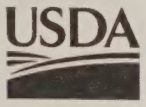

United States
Department of
Agriculture

**Agricultural
Research
Service**

August 2000

110 Years of Biological Control Research and Development in the United States Department of Agriculture

1883–1993

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110 Years of Biological Control Research and Development in the United States Department of Agriculture

1883–1993

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W.C. Kauffman, editors

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ABSTRACT

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Research and implementation of biological control, briefly defined as the use of natural enemies and other beneficial organisms to control pests, began in North America with the first introduction of an exotic natural enemy in late 1883 by the United States Department of Agriculture (USDA). USDA's biological control programs have addressed many agricultural pests and have utilized a variety of natural enemies and antagonists. This report provides a brief chronicle of progress in these areas. Many successes have been demonstrated in USDA's classical biological control programs, saving growers more than $2 billion during just the past decade. Considerable progress has also been made toward the practical use of augmented insect and nematode natural enemies and in the development of pathogens for control of insects and weeds.

Keywords: agricultural pests, antagonists, arthropod pathogens, arthropods, augmentation, biological control, classical, history, competitors, insects, microbial control, mites, natural enemies, nematodes, organism introductions, plant pathogens, weeds

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This book would not have been possible without the help of many persons, mostly within the Agricultural Research Service (ARS), but including scientists from the Forest Service (FS) and Animal and Plant Health Inspection Service (APHIS). The authors involved in the main part of this book are given in the specific sections, and their affiliations and locations are listed below. The names, affiliations and locations of the scientists who reviewed texts of the various sections are also listed; since this is a history of USDA research, almost all reviewers were USDA personnel. The help of all of these individuals in telling the story of biological control research and implementation in the U.S. Department of Agriculture has been, of course, invaluable. Authors and reviewers of Appendices II and III, with their affiliations and locations, are given in the respective Appendices, along with other acknowledgments.

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INTRODUCTION

By J. R. Coulson, D. A. Nordlund, and R. J. Cook

A. DEFINITION OF "BIOLOGICAL CONTROL" FOR THIS HISTORY

The subject of this history, as indicated by its title, is biological control. It is important to note, however, that the pest management/control community is still working toward a consensus regarding exactly what constitutes biological control. There are two basic schools of thought, one arising from the field of entomology for control of arthropods and weeds and the other from the field of plant pathology for control of microorganisms as plant pathogens. It is also important to note that contributors to this publication do not all define biological control in the same way and thus, for the purposes of this publication, some boundaries to the definition are needed.

The entomological tradition supports a limited view of biological control, a term first coined in 1919 by H. S. Smith, University of California (Smith 1919), and defined by DeBach and Schlinger (1964) as: "The actions of parasites, predators and pathogens in maintaining another organism's density at a lower average than would occur in their absence." This was not the first definition and there have been other more recent ones (Huffaker and Messenger 1976; Coppel and Mertins 1977). It is probably the most succinct definition, and restricts biological control to interactions which generally involve a density dependent relationship between the biological control agent and the organism being controlled. This is an important unifying concept. Under DeBach's definition there is natural biological control, which is extremely important in maintaining the populations of many organisms at relatively low levels, and applied biological control, which involves active intervention by humans.

In the plant pathology tradition, the term biological control has been defined (Garrett 1965; Baker and Cook 1974) broadly so that any organism (except humans) can be a biological control agent, whether the interaction involves a density dependent interaction or not. Somewhat equivalent to DeBach's "natural" and "applied" biological control, plant pathologists include both the use of practices to enhance or take advantage of "resident antagonists" (actions analogous to "conservation of biological control agents" in entomology), and the use of "introduced antagonists" (analogous to "augmentation," or more rarely "classical," biological control in entomology). The plant pathological concept of biological control includes approaches that lower the population of pathogens, but also approaches that arrest or retard disease development or reproduction of the pathogen on or within the diseased plant. This tradition led to the recent proposal of a very broad definition for biological control: "The use of natural or modified organisms, genes, or gene products to reduce the effects of undesirable organisms (pests), and to favor desirable organisms such as crops, trees, animals, and beneficial insects and microorganisms" (National Academy of Sciences 1987; Cook 1988). Under this definition, naturally occurring interactions as well as a wide range of biologically based pest management techniques, including sterile male technique and host resistance, are all considered biological control.

The different approaches to and definition of biological control used in plant pathology compared with entomology are not surprising, considering the nature of the agent or process to be controlled

and the agents used for control. The target is always a plant pathogen, either a fungus, bacterium, or virus. The biological control agent is likewise either a fungus, bacterium, or virus. Biological control in plant pathology is thus microbe against microbe. The meeting ground between the agent and target may be independent of plants, e.g., in soil, but most commonly is on or within plants during the disease-producing process. This accounts for the emphasis on interrupting or retarding processes such as infection or other events associated with the development of plant disease. In many respects, this is analogous to biological control of arthropods, where the control agent is most often another arthropod, usually quite unrelated taxonomically to the target, and can also be another invertebrate or a microbial pathogen. The meeting ground can also be on or independent of the host organism. But in entomology, the emphasis is on reducing the numbers of the target organism and thus the damage to the host plant or animal, rather than on limiting a process.

For the purposes of this history, we will use a definition slightly altered from that used for the U.S. Department of Agriculture (USDA), Agricultural Research Service (ARS) biological control workshop in 1987 (King et al. 1988): "Use/management of naturally-occurring, introduced, or genetically-modified natural enemies (predators, parasites/parasitoids, and pathogens of pests) and other selected beneficial organisms (antagonists, competitors, and allelopaths), and their products, to regulate populations and effects of pests (invertebrate pests of useful plants, animals, man, terrestrial and aquatic weeds, and plant pathogens)." The use of the term "biological control agent" in this paper therefore includes both the "natural enemies" and "other beneficial organisms" included in this definition.

The pest management community does not have a shared conceptual model for biological control, and thus, some will feel that the definition used here is too broad while others will feel that it is not broad enough. Issues, such as the use of dung beetles to destroy fly breeding habitat, which under DeBach's definition, would not be considered biological control, will be discussed, and dung beetles considered as "biological control agents". Then there are the microbial agents such as the endophytes--fungi and bacteria that live in plants--that protect their host plants against certain insect pests by production of toxic substances such as alkaloids (Siegel et al. 1987), but without directly or necessarily reducing the pest population. These agents do not fit under the categories of parasites, predators, or pathogens, but do fit more logically in the plant pathology concept of "antagonists," and limiting a "process" (the process by which the pest attacks the plant), and can thus be included in the definition used here. On the other hand, host resistance, pheromones, and the sterile male technique, which are considered biological control under the broad definition proposed by the National Academy of Sciences (NAS) (1987), will not be discussed. The proper definition for "biological control" is still being discussed in the scientific literature (Dietrick 1988; Garcia et al. 1988; Gabriel and Cook 1990), and may never be entirely resolved. The broader term "biologically based" methods of control has been used by USDA-ARS to encompass the use of natural enemies and antagonists as well as the many other pest management techniques included in the NAS definition of biological control, most recently for a 1993 ARS-sponsored symposium (Lumsden and Vaughn 1993).

There is a further complication concerning microorganisms, whether for use to control plant pathogens, invertebrates, or weeds, that deserves mention here, since definitions are also involved. This concerns the different regulatory mechanisms affecting the introduction and development of microorganisms as pest control agents, as compared to the introduction and use of invertebrate biological control agents. The U.S. Environmental Protection Agency (EPA) considers all organisms used for pest control purposes as "pesticides," in accordance with the definitions used in the Federal Insecticide, Fungicide and Rodenticide Act (FIFRA). Though the EPA has exempted invertebrate organisms (including arthropods and nematodes) from regulation under FIFRA, relying on adequate regulation of these organisms by the USDA, microorganisms (including fungi, bacteria, protozoans, viruses, and rickettsia) are still regulated by EPA under FIFRA as "microbial pesticides." This requires long-term intensive study such as performance trials and safety tests for the introduction and

use of these organisms as pest control agents, which can include tests originally developed for chemical pesticides. This can be a severe deterrent if, as in most cases, development of a commercial product is intended, which requires registration by the EPA. The USDA supports research on these pest control agents to the point where they can be patented and transferred as a technology to the private sector. And the private sector will only further develop and license them for commercialization if a profit can be made, which often depends upon a broad target host spectrum and high degree of efficacy of the product, and is negatively impacted by the high cost involved in the testing and development of the product, caused largely by costs associated with meeting existing regulation requirements. As noted in the latter portions of this history, a number of regulatory changes are currently being discussed in the EPA and USDA that will affect the introduction and use of both invertebrate and microbial biological control agents in the future.

B. SCOPE AND ORGANIZATION OF THIS HISTORY

The original intent for the compilation of this history was to help commemorate the first centennial anniversary of biological control in the United States, an event celebrated by two international symposia in 1989 organized by the University of California and the USDA, and sponsored or supported by several other organizations (University of California 1989; U.S. Department of Agriculture, Animal and Plant Health Inspection Service, USDA, 1989a). An early draft of this history formed the basis for a USDA article relating to this anniversary (Morrison 1989). Though the anniversary celebrated the first successful classical biological control program, that is, the 1888-89 introduction and establishment of the vedalia beetle that controlled the introduced cottony cushion scale pest of citrus in California, biological control activities in the USDA began prior to 1888. The initiation of USDA biological control research can be considered to have begun in 1883-84 with the first successful introduction of an exotic natural enemy to control a pest: the braconid parasite *Cotesia glomeratus* for control of the imported cabbageworm. Though establishment of the natural enemy in the United States occurred, this did not result in control of the pest for which it was introduced, unlike the case of the vedalia beetle. Also, because of the time required to complete the manuscripts for this history, the 1989 centennial date has long since passed. This has resulted in the 110-year period now covered by this history, which covers events from 1883/84 through 1992/93, and includes reference to some literature published in 1994/95. The Epilogue to this History includes a discussion of ARS' classical biological control program with comments on some administrative events impacting that program that occurred subsequent to the 1993 cutoff, i.e., 1994-1999.

The first portions of this history to be completed were those relating to the biological control programs of the early USDA bureaus and divisions and of USDA's Agricultural Research Service (ARS), following its creation in 1953. Since biological control activities were conducted in other USDA agencies, manuscripts were also solicited from the Forest Service (FS) and Animal and Plant Health Inspection Service (APHIS). A primary delay in assembling this history was in compiling the histories of the Forest Service and ARS insect pathology research. The considerable efforts expended and information collected resulted in histories of these two areas in much greater detail than compiled for other sections of the overall history. Consequently, these detailed histories have been placed *in toto* as appendices, but they are briefly summarized in the body of the overall history to correspond more closely to the treatment accorded other sections.

This has, however, resulted in a relatively brief history of the early periods and of ARS's biological control programs, wherein little mention is made of the many individuals who were involved in the early periods and ARS programs, particularly in classical biological control; their contributions can be noted primarily by the many literature references cited in those sections that record their work, and in the major historical summaries cited (Clausen 1956, 1978; Habeck et al. 1990; Nechols et al. 1995), and the references cited therein. (Details of some early work on forest insects mentioned in

Chapters 1 and 2 are given in Appendix III, and more details concerning arthropod pathogens are given in Appendix II.)

Basic research in support of biological control programs is not specifically addressed in this history; the demarcation between basic and applied research impacting biological control is often difficult to distinguish.

This is a chronicle of the **USDA** biological control programs, and little mention is made of the many valuable contributions to biological control made by colleagues in other federal and state institutions. In particular, the considerable involvement of the University of California in classical biological control and in insect pathology from the inception of those disciplines in the United States, and the contributions of other institutions such as the Hawaiian Sugar Planter's Association and Hawaiian Department of Agriculture, various State Agricultural Experiment Stations and Universities in Florida, Massachusetts, Texas, Wisconsin, and many other states, and state agencies in California, Colorado, Maryland, Massachusetts, New Jersey, Oregon, Pennsylvania, Virginia, Washington, and other states that have been involved in many various aspects of biological control, must be acknowledged here. However, little mention of these is made in this history; their contributions are discussed in other histories of biological control and in many biological control textbooks cited herein (Steinhaus 1946, 1949; Clausen 1956, 1978; Sweetman 1958; DeBach and Schlinger 1964; Doutt 1964; Hagen and Franz 1973; Baker and Cook 1974; Huffaker and Messenger 1976; Simmonds et al. 1976; Coppel and Mertins 1977; Luck 1981; van den Bosch et al. 1982; Cook and Baker 1983; Funasaki et al. 1988; Lashomb et al. 1988; Habeck et al. 1990; Hornby 1990; DeBach and Rosen 1991; Stirling 1991; TeBeest 1991; Tjamos et al. 1992; Nechols et al. 1995; and Van Driesche and Bellows 1996).

Much of the research and other activities reported in this publication were conducted by USDA scientists in cooperation with state and university colleagues. Histories of two pertinent USDA agencies are missing from this compilation – the Cooperative State Research Service (CSRS) and Extension Service (ES); at the end of 1993, these were combined into the new Cooperative State Research, Education, and Extension Service (CSREES). The primary function of these agencies has been the administration of federal funds that go to the State Agricultural Experiment Stations (SAES) and Cooperative Extension Services (CES), respectively, at the land-grant universities throughout the United States. In addition, the CSRS/CSREES has provided funds for a number of Regional Research Projects that have involved cooperative research between SAES and USDA scientists, including several biological control projects. Recent publications of two of those regional projects are particularly noteworthy here, recording the results of long-term cooperative SAES/USDA biological control research in the Southeastern and Western regions of the United States (Habeck et al. 1990; and Nechols et al. 1995, respectively).

This history of USDA biological control programs is generally organized into four chronological periods, 1883/84-1933, 1934-52, 1953-72, and 1973-93. These correspond to four periods initiated by major organizational changes in USDA, which have had their impacts, some good, some bad, on biological control research and development/implementation programs within the department. The history concerns biological control activities of the old Divisions and Bureaus that were combined in 1952/53 to form ARS. Some units were placed in the Forest Service (FS) at that time. In 1971, additional units were removed from ARS to form the Animal and Plant Health Inspection Service (APHIS). Reviews of biological control activities in the latter two USDA agencies are included in this history.

Within each of the four main historical periods, the history of early studies and ARS research is further organized by the agricultural pests targeted for biological control, i.e., arthropods (insects, mites, and ticks), weeds, plant nematodes, and plant pathogens. And finally, the sections on

arthropod pests are further organized by the type of natural enemy or other organism used for control, i.e., arthropod parasites (parasitoids) and predators, arthropod-parasitic nematodes, and arthropod pathogens. The last section on weeds is similarly organized by natural enemy, i.e., invertebrate weed feeders and weed pathogens.

The sections on Forest Service and APHIS are differently organized, in accordance with the treatments preferred by their authors and editors, and are general overviews of biological control activities in those two agencies. As noted above, detailed treatment of the Forest Service activities appears as an Appendix.

Included in the Indexes to this history are all scientific and common names of pest and beneficial organisms mentioned in the text of the main body and appendices, cross-referenced and with reference to the higher taxa to which the organisms belong. Common names of arthropods not approved by the Entomological Society of America (ESA) (Stoetzel 1989) appear in quotes in the text. Other texts used in compiling the Indexes are mentioned therein.

CHAPTER I
1883-1933

A. BIOLOGICAL CONTROL OF ARTHROPODS (INSECTS, MITES, AND TICKS)

1. Arthropod Biological Control Agents

a. Classical biological control (introduction of biological control agents). By J. R. Coulson

During the early years of the U.S. Patent Office's Bureau of Agriculture (1853-62) and its successor the Department of Agriculture (USDA, 1862-81), the several bureau and department entomologists (T. Glover, 1853-59 and 1862-78; C. V. Riley, 1878-79; and J. H. Comstock, 1879-81) published observations on natural enemies of agricultural pests. Concurrent observations were being made by several State Entomologists, some of whom (A. Fitch, New York; B. Walsh, Illinois) suggested the importation of parasites of introduced pests. Some of the State Entomologists (C. V. Riley, then Missouri State Entomologist; and W. LeBaron, Illinois State Entomologist) began within-state redistribution of parasites in the 1870s. Riley made the very first international shipment of an insect natural enemy in 1873, sending specimens of a predaceous mite to France to control the grape phylloxera. (Riley 1893; Doutt 1964; Rainwater and Parencia 1981.)

It was not until the establishment of the Division of Entomology in 1881 under its Chief, C. V. Riley, that the USDA initiated research on what is now known as classical biological control. Riley arranged the first importation and establishment of an insect parasite in the U.S. (District of Columbia, Iowa, Nebraska and Missouri) in 1883-84, the braconid *Cotesia glomeratus*, a European parasite of the imported cabbageworm. He was also responsible for the highly successful importation of the so-called vedalia beetle, *Rodolia cardinalis*, from Australia in 1888-89 into California for the control of the cottony cushion scale, *Icerya purchasi*. This scale had become a severe threat to the infant California citrus industry. The vedalia beetle quickly became established in California. By the end of 1889 it had caused a spectacular decline in scale populations there. Oddly enough, Riley had been forced to resort to a subterfuge of sorts to obtain from the U.S. Congress the necessary funds ($2,000) to support the foreign travel of a USDA entomologist (A. Koebele) to Australia for collection of natural enemies of the scale. (Riley 1893; Doutt 1958, 1964; Clausen 1956, 1978; Caltagirone and Doutt 1989.)

The spectacular success of the vedalia beetle led to a rapid expansion of introductions and other use of natural enemies in California, and also in Hawaii. Other than financing of one further exploration in Australia by Koebele, the USDA played little part in biological control during Riley's remaining years as the Division Chief (he served as Chief during 1881-1894), and even in the very early years of his successor, L. O. Howard, Chief of the Division of Entomology, 1894-1904 (and later of the Bureau of Entomology, 1904-27).

In fact, the relationship between the USDA and the California programs became strained, primarily due to Howard's concerns about possible placement of too much emphasis on importation of natural enemies at the expense of other pest control measures in California and a perceived reckless handling

of importations. These concerns were eased at the passage of the Federal Plant Quarantine Act in 1912, and appointment in 1913 of H.S. Smith, a former USDA entomologist, as superintendant of the state insectary at Sacramento (built in 1907). With this appointment, Smith was thus placed in charge of California's natural enemy importations; he was made an official collaborator of the USDA. In 1931, the California biological control importation program was formalized under a three-way Memorandum of Agreement involving USDA, University of California, and the California Department of Agriculture. This ongoing agreement has been updated and renewed several times (for the most recent draft, see Appendix I.C), and sets forth procedures to be followed and certain applicable restrictions in regard to the USDA and University programs in California. (Clausen 1956; Doutt 1964; Hagen and Franz 1973; Simmonds et al. 1976; Rainwater and Parencia 1981.)

While the natural enemy importation programs in the states of California and Hawaii quickly expanded, early USDA importations were limited to a few natural enemies of the Hessian fly from England (1890-94), San Jose and white peach scales from Japan and China (1895-96, 1901-02), barnacle and Florida wax scales from Italy (1895-98), and boll weevil from Guatemala (1904). With the exception of the Guatemalan predator of the boll weevil, which was brought directly to Texas, these shipments were initially received at the insectary at division headquarters in Washington, DC. From there they were disseminated to division entomologists in Louisiana (for barnacle and wax scales) and several eastern and midwestern states. Two of the predators and one parasite were established, but with little effect on the pests. (Clausen 1956, 1978.)

In 1905, USDA began its first large-scale biological control program, embarking on explorations in Europe and to a lesser extent Japan for natural enemies of the gypsy moth and browntail moth. These two introduced pests had become severe pests of forest and other trees in Massachusetts and other areas of New England. Importations and releases of natural enemies, first begun in cooperation with the State of Massachusetts (1905-11), were made during 1906-14 and 1921-33. Explorations were conducted by USDA entomologists of the Bureau of Entomology's Division of Forest Insect Investigations (or variously Gipsy Moth and Brown-tail Moth Investigations). Shipments were received at the Bureau's newly established Gypsy Moth Laboratory at Melrose Highlands, MA, for emergence, identification, culture, and dissemination of the natural enemies. The program resulted in the establishment of nine species of parasites of the gypsy moth, seven of the browntail moth, and two predators of both moths. Although the introduced natural enemies contributed to limiting populations of the gypsy moth, continuous economic control of this pest was not achieved. However, substantial control of the gypsy moth at least in New England can be claimed, since outbreaks there were reduced in frequency, duration, and severity. Such population suppression appears to have spread into areas more recently invaded by the gypsy moth. In addition, the established browntail moth parasites, along with others introduced later in connection with the satin moth program, are generally considered to be the major factor in controlling the browntail moth in New England.

Many basic biological control concepts, principles, and procedures were developed as a result of this program, which involved a number of state and USDA entomologists who were later to become key personnel in the USDA and California biological control programs. (Howard and Fiske 1911; Burgess and Crossman 1929; Clausen 1956, 1978; Dowden 1962; Hagen and Franz 1973; Elkinton and Liebhold 1990; Williams et al. 1990, 1992, 1993; Berryman 1991.)

During 1905-18, the Bureau of Entomology imported parasites and predators of the elm leaf beetle (from Europe, 1907-08 and 1917), citrus whitefly (from India, 1910-11), alfalfa and clover leaf weevils (from Europe, 1911-13), and sugarcane borer (from Cuba, 1915), and transferred (without success) some of the established gypsy moth natural enemies from New England to New Mexico in an attempt to control the range caterpillar. The alfalfa weevil program was USDA's second major importation program, and resulted in the establishment of several species of parasites in Utah where this European weevil had been recently introduced accidentally. The most important parasite

subsequently dispersed widely with the weevil in western states. A parasite of the clover leaf weevil, an earlier introduced pest, was also established, in the eastern U.S., as an incidental result of this program. There were mixed results from the other programs, with some establishments but little economic control. (Chamberlin 1924; Clausen 1956, 1978.)

An important event occurred in 1919 with the founding of a USDA laboratory in Europe. This laboratory was established at Auch in southern France by W.R. Thompson of the Bureau of Entomology's Division of Cereal and Forage Insects Investigations for the conduct of the large-scale European corn borer program initiated that year (and which continued through 1938). The European corn borer was first discovered in the U.S. in 1917 and quickly became a major pest. Shipments of natural enemies were made initially directly to the Bureau's European Corn Borer Laboratory at Arlington, MA. Of 24 parasite species imported, six became established in the U.S. but failed to provide satisfactory control of the borer. Additional studies in Europe were made at the laboratory in France on natural enemies of the alfalfa weevil (1921-28), European earwig (for Oregon, 1924-31), and peach twig borer (for California, 1931), resulting in establishment of additional parasite species in the U.S. From 1922 until his retirement in 1960, H.L. Parker was in charge of the USDA laboratory in Europe, soon to be known as the European Parasite Laboratory. This Laboratory has been moved to several locations in France (and to South America, see Chapter II) throughout its existence, the last being at Béhoust, near Paris, prior to its consolidation with the ARS Rome laboratory at Montpellier to become the European Biological Control Laboratory in 1991 (see Chapter IV). (Baker et al. 1949; Drea 1981.)

A second USDA overseas laboratory was established by the Bureau's Division of Deciduous Fruit and Shade Tree Insects Investigations in Japan by 1922. Explorations were conducted from this and other oriental field stations in Japan, Korea, and China for natural enemies of Japanese beetle (1920-33), gypsy moth (1921-22), oriental beetle (1925-26 and 1932), Asiatic garden beetle (1927-34), oriental moth (1929-30), European corn borer (1929-36), and oriental fruit moth (1929-39). These oriental field stations were consolidated into one laboratory at Yokohama, Japan, in 1932, under the leadership of G.J. Haeussler (1932-34), later to be called the Asian Parasite Laboratory (see Chapter II). (Clausen et al. 1927; Allen et al. 1940; Haeussler 1940; Gardner and Parker 1940; Clausen 1956, 1978.)

Another USDA overseas laboratory was established in Hungary in 1926 as the Gypsy Moth Laboratory, later Central European Investigations, by R.T. Webber and C.F.W. Muesebeck of the Bureau's Division of Forest Insect Investigations. Projects conducted there, in addition to that on gypsy moth, included those on satin moth (1927-34), "birch leafmining sawfly", *Heterarthrus nemoratus* (1930-34), European pine shoot moth (1931-1934), larch casebearer (1932-34), and some exploratory work on the beech scale. (Burgess and Crossman 1929; Dowden and Berry 1938; Clausen 1956, 1978.) Another foreign laboratory was established in 1928 in Mexico by A.C. Baker of the Bureau's Division of Insects Affecting Fruit and Shade Trees, to study insect pests of tropical and subtropical crops and ornamentals, including fruit flies. (McPhail and Bliss 1933; Baker et al. 1944.)

Other importations made by USDA during the remaining tour of duty of L.O. Howard and of his successor C.L. Marlatt, Bureau Chief from 1927-1933, included natural enemies of Mexican bean beetle from Mexico (1922-23 and 1929-30), sugarcane borer from South America (1928-32), and the gray sugarcane mealybug from Hawaii (1932). Also, explorations for natural enemies of the beet leafhopper were begun (1926-28), natural enemies of citrus blackfly were introduced into Cuba from Malaya (1930), a native parasite of the Nantucket pine tip moth from Virginia was successfully established in Nebraska, and a native parasite of the woolly apple aphid was successfully recolonzied from the eastern to northwestern U.S. (1930-31) and subsequently to several other countries.

(Clausen and Berry 1932; Baumhofer 1932; Jaynes 1933; Landis and Howard 1940; Clausen 1956, 1978.)

Significant accomplishments of USDA's classical biological control programs during 1883-1933 included not only the development of concepts, procedures, and principles of biological control, and the training of numerous scientists in this new field of pest management, but also the establishment of numerous parasites and predators of many of the introduced insect pests in the U.S. Some of these have contributed to the substantial or appreciable suppression of economic populations of such pests as the oriental, satin, browntail, and gypsy moths in New England and the alfalfa weevil in large areas of western U.S., and at least partial suppression of populations of sugarcane borer in Florida, European corn borer and Japanese beetle in eastern U.S., and the European earwig in the Northwest. Complete control of the cottony cushion scale in California and citrus blackfly in Cuba was obtained. In addition, movement of native parasites from eastern U.S. caused substantial control of the western pine tip moth in Nebraska and the woolly apple aphid in northwestern U.S. and in several foreign countries. Many other insect pests are reported to have been completely, substantially, or partially controlled as a result of the state and university biological control programs in California and Hawaii during this period. (DeBach 1964; Laing and Hamai 1976; Luck 1981; and DeBach and Rosen 1991.)

The intense interest in biological control generated by the successful cottony cushion scale control began to wane during the latter part of this early period. A count of research papers shows that the ratio of those devoted to biological control research versus those related to insecticide research shifted from a 1:1 ratio in 1915 to 0.3:1 in 1925, the beginning of a trend that continued into the 1940s (Sailer 1973), and perhaps reflected disappointment in the results of the USDA biological control program, despite the substantial achievements noted above. L.O. Howard warned of over expectations for biological control, while also warning of too easy discouragment, in a paper setting forth his assessment of the USDA and other biological control programs shortly before his retirement (Howard 1926).

b. Augmentation and conservation of arthropod biological control agents. By D. A. Nordlund, J. R. Coulson, and E. G. King

Augmentation is an approach to applied biological control that involves actions taken to increase populations of, or beneficial effects of biological control agents (Rabb et al. 1976; DeBach and Hagen 1964; Ridgway and Vinson 1977). This approach may involve indigenous or introduced biological control agents. There are two basic strategies for augmentation: periodic release and environmental manipulation.

Periodic releases of the biological control agent is the approach to augmentation that has received the most attention. Periodic releases may be inoculative or inundative and may involve field-collected or laboratory- reared organisms. Inoculative releases involve a relatively small number of the biological control agents and depend on the progeny of the released organisms to suppress the pest population (DeBach and Hagen 1964). Inoculative releases, for example, are appropriate for the reintroduction of a biological control agent into an area in which it cannot overwinter, but is effective during the growing season. Inundative releases, on the other hand, involve releases of relatively large numbers of the biological control agent and depend on the actions of the released individuals for pest suppression (DeBach and Hagen 1964; Flanders 1930, 1951; Stinner 1977). These releases require large-scale cultures of the biological control agent. They are intended to provide a relatively rapid suppression of the pest population, but are not expected to provide any continuing population suppression. Thus, inundative releases are repeated on an as-needed basis throughout the growing season.

Environmental manipulation is the second approach to augmentation. One of the earliest known examples of environmental manipulation to increase the effectiveness of a predator is the practice in China, by 300 AD, of constructing bamboo runways to provide predatory ants easy transit from one pest-infested citrus tree to another (Flint and van den Bosch 1981). Environmental manipulation can take a variety of forms and is differentiated from cultural controls in that its direct effect is intended to be on the biological control agent, not on the pest.

"Conservation" is an approach to applied biological control that involves actions taken to protect or maintain existing populations of biological control agents (van den Bosch and Telford 1964; Rabb et al. 1976). In practice, this means not taking actions that have a negative impact on the populations of biological control agents (Nordlund 1984). It can be difficult to differentiate between augmentation and conservation. Thus, Nordlund (1984) suggested dropping this terminology and simply using periodic release and environmental manipulation. However, the augmentation and conservation terminology is still in general use.

The reality is that applied biological control usually involves a variety of approaches. When conducting a release program, whether classical importation or augmentation, it is necessary to avoid actions that have a negative effect on the population of biological control agents. Thus, conservation should always be an important aspect of biological control. In addition, environmental manipulation, to improve the effectiveness of a release program (or biological control agents that have been conserved), is also important. These various divisions are designed to assist in our communication, but are not generally expected to be exclusive and stand alone biological control approaches.

Early large-scale augmentation attempts, including those by the USDA to control the boll weevil (1906-07) and house flies (1914) in Texas, and by the University of Kansas to control the greenbug (1907), utilized native parasites (Pierce 1908; Clausen 1956). These were the forerunners of subsequent release programs utilizing the native *Hippodamia* ladybug for aphid control in vegetables in California from 1910, the introduced predator *Cryptolaemus* against mealybugs in California from 1910, and the native parasite *Macrocentrus ancylivorus* against the introduced oriental fruit moth by the USDA and several states in many areas of the U.S. from 1929. Other early USDA augmentation programs included the use of a native egg parasite against the range caterpillar in New Mexico (1930-32), *Trichogramma* species against the pecan nut casebearer in Georgia (1931) and the oriental fruit moth in New Jersey (1930-31), and large-scale culture and release of an imported tachinid parasite of the Mexican bean beetle (1930-1935) that involved releases in 19 states. Augmentation received an important boost with the development of mass rearing techniques for *Trichogramma* egg parasites by University of California researchers by 1930. (Flanders 1930; Allen and Warren 1932; Clausen 1956.)

The history of USDA research and implementation of environmental manipulation and conservation programs in biological control is difficult to compile, since research results appear in papers that are not usually indexed to these subjects, and are thus difficult to identify. But these approaches are once again becoming important as many of the chemicals once used for pest control are being banned for use in many agricultural systems.

2. Arthropod-Parasitic Nematodes. By J. R. Coulson and W. R. Nickle

Although a number of observations of plant nematode problems in agriculture had been made by USDA scientists, a major role in the development of the science of nematology was to be played by N. A. Cobb, known as the "father of nematology" in the U.S. Cobb was hired by the USDA in 1907, serving first in the Office of Agricultural Technology in USDA's Bureau of Plant Industry, where he continued his studies on nematodes and plant pathology, which eventually led to the formation in the

1920s of the Nematology Investigations, later the Division of Nematology, within that Bureau, with Cobb serving as the Division's first Chief until his death in 1932.

Early work on the taxonomy and biology of insect-parasitic nematodes was conducted for the most part in Europe. However, among American scientists who first recognized the potential use of nematodes as biological control agents of insects were the leaders of USDA's Division of Nematology, beginning with Cobb, based on his experience with three entomophilic nematodes (Cobb 1927). G. Steiner and J. R. Christie joined Cobb at the USDA farm in Washington, DC, and produced a long series of papers on insect nematology. Their work on *Agamermis decaudata*, a nematode parasite of grasshoppers and other insects, is considered a classic (Cobb et al. 1923). However, the advent of the Japanese beetle research in the 1920s, and the discovery of nematodes attacking this pest, resulted in more intensive research on the potential biological control of insects by nematodes, in the early 1930s. This early work on an apparently indigenous nematode described by the USDA taxonomist, Steiner, was conducted by the New Jersey Department of Agriculture in cooperation with the USDA Japanese beetle program in New Jersey. Thus, during this early period, most of the nematology research effort in the USDA was centered around insect-parasitic nematodes. After Cobb's death in 1932, Steiner became head of the Division of Nematology (1932-56) and the emphasis moved to research on plant nematodes, though Steiner continued studies on the taxonomy of mermithids, an important insect-parasitic group of nematodes. See also Section C below on biological control of plant nematodes. (Clausen 1956; Fleming 1968; Dowler and Van Gundy 1984; Nickle and Welch 1984.)

3. Arthropod Pathogens. By J. R. Coulson, H. Shimanuki, and P. V. Vail

As in the case with insect-parasitic nematodes, early studies on insect pathogens and their use in control of pests took place in Europe (Steinhaus 1964). As noted by Steinhaus (1949), in order for insect pathology/microbial control to develop as a distinct discipline, separate projects dealing solely with this subject were needed. Two such projects, the study of the diseases of the honey bee and their control and, later, in 1922, an extensive program on pathogens of the newly introduced Japanese beetle, were initiated by the USDA. Many of the early studies relied heavily on surveys and were descriptive in nature. However, the studies by G. F. White (1906-1920) noted below provided the basis of understanding of the foulbroods and also therapeutic measures for these and other bee diseases. Intensive programs on bee diseases continue to this day.

Though there were some early attempts made by USDA entomologists to use pathogens for control of insect pests, insect pathology research in the USDA essentially began in the Bureau of Entomology's Division of Bee Culture Laboratory at Somerset, MD, in 1905. Research on honey bee diseases was conducted there under E. F. Phillips, leader of the Investigations, 1906-24 (Phillips 1906, 1908). He was joined at Somerset by G. F. White in 1907 and in 1916 by A. P. Sturtevant, who was transferred in 1926 to the Investigations' Field Laboratory at Laramie, WY. It was Phillips, writing in the preface of White's 1906 publication, who differentiated and named American foulbrood and European foulbrood diseases of bees. Subsequently, White and Sturtevant published several papers on these and other diseases of the honey bee (White 1906, 1907, 1912, 1919, 1920; Sturtevant 1932, 1936).

The early studies by USDA personnel on the use of pathogens for control of insect pests included: (1) dissemination of diseased chinch bugs infected with a native fungus pathogen in Minnesota and Kansas, 1888-96 (Billings and Glenn 1911); (2) introduction of fungal pathogens of grasshoppers imported from South Africa in 24 states, 1900 (Howard 1902); (3) experiments with apparently native fungi of the browntail moth in New England, 1908-11 (Speare and Colley 1912) and of the citrus whitefly in Florida, 1910-11 (Morrill and Back 1912); and (4) studies of fungal pathogens of the gypsy moth imported from Japan, 1910 (Speare and Colley 1912) and of the European corn borer

imported from China, 1931-32 (Bartlett and Lefebvre 1934). The Japanese fungal pathogen of gypsy moth, later described as *Entomophaga maimaiga*, was reintroduced in the 1980s, and has proven to be an effective control agent; see Chapter IVB3 and Appendix II. A virus disease of the gypsy moth, apparently introduced during the gypsy moth biological control importation program, first appeared in New England in 1907, and assumed epidemic proportions in heavy gypsy moth populations (Glaser 1915). But the first intentional attempts to utilize insect viruses for insect control in the U.S. did not take place until many years later. The lack of a concerted effort on pathogens, either native or introduced, was noteworthy.

A major impetus in U.S. research on use of insect pathogens occurred as a result of the Japanese beetle program, when the bacterial milky spore or milky disease of this pest was discovered in New Jersey in 1933; G. F. White had just been transferred to the Japanese beetle laboratory in New Jersey, and was involved in the identification of the organism (Hawley and White 1935). Research efforts at Moorestown, NJ, on the Japanese beetle were intensified with the work of G. E. Spencer, R. W. Glaser, and H. Fox, and expanded in the 1930s to include White, I. M. Hawley, and S. R. Dutky. This early work evolved into extensive studies on all aspects of the use of the "milky disease" organism(s) as microbial agents. Use of the "milky disease" bacterium to control Japanese beetle continues today, as does research to further understand and utilize this organism. The importance of this pathogen for control of the Japanese beetle has been discussed by Steinhaus (1949, 1964), Clausen (1956), Fleming (1968), and Cameron (1973), and a bibliography of the bacteria was prepared by Klein at al. (1976).

B. BIOLOGICAL CONTROL OF WEEDS. By J. R. Coulson

Credit for initiation of biological control of weeds in the U.S. goes to the Hawaiian Sugar Planter's Association, which financed the collection in Mexico of natural enemies of lantana, an introduced weedy plant in Hawaii, for shipment and release in Hawaii in 1902. Though biological control of weeds quickly developed in other areas of the world, it was not until the 1940s that such research was conducted in the continental U.S., first by the University of California, 1940-42, and beginning in 1944 by the USDA in cooperation with the University of California. (See Goeden, 1978.)

C. BIOLOGICAL CONTROL OF PLANT NEMATODES. By R. M. Sayre and J. R. Coulson

The first natural enemy of nematodes, a nematode-trapping fungus, was discovered in the mid-1800s, and additional natural enemies were discovered in the early 1900s. Interest in use of these to control plant-parasitic nematodes developed early, and greenhouse tests were conducted, but no field tests were done. Again, N. A. Cobb and other nematologists of USDA's Nematology Investigations (later Division) of the Bureau of Plant Industry played a major role in this research (see the Section A.2 above on insect-parasitic nematodes for notes on the early history of insect nematology in the U.S.). Interest waned when low-cost nematicides became available in the 1940s, but began again in the 1970s when use of these nematicides were being lost due to actions by the Environmental Protection Agency (EPA). Knowledge of natural enemies of nematodes is still inadequate and there are still very few nematologists involved in research on biological control of plant-parasitic nematodes in the U.S. (Sayre 1971, 1988; Mankau 1973, 1980; Kerry 1981; Smart 1986.)

In the year 1889, the beginning of this historical survey, N. A. Cobb, founder of the science of nematology in the U.S., had just received his doctorate from the University of Jena. It was some two years after his appointment to the USDA in 1907 that he succeeded in adding to his assigned studies investigations on nematodes. Even then, it would be another decade before he was to propose that predaceous soil nematodes might serve as agents for the biological control of plant-parasitic nematodes (Cobb 1920). G. Thorne, J. R. Christie, W. E. Chambers, E. G. Titus, and G. Steiner, who joined the USDA Nematology Investigations early, were trained or greatly influenced by Cobb. (As

an example, Steiner was also to propose that *Mononchus* nematodes, through their predaceous habits, were bioregulators of plant-parasitic nematode populations [Steiner and Heinly 1922].) Consequently, like Cobb, each was a keen observer of the morphology of healthy nematodes and recognized parasites and predators present in nematode samples. They incorporated information on the antagonists of nematodes into taxonomic descriptions of new nematode species. This practice resulted in a body of information on natural enemies of nematodes being scattered throughout the taxonomic literature (Thorne 1961). The first attempt to bring together all the literature on parasites of nematodes was not until 1946 (Dollfus 1946) and the next was over 40 years later (Poinar and Jansson 1988).

Some of these early investigators even recognized the occurrence of natural crashes in the populations of plant nematodes, and attributed the declines to one or more of the associated antagonists. Generally, most investigators did not subject their conjectures on population declines to any further rigorous tests either in greenhouse or field plot studies. Perhaps the effort by Thorne (1927) to show the economic importance of *Mononchus* species came the closest to good documentation of a biological agent for control of the beet cyst nematode (though he cast doubt on whether biological control of the nematode was possible under the soil conditions of Utah).

In this same 1927 paper, Thorne also discussed and illustrated a "sporozoan" parasite of nematodes that he later described as *Duboscqia penetrans* (Thorne 1940). The species was transferred first to genus *Bacillus* (Mankau 1975) and later to *Pasteuria* (Starr and Sayre 1985). Starr and Sayre (1988) redefined *P. penetrans* as limited to attacking root-knot nematodes and described a sibling species, *P. thornei*, attacking root-lesion nematodes.

At the end of this early period, upon the death of Cobb in 1932, Steiner assumed leadership of USDA's Division of Nematology. He served in that capacity until 1956.

D. BIOLOGICAL CONTROL OF PLANT PATHOGENS. By R. J. Cook

Much of the effort on the biological control of plant pathogens during 1889-1933 was made by state, university, and foreign scientists, though USDA scientists made key contributions during this period. However, most of the more intensive research in this field has occurred only in recent years. (Cook 1981; Cook and Baker 1983; Baker 1987; Hornby 1990.)

The first reference to biological control in plant pathology literature was made by a German plant pathologist, C. F. von Tubeuf, in 1914. It was only seven years later that C. Hartley, of USDA's Bureau of Plant Industry, Office of Investigations in Forest Pathology, made the first attempt at direct introduction of microorganisms into soil for biological control of a plant pathogen (Hartley 1921). He tested 12 fungi and one bacterial strain in steamed nursery soil for their antagonistic potential against damping-off of pine seedlings caused by *Pythium debaryanum*. Significantly less damping-off occurred in the treated soil compared with the same soil without the introduced fungi. Hartley's report was followed by papers by scientists in the United Kingdom and Canada reporting successful control of common scab of potatoes and take-all of wheat in sterilized soil by antagonistic fungi or bacteria introduced into such soils (Millard and Taylor 1927; Sanford and Broadfoot 1931; Henry 1931; Baker 1987; Cook 1988).

Soil steaming and fumigation have been used extensively in nurseries, greenhouse beds, and open fields since Hartley's classic work, but nearly 50 years passed before microorganisms would again be tested for their potential to enhance or extend the control of soilborne pathogens provided by these heat or chemical treatments.

Except for the work by Hartley, there are no published reports of USDA plant pathologists having attempted to control either fungal or bacterial diseases with introduced antagonists during this early period. The emphasis instead was on collection and release of genes for resistance to plant diseases. While entomologists were exploring the original homes of naturalized insect pests and collecting and importing their natural enemies, USDA plant pathologists, cooperating with plant geneticists, were exploring the original homes of plant pathogens to collect germplasm of the plant hosts as a source of resistant genes for deployment in U.S. crops.

During these same early years, plant pathologists attempted the approach used by entomologists, with emphasis on antibiotic-producing fungi introduced into raw soil for biological control of root pathogens, since there was a general lack of resistance genes for defense against fungal root pathogens. It was learned early, however, that raw soil has remarkable resiliency against the introduction of alien microorganisms or the establishment of native organisms at populations above natural levels. Indeed, these early attempts were so consistently unsuccessful that all further efforts along these lines would be abandoned for the next 50 years.

In 1929, H. H. McKinney of the USDA Bureau of Plant Industry, reported the results of his research on inoculation of tobacco plants with various mixtures of mild and severe strains of the "green mosaic" and "yellow mosaic" viruses, and showed that plants first inoculated with one virus were protected from infection of another closely related virus or a mild strain of the same virus (McKinney, 1929). Thus became known the phenomenon of "cross protection," which has been shown to have general applicability for most, if not all, major groups of plant viruses. This approach to biological control of plant viruses, i.e., inoculating plants with a mild strain to protect them for part of their productive life against a severe strain of the virus, is now used on nearly every continent. U.S. plant virologists have studied cross protection extensively in the laboratory since McKinney's discovery, but consider its use as a last resort because of risk that a mild virus of one crop could be severe or act synergistically with other viruses in other crops. This problem may now be overcome as a result of recent discoveries discussed later in this history.

CHAPTER II
1934-1952

A. BIOLOGICAL CONTROL OF ARTHROPODS (INSECTS, MITES, AND TICKS)

1. Arthropod Biological Control Agents

a. Classical biological control (introduction of biological control agents). By J. R. Coulson

Until 1934, all USDA foreign explorations and introductions and releases of natural enemies and other biological control agents were handled independently by the various commodity-oriented Investigations (or Divisions) of the Bureau of Entomology. In 1934, the Bureau of Entomology was combined with the old Bureau of Plant Quarantine to form the Bureau of Entomology and Plant Quarantine (BEPQ). Chiefs of this new Bureau were L. A. Strong (1934-41), P. N. Annand (1941-50), and A. S. Hoyt (1950-53). Within this new Bureau, there was formed in 1934 a Division of Foreign Parasite Introduction, which was charged with the responsibility for all Bureau exploration for, and importation of, foreign insect parasites and predators and their distribution to the various other Bureau Divisions for utilization in their biological control programs. This was the first agency in the USDA providing centralized direction of natural enemy introductions, and such an agency, under various names, continued until 1972. (Clausen 1956; Rainwater and Parencia 1981.)

The Division was placed under the direction of C. P. Clausen, who continued in that position until his retirement in 1951 (at which time he became Chairman of University of California's Department of Biological Control). In addition to his responsibilities for planning and directing activities concerned with collecting, importing, and handling foreign insect natural enemies up to the time of their release to the appropriate Division for colonization and/or propagation, he continued other activities assigned to him including coordination of the work conducted by the other Divisions and cooperating states on the utilization of parasites and predators. For a short period during World War II, a Control Investigations Division was established, with Clausen serving also as its director. Thus, the foreign parasite introduction program was for this short period effectively under single management with control of both foreign and domestic work (Sailer 1981b).

The two biological control laboratories in Europe were consolidated in 1935 when the Budapest laboratory (with W. F. Sellers in charge) was closed, and in 1936 the European Parasite Laboratory (EPL) was moved to St. Cloud near Paris. In 1939, this laboratory, which since 1922 had been headed by H. L. Parker, was closed due to the onset of World War II. During 1934-39, work at the EPL was conducted on natural enemies of the European corn borer, Hessian fly, European earwig, alfalfa weevil, asparagus beetle, pink bollworm, elm leaf beetle, European pine shoot moth, larch casebearer, pea weevil, and codling moth. Releases of European parasites of the larch casebearer in the 1930s made by both the USDA and Canada programs resulted in the establishment of two parasites (*Agathis pumila* and *Chrysocharis laricinellae*) which have provided substantial control of the pest in eastern U.S. and eastern Canada; with additional releases, this control was later expanded to western U.S. after spread of the pest there (see Appendix III below). (See references for the

various EPL projects cited in Chapter I and especially Clausen 1956, 1978; Dowden 1962; and Drea 1981.)

Projects during 1934-41 at the Asian Parasite Laboratory (APL) in Japan, which was headed by R. W. Burrell from 1934 until closing of the laboratory in November 1941, included studies of the natural enemies of the oriental fruit moth, European corn borer, Comstock mealybug, Japanese beetle, Asiatic garden beetle, elm leaf beetle (for California), and European spruce sawfly (for Canada). Shipments of natural enemies of the first three pests were sent to Division of Fruit Insects' laboratories at Moorestown, NJ, which also functioned as a quarantine receiving station. The oriental fruit moth project was another major USDA program entailing large scale rearing of the oriental parasites and their release in many Eastern states; only one of the parasites became established in the U.S. The Comstock mealybug program resulted in establishment of three parasites and commercial control of this pest was soon obtained in the eastern U.S. (See references for the various APL projects cited in Chapter I and Haeussler and Clancy 1944; Allen 1962; and Clausen 1956, 1978.)

An European parasite of wheat stem sawflies obtained from the Canadian Department of Agriculture was released by USDA in the eastern U.S. in the 1930s. At first, no establishment was recorded (Clausen 1956), but much later the species (*Collyria coxator*) was found to be established, together with a second introduced parasite, in the eastern U.S., where complete control of the European wheat stem sawfly has been obtained (Streams and Coles 1965; Filipy et al. 1985). Other importations were made during the pre-war period of parasites of the sugarcane borer from Puerto Rico (where they had originally been established from Brazil) for Louisiana and Florida, and of the pink bollworm from Egypt, Korea, and Hawaii. (Clausen 1956, 1978.)

In 1935-36, special funds were made available to USDA for a 1-year study of insect pests in Hawaii and Puerto Rico. Some of these funds were assigned to the Division of Foreign Parasite Introduction to conduct explorations for parasites of the Mediterranean fruit and melon flies for Hawaii, and importations of natural enemies of other insect pests for Puerto Rico. Fruit fly parasites were imported into Hawaii from four explorations (in West and East Africa, Brazil, India, and Sri Lanka) and from the Fruit Fly Laboratory in Mexico City, but there were no establishments, largely due to shipping problems and a precipitant cessation of funding (Clausen et al. 1965). A Division field station was established at Mayaguez, PR, under K. A. Bartlett, in cooperation with the federal experiment station there. Work concerned parasites of the sugarcane borer, West Indian fruit fly, coconut scale, pineapple mealybug, pink bollworm, limabean pod borer, white peach scale, and other pests. Parasite shipments were received from South American explorations, from Hawaii, the Mexico City laboratory, and mainland U.S. These Division efforts in Hawaii and Puerto Rico were concluded in late 1936.

In 1937, a parasite quarantine receiving station was established within the Division of Foreign Parasite Introduction at the U.S. Entomological Laboratory at Moorestown, NJ. Laboratory facilities were constructed to enable foreign shipments to be received and handled under quarantine conditions, and for breeding of the parasites for shipments to other agencies throughout the U.S. This receiving facility, established at Moorestown in 1928, was to be the first of several such USDA biological control quarantine facilities. Personnel of the Moorestown Receiving Station were moved to new, improved quarters at the new Plant Quarantine Building at Hoboken, NJ, from 1940 until 1944, when the Hoboken facility was closed (Clausen 1956). T. R. Gardner was in charge of the receiving facilities at Moorestown and Hoboken from 1937-43, when H. D. Smith was placed in charge. After closure of the Hoboken quarantine facility, shipments of imported natural enemies were received during 1945-52 at several Bureau of Entomology and Plant Quarantine field stations, the most important being the Division of Fruit Insects and Division of Cereal and Forage Insects laboratories at Moorestown, NJ, using the quarantine facilities there, and the newly opened Division of Foreign Parasite Introduction facility at Albany, CA (see below).

In 1938, additional studies were assigned to the Division of Foreign Parasite Introduction involving investigation of the effects of chemical and other control methods on populations of natural enemies. These studies were initiated at field stations in Orlando, FL (1938-40), Kearneysville, WV (1938-41), and Whittier, CA (1938-43). The major pests investigated included codling moth, strawberry leafroller, citrus whitefly, and several citrus scale insects.

In 1938-39, a Division entomologist (P. A. Berry) conducted a survey of whitefringed beetles in South America, with little success in finding natural enemies.

During World War II, the Division's Japanese and European laboratories were closed. The American personnel of the European Parasite Laboratory were sent to open a South American Parasite Laboratory in Montevideo, Uruguay, headed by H. L. Parker, which operated from January 1940 to November 1946. Explorations were conducted in various areas of South America, and temporary field stations were opened in Brazil and Peru. Over 300 shipments of natural enemies were sent from South America during this period. Most of the shipments were made to Hoboken, but some were made directly to other Bureau laboratories in Florida and Louisiana, and to the University of California. Major insect pests studied included Mexican bean beetle, pink bollworm, vegetable weevil, pea weevil, vetch bruchid, sugarcane borer, fall armyworm, corn earworm, and cotton leafworm. (Parker et al. 1950, 1953.)

In 1936, a parasite of the asparagus beetle established in the eastern U.S. was collected in Ohio and established in Washington, which has resulted in partial, though not commercial, control of this pest in the latter state. Similarly, a cooperative University of California-USDA program in 1943 was successful in establishing in California an important parasite of the San Jose scale from the eastern U.S. This parasite has provided partial control of that pest in California. (Clausen 1956; DeBach 1964).

The citrus blackfly, which had been discovered in Mexico in 1935, spread rapidly throughout the citrus-growing areas of that country, and by 1950 was threatening citrus-growing areas of the U.S. In 1938 and again in 1943, the Mexican Department of Agriculture, in cooperation with USDA's Division of Foreign Parasite Introduction, obtained and released the parasite that had successfully controlled this pest in Cuba; successful control was obtained only in areas of high humidity in Mexico. In 1943, a working agreement was negotiated by the governments of Mexico and the U.S. on biological, chemical, and quarantine measures to control this serious pest of citrus. In 1948-49, Division entomologists explored in Malaya, India, and Pakistan, and made many shipments of citrus blackfly parasites to the Division quarantine receiving laboratory at Mexico City, from which the parasites were disseminated and released in the principal citrus-infested areas of Mexico. This program resulted in the establishment of three Asian parasites and the subsequent complete economic control of the citrus blackfly in Mexico by 1953-55. This biological control success was to be repeated in Texas and Florida, when the citrus blackfly invaded those areas in the 1970s. (Smith and Maltby 1964; Thompson et al. 1986.)

The discovery of the oriental fruit fly in Hawaii in 1946 resulted in funding for USDA foreign explorations and the establishment of another cooperative biological control importation program directed against this and other introduced fruit flies in Hawaii. In order to coordinate all phases of the project properly and prevent duplication of effort by the large number of participating agencies, a Memorandum of Agreement was established in 1948 involving USDA's Bureau of Entomology and Plant Quarantine, the Hawaiian Agricultural Experiment Station, the Hawaiian Sugar Planters' Experiment Station, the Pineapple Research Institute, and the University of California. Major responsibility for foreign exploration was assigned to the Bureau's Division of Foreign Parasite Introduction. During 1947-51, numerous shipments of over 25 species of parasites and predators were sent to Hawaii from the Philippines, Malaysia and other areas of Southeast Asia and Oceania,

southern China, Taiwan, India, Sri Lanka, and various areas of Africa, Brazil, Mexico, and Australia. During 1947-62, field releases were made of 29 species of parasites and one species of predator, and seven of the imported parasite species became established. Though full economic control was not attained, these and earlier established parasites are responsible for a considerable degree of parasitization and substantial reduction of fruit fly populations in Hawaii. (Clausen et al. 1965.)

In 1944, the Division of Foreign Parasite Introduction established a laboratory at Albany, CA, headed by J. K. Holloway, in cooperation with the California Agricultural Experiment Station, to study the biological control of weeds (see below) and insect pests. And in January 1947, after the closing of the South American Parasite Laboratory, the Division's European Parasite Laboratory was reopened in France, under H. L. Parker. Projects initially assigned to the EPL included work on the European corn borer, sweetclover weevil, European chafer, and European elm scale, fig scale, and navel orangeworm in cooperation with the University of California. In 1950, projects on the European wheat stem sawfly, green peach aphid, omnivorous leaftier, and Rhodesgrass mealybug were added. Work on weeds had also begun there, in 1947 (see below). In June 1952, USDA explorations for natural enemies of the pink bollworm were begun in India, which resulted in the establishment of a USDA laboratory there that was maintained until 1958. G. W. Angalet was in charge of the Indian laboratory.

In 1942, the Bureau of Entomology and Plant Quarantine was placed administratively under the Agricultural Research Administration of USDA. In April 1952, the Bureau's Division of Foreign Parasite Introduction was abolished and its personnel and functions combined with the Bureau's Division of Bee Culture to form the Division of Bee Culture and Biological Control, with its integral Biological Control Section absorbing the functions of the former Division of Foreign Parasite Introduction. Chief of the new Division was J. I. Hambleton, and T. R. Gardner was in charge of the Biological Control Section. (Gardner and R. Latta had been acting in charge of the Division of Foreign Parasite Introduction since Clausen's retirement in January 1951.) All parasite receiving activities at Moorestown, NJ, were placed under this new Division, and D. W. Jones, formerly with the Division of Cereal and Forage Insects, assumed leadership of the new Division's Foreign Parasite Introduction Station at Moorestown in July 1952.

Significant accomplishments of the USDA's classical biological control program during 1934-1952 included complete control of the citrus blackfly in Mexico (which was to be extended to Texas and Florida when that pest reached the U.S. in the 1970s) and of the European wheat stem sawfly and Comstock mealybug in the eastern U.S., substantial control of the larch casebearer in New England, and significant but partial population suppression of the San Jose scale, elm leaf beetle, and fig scale in California, and of the asparagus beetle in Washington State (Clausen 1956; Dowden 1962; DeBach 1964; DeBach and Rosen 1991; and Appendix III below). The two major USDA biological control importation programs, on the European corn borer and oriental fruit moth, had somewhat disappointing results. Six species of corn borer parasites were established in the U.S. and at first provided appreciable field control of this pest. However, the most effective of the introduced parasites, a tachinid fly, *Lydella thompsoni*, disappeared from the Corn Belt in the late 1950s, and corn borer populations rose. "At best it may be said that *L. thompsoni* bought the time needed to develop and place in production the borer-resistant hybrid varieties of corn" (Sailer 1973). Only one of the many oriental fruit moth parasites imported became established in the U.S., and it provides little control. However, the significant accomplishment in regard to the biological control program against this pest relates to augmentation (see below).

The interest in biological control further declined during this period, with a continued shift toward insecticide research. The ratio of insecticide to biological control papers at the beginning of World War II was 6 to 1, and by 1946, 20 to 1, due to the development of DDT and many other synthetic insecticides. This trend is perhaps reflected in the organizational changes of 1952 noted above, i.e.,

the abolishment of the Division of Foreign Parasite Introduction and its submersion into the Division of Bee Culture and Biological Control. However, by 1955 the trend had begun to reverse, the publication ratio then being 7 to 1. Despite these trends, the number of entomologists engaged in biological control research in the USDA increased up to the beginning of World War II to a high of about 40, and there was a subsequent decline during the 1940s, with a low of 5.5 scientific man-years (SYs) by 1954. During this period, more state organizations, in addition to those in California and Hawaii, became involved in the overall biological control program, wherein the USDA performed the initial exploration and importation phases and the states performed colonization and recovery phases. (Clausen 1956; Sailer 1973.)

b. Augmentation and conservation of arthropod biological control agents. By J. R. Coulson

Augmentation and conservation approaches during this period were focused on the oriental fruit moth program. A native species, *Macrocentrus ancylivorus*, a parasite of the strawberry leafroller, was found to attack the newly introduced pest moth, and attained a high degree of parasitization. Culture of this parasite and its release against the oriental fruit moth began as early as 1928, and the USDA mounted a large-scale release program in all infested areas of the eastern U.S. from 1929 to 1935, during which 50% reduction of fruit injury was frequently reported. When the pest invaded California in 1942, *Macrocentrus* became the first parasite to be mass reared and released in an attempt to eradicate or prevent further spread of a pest. University of California researchers developed a low-cost, highly effective method for its mass culture, and millions were reared and released annually during 1944-46. Although overall eradication was unsuccessful, some infestations were eliminated. The parasite continues to be utilized in a number of state biological control programs to the present. However, in general, interest in the augmentation and conservation approaches to biological control, as well as in importation, waned as highly effective insecticides were discovered and came into general use. (Finney et al. 1947; Clausen 1956; Allen 1962; Sailer 1973, 1976.)

2. Arthropod-Parasitic Nematodes. By J. R. Coulson

In 1934, the Bureau of Plant Industry was combined with other units and became the Bureau of Plant Industry, Soils, and Agricultural Engineering. The Division of Nematology continued under this Bureau, with its Chief, G. Steiner, 1932-56. Research on insect-parasitic nematodes continued at a few Division locations, though most of the research continued to emphasize plant nematodes. (See also Section C below on biological control of plant nematodes.)

Considerable research was conducted during the 1930s on the biology and culture of the nematode *Neoaplectana* (now *Steinernema*) *glaseri*, discovered parasitizing the Japanese beetle in New Jersey, and a bacterium was discovered to be associated with it which caused the death of the Japanese beetle grubs. With the development of methods of mass culture of the nematode on artificial media, a large-scale colonization program was conducted in New Jersey in 1940 by the New Jersey Department of Agriculture in cooperation with the USDA and Rockefeller Institute for Medical Research at Princeton. A similar program was conducted later in Maryland. These first efforts to utilize nematodes for insect control did not produce effective control, and interest in the use of nematodes waned. Another nematode of this genus was discovered in 1954, which rekindled this interest; see Chapter III. (Fleming 1968.)

3. Arthropod Pathogens. By J. R. Coulson, J. R. Adams, H. Shimanuki and P. V. Vail

During this period, research on honey bee diseases, their control, and bee resistance to them, was conducted in the new Bureau of Entomology and Plant Quarantine created September 1, 1934, in the Bureau's Division of Bee Culture, under the leadership of J. I. Hambleton, 1924-52. This work was

primarily conducted at the Bee Culture unit at Beltsville, MD, and at the Laramie, WY, field station, by C. E. Burnside, E. C. Holst, A. P. Sturtevant and colleagues (Burnside 1934; Woodrow 1941a, 1941b; Burnside and Revell 1948; Holst 1946; Burnside et al. 1949; Sturtevant 1949). For a brief period, 1952-1953, the Division of Bee Culture was combined with the Division of Foreign Parasite Introduction to form the Division of Bee Culture and Biological Control of the Agricultural Research Administration (see section A.1.a in this Chapter), with W. J. Nolan heading the Section of Bee Culture Research. (More information on USDA research on bee diseases is included in Appendix II.)

At other Bureau of Entomology and Plant Quarantine locations throughout the U.S. administered by several Bureau Divisions, there were significant successes in utilizing pathogens for insect control. The first was the development by the USDA of the bacterial milky spore disease, *Bacillus popilliae*, found attacking the Japanese beetle in New Jersey (see Chapter I), into a highly effective, and economical control for that introduced pest. The Japanese beetle was discovered in New Jersey in 1916, and soon became a severe, rapidly spreading economic pest, in part due to the absence of natural enemies. By the late 1930s, the USDA Japanese Beetle Laboratory at Moorestown, NJ, had expanded its staff to include R. T. White, I. M. Hawley, and S. R. Dutky. Research at the laboratory evolved into studies on most aspects of the use of the milky disease organism as a microbial control agent. Searches for diseased beetle grubs in New Jersey and studies of pathogens found were also conducted by Dutky and others. A bacterial microorganism was discovered, later described by Dutky as *B. popilliae*, that successfully controlled the grubs of this pest (Dutky 1940, 1941a-c, 1963; White and Dutky 1940). Methods for producing spores of the *Bacillus* and for storing and distributing them were developed. Procedures for mass production included injection of grubs with a microinjector, since the organism was not infectious *per os* (Dutky 1942a, 1947; Dutky and Fest 1942). Dutky then developed a spore dust formulation and application procedures for its effective use (Dutky 1942b). The spores were colonized in large areas of turf during 1939-53 in 14 states and the District of Columbia, providing effective suppression of Japanese beetle populations. *Bacillus popilliae* was further developed into the first commercial microbial pesticide, first officially registered for use in the U.S. in 1948. Dutky also studied other pathogens affecting the Japanese beetle, including the bacteria found in association with the nematode *Steinernema glaseri*, noted in the previous section. The Insect Pathology Unit of the Moorestown laboratory was moved to Beltsville, MD, in 1954 (see Chapter III).

A second success in the utilization of insect pathogens for insect control was the development by the University of California of a nuclear polyhedrosis virus (NPV) as an effective control of the alfalfa caterpillar in California in the 1940s and early 1950s. Experiments with viruses were also conducted by Canadian researchers in the 1940s and 1950s for use against introduced forest insect pests. An exotic NPV virus was introduced into Canada from Sweden and utilized against the European pine sawfly in Ontario. Researchers from USDA's Division of Forest Insect Investigations conducted similar studies in the U.S. in 1951-52, with excellent results. The virus became widely used in both Canada and the U.S. (Bird et al. 1950; Dowden and Girth 1953; and Benjamin et al. 1955.)

Toward the close of this period, research was being conducted on another insect bacterium, *Bacillus thuringiensis*, that led to the production of the most widely accepted, commercial microbial pesticide in use today. These successes increased interest in microbial control of insects, and insect pathology laboratories were established by the University of California in 1945, by the Canadian Department of Agriculture in 1946, and by the USDA in 1953. By the late 1950s and early 1960s, many other USDA laboratories began programs on insect pathology/microbial control. (Clausen 1956; Sweetman 1958; Steinhaus 1964; Hall 1964; Heimpel 1974; Dutky 1991.)

B. BIOLOGICAL CONTROL OF WEEDS. By J. R. Coulson

Following initiation of the use of insects for control of weeds in Hawaii, several other countries, including Australia, New Zealand, Fiji, India, and South Africa, became interested in this aspect of biological control in the 1920s and 1930s. The spectacularly successful control of the introduced prickly pear cactus in Australia by an insect introduced from South America kindled this interest even more.

Biological control of weeds in North America began with joint USDA-University of California research on prickly pear cacti on Santa Cruz Island, California, in the late 1930s (Goeden et al. 1967; Goeden 1993). But it was not until 1944 that permission was granted for the introduction of exotic insects into the continental U.S. to control weeds. As noted above, USDA's Division of Foreign Parasite Introduction established a laboratory under J. K. Holloway at Albany, CA, that year for research on the biological control of weeds in cooperation with the University of California, and in 1947, added research on natural enemies of introduced weeds to its European Parasite Laboratory in France. Initial target weeds for study at EPL included common St. John's-wort, from 1947, and gorse, from 1948. Common St. John's-wort, or Klamath weed, a rangeland weed, mildly poisonous to livestock, was introduced about 1900 into California, Oregon, and Washington, and by 1944 occupied over two million acres of otherwise useful rangeland in California alone. The weed was also a pest in Australia, and European insects were studied and introduced into that country beginning in 1928; control of the weed was good in localized areas there. A similar program was authorized for the U.S., and importations of the European insects established in Australia were begun in October 1944, from Australia, importations from Europe being impossible due to the war. Two species of beetles became established almost immediately, and by 1947 no further importations of those beetles were needed. In 1950, millions of the beetles were collected in California for recolonization.

At the close of the war, research on other European enemies of common St. John's-wort/Klamath weed was begun at the reopened European Parasite Laboratory in 1947, and shipments were made to California. By 1954, populations of the weed in California were reduced to the level of a roadside weed, and is now estimated to occupy less than 1% of its former abundance. The replacement vegetation was comprised primarily of native plants. Grateful California ranchers erected a monument in Fortuna, Humboldt County, to the beetles responsible for this control, the benefits of which are estimated at $23,000,000 per year over previous control costs plus weight gain in cattle. Much of these benefits extended to Oregon, Washington, Idaho, and other western states. (Holloway 1964; Huffaker and Kennett 1959; Huffaker et al. 1976; Goeden 1978.)

C. BIOLOGICAL CONTROL OF PLANT NEMATODES. By R. M. Sayre

As noted in the above section on insect-parasitic nematodes, the USDA Division of Nematology Investigations continued, under the leadership of G. Steiner (1932-56), within the newly reorganized Bureau of Plant Industry, Soils, and Agricultural Engineering, formed in 1934. This Bureau was placed administratively under USDA's Agricultural Research Administration in 1942.

In 1935, C. Drechsler, a USDA plant pathologist, was relocated from downtown Washington, DC, to the newly opened research facility at Beltsville, MD. There, he continued studies on the numerous soil fungi parasitizing amoebae, tardigrades, testaceous rhizopods, and nematodes. Drechsler was not a nematologist, but a mycologist in the Bureau's Horticultural Crops Research Division. His work was of direct benefit to the science of nematology. At retirement in 1962, he had published over 180 papers, some sixty of which included descriptions of new species of nematode-destroying fungi. These publications, even today, serve as guides to others in their search for fungi that might be used as biological control agents of nematodes. Although he suggested that fungi were regulators of

nematode populations, he never determined which fungal species might best be used in a practicable method for control of nematodes in agricultural soils.

During this period, there was one landmark field plot study, that of M. B. Linford and others of the Pineapple Experiment Station, University of Hawaii (Linford 1938). In field plots, they found reductions of soil populations of root-knot nematodes during the decomposition of organic matter that had been added to the soils. They attributed this reduction of nematodes to the fact that organic matter may have stimulated the activities of the many soil antagonists of nematodes. This was, perhaps, one of the first field tests that demonstrated biological control of nematodes.

In 1940, G. Thorne published on the life cycle of a "protozoan" parasite of a *Pratylenchus* nematode species (Thorne 1940). Again, as in his 1927 paper (Thorne, 1927), he pointed out the potential of this organism as a biological control agent.

In the same year (1935) that Drechsler moved to Beltsville, A. L. Taylor established a USDA field station at Tifton, GA. Later, Taylor served as a technologist for Shell Oil Company, 1946-49, where he did pioneering work towards the development of a volatile nematicide suitable for injection into soils. His work helped lead the way to the discovery and development of volatile D-D (1,3-dichloropropene and 1,2-dichloropropane) mixtures, EDB (1,2-dibromoethane), and DBCP (1,2-dibromo-3-chloropropane) in 1943, 1945, and 1954, respectively. (Christie, the USDA nematologist, determined the efficacy of EDB [Christie 1945].) These nematicides were to profoundly change the management practices used to control plant-parasitic nematodes. Attention was diverted from previously used methods to a single chemical tactic. This control approach dominated the thinking and actions of most nematologists for the next two decades.

D. BIOLOGICAL CONTROL OF PLANT PATHOGENS. By R. J. Cook, G. C. Papavizas, and J. R. Coulson

Considerable research on plant pathogens and their control was conducted during this period by many plant pathologists in various units of USDA's Bureau of Plant Industry, Soils, and Agricultural Engineering (Stefferud 1953). However, though some research on biological control of plant pathogens was conducted elsewhere (Wood and Tveit 1955), there was little study in this area within the USDA during this period.

Hurley Fellows and C. H. Ficke, both of USDA's Bureau of Plant Industry, Cereal and Forage Crop Disease Investigations, at Manhattan, KS, worked on root diseases of wheat. Their pioneering studies on take-all caused by *Gaeumannomyces graminis* var. *tritici* included significant observations on biological control (Fellows and Ficke 1934). Workers in Canada and Texas had shown earlier that root rots could be controlled by intensifying the activity of soil saprophytes by use of green or barnyard manure. Fellows and Ficke demonstrated this same effect for wheat take-all using various sources of organic materials, including chicken manure. Studies by F. E. Clark, of USDA's Bureau of Plant Industry, Soil and Fertilizer Investigations, showed that the suppressive effect of organic amendments on take-all and Phymatotrichum root rot was the result of intensified antagonism of the causal pathogens by microorganisms stimulated by the added substrates (Clark 1942). Fellows and Ficke (1934) had reported that take-all disappeared after about the fourth year of continuous wheat, and severe disease in the second and third years of wheat monoculture, an observation that would prove to be one of the first reports of biological control being responsible for "take-all decline." However, proof that take-all decline results from spontaneous biological control would not emerge until the 1960s (see below).

CHAPTER III
1953-1972
AGRICULTURAL RESEARCH SERVICE

A. BIOLOGICAL CONTROL OF ARTHROPODS (INSECTS, MITES, AND TICKS)

1. Arthropod Biological Control Agents

a. Classical biological control (introduction of biological control agents). By J. R. Coulson and W. H. Day

In November 1953, the old Agricultural Research Administration became the Agricultural Research Service (ARS), and the Bureau of Entomology and Plant Quarantine was abolished, its regulatory functions being placed into the Plant Quarantine and Plant Pest Control Branches (later Divisions) under ARS, and its research functions being placed in the newly formed Entomology Research Branch (raised to Division in 1957). Forest entomology was removed from ARS and placed in USDA's Forest Service (see notes on subsequent biological control activities in the Forest Service in Chapter V), and research on stored-products insects was assigned temporarily to the Agricultural Marketing Service, but later was returned to ARS. E. F. Knipling was designated Chief (Director in 1957) of the new Entomology Research Branch/Division and remained in charge until 1971. C. H. Hoffmann and H C Cox served as Division Directors from January 1971 until June 30, 1972, when the Division was abolished, and after 91 years (1881-1972), entomology ceased to be a separate entity within the USDA. (Rainwater and Parencia 1981.)

At the start of this period, there was an increasing awareness of problems caused by emphasis on chemical control of pests: development of insect resistance to chemical pesticides; concern over pesticide residues; and new pests developing due to destruction of their natural enemies by broad-spectrum pesticides. A 1953 review of the entomological research program indicated the need to make a substantial shift from chemical control to biological control, and this was immediately implemented by the Entomology Research Branch/Division, which increased research on alternative methods of pest control, and strengthened research on parasites, predators, and pathogens. This was reflected in an increase in the number of man-years devoted to biological control of insect crop pests from 5 in 1954 to 52 by 1965, and in the number of man-years devoted to biological control of weeds from 0.5 in 1954 to 6 in 1965. But due to general curtailment of government expenditures, the total number fell to 43 by 1972 (Sailer 1973).

On July 1, 1954, the Biological Control Section was removed from the old Division of Bee Culture and Biological Control and combined with the Insect Identification Section of the old Division of Insect Detection and Identification to form the new Insect Identification and Parasite Introduction (IIPI) Research Section (or Laboratory), which was raised to Branch status in 1957. Chiefs of this Section/Branch were P. W. Oman, 1954-60, W. H. Anderson, 1960-67, and R. I. Sailer, 1967-72. The IIPI was abolished with the Entomology Research Division on June 30, 1972. This reorganization effectively ended, after 38 years (1934-72), the centralized leadership and coordination of USDA's

foreign and domestic classical biological control importation programs that proved so successful for biological control.

The IIPI was given responsibility for conducting research in foreign areas, and for directing work at, and maintaining, all USDA biological control quarantine receiving stations in the U.S. Other commodity-oriented Sections/Branches of the Division were responsible for all aspects of parasite and predator studies that concerned pests within the scope of their commodity responsibilities. These included work with exotic species from the time natural enemies were cleared from quarantine and research on the effects of pesticides on the insects and their natural enemies. These types of research were conducted in close coordination and cooperation with IIPI. The combination of parasite/predator research with insect systematics was intended to facilitate maximum identification service for biological control, and to permit the use of USDA taxonomists in initial biological control surveys, collections, and field identifications.

At the time of the 1953-54 reorganization, three foreign laboratories reported to IIPI: Mexico City, Mexico (1953-57) (H. D. Smith in charge), New Delhi, India (1953-58) (G. W. Angalet in charge), and the European Parasite Laboratory (EPL) near Paris, France (1953-72) (directed by H. L. Parker, 1953-60; R. I. Sailer, 1960-65; R. J. Dysart, 1965-69; J. J. Drea, 1969-80). Each laboratory was staffed by a single American entomologist, and the Indian and European laboratories had additional local staff. A second American was added to the EPL in the early 1960s. Other IIPI foreign locations were established later during this period for studies on the biological control of weeds (see section B below).

Work at the Mexico City laboratory was essentially the continuation of the citrus blackfly project discussed in Chapter II, cooperation in various aspects of biological control with the Mexican Department of Agriculture, and studies of natural enemies of citrus pests in the Rio Grande Valley of Texas. Work at this location was terminated at the end of 1957.

Major work at the New Delhi laboratory concerned natural enemies of the pink bollworm (1952-54) and spotted alfalfa aphid (1955-58). Miscellaneous observations and opportunistic collections of natural enemies of other U.S. pests were made in India, including, but not limited to, bollworm, epilachnine beetles, citrus whitefly, California red scale, Rhodesgrass mealybug, pea aphid, and the weed puncturevine. This laboratory was closed in 1958.

Studies at the European Parasite Laboratory concerned natural enemies of several weeds (see Section B below) and a number of insect pests including the following: sweetclover weevil, for North Dakota (1953-62); wheat stem sawfly, for North Dakota, Nebraska, and Montana (1953-55); Rhodesgrass mealybug, for Texas (1953-59); European chafer, for New York (1953-60); green peach aphid, for western and eastern states (1953-58); omnivorous leaftier, for the Pacific Northwest (1954-55); cherry and apple maggots (1954-64); yellow clover aphid (1955-56); vetch bruchid (1955-65); spotted alfalfa aphid (1955-56); alfalfa weevil (1959-72); alfalfa and clover seed chalcids (1959-64); pea aphid (1959-69); balsam woolly adelgid (1959-64); European pine shoot moth (1961-65); face fly (1961-67); lygus bugs (1962-65 and 1970-72+); cereal leaf beetle (1963-73); grasshoppers (1963-71); smaller European elm bark beetle (1963-68); imported cabbageworm (1967-69); greenbug (1968-71); "linden aphid" (*Eucallipterus tiliae*), for California (1969-70); alfalfa snout beetle, for New York (1970-72); elm leaf beetle, for California (1971-73); and gypsy moth (1972+).

Two domestic field locations also reported to IIPI in 1953 - an East Coast Parasite Receiving Station located at Moorestown, NJ (1953-73) (headed by D. W. Jones, 1953-60; L. B. Parker, 1961-63; M. H. Brunson, 1963-70; L. W. Coles, 1970-71; W. H. Day, 1971-78), and West Coast Parasite Receiving Stations located at Albany, CA (1953-57) (J. K. Holloway in charge), and Riverside, CA (1957-68) (headed by B. Puttler, 1957-59, and D. W. Clancy, 1961-68), and operated in cooperation

with the California Agricultural Experiment Stations at Albany and Riverside, respectively. The New Jersey station received most of the parasite/predator shipments from the Indian and European stations. The California station at Albany was responsible mostly for receipt of shipments of natural enemies of weeds (see section B), but also received parasite/predator shipments from the European station that were destined for use in western states, and from University of California explorers (e.g., a number of shipments of beet leafhopper parasite material from Morocco and Egypt was received at the Albany station from 1953-54). The Receiving Stations were responsible for clearing foreign material through quarantine to assure that only beneficial species were released from quarantine, and for distribution of the material to State and federal researchers and action agencies for study and field release. Personnel at both the East Coast and West Coast stations also participated in research programs involving release and evaluation of exotic natural enemies in their respective areas. Projects at the Riverside location included spotted alfalfa aphid, alfalfa weevil (for the East Coast), Egyptian alfalfa weevil, elm leaf beetle, limabean pod borer, pea aphid, lygus bugs, cabbage looper, Comstock mealybug, and vegetable weevil. In the early years, the New Jersey station was mainly involved only in quarantine clearance, culture, and distribution of the imported natural enemies received. However, in 1956, breeding of aphid parasites and predators for release in New Jersey was begun, and some sweetclover weevil parasites were released in New Jersey and Delaware beginning in 1957. Other more extensive release and field evaluation projects soon developed at the Moorestown location, including those on wheat stem sawfly (1957-64), pea aphid and other aphids (1958-72+), alfalfa weevil (1958-72+), apple, cherry and blueberry maggots (1959-62), lygus bugs (1962-72+), face fly (1966-69), Mexican bean beetle (1967-68), and alfalfa blotch leafminer (1971-72+). The station's major project on alfalfa weevil biological control was an outstanding success (see below).

In 1965, a third domestic location was added to IIPI, a newly constructed Biological Control of Insects Research Laboratory at Columbia, MO. Directors of this Laboratory were F. R. Lawson (1965-70) and C. M. Ignoffo (1971-1989). The purpose of the Laboratory was to develop and test new principles and methods of using parasites, predators, and pathogens against major insect pests, with emphasis on reduction of pest populations over large areas by integration of biological control measures with other control measures such as pesticides, sterile insect techniques, attractants, cultural methods, etc. Initial projects at the Laboratory included biological control of 1) insect pests of cole crops, 2) insect pests attacking leaves and stems of crop plants, 3) insects attacking roots of plants, and 4) flies attacking man and animals. These included research on host and parasite rearing (including *Trichogramma* egg parasites), field observations and experiments (primarily with cabbage insects and cutworms), and work on integrated control of livestock insects (primarily horn fly). In this period, research at this Laboratory demonstrated successful control of cabbage insect pests by use of parasites and pathogens (Parker et al. 1971; see Augmentation section below).

During this period, IIPI and other Entomology Research Division Branches followed the custom begun in the Bureau of Entomology and Plant Quarantine era of requiring all foreign and domestic locations to submit quarterly reports of their activities. These reports have been important sources of information when projects have been reopened after a period of years, or when new personnel became involved in an old project. They have been of special importance for foreign explorations, and in the preparation of this history.

In 1958, the Foreign Agricultural Research Grant Program was initiated under authority of U.S. Public Law 480 (the Agricultural Trade, Development, and Assistance Act of 1954). This program continues today as the Special Foreign Currency (SFC) program. P.L. 480 authorizes USDA to use U.S.-owned foreign currencies to support cooperative agricultural and forestry research on problems of interest to the U.S. and participating foreign countries. This program, which until 1978 was administered by ARS, has been of special importance to USDA's biological control programs, and its taxonomy programs. From 1959-72, IIPI scientists were "cooperating, or sponsoring, scientists" on

numerous biological control and taxonomic projects in Brazil, Colombia, Uruguay, Egypt, Morocco, India, Pakistan, Taiwan, Korea, Israel, Yugoslavia, and Poland. The biological control projects generally concerned surveys for natural enemies of certain crop pests, or in certain crop or ecological situations, and represented a considerable expansion of USDA's biological control exploration program. Extensive valuable information was accumulated concerning the natural enemies of insect and weed pests in these areas, much of which remains in unpublished reports, which are on file in the ARS Biological Control Documentation Center. Later projects concerned research on techniques for culturing or otherwise utilizing specific types of natural enemies. Taxonomic projects under the P.L. 480 program contributed important information on the systematics of parasitic and predaceous groups, including descriptions of new species of importance to biological control. Many of the natural enemies discovered or described during these various projects were imported for study and release against insect and weed pests in the U.S. Projects in the U.S. which benefitted included those concerning the balsam woolly adelgid, cereal leaf beetle, gypsy moth, corn earworm/ bollworm/tomato fruitworm, various aphids and scale insects, European corn borer, sugarcane borer and other stalk borers, *Trichogramma* egg parasites, beneficial and non-beneficial lady beetles, plant bugs, dung beetles, fruit flies, and leafminer flies, among others.

In addition to these overseas activities, personnel of ARS' Plant Protection Division (PPD) (now the Plant Protection and Quarantine Programs of the Animal and Plant Health Inspection Service) were involved, from 1967-69, in shipment of large quantities of several gypsy moth parasites from Spain. These parasites were collected in connection with PPD's studies on sex attractants there, and PPD financed collections of gypsy moth parasites in Yugoslavia in 1970. These parasites were cleared in ARS quarantine at Moorestown, NJ, and made available for release by PPD and state personnel in several northeastern states, especially NJ and PA (Reardon and Coulson 1981).

Significant accomplishments resulting from ARS's biological control importation program during 1953-72 included, but are not limited to, the control of three serious introduced pests, the cereal leaf beetle and the alfalfa weevil in the eastern U.S., and the Rhodesgrass mealybug in Texas.

The cereal leaf beetle (CLB), a European species, was discovered to be established in Michigan in 1962, and was quickly recognized as a major threat to U.S. small grain production. ARS studies at the European Parasite Laboratory began in 1963 and resulted in the discovery and importation of five species of parasites of the beetle through ARS quarantine. Since there were no IIPI units within working distance of the pest populations, release and establishment work was conducted first under cooperative agreements with universities in Michigan and Indiana. In 1966, the Plant Protection Division of ARS (which in 1971 became the Plant Protection and Quarantine Program (PPQ) of USDA's new regulatory agency, the Animal and Plant Health Inspection Service [APHIS]), established a laboratory in Michigan to culture and/or otherwise disseminate and release the introduced parasites. By 1972, four of the European parasite species were established in the U.S., and through the efforts of PPQ were soon disseminated and established throughout the expanded range of the CLB, which soon covered most of the northeastern U.S. and some parts of eastern Canada. Though the absence of research involvement in much of the domestic phase of this program long prevented a thorough, detailed evaluation of its results, the program is recognized as an outstanding success, the parasites being credited with economic control of this pest. Heavy crop losses (as high as 55% in spring grains and 23% in winter grains; R. J. Dysart, personal communication, 1984) reported during the late 1960s in the Midwest were nearly eliminated, and this pest seldom reached damaging levels as it later expanded its range. An assessment of the benefits of this program made in 1978 by the APHIS laboratory in Niles, MI (W. H. Day, unpublished data, 1988; see Table 1) noted a conservatively estimated annual savings of $14,000,000 due to cessation of many pesticide applications previously applied for this pest; e.g., 1.6 million acres were treated in 1966, but only 20,000 acres in 1981 (R. J. Dysart, personal communication, 1984). Incidentally, this was the first example in which a pest of an annual crop in a temperate continental area was successfully controlled

by imported parasites. Previous successes had been with pests of perennial crops. (Dysart et al. 1973; Sailer 1973, 1981a; Coulson 1976; Burger 1980; Haynes and Gage 1981; Lampert and Haynes 1985; DeBach and Rosen 1991.) See also Chapter VI for more complete information on the APHIS program, including updated cost:benefit information.

In 1951, the alfalfa weevil, which had been present in the western U.S. since the early 1900s, was found in Maryland and by 1971 had spread throughout most of the eastern U.S. It became the number one pest of alfalfa in the East, requiring regular insecticidal treatments to prevent total crop destruction in most cases, and in some cases, especially in the Southeast, farmers were forced to shift from alfalfa production to less desirable forage crops. The discovery of insecticide residues in milk, a result of cows eating alfalfa contaminated with the hazardous pesticides in use at the time, was an additional serious problem. IIPI scientists at the European Parasite Laboratory and the New Jersey parasite receiving facility began a parasite importation program in 1957. The weevil parasite established earlier in the West, was successfully recolonized by ARS in New Jersey by 1959 and quickly spread throughout the East. However, it soon became clear that one parasite species would not provide adequate biological control of this pest. By 1965, five parasite species were established in the New Jersey-eastern Pennsylvania area and began to disperse throughout the Middle Atlantic States. (A total of seven species were eventually established; Dysart and Day 1976; Dysart 1989; Bryan et al. 1993.) The New Jersey Department of Agriculture developed a strong parasite distribution program, aided by the ARS Moorestown station, that resulted in rapid expansion of parasite populations in that state. By 1970, weevil populations there had decreased and only 8% of New Jersey farmers used insecticides for the weevil, as compared to 94% in 1966, saving farmers $3,000,000 in 1970 in this state alone. ARS Moorestown personnel also collected and disseminated the parasites to other states from 1965-72, and the parasites continued to increase and spread. By 1978-79, their effects on the weevil were significant, saving farmers in an 11 state area in the Northeast about $8,000,000 annually due to cessation of previously applied insecticidal treatments. A more recent estimate (W. H. Day, unpublished data, 1988; see Tables 1 and 2) of such savings to farmers in 18 eastern states as the parasites' ranges have increased further is, by 1986, nearly $49 million annually. Adjusted for inflation to 1993, this annual savings represents $63,700,000! This is a considerable return for an estimated total cost of about $1,000,000 for the ARS importation program. The dissemination of the parasites by ARS personnel was recognized as detracting from the ARS research programs, and this work was assumed by APHIS in 1980. Improvements in this aspect of biological control, i.e., implementation, are discussed in subsequent chapters. (Sailer 1973, 1981a; U.S. House of Representatives 1973; Coulson 1976; Day 1981; Lashomb et al. 1988; Moffitt et al. [1990]; Bryan et al. 1993.)

The Rhodesgrass mealybug, an oriental species, was first identified in the U.S. in 1942 and quickly became a major pest of forage and lawn grasses in Texas in the 1940s. A parasite of the mealybug known from Hawaii was imported and established in 1949 and was reared and released in large numbers by the Texas Agricultural Experiment Station (TAES) in cooperation with the USDA. Mealybug parasites were also sent to Texas from USDA's European Parasite Laboratory in the 1950s. These attempts provided little control of the mealybug. In 1956, the ARS entomologist at the Indian station discovered an undescribed parasite attacking the mealybug, now known as *Neodusmetia sangwani* (Subba Rao). This species was introduced into Texas in 1959 where it became established and control of the mealybug was quickly demonstrated. Methods were developed by the TAES to distribute the parasite throughout Texas rangelands in the 1960s, and the Rhodesgrass mealybug was eliminated as a pest of forage grasses in Texas by 1970. A 1979 cost:benefit analysis indicates that this successful control represents an annual savings of almost $17,000,000 in reduced costs for turf grass maintenance alone, and additional profits from increased calf sales exceeding $177,000,000. Total cost of the project in Texas was less than $200,000. The parasites have also been established in Florida with nearly similar results. (Sailer 1973; Dean et al. 1979; DeBach and Rosen 1991.)

In addition to these three successful classical biological control programs, other accomplishments during 1953-72 included the establishment of parasites and predators of a number of other introduced insect pests in the United States, of which the most noteworthy are the spotted alfalfa aphid and the pea aphid. The spotted alfalfa aphid appeared in California in 1954 and quickly spread across the southern U.S., inflicting severe damage to alfalfa crops. The USDA and University of California began a cooperative biological control program in 1955 that resulted in establishment of three parasites and their rapid dispersal across the range of the aphid. In the meantime, strains of alfalfa were being developed that were resistant to the aphid. By 1958, spotted alfalfa aphid outbreaks had subsided due to a combination of plant resistance and parasitism, and aphid populations remain below economic levels today. The pea aphid was a much earlier introduction, being found in North America in the 1870s (Davis 1915), and by the 1950s was distributed throughout the continental U.S. as a very important pest of peas, alfalfa, and other leguminous crops. In the late 1950s, parasites were introduced by ARS from India and Europe, established, and quickly dispersed throughout the U.S. After the mid-1960s, there was a marked reduction in reports of damage caused by the pea aphid. It has been estimated that an annual savings of over $36,000,000 has resulted from a 30% reduction in alfalfa acreage no longer treated for this pest (W. H. Day, ARS, unpublished data, 1988); adjusted for inflation, the savings represent $47,300,000 in 1993 dollars (see Table 1). A third introduction of note was that of the staphylinid face fly predator, *Aleochara tristis*, which was the first natural enemy of livestock pests introduced by ARS. This species was imported in 1965, cultured in Nebraska, and released in several western and eastern states. It became established in Nebraska, but has had little apparent impact on the pest to date. (van den Bosch et al. 1959; DeBach 1964; Drea 1966; Sailer 1973; U.S. House of Representatives 1973; Angalet and Fuester 1977.)

Thus, the results of USDA's classical biological control program during this period have produced a total, conservatively estimated benefit of at least $115,000,000 a year, or $150,000,000 in 1993 dollars, benefits that accrue annually! These savings figures compare very well with the estimated total costs ($20,000,000) of research by both Federal and State agencies to find, establish, and utilize natural enemies of insect and weed pests from 1888 to 1976 (Sailer 1976), and with the estimated $420,000,000 spent annually on insecticides in the 1960s (Sailer 1973).

It was during this period that Rachel Carson published Silent Spring (1962), which increased public concern about the effects of pesticides in the environment, which in turn led to an increased interest in biological control and other nonchemical methods of pest control. In regard to classical biological control, USDA's Insect Identification and Parasite Introduction Research Branch (IIPI) gradually broadened the scope of its activities to include not only foreign exploration and importation activities, but also domestic release and evaluation activities on pests located within working distances of its domestic research locations. Thus in effect, there was single, close administrative coordination of the alfalfa weevil parasite importation program from its foreign exploration and quarantine receiving aspects, to its release and evaluation (establishment and effectiveness) phases, and resources (funds, personnel, etc.) could be readily shifted from one area to another as dictated by program needs. This is seen by many to be an ideal situation for optimal conduct of parasite introduction programs, and seems to have paid off in the case of the alfalfa weevil program. There was, however, a need for a better method of dissemination of effective, established parasites, in the case of the alfalfa weevil program, to include non-research input. This goal was accomplished at the state level, very effectively by the New Jersey Department of Agriculture, but was not addressed until later at the federal level, in the period after 1972. (Sailer 1974, 1976b, 1981b; Coulson 1976; Lashomb et al. 1988.)

b. Augmentation and conservation of parasites and predators. By D. A. Nordlund, E. G. King, C. J. DeLoach, and P. V. Vail

During this period, Rachel Carson (1962) published Silent Spring. Though the problems cited by Carson were recognized by many in the scientific community, her book attracted the attention of the general public. The resulting public outcry against the indiscriminate use of conventional pesticides resulted in a considerable increase in research to develop alternative pest management techniques. Evidence of pests developing resistance to pesticides and of the harmful effects of pesticides on non-target organisms also increased. Several relatively new approaches to the control of insect pests, including the use of pheromones and hormones, came into the limelight. Integrated pest management (IPM), which is, to a great extent, a conservation approach, also began to take on an increased role in pest management. Biological control also received attention and there was increasing awareness on the part of biological control workers that not all of the insect pest problems in the U. S. were amenable to the classical importation approach. Many of the pests are native and have a full complement of natural enemies already attacking them. Researchers also began to realize that the annual row crop agroecosystem is, because of the disruptions that occur in such systems, a difficult place for natural enemies to work without man's assistance. Thus, augmentation and conservation began to receive increased attention, at least during the latter part of this period.

Much of the biological control work conducted by ARS scientists during this period was basic biological and ecological studies of parasites and predators that could possibly be used in augmentation or conservation programs. Though a number of pests were involved in the research that is discussed here chronologically, the major targets of such research during this period included lepidopterous and hemipterous pests in cotton, lepidopterous pests in cabbage, and scale insect pests in citrus. Research on the use of *Trichogramma* continued in ARS and elsewhere in the U.S., but utilization of these biological control agents was most intensive in other countries, such as the USSR, China, and Mexico.

Lawson (1959) studied natural enemies of the tobacco and tomato hornworms and found that egg and larval predators, especially *Polistes* wasps, and *Cotesia* (=*Apanteles* s. lat.) parasites caused significant pest mortality. DeLoach and Rabb (1971, 1972) found that the tachinid, *Winthemia manducae*, caused significant losses of hornworm prepupae. These natural enemies often maintained complete control of the pests and significantly reduced crop losses. Finney et al. (1960), of the University of California at Berkeley, in cooperation with ARS's Ben Puttler, developed rearing techniques for three hymenopterous parasites of the spotted alfalfa aphid. These techniques were developed to facilitate an augmentation program against this pest. Puttler (1961) studied the biology of *Hyposoter exiguae*, a parasite of lepidopterous larvae. Wene and Sheets (1962) studied the role of predatory insects in the Salt River Valley (Arizona) area cotton and found that the naturally occurring predators could not maintain control of lygus bugs (*Lygus* spp.), whitemarked fleahopper and western plant bug, and cotton leafperforator (or the saltmarsh caterpillar). Also in 1962, Burrell and McCormick reported that releases of *Trichogramma* against the sugarcane borer resulted in no significant increase in parasitism of borer eggs.

In 1962, under the leadership of Orin Hills, a biological control program was initiated at the Western Vegetable and Sugarbeet Investigations, Mesa, AZ. Initially, the objective was to catalog the parasites of noctuids attacking vegetable and row crops in the desert areas of the southwestern U.S. R. W. Brubaker assumed responsibility for, and expanded this program to include surveys of the relative abundance of several parasites of noctuids, with particular emphasis on tachinids (Brubaker 1968). Following these surveys, three species were selected for further study, in support of augmentative releases to control the cabbage looper and the beet armyworm on an area wide basis. These studies led to the integration of the use of parasites with other methods, such as pheromone-baited light traps and sterile insect techniques then being developed at the laboratory.

The parasites initially selected were *Lespesia archipivora*, a tachinid parasite of the beet armyworm, and two parasites of the cabbage looper: *Copidosoma truncatellum*, a polyembryonic egg-larval hymenopteran; and *Voria ruralis*, a tachinid. Rearing of these parasites was facilitated by development of semi-artificial diets for their hosts (Henneberry and Kishaba 1966; Shorey and Hale 1965; van der Zant 1966). Various biological, behavioral, and efficacy studies were also conducted with these parasites (Brubaker 1968). Brubaker, who retired in 1970, was replaced by C. Soo Hoo. Field cage and behavioral studies were subsequently conducted with the two tachinids (Soo Hoo et al. 1974), which demonstrated that *V. ruralis* could provide high levels of parasitism.

Biological control related research began increasing significantly about 1966. That year, Dolphin and Cleveland (1966) reported their studies of *Trichogramma minutum* as a parasite for use against the codling moth and redbanded leafroller. The behavior of *Campoletis flavicincta* (as *perdistinctus*), a parasite of the tobacco budworm, was studied by Noble and Graham (1966). Knipling (1966) developed theoretical predator/prey ratios required to obtain various levels of control in periodic release programs. Kieckhefer and Miller (1967) studied aphids and aphid predators in South Dakota cereal crops and found that aphid population increases in cereal crops were primarily dependent on movement from other crops. Hendricks (1967) studied effects of wind on dispersal of *Trichogramma semifumatum* and worked on release technology for this egg parasite. Burrell (1967) studied parasites that attack the armyworm. Champlain and Sholdt (1967a,b) studied the basic biology of the generalist predator *Geocoris punctipes*. Streams and Fuester (1967) studied *Oomyzus* (=*Tetrastichus* s. lat.) *incertus*, an imported parasite of the alfalfa weevil, while Hagen and Manglitz (1967) studied parasitism of the alfalfa weevil in the western plain states. Puttler (1967) found that encapsulation of *Bathyplectes curculionis* eggs by the weevil was common in the eastern U.S., but not in the western U.S. Lingren et al. (1968) studied consumption of *Heliothis* (s. lat.) spp. eggs and larvae by several common arthropod predators. Puttler and Dickerson (1968) studied the biology of *Apanteles forbesi*, a parasite of the bristly cutworm. Clancy (1968) studied the distribution and parasitization of *Lygus* spp.

In 1969, Marston and Ertle reported on some basic studies of parasitization by *Trichogramma minutum*, while Lewis and Redlinger (1969) tested the eggs of almond moth as hosts for *Trichogramma evanescens*. Ridgway and Jones (1969) reported on inundative releases of the common green lacewing for control of *Heliothis* (s. lat.) spp. on cotton. Adams et al. (1969) reported on the biology of *Bracon mellitor*, a parasite of the boll weevil and suggested that inundative releases of this parasite could be effective if mass production techniques could be developed. Clancy (1969) reported that the tachinid parasite *Voria ruralis* showed promise as a biological control agent of the cabbage looper. Bryan et al. (1969) conducted studies on the role of temperature in development of *Microplitis croceipes* and selected 30°C as the optimal temperature for rearing this important parasite of *Heliothis* (s. lat.) species. Maltby et al. (1969) found a new species of *Trichogramma* that was adapted to the cereal leaf beetle, an introduced pest; they suggested that selective breeding of the parasite could improve its efficiency. Fye and Larsen (1969) conducted a preliminary evaluation of *Trichogramma minutum* as a biological control agent of lepidopterous pests of cotton. They found this species to be of little value because: 1) the rate of dispersion was slow and distances limited; 2) mortality of broadcast parasitized host eggs would be quite high, and timing of applications would be difficult; 3) searching capability of the wasps in complex situations was relatively poor; 4) longevity and ovipositional periods were short; and 5) high temperatures limit the activity of the adult female.

Lewis (1970) described the life history and anatomy of *Microplitis croceipes*, a parasite of *Heliothis* (s. lat.) larvae, and Lewis and Burton (1970) described a rearing procedure for this parasite. Lingren et al. (1970) evaluated host and host age preference of *Campoletis flavicincta* (as *perdistinctus*) to determine the most appropriate host for use in mass rearing. Graham (1970) studied parasitization of several lepidopterous pests by *Trichogramma semifumatum* in the Lower Rio Grande Valley of Texas and reported that, though *T. semifumatum* is an important mortality agent in tomato and corn,

demand for insect-free produce mitigated against their use. The importance of *T. semifumatum* in cotton was difficult to measure because of insecticide use. Ridgway et al. (1970) developed a mass rearing system for the common green lacewing (*Chrysoperla carnea*). Hoffman et al. (1970) reported on techniques for collecting, holding, and determining parasitism of lepidopterous eggs. Jackson et al. (1970) reported on the developmental biology of *Leschenaultia adusta*, a tachinid fly attacking the saltmarsh caterpillar, and suggested spraying laboratory-produced parasite eggs in the field. Bryan et al. (1970) reported on a comparison of two species of *Eucelatoria*, tachinid flies parasitic on *Heliothis* s. lat. Stoner (1970) studied the plant-feeding behavior of the predaceous bug *Geocoris punctipes*. Parker (1970) studied the seasonal mortality of the imported cabbageworm and the effect of introducing *Trichogramma evanescens*. This was the initial study for a later biological control program using *T. evanescens* (discussed below). Schmidt (1970) also studied the biology of *T. evanescens*.

ARS scientists also began to realize that environmental manipulation strategies could play an important role in biological control. Reed et al. (1970) suggested that the lower numbers of brown soft scale found on citrus trees near windbreaks, could, in part, be due to increased efficiency of parasites when they are sheltered from the wind.

Parker and Pinnell (1971) studied several species of *Trichogramma* to determine if and how they overwintered in Missouri. Day et al. (1971) studied the distribution of *Microctonus aethiopoides* and *M. colesi*, two important parasites of the alfalfa weevil, in the eastern U.S. McCoy and Selhime (1971a, b) studied the influence of natural enemies, including the parasite *Cheiloneurus inimicus*, on black scales (*Saissetia* spp.) on citrus in Florida. Butler and May (1971) studied feeding of the common green lacewing on eggs of *Heliothis* (s. lat.) spp. Stoner and Surber (1971) studied the influence of temperature on the development of *Anaphes iole* (as *ovijentatus*), an egg parasite of *Lygus hesperus*. Lewis and Jones (1971) began their reports of studies on semiochemicals with a publication on the kairomone from *Heliothis* (s. lat.) spp. that stimulates host-seeking by *Microplitis croceipes*. Elsey and Stinner (1971) studied the biology of *Jalysus spinosus*, a predaceous stilt bug found in tobacco. Arbogast et al. (1971) reported on the developmental stages of the warehouse pirate bug (*Xylocoris flavipes*), an important predaceous bug in the stored product environment.

In late 1964, ARS established the Biological Control of Insects Research Laboratory (BCIRL) at Columbia, MO, under the direction of F. R. Lawson. The primary project until Lawson's retirement in 1971 was biological control of pests of cabbage and other cole crops, including the imported cabbageworm, cabbage looper, diamondback moth, and green peach, cabbage and turnip aphids. This research is particularly interesting because it combined parasite importation, periodic releases, the use of both parasites and pathogens, and environmental manipulation techniques (Parker et al. 1971; Parker 1971). In this program two imported parasites, *Trichogramma evanescens* and *Cotesia* (=*Apanteles* s. lat.) *rubecula*, were released periodically in cabbage along with fertile hosts, the imported cabbageworm. The goals of the program were to: 1) introduce more effective parasites, 2) increase parasite density and synchronize parasite populations with host populations, and 3) increase host density to insure an adequate host supply for maintaining continuity of the parasites. These experiments resulted in 96% of the cabbage plants in treated plots producing grade A, No. 1 heads, whereas none of the plants in control plots produced marketable heads. A naturally-occurring "polyhedrosis virus", prepared by grinding as few as four infected looper larvae per acre, along with *Trichogramma* parasitization, controlled 100% of the cabbage loopers (Parker 1971). The bacterial insecticide, *Bacillus thuringiensis*, was also used to control the lepidopterous pests (Biever et al. 1994). The aphids were normally controlled by parasites, predators, and pathogens in the absence of chemical pesticides (C. J. DeLoach, unpublished data). This program was an excellent example of how a variety of biological control approaches could be integrated into an effective Integrated Pest Management (IPM) program. Variations of this IPM program were successfully demonstrated at several commercial vegetable farms in Missouri (Biever et al. 1994), but a final pilot field test that

would have demonstrated the practicality of the program to producers was never carried out in Missouri. The mission of the Columbia laboratory was altered under its new Director, C. M. Ignoffo, in 1971; i.e., soybean insects became the new targets for biological control research, with emphasis placed on insect pathology. However, a highly effective biological control-IPM program for insect pests of cabbage, based on these early studies, was later developed and implemented in Washington and Texas (Biever et al. 1994); see Chapter IV.

There was also considerable interest in the use of the predaceous larvae of the common green lacewing for augmentation programs during this period. Lingren et al. (1968) and Ridgway and Jones (1968, 1969) demonstrated the effectiveness of augmentative releases of the lacewing for suppressing *Heliothis* (s. lat.) spp. in cotton. However, the number of lacewing larvae required to suppress *Heliothis* (s. lat.) below the economic injury level was nearly 1 million/ha. These tests culminated in a series of releases in small plots at rates of 227 to 494 thousand larvae/ha where a peak *Heliothis* (s. lat.) spp. larval population of 44,460/ha was reduced 96% and cotton yield increased three-fold over the untreated check. From other small plot studies, the researchers concluded that releases of 123,000 predator larvae/ha might provide effective control of *Heliothis* (s. lat.) spp. in cotton. The need for such large numbers again pointed out the need for improved rearing systems for biological control agents. Rearing of common green lacewing was reviewed by King and Morrison (1984) and Nordlund and Morrison (1991).

One of the major impediments to economical inundative release programs is the high cost of producing sufficient numbers of insects. A major factor in the production cost is the necessity of producing large numbers of hosts or prey. This realization led to efforts to develop *in vitro* rearing techniques for parasites and artificial diets for predators. ARS efforts to develop artificial diets for predators includes those of Vanderzant (1969, 1973), who developed an artificial diet for larval and adult common green lacewings. This diet worked, but the presentation system was inefficient. Efforts to develop an encapsulation device were only somewhat successful (Anonymous 1971; Martin et al. 1978), as the equipment was quite costly and cumbersome. Sterility of the diet was also a problem.

Elsey studied the predaceous stilt bug *Jalysus spinosus* in tobacco in North Carolina (Elsey 1971, 1972, 1974, 1975; Elsey and Stinner 1971). Although tobacco budworm populations were not reduced, some suppression of tobacco hornworm populations did result from early season releases of this insect.

Hart (1972) tested *Microterys flavus*, an encyrtid parasite of brown soft scale, in citrus groves in the lower Rio Grande Valley of Texas. Apparently, this parasite and other natural enemies were largely eliminated by insecticide drift from nearby cotton fields. When chemical treatment was stopped and *M. flavus* was released inoculatively, biological control of the brown soft scale was reestablished.

Lewis et al. (1971) demonstrated that *Trichogramma evanescens* perceived chemicals left by adult moths near oviposition sites, as first demonstrated by Laing (1937), and in 1972 they reported that moth scales were the source of a kairomone that stimulates host-selection behavior by this parasite. These studies resulted in considerable and continuing interest in the roles played by semiochemicals in the host- and prey-selection behavior of parasites and predators.

In conclusion, the period 1953-72 saw an increased interest in the development of alternatives to conventional pesticides, including the augmentation and conservation of parasites and predators. Much of the work conducted by ARS scientists during this period involved basic biological and ecological studies of potential biological control agents. At least two studies demonstrated the technical feasibility of augmentation. One involved the use of the parasites *Trichogramma evanescens* and *Cotesia rubecula* against imported cabbageworm in cabbage (Parker et al. 1971, Parker 1971), and the other involved the use of the predator common green lacewing against

Heliothis (s. lat.) spp. in cotton (Ridgway and Jones 1968, 1969). These programs demonstrated the need for improved rearing techniques, particularly the need for artificial diets. Studies on semiochemicals influencing the host and prey selection behavior of entomophagous insects also began during this period; continuing research in this area is discussed in Chapter IV, section B.1.b.

2. Arthropod-Parasitic Nematodes. By W. R. Nickle, J. R. Coulson, and P. V. Vail

With the establishment of the Agricultural Research Service (ARS) in 1953, the old Bureau of Plant Industry, Soils, and Agricultural Engineering was abolished and much of its research functions was placed into the newly formed Crops Research Branch. This Branch was raised to Division status in 1957 and its name was changed to Plant Science Division late in this period. Nematology Investigations, under the leadership of A. L. Taylor (1956-64) and J. M. Good (1964-72), continued as a unit of this Division's Crops Protection Research Branch. See also section C below on biological control of plant nematodes.

In 1954, a nematode from the codling moth was found by ARS insect pathologists (Dutky and Hough 1955) in the U.S., and was designated by an accession number "DD-136." The same species was found from the codling moth in the same year in Europe, where it was described as *Neoaplectana carpocapsae*. This nematode, now known as *Steinernema carpocapsae,* has many insect hosts and is known to vector a bacterium that kills the host. S. R. Dutky worked on this nematode-bacterium association for many years at the ARS Insect Pathology Pioneering Laboratory at Beltsville, MD. Early work in the 1950s and early 1960s and subsequent research by ARS and university nematologists in the U.S. and by foreign researchers, led to the eventual commercialization of this nematode by private companies in the 1980s. It is currently the most widely used nematode for insect control in the U.S. and throughout the world. (Poinar 1979; Nickle 1984; and references therein.)

ARS studies with other nematodes for insect control during this period concerned nematodes attacking the face fly (Stoffolano and Nickle 1966; Nickle 1967), and mosquitoes (Chapman et al. 1967; Petersen et al. 1968, 1969; Chapman 1974; Petersen and Willis 1972; Nickle 1972), and discovery of a new mermithid species (*Filipjevimermis leipsandra*) attacking cucumber beetles (*Diabrotica* spp.) (Cuthbert 1968; Poinar and Welch 1968). Host ranges of mermithid nematodes infecting mosquitoes as well as preliminary mass production methods for those organisms were developed by Petersen et al. (1969) and Petersen and Willis (1972). Work on the mosquito nematode (*Romanomermis culicivorax*) led to the development of the first commercial use of nematodes for pest control in the 1970s. It was also not until after 1972 that the first importations of exotic nematodes were made into the U.S. for insect control (see Chapter IV).

Considerable advances were made during 1953-72 in the systematics of insect-parasitic nematodes; see Poinar, 1979, and Nickle, 1984. In 1965, W. R. Nickle joined the Nematology Investigations unit at Beltsville, MD. His efforts were to be concentrated on the systematics of insect-parasitic nematodes and their use in biological control of pest soil insects.

3. Arthropod Pathogens. By P. V. Vail, J. R. Coulson, J. R. Adams, and H. Shimanuki

In the late 1940s and early 1950s, E. A. Steinhaus, one of the preeminent leaders in the development of insect pathology in the U.S., began research, teaching and graduate programs in insect pathology at the University of California. He was a stong proponent of both basic and applied insect pathology/microbial control research. In the early to mid-1950s, his graduate students expanded the base of insect pathology in the United States and throughout the world, and these graduates in turn trained the "second generation" of insect pathologists. These developments led to the acceptance of insect pathology as a discipline within biological control. This, combined with the foresight of E. F. Knipling, Director of the ARS Entomology Research Division, led to establishment of insect

pathology/microbial control programs at many ARS laboratories throughout the United States. During these years, significant advances were made in both basic and applied insect pathology.

One of the first actions taken by the newly formed Entomology Research Division was the creation in 1954 of the Insect Pathology Pioneering Research Laboratory at Beltsville, MD. The Insect Pathology Unit of the Japanese Beetle Laboratory at Moorestown, NJ, was moved to Beltsville as part of this new Laboratory, which was headed by C. G. Thompson (1953-1961). Subsequent leaders of the unit, later called simply Insect Pathology Laboratory (and yet later Insect Biocontrol Laboratory), were A. M. Heimpel (1961-1979) and J. L. Vaughn (1979-present). The purpose of this Laboratory was to conduct basic research in support of more applied insect pathology/microbial control programs at the ARS field locations.

Similar units devoted specifically to insect pathology research had already been established in the University of California at Berkeley in 1945 by Steinhaus, and in Canada in 1950 by J. W. M. Cameron.

Research on honey bee diseases and their control continued in the Entomology Research Division's Apiculture Research Branch (briefly the Beekeeping and Insect Pathology Section) at locations in Beltsville MD, Laramie, WY, and elsewhere. Techniques were developed for controlling pests and diseases of the honey bee at Beltsville, MD (Cantwell and Lehnert 1968; Cantwell and Smith 1970; Cantwell et al. 1972). The first record of chalkbrood in the alfalfa leafcutting bee in North America was reported by Baker and Torchio (1968) at Logan, UT. Chalkbrood in the alkali bee was also studied (Batra and Bohart 1969). Tylosin lactate was discovered as a treatment for American foulbrood (Hitchcock et al. 1970) and methods to control other bee diseases were investigated (Moffett et al. 1969). New application techniques to enhance the efficacy of foulbrood control agents were developed (Wilson et al. 1970, 1971; Wilson and Elliott 1971). A diagnostic service for bee diseases was established during this period at the Beltsville laboratory, and continues to the present day. (See Beltsville laboratory's research in Appendix II.)

Research on insect pathogens was also initiated during this period at other ARS locations under the administration of several Research Branches of the Entomology Research Division. In the 1950s, studies were begun by ARS researchers at Brownsville, TX, and Whittier (later Riverside), CA, on insect viruses, and at Ankeny, IA, and Mississippi State, MS, on other pathogens. In the 1960s, research on the bacterial pathogen *Bacillus thuringiensis* (Bt) was begun at the Brownsville station, through the research of H. T. Dulmage from 1960 to the 1980s. Over 1,000 isolates of Bt were purified, propagated, and tested for efficacy. These isolates are now in a collection at the ARS laboratory in Peoria, IL (Dulmage and Beegle 1982). Dulmage was also deeply involved in the development of standardization of commercial Bt formulations based on comparison with an industry accepted standard (Dulmage 1973 a and b). Various other pathogens were studied at other Entomology Research Division locations in Arizona, California, Florida, Illinois, Missouri, Montana, South Dakota, and Texas (see Appendix II).

In 1957, research at Ankeny, IA, showed the deleterious effects of the protozoan pathogen *Nosema pyrausta* on populations of the European corn borer, including reduced fecundity of adults (Zimmack and Brindley 1957; Lewis et al. 1971); occasionally, negative impacts on beneficial insects were noted. Also at Ankeny, the fungus *Beauveria bassiana* was shown to reduce corn borer populations to near 90% (York 1958). Beginning in 1961, research at Peoria, IL, emphasized fermentation systems for production of *Bacillus popilliae* spores; although vegetative cells could be produced, they were not successful in producing spores. At Peoria, several techniques led to successful sporulation (Rhodes et al. 1965); however, development of high sporulation rates remain an enigma to insect pathologists and microbiologists today.

Early ARS tests with nuclear polyhedrosis viruses (NPVs) using spray and autodissemination techniques were conducted in southern California (Elmore 1961; Elmore and Howland 1964). ARS and University of California scientists conducted extensive studies on a virus isolated from the citrus red mite over a period of about 14 years. These studies included characterization (Smith et al. 1959; Reed and Hall 1972; Reed and Desjardins 1982). Also studied were methods of transmission (Reed et al. 1975) and potential methods of use (Gilmore and Munger 1963; Reed et al. 1973).

Intensive studies were conducted at Brownsville, TX, in the 1960s to develop NPVs infectious to the *Heliothis/Helicoverpa* complex and cabbage looper as microbial control agents (Ignoffo 1964, 1965a and b, 1965b, 1966d, 1973). These and later studies (Ignoffo et al. 1965; Ignoffo 1966a and b and c; Ignoffo and Couch 1981) led to the first registration of a baculovirus for agricultural use. Of importance was that newly developed artificial diets (Vanderzant et al. 1962) for the host insect were utilized for mass production of the virus. As a part of a project for area-wide suppression of the boll weevil, McLaughlin (1962) demonstrated that *Beauveria bassiana* could infect overwintering insects when applied to hibernation sites. Several protozoan pathogens of the boll weevil were also studied during this period (e.g., McLaughlin 1967). Granular formulations of *Bacillus thuringiensis* provided the stimulus to develop this organism for European corn borer control (Raun, 1963; Raun & Jackson, 1966). Lists of parasites and pathogens of mosquitoes, including viruses, protozoa, and nematodes, were developed at ARS laboratories at Lake Charles, LA, Gainesville, FL, Kerrville, TX, and Fresno, CA.

Successful use of *Bacillus thuringiensis* β-exotoxins led to methods of reducing populations of horn fly larvae infesting cattle dung and also adult fly populations on range cattle (Gingrich 1965; Gingrich and Eschle 1966, 1971). Sutter and Raun (1966, 1967) were the first to show that *B. thuringiensis* crystals damage insect midgut cells allowing the contents to enter the hemocoel causing septisemia. Control of the corn earworm and fall armyworm with NPVs was investigated by Young and Hamm (1966) and Hamm and Young (1971). NPVs were found to be of two types, either with the capsids embedded singly or in multiples in the polyhedron matrix (Heimpel and Adams 1966). A number of other viruses were also described by scientists in the Insect Pathology Pioneering Laboratory and other ARS laboratories during this period.

Two new microsporidians and a poxvirus were described from grasshoppers (Henry and Jutila 1966; Henry 1967, 1969a, 1971b; Henry et al. 1969). These pathogens would later be developed as microbial control agents for rangeland grasshoppers. *Nosema locustae* was eventually registered for this purpose by the Environmental Protection Agency (see Chapter IV). The manifold effects of a cytoplasmic polyhedrosis virus on cabbage looper was determined (Vail et al. 1967). A multiply-occluded NPV was isolated having a broad host range for many lepidopterous pests (Vail et al. 1971). This virus is a candidate as a microbial control agent and is now used extensively in medical research. A number of pathogens were reported from Coleoptera and were field tested at various locations (Daum et al. 1967; McLaughlin 1967; McLaughlin et al. 1967; Cuthbert 1968). Early studies on the impact of *Beauveria bassiana* on mosquitoes was demonstrated (Clark et al. 1968). Extensive studies on ultrastructure, taxonomy, basic pathology, and transmission of protozoans infectious to lepidopterous and coleopterous postharvest pests were determined at Fresno, CA (Kellen and Lindegren 1968, 1971). A landmark discovery was made when "species" of *Thelohania* in larval and *Nosema* in adult mosquitoes were found to be the same species (Hazard and Weiser 1968). A pathogenic strain of *Bacillus cereus* was isolated from the cigarette beetle (Thompson and Fletcher 1972). In 1968, the ARS fire ant project began and included a component for the development of microbial control agents. Cell cultures from various insects, but primarily Lepidoptera and Orthoptera, were being established at numerous ARS laboratories to facilitate basic and applied research on pathogens.

Basic studies on the chemistry, characterization and mode of action of *Bacillus thuringiensis* led to further understanding of this and related bacterial pathogens (Faust and Dougherty 1969; Faust et al. 1971 a and b). At Manhattan, KS, intensive studies were conducted on *B. thuringiensis* metabolism, origin and function of parasporal crystals and spore coat proteins (Bulla et al. 1970 a and b, 1971 a and b; Bulla and St. Julian 1972 a and b). Significant reductions of grasshopper field populations by the use of *Nosema locustae* were demonstrated (Henry 1971a) and the known host range of this protozoan was expanded to include 58 species of grasshoppers and other Orthoptera from throughout the world (Henry 1969b). Formalin was found to be an excellent antiviral agent for a number of viruses (Ignoffo and Garcia 1968; Vail et al. 1968; Bullock et al. 1969). Studies of viruses of stored product insects were initiated by Hunter at the Fresno location (Hunter and Dexel 1970; Hunter and Hoffmann 1970). Complete and continued replication of baculoviruses, as well as titration methods and cell line nutritional requirement studies were reported by scientists of ARS Arizona and Beltsville laboratories (Goodwin et al. 1970; Vail et al. 1973; Hink and Vail 1973). These were the first studies to show complete replication of baculoviruses as well as end point and plaque assay procedures, important to further studies on the molecular biology of these organsisms. Entomophagous insects such as sarcophagid flies as well as birds were demonstrated to disseminate occlusion bodies of a nuclear polyhedrosis virus (Hostetter and Biever 1970). The first RNA virus (crystalline array) was isolated from an arthropod, the twostriped grasshopper (Jutila et al. 1970).

The "Heliothis NPV" (i.e., the NPV of corn earworm) was registered in 1970 by the U.S. Food and Drug Administration, the first baculovirus to be registered and mass produced for commercial use, and was registered by the Environmental Protection Agency in 1975 (Benz 1986). A summary of the research and development of this virus is provided by Ignoffo (1973) and Ignoffo and Couch (1981).

The pink bollworm, cotton leafperforator and diamondback moth were reported as hosts of the alfalfa looper NPV (Vail et al. 1971, 1972). The serious effects of ultraviolet light on persistence of baculoviruses was demonstrated (Bullock 1967; Bullock et al. 1970). A significant increase in basic knowledge of the inactivation of microbials by sunlight led to a number of protectants to stabilize microbial pesticides (Ignoffo and Batzer 1971). A pioneering study on the influence of *Rickettsiella* on the navel orangeworm was conducted by Kellen et al. (1972).

Research progress at ARS stations listed above, as well as in all other ARS locations where insect pathology research was initiated in the 1970s and 1980s after elimination of the Entomology Research Division, is discussed in Appendix II, arranged by location. For general information on the history of insect pathology during 1953-72, see Sweetman 1958; Steinhaus 1964; Hall 1964; Burges and Hussey 1971; Heimpel 1974; and references cited therein.

B. BIOCONTROL CONTROL OF WEEDS. By J. R. Coulson and L. A. Andres

As noted in the section A.1.a, research on natural enemies of weeds was included in the program of the ARS Insect Identification and Parasite Introduction Research Branch (IIPI). As such, research in this area commenced at the ARS European Parasite Laboratory in 1947. Target weeds at the EPL during 1953-59 included Klamath weed (or common St. Johnswort) (1953), gorse (1953, 1956-59), tansy ragwort (1956-59), Scotch broom (1956-59), Mediterranean sage (1956-59), Dalmatian toadflax (1956-59), Italian thistle (1956-59), puncturevine (1957-59), and hemp broomrape and Canada thistle (1959).

In 1959, weed projects shifted to the new laboratory in Italy, see below. Shipments of natural enemies of several of these weeds were sent to the ARS station at Albany, CA, and to Hawaii in some cases. Results of the Klamath weed project are discussed in Chapter II.

Since most of these California weeds were believed to be of Mediterranean origin, work was phased out at the laboratory in France and shifted to a new ARS Biological Control of Weeds Laboratory established by L. A. Andres in Italy in 1959, which was developed specifically for the weed work. Directors of this laboratory during this period were L. A. Andres (1959-64), K. E. Frick (1965), B. D. Perkins (1965), and P. H. Dunn (1965-72). During 1959-72, target weeds at this new IIPI laboratory included over a dozen weeds common to the western states, including: gorse (1959-60), puncturevine (1959-62), Scotch broom (1959-66), Italian and slenderflower thistles (1959-60, 1966-67), other carduine thistles (1959, 1963-65) with concentration on musk thistle (1966-72), Dalmatian toadflax (1959-69), Mediterranean sage (1959-72), tansy ragwort (1961-66), cruciferous weeds (1966-68), and Russian thistle (1967-72). The laboratory in Italy was under the administrative and technical direction of IIPI's Beltsville, MD, and Albany, CA, offices, respectively.

Concurrent with the initiation of weed work at the EPL, a station was established by IIPI in Iran, in 1956, to study natural enemies of the poisonous western rangeland weed, halogeton, in Iran and Afghanistan. This station was headed by G. B. Vogt (1956), C. J. Davis (1957), and J. J. Drea (1957-59). Despite extensive surveys, good study populations of the weed could not be found, and the station was moved to Morocco in 1959, where research continued through 1962, under J. J. Drea. The most promising natural enemy, a moth species, studied during this period was found to be unsuitable for introduction into the U.S.

Additional surveys for natural enemies of western rangeland weeds were made by ARS explorers in the USSR in 1965 under the auspices of a U.S.-USSR scientist exchange program (Coulson 1981a), and in India, Pakistan, Egypt, Israel, Poland, and Yugoslavia as a result of the Special Foreign Currency (or PL-480) program discussed above.

Most of the natural enemies found during overseas studies to be promising control agents of these western weeds were sent primarily to the newly constructed ARS Biological Control of Weeds Research Laboratory and quarantine facility at Albany, CA, for further evaluation. Directors of IIPI's Biological Control of Weeds Investigations and the Albany weed laboratory during this period were J. K. Holloway (1953-64) and L. A. Andres (1964-72). Some natural enemies of thistles were sent to Virginia; see below.

In 1957, an interagency Subcommittee (later Working Group) on Biological Control of Weeds was established by the joint Weed Committees of the USDA and U.S. Department of Interior. This was done at the request of biological control of weed researchers who recognized the need for wide discipline participation in making decisions regarding selection of appropriate test plant species and the safety of introductions of foreign natural enemies of weeds. This group recommended plant species to be included in pre-release safety studies, reviewed detailed results of studies prior to recommending approval of proposed releases, and also provided comments on whether conflicts of interest existed concerning the targeted weeds. (Klingman and Coulson 1982-83; Coulson and Soper 1989; Coulson 1992a.)

Significant accomplishments of the research on rangeland weeds during 1953-72 included the establishment in the U.S. of a number of insect natural enemies of Canada, milk, musk, plumeless, and Italian thistles, tansy ragwort, gorse, Scotch broom, Mediterranean sage, and puncturevine. The success of the Klamath weed project extended into the early part of this period. Of the new target weeds, the most successful results were obtained on tansy ragwort, musk thistle, and puncturevine.

Tansy ragwort is a poisonous European weed in pastures and rangeland of the northwestern U.S. The ARS research on this weed was carried out primarily at the Albany laboratory (J. K. Holloway, L. A. Andres, K. E. Frick, R. B. Hawkes), the Paris laboratory (H. L. Parker), and the Rome laboratory (L. A. Andres, K. E. Frick). A total of three European insects were successfully introduced for

biological control of tansy ragwort in the United States. Two of these, the cinnabar moth (*Tyria jacobaeae*) and the "ragwort flea beetle" (*Longitarsus jacobaeae*), have been primarily responsible for excellent control of this weed. A third insect, the "ragwort seed fly" (*Botanophila seneciella*), was first introduced in 1966 and successfully established in some areas, but its impact is largely unknown. Initially, the leaf- and flower-feeding cinnabar moth, released in 1959, provided some relief, but it was not until the release of the root- and leaf-feeding beetle, beginning in 1969, that dramatic control of this weed occurred. Tansy ragwort has been reduced to less than 1% of its former densities at study sites in northwestern California and western Oregon (the only areas where impact studies have been carried out). The replacement vegetation has been chiefly native plants and more benign weeds. In Oregon alone, the savings from the control of tansy ragwort have amounted to ca. $5 million annually, with an estimated cost:benefit ratio of 1:14. Field evaluation studies were carried out in California by ARS personnel, and in Oregon by personnel of Oregon State University and the Oregon Department of Agriculture. (See references cited below.)

Musk thistle is a serious pest of pastures and rangelands throughout the U.S. Much of the domestic research on the musk thistle insects received from the ARS laboratory in Europe was funded under a cooperative agreement with scientists of the Virginia Polytechnic Institute and State University (VPI). A European seed weevil, initially released in Canada, was tested by ARS scientists and disseminated and established throughout the U.S. from European and Canadian stock, and later from populations initially established in Montana and Virginia. The weevil effected substantial reduction of musk thistle populations in many locations, and had additional effects on plumeless, milk, and Italian thistles. However, testing began on additional insect enemies of these thistles deemed required for better control, and these were eventually introduced during the next period (1972-93).

Puncturevine is an introduced spiny weed of roadsides, cultivated crops, pastures, and rangeland throughout most of the U.S. Two species of European weevils were successfully introduced from Italy and have established and spread in California and southwestern and central states from Texas north to Nebraska. Of 57 puncturevine-infested California counties surveyed in 1975, 32 reported a major decrease in puncturevine populations as a direct result of the weevils. This represents an estimated annual savings in treatment costs for California alone of $1,700,000. The overall one-time cost of the puncturevine project was estimated to be $360,000, one-fifth of the resulting annual benefits.

For references to research results for rangeland weeds during this period, see Parker 1960; Frick and Holloway 1964; Frick and Andres 1967; Frick 1969, 1970 a and b, 1978; Andres and Goeden 1971; Kok and Surles 1975; Rees 1977; Goeden 1978; Hawkes and Johnson 1978; Maddox and Andres 1979; Batra et al. 1981; Hawkes 1981; Huffaker et al. 1983; Piper 1986; Julien 1987, 1992; Pemberton and Turner 1990; McEvoy et al. 1991; Isaacson and Radtke 1993; Andres and Rees 1995; Turner and McEvoy 1995.

Beginning in 1959, ARS pioneered a new thrust in biological control, the biological control of aquatic weeds. Since 1899, the U.S. Army Corps of Engineers has been charged with the responsibility of controlling aquatic weeds in the nation's navigable waterways; these activities were expanded in 1945. As part of these expanded efforts, the Corps of Engineers began in 1959 to fund ARS research to explore the feasibility of biological control of alligatorweed and waterhyacinth, two of the most serious weeds of waterways in the southeastern U.S., and subsequently has funded such research involving other aquatic weeds. Working under the technical direction of the ARS Albany laboratory, an IIPI taxonomist, G. B. Vogt, conducted surveys for natural enemies of these two weeds in South America, their original homeland, during 1960-62, and an ARS laboratory was established by D. M. Maddox in Argentina in 1962 to study further the promising insect enemies found. IIPI entomologists in charge of the Argentine lab were D. M. Maddox (1962-67), B. D. Perkins (1968-71), and C. J. DeLoach (1971-72). An SFC (PL-480) project to study the biologies of the

natural enemies of these weeds in Uruguay was also established. Three insect enemies of alligatorweed were introduced and established in the U.S. in 1964-71; prior quarantine studies, initial domestic field releases and subsequent evaluation studies were conducted by scientists from the ARS Albany, CA, laboratory. In 1970, IIPI established the Insect Enemies of Aquatic Weeds Laboratory at Gainesville, FL, with N. R. Spencer in charge, to conduct further research on the biological control of these and other aquatic weeds in the Southeast. In 1972, IIPI stationed an entomologist (B. D. Perkins) at USDA's Aquatic Weeds Research Laboratory at Fort Lauderdale, FL, to handle release and evaluation of natural enemies of both alligatorweed and waterhyacinth in Florida. Two of the introduced alligatorweed insects spread rapidly throughout the southeastern U.S., with spectacular results in some areas, and in general causing a substantial reduction in alligatorweed infestations in many areas of the Southeast. An early (1976) and very conservative estimate of the benefits of this control of alligatorweed in terms of herbicidal treatments no longer required was $400,000 annually, at an estimated total cost of ARS research of $1 million. Results of a 1981-82 survey of alligatorweed in ten southern states conducted by the Corps of Engineers showed that of the 97,000 problem acres of the weed in 1963, less than 1,000 problem acres remained in 1981 (Cofrancesco 1993). The first of the natural enemies of waterhyacinth was not introduced (through the Albany quarantine facility) until 1973.

Explorations for natural enemies of aquatic weeds were also conducted under the SFC or PL-480 program in India, Pakistan, and Yugoslavia, the weeds involved being waterhyacinth and the submersed weeds Eurasian watermilfoil and hydrilla. The Weeds Investigations unit of the Crops Protection Research Branch, Crops Research Division, ARS, supported a number of these projects as did IIPI. There was considerable cooperation between these two research branches in the biological control of weeds research programs.

For some references on the early aquatic weed research, see Andres and Goeden 1971; Maddox et al. 1971; Perkins 1973; Spencer and Coulson 1976; Andres 1977; Coulson 1977.

The successes obtained in the biological control of weeds program, including Klamath weed, alligatorweed and tansy ragwort, led to a marked expansion of effort in this area. As reported above, during 1959-72, two foreign laboratories (Italy and Argentina) and two domestic laboratories (for research on aquatic weeds) were established by the IIPI, and a new quarantine facility was constructed (in 1963) at Albany, CA, and the staff there increased to four scientists. At the time of the 1972 reorganization, plans were underway for additional IIPI laboratories, with quarantine facilities at Stoneville, MS, and Temple, TX, for biological control of southern pasture and row crop weeds, and brush and other weeds of southwestern rangelands, respectively. Similar efforts on northeastern weeds was not established until 1974.

C. BIOLOGICAL CONTROL OF PLANT NEMATODES. By R. M. Sayre

As noted in the above section A.1.2 on insect-parasitic nematodes in this Chapter, Nematology Investigations continued in the new ARS Crops Research Division, created in the 1953 reorganization (name changed to Plant Science Division late in this period). The subsequent 20 years was the period of most rapid growth in numbers of nematologists at universities, in industry, and at federal laboratories. The demonstration of the economic importance of nematodes in crop production was made possible only by utilizing the newly discovered effective nematicides. These two factors became the driving force for the increase in numbers of nematologists. The demonstrated increase in crop yields in field plots that had been treated with nematicides was not overlooked by administrators. Some universities allowed formation of independent departments of nematology, while others permitted changes in the names of entomology and plant pathology departments to include nematology, and hired new personnel for these departments. In 1956, the USDA, partially in acknowledging the importance of nematicides in crop production and in recognizing A. L. Taylor's

leadership in nematicide development, named him leader of the Nematology Investigations, a post he held until his 1964 retirement. The Society of Nematologists was formed in 1961, and the first estimates of crop losses caused by nematodes were assembled and published by the Society (Feldmesser et al. 1971).

The study of possible biological control agents of nematodes languished in the USDA at first. But some research activity in this area continued at universities. Culminating in 1965, the studies of Rodriguez-Kabana et al. (1965) were to report the first instances of biological control of a plant nematode which was mediated by a bacterium.

The 1962 publication of Rachel Carson's book Silent Spring (Carson 1962) resulted in an increase in federal funding and an ensuing increase in numbers of federal nematologists. In 1965, under the new leadership of J. M. Good, eight new positions were created in the Nematology Investigations unit in order to meet the national need for finding methods of controlling nematodes other than reliance on chemical nematicides. Five positions, at scattered research stations in the U.S., were crop-oriented toward the nematode problems in their regions. The remaining three positions were allotted to Beltsville, MD. Two were filled by nematode taxonomists to study certain groups of nematodes (see section on insect-parasitic nematodes in this Chapter). The third was designated for research on the biological control of plant-parasitic nematodes, and was filled by R. M. Sayre. His research during this period considered the soil invertebrates (i.e., amoebae, tardigrades, and turbellarians) antagonistic to nematodes. Also, the use of sewage sludge as a soil organic amendment to control nematodes was investigated, as was the use of the water mold, *Catenaria* sp., as a possible biological control agent (Sayre 1971).

In the late 1960s, additional USDA funds were made available as grants to universities and other research organizations. Three grants involving biological control of nematodes were made as follows: (1) R. Mankau, University of California, Riverside, who initiated a program that was eventually to lead to the discovery of at least two potential biological control agents; one was a promising bacterial disease of plant nematodes currently designated as a *Pasteuria* species, the other being a nematode-trapping fungus. (2) G. C. Smart, University of Florida, reexamined certain predaceous nematodes for their potential to control crop pest nematodes (Smart 1986). (3) D. C. Norton who began a program studying soil factors influencing nematodes, that led to the publication of "Ecology of Plant-Parasitic Nematodes" (Norton 1978).

D. BIOLOGICAL CONTROL OF PLANT PATHOGENS. By G. C. Papavizas and R. J. Cook

Biological control in plant pathology was born as a concept in the USDA in 1955. In the early part of that year, V. R. Boswell, Chief of the Vegetable and Ornamentals Research Branch of the new ARS Crops Research Division, submitted a proposal to the American Society for Horticultural Science (ASHS) suggesting the creation of a Committee of the Division of Biology and Agriculture with the subject of "Biological Control of Soil-Borne Plant Pathogens." The ASHS approved the proposal and submitted it to the Divison of Biology and Agriculture of the National Research Council on October 3, 1955. The proposal contained information on the economic problem, description of more than 40 soilborne plant pathogens, estimated annual expenditures by private farm enterprises for disease-control measures, technical problems, and a plan to work on cultural and biological control. Based on this proposal, the U.S. Congress appropriated a small amount of funds to perform research in ARS on soilborne plant diseases. Following the advice of Boswell, the Crops Research Division created at Beltsville, MD, the Mushroom and Microbiology Investigations, a new unit within Boswell's Branch, and appointed E. B. Lambert, a mushroom expert, as Investigations Leader. The Microbiology Group was composed of two scientists, C. B. Davey and G. C. Papavizas, who joined ARS in 1957, and was charged with the responsibility of developing a research program on soilborne plant pathogens. After publication of Rachel Carson's book "Silent Spring" (Carson 1962), additional

funds were added to the Microbiology Group in FY 1965. In 1966, Papavizas became Investigations Leader and recruited four more scientists, thus increasing man-years in the unit from 2.0 in 1957 to 6.0 in 1966. Davey, who left ARS in 1962, was replaced by W. A. Ayers. Except for a change of the Division name from Crops Research to Plant Science Division late in the period, this organizational structure continued until 1972 when ARS underwent a major reorganization.

The research of the Microbiology Group during this period centered on systems ecology of the harmful microbes that cause diseases on or through the root systems. The Group developed methods to isolate and enumerate several important and widespread soilborne plant pathogens from the soil and plant rhizosphere; advanced new and intriguing concepts in soil-microorganism-plant interactions, behavior of plant pathogenic organisms in soil, and fundamental principles on the manner in which organic and inorganic constituents influence the ecology and behavior of important plant pathogens; developed the theory of competitive saprophytic activity and its exploitation in enumerating and controlling *Rhizoctonia*; studied the impact of chemical agents on nontarget microorganisms; and unravelled the enzymatic mechanisms of *Aphanomyces* and *Rhizoctonia* instrumental in disease development. (Papavizas 1973.)

While scientists of the Mushroom and Microbiology Investigations were studying systems ecology and laying the foundation for research to follow at Beltsville, a small group of ARS scientists at the Tidewater Research Station at Holland, VA, developed the "non-dirting" control of the peanut stem rot disease caused by *Sclerotium rolfsii* (Garren and Duke 1958).

Meanwhile, USDA plant pathologists in the State of Washington were studying natural or induced suppression of soilborne plant pathogens by resident antagonists in soils, following up on earlier discoveries that biological control of such pathogens was most productively directed at enhancement of resident antagonists. ARS scientists at Prosser, WA, demonstrated that soils cropped repeatedly to potatoes under irrigation became microbiologically suppressive to common scab caused by *Streptomyces scabies* (Menzies 1959), and that soils of the Columbia Basin and Yakima Valley irrigation districts where common beans were grown ranged between extremes of highly favorable (conducive) and highly unfavorable (resistant or suppressive) to the bean root-rot pathogen, *Fusarium solani* f. sp. *phaseoli* (Burke 1965). In 1969-71, R. J. Cook and associates, ARS, Pullman, WA, demonstrated that a factor, associated specifically with soils from fields where wheat take-all disease had declined, could be transferred to and expressed in other fields (Baker and Cook 1974). This work at Pullman on biological control responsible for take-all decline was continued during 1973-present (see Chapter IV).

A major event during this period was the convening in 1963 at Berkeley, CA, of the First International Symposium entitled "Ecology of Soilborne Plant Pathogens - Prelude to Biological Control." The idea for this symposium grew from the activities of the ASHS Committee on Biological Control of Soilborne Plant Pathogens, mentioned above. (Baker and Snyder 1965). Of the 40 papers, none were on introduced antagonists, the emphasis being instead on soils, plants, resident antagonists, and biological control through soil microbiologies and the plant. In contrast, the Sixth International Symposium on Ecology of Soilborne Plant Pathogens held in Kyoto, Japan, in 1988, covered this same range of topics, but in addition about half of the papers dealt in one way or another with specific antagonists manipulated or introduced for biological control purposes.

Research on the biological control of foliar plant pathogens was initiated in 1970 at the ARS laboratory at Oxford, NC. This research continued and is discussed in Chapter IV, section E.

Table 1. Benefits of Some USDA Classical Biological Control Programs, 1963-87[1,2]

Pest	States	A Acres Infested (X1000)	B Not Treated	Total Savings per Year	Year Calculated[3]
Alfalfa weevil	18	5,767	85%	[4] $ 48.9 million	1986
Alfalfa blotch leafminer	10	2,049	100%	[5] 13.2 million	1978
Pea aphid (on alfalfa only)	22	13,494	[6] 30%	[4] 36.4 million	1984
Cereal leaf beetle	5	1,341	55%	[7] 14.0 million	1978
Annual Savings				[2]$ 112.5 million	

[1] Prepared by W. H. Day, ARS Beneficial Insects Research Laboratory, Newark, DE, September 1988. Benefits from promising projects still in early stages (e.g., euonymus scale, birch leafminer, tarnished plant bug) are not included.

[2] 1993 savings (adjusted for inflation) would exceed $146,000,000.

[3] The older data underestimate present savings considerably because of subsequent increases in crop value, cost of pesticides, and parasite and pest ranges. In terms of 1993 dollars, these figures are respectively: 63.7, 17.2, 47.3, and 18.2 million dollars, for a total of $146,400,000 annual savings.

[4] Calculated as A X B X $10/acre, conservative costs of one insecticide treatment/year eliminated by biological control; savings due to reduced environmental damage are additional. For alfalfa weevil, see Table 2 and Day, 1981.

[5] Damage is usually less than costs of control, so this figure is the average yield loss ($6.44/acre) that was prevented by the biological control of this pest. Infested area (and savings) is considerably larger in 1988. See also Hendrickson & Plummer, 1983.

[6] 100% of acreage that formerly needed treatment in an average year. For pea aphid, savings to peas are additional but appropriate data have not been found.

[7] APHIS data for crop losses; parasite ranges are much greater in 1988, so savings are commensurately larger. See also Chapter VI below.

Table 2. Estimated Annual Savings to Farmers and Consumers from the Alfalfa Weevil Biological Control Program in the Northeastern United States[1]

State[2]	A Acres of Alfalfa[3] (X1000)	B % Not Treated[4]	A X B Acres Not Treated (X1000)	Net Savings[5]
ME	27	90	24.3	$ 243,000
VT	115	90	103.5	1,035,000
NH	19	90	17.1	171,000
MA	30	90	27.0	270,000
RI	3	90	2.7	27,000
CT	23	90	20.7	207,000
NY	940	90	846.0	8,460,000
PA	840	90	756.0	7,560,000
NJ	45	90	40.5	405,000
DE	7	90	6.3	63,000
MD	80	80	64.0	640,000
VA	88	50	44.0	440,000
WV	100	80	80.0	800,000
OH	600	90	540.0	5,400,000
IN	420	80	336.0	3,360,000
IL	800	70	560.0	5,600,000
MI	1,400	90	1,260.0	12,600,000
KY	230	70	161.0	1,610,000
Totals			4,889.1	[6] $ 48,891,000

[1] Prepared by W. H. Day, ARS Beneficial Insects Research Laboratory, Newark, DE, September 1988.

[2] States that primarily benefitted from the ARS program. Additional states to the west and south (recent APHIS program) are now experiencing increasing parasite impact, and are producing savings which are not included here.

[3] For 1984 (1985 USDA data, most recent available; does not change much from year to year).

[4] Estimates (conservative) by W. H. Day, averages of 1985-86.

[5] Calculated as A X B X $10/acre for insecticide and application costs; savings due to reduced environmental damage are additional.

[6] $63,723,000 in 1993 dollars (adjusted for inflation); see Table 1. APHIS figures following their extensive parasite distribution program (Bryan et al. 1993) provide an increase in savings for the entire USDA alfalfa weevil biological control program to a total of an estimated $88,000,000 annually, measured in 1987 dollars (Moffitt et al. [1990]).

CHAPTER IV
1973-1993
AGRICULTURAL RESEARCH SERVICE

A. ORGANIZATIONAL CHANGES AND GENERAL EVENTS. By J. R. Coulson

In 1972, the Agricultural Research Service (ARS) underwent a massive, far-reaching reorganization. The regulatory and control programs of ARS had already been removed in 1971 and placed in the newly formed Animal and Plant Health Inspection Service (APHIS). In 1972, the remaining research, discipline-oriented Divisions, including the Entomology Research Division and the Plant Science Division (previously Crops Research Division), were abolished. The many research units throughout the country and overseas, formerly administered by the several Research Branches of these Divisions, were placed administratively into 29 Areas in four Regions in the U.S., and an International Programs Division. The rationale for this reorganization was to enhance and increase multidisciplinary research, to bring management of research programs closer to area and regional problems, to increase cooperation between ARS and state experiment station scientists and other regional and local groups, and to eliminate a number of research administrative and support positions with a corresponding return of resources to productive research. To provide leadership and continued focus on the national aspects of ARS programs and to provide coordination of research by commodity, discipline, and program areas, a National Program Staff (NPS) was established, as were several other planning and coordinating bodies.

A reorganization of such a broad scope was naturally controversial, and many serious doubts and questions were raised both within ARS as well as in outside scientific circles and in the U.S. Congress. There was, for example, considerable concern expressed over the effect of the elimination of entomology as a distinct entity in the USDA, a status it had held since the establishment of the first Division of Entomology in the Department in 1881. However, research programs within ARS continued with varying degrees of difficulty caused by adjustment to new administrative and coordination channels, an increase in paperwork at the scientist level (as a result of the loss of some administrative levels and increase in others), and the movement or loss of a number of senior scientists and science administrators (during the first year of the reorganization, 106 employees were transferred from the Washington, DC, and Beltsville, MD, administrative areas to the field, including 34 former program administrators, and there were 99 retirements [U.S. House of Representatives 1973]). ARS biological control programs were both positively and negatively affected by the reorganization. Classical biological control, with its need for close coordination of overseas exploration and domestic quarantine and field research aspects, was particularly badly affected; see sections B.1.a and C.1 below.

Part of the reason for the negative impact on ARS biological control programs, at least in the beginning, was the fact that there was no Staff Scientist responsible for biological control on the National Program Staff until 1976, when D. E. Bryan was appointed to that position. That position was also given the responsibility for ARS research in insect taxonomy. Also, it was not until 1976 that ARS National Research Program (NRP) documents were developed, for biological control as well as for other ARS research programs. The NRP documents outlined a 10-year plan describing

current technology in the various research program areas, identified national research objectives, described methods for achieving those objectives, and provided the accounting and reporting system by which those program areas were planned and managed. The responsibility for coordinating research for each NRP was assigned to a NPS Staff Scientist (later designated as National Research Program Leader). Though biological control was an integral part of the research of a number (initially 10) of NRPs, a special NRP (no. 20260) was established to deal with the exploration for, and introduction, augmentation, and conservation of biological agents for the control of insects, weeds, plant pathogens, and other pests, and for insect and mite taxonomy (USDA 1976a).

Prior to the appointment of Bryan and establishment of NRP 20260, biological control matters were handled in the NPS by NPS Staff Scientists for weeds (W. B. Ennis) and bees (M. D. Levin). In addition, a number of Technical Advisors (TAs) were designated, first (1974) on a regional basis and later on a national basis, to assist NPS scientists in the planning and assessment of research and provide counsel on technical matters both to NPS and to ARS scientists and administrators in the field; there were nine TAs for the various aspects of biological control (for a list of TAs, see USDA 1980b). The TA system was abolished in 1981.

Recognizing the special coordination needs for biological control research, particularly in classical biological control, there was established in 1973 an ARS Working Group on Natural Enemies of Insects, Weeds, and Other Pests (WGNE); see section B.1 below on classical biological control for more detail on its establishment. ARS insect pathology programs continued to have informal coordination of activities by means of periodic research meetings. These meetings provided a mechanism for easy information exchange and development of cooperative research. Partly due to financial constraints, these meetings were no longer held after the mid-1980s.

The WGNE consisted of two biological control specialists, of appropriate disciplines (including insect pathology), from each of the four ARS Regions, and a member from the International Programs Division, and was chaired by Drs. Ennis and Levin from 1973-75, and Dr. Bryan from 1975 until his retirement in 1979. Liaison members were also appointed to represent APHIS, the Forest Service (FS), the Cooperative State Research Service (CSRS), and the Environmental Protection Agency (EPA). The WGNE Charter, as finalized at the first WGNE meeting, is presented in Appendix I.A. Some of the functions performed by the WGNE were: (1) establishment of priorities for research at the ARS overseas biological control laboratories; (2) assessment of biological control quarantine facility capabilities and needs; (3) recommendations on proposals for biological control explorations; (4) compilation of annual rosters of ARS biological control researchers; (5) preparation of annual reports of ARS biological control activities for the ARS Administrator and NPS; (6) preparation of ARS guidelines for introduction of exotic biological control agents, a still unfinished task (Coulson and Soper 1989; Coulson et al. 1991); (7) review and prioritization of proposals for foreign biological control explorations for funding from the ARS Administrator's foreign exploration funds; and (8) provision of solicited information and advice in many areas of biological control for the NPS. Similar biological control committees or working groups were established in the Southern and Northeastern Regions of ARS during the early years following the reorganization, which served coordination and information gathering and dissemination purposes within the regions and for the WGNE. These regional groups were disbanded with the abolition of the ARS Regions in late 1984.

In 1976, in partial response to the Secretary's Memorandum No. 1890 concerning USDA's Program for Environmental Quality, an interagency Work Group on Biological Pest Control Agents (WGBCA) was established in the USDA under the aegis of USDA's Office of Environmental Quality Activities (OEQ), to provide assistance in formulating USDA policies and coordination in the area of biological control research. Membership of the WGBCA included representatives from the National Program Staffs of ARS and APHIS' Plant Protection and Quarantine (PPQ), and from CSRS, FS, the

Extension Service (ES), Economic Research Service (ERS), and the Office of General Counsel, and the Pesticide Coordinator from the Secretary's office. The ARS NPS Staff Scientist, D. E. Bryan, served as Chairman. The Charter of the WGBCA is presented in Appendix I.B.

One of the WGBCA's first tasks was the organization of a federal-state task force that produced the 1978 publication "Biological Agents for Pest Control - Status and Prospects" (USDA 1978). This publication highlighted a number of opportunities for expanded use of beneficial organisms for pest control, and included an appendix indicating the statutory authorities for the USDA to undertake research, education, or regulatory action on biological agents for pest control. As a direct result of one of the 11 major recommendations made and published by this task force, the ARS Biological Control Documentation Center, with its planned databases, was established in 1982 (Coulson 1988, 1992b). As per the task force recommendation, the Documentation Center was developed to serve as "a national information storage and coordinating system specifically designed for assembling and collating domestic and international information relevant to all biological agents that might be used for pest control" and was designed to provide information for ARS and other biological control scientists and for the ARS National Program Staff. Many of the sections of this history of USDA biological control have been prepared from published and unpublished documents on file in the Center.

Several interagency subcommittees were established by the WGBCA, including one to deal with evaluations of proposed introduced biological control agents (see section B.1 below on classical biological control), another to work with EPA and the U.S. Department of Interior in considering changes in conditions specified in Section 25(b) of the Federal Insecticide, Fungicide, and Rodenticide Act (FIFRA) concerning regulation of biological control agents, and a third to work with APHIS to draft proposed legislation concerning regulation of the importation of biological control agents. The WGBCA was disbanded when USDA's Office of Environmental Quality was abolished in 1981.

In late 1977-early 1978, ARS was part of another reorganization within the USDA which resulted in the establishment of a Science and Education Administration (SEA) encompassing the former agencies ARS, CSRS, Extension Service, and other units. The establishment of SEA was to reflect an equal emphasis for the major mission/activities of Federal and cooperative research, extension, teaching, and libraries, while simultaneously providing a strong focus addressing major national programs in these mission/activities, by means of an extensive joint program and planning staff composed of Federal and non-Federal personnel. The ARS became first "Federal Research" (FR) and later "Agricultural Research" (AR) under this new organizational structure; CSRS became "Cooperative Research" (CR). Another USDA reorganization in 1981 restored the previous organizational structure and AR became once more ARS. Other than changes in the top administration and in reporting procedures, etc., there was little effect of these reorganizations on AR/ARS research programs, including biological control. (A similar reorganization was announced in 1993; see below.)

Also in 1978, another new agency was established in the USDA, the Office of International Cooperation and Development (OICD). Until that year, USDA's international programs were distributed among a number of agencies, including ARS' International Programs Division (IPD). OICD was established to improve the management of these programs. Since the 1972 ARS reorganization, IPD (later International Program Staff) had been responsible for administration of ARS' overseas laboratories, including those devoted to biological control, and had also administered the PL-480, or Special Foreign Currency Program, insofar as it related to ARS research. The latter was placed under OICD in 1978, together with many IPD personnel. OICD also became responsible for scientist exchange programs with a number of countries, through which many biological control exchanges have since taken place, beginning with several important exchanges with the People's

Republic of China (Wong 1982). See also Hedlund 1986, for other OICD programs of importance to biological control. (At the end of 1993, OICD became part of USDA's Foreign Agricultural Service.)

In 1981, an International Activities (IA) office was established in ARS and administration of ARS overseas laboratories was placed under this office, along with responsibility for ARS international interests, and IPD was soon abolished. Supervisors of this office, and thus administrators of ARS' overseas laboratories, have been B. M. Kopacz (1981-86) and D. R. Kincaid (1986-91); R. S. Soper served as IA Director, in an acting capacity, from 1991 until his appointment as Assistant Administrator of the newly created Office of International Research Programs in 1992.

One of the rationales for the 1972 reorganization was to effect an enhancement and increase in multidisciplinary research within ARS. That this was a successful outcome of the reorganization is reflected in the mixture of entomology, nematology, weed science, and plant pathology in the various biological control coordinating bodies established in ARS since 1972, from the mixture of these disciplines in the task force that developed the 1978 publication on biological control agents (USDA 1978), and by the fact that the 1980 Beltsville Symposium on biological control was the first such symposium to bring together these four disciplines (Papavizas 1981; Cook 1981). Such a mixture of disciplines has been the case in subsequent biological control workshops and conferences, such as those of 1983, 1984, 1987, and 1991 noted below.

After the 1979 retirement of D. E. Bryan, first NPS Staff Scientist for Biological Control and Insect Taxonomy, that NPS position was not immediately filled, its duties being temporarily carried out by M. T. Ouye. J. J. Drea was appointed to the NPS biological control position in October 1980 and served in that capacity until an NPS reorganization in late 1982. During 1979-82, NPS use of the WGNE languished; the last (sixth) meeting of the group having taken place in 1978, and the group was effectively dissolved by the end of 1982.

Thus, by 1983, biological control was once again without focused representation on the NPS. Instead, an NPS Biological Control "Matrix Team" was established, one of many such NPS Teams established in 1983. The Team consisted of NPS specialists in plant pathology, weed science, and plant, man-and-animal, and post-harvest entomology. NPS scientists representing other areas were added at later dates. From 1983 to 1987, the Team was variously chaired by W. Klassen, R. D. Jackson, and J. E. Wright, none of whom were biological control specialists. The duties of the Team were to develop and implement a national research plan for biological control, provide scientific and technical coordination and leadership for the overseas and domestic biological control laboratories including identification and prioritization of research thrusts, and provide leadership and coordination of interagency biological control research activities.

During 1983-87, there were several "adjustments" in the organization and management of ARS, including elimination of the four Regions and their administrative offices, and reduction in the number of Areas, first to 11 and later to eight, with their Directors reporting directly to the ARS Administrator, and the initiation of a totally new management system for ARS research. The NRPs established in 1976 were abolished, and a new ARS Program or Strategic Plan was formulated (USDA 1983a), which was followed by 6-Year Implementation Plans that were to be continuously updated (USDA 1983b, 1985). Research was to be managed even more strictly than before by CRIS (Current Research Information System) Work Units, which were to be developed by ARS scientists and approved by line administrators and the NPS, and which were grouped by the various research Approaches, Approach Elements, and Problems within the six ARS Objectives. The latest Implementation Plan, at this writing, was for 1992-1998 (USDA 1991).

As a result of increasing concerns from public and scientific sectors about environmental contamination and the need for increased use of nonchemical methods of pest control, a number of

interdisciplinary workshops and conferences on biological control were held during 1983-87, which brought together scientists of various disciplines to make recommendations for the future direction of research in the various aspects of biological control, and to take advantage of the many new possibilities resulting from current biotechnological research. Many other recommendations for improving biological control research programs had been made previously by the cooperative USDA task force in 1978 (USDA 1978), and in papers delivered at the interdisciplinary USDA Symposium at Beltsville, MD, in 1980 (Papavizas 1981). The next interdisciplinary meeting was the National Interdisciplinary Biological Control Conference organized by CSRS and attended by many university, state agricultural experiment station, and ARS scientists, held in February 1983 at Las Vegas, NV. The Proceedings of this Conference contains many recommendations for future research areas and operational needs (Battenfield 1983). This was followed in March 1984 by the ARS Research Planning Conference on Biological Control organized by the NPS Biological Control Matrix Team and held at Laurel, MD. And finally, in July 1987, an ARS Workshop on Research Priorities in Biological Control was held at Beltsville, MD, during which the ARS National Biological Control Program (NBCP) was established. Proceedings of these two meetings are also replete with many recommendations on research and operational/coordination needs (USDA 1984a; King et al. 1988). Concern over the lack of effective coordination of biological control programs was a common theme in all of these meetings. The establishment of the NBCP was for the purpose of unifying, improving coordination of, and expanding research on, the use of biological agents for pest control within ARS, in full cooperation with other federal and state biological control organizations (King et al. 1988).

Also in 1987, a Research Briefing Panel on Biological Control in Managed Ecosystems was established by the National Academy of Sciences Committee on Science, Engineering, and Public Policy (COSEPUP) which resulted in a published report (NAS 1987). Along with a number of recommendations for future biological control research, the Report contained a broad and controversial definition of biological control. (See Dietrick 1988; Garcia et al. 1988; Gabriel and Cook 1990, and the Introduction to this History.)

In April 1988, biological control once more became represented on the ARS National Program Staff (NPS), with the appointment of R. S. Soper to the position of National Program Leader (NPL) for Biological Control (to which insect taxonomy was later added). One of Soper's first actions was the establishment of Biocontrol Working Groups (BWGs) consisting of Federal, State, and university biological control specialists in various disciplines to provide guidance to the ARS Biological Control "Matrix Team" in technical matters pertaining to the further development of the ARS National Biological Control Program. The BWGs established during 1989-90 were on Microbial Biological Control, Augmentation and Conservation Biological Control, Classical Biological Control, Ecology, and Natural Products. In addition, Soper began the development of a Plan for Biological Control for the 21st Century. And in 1990 an Interagency Biological Control Coordinating Committee (IBC^3) was created, consisting of members from APHIS, ARS, CSRS, the Forest Service and Extension Service, with liaison representatives from other agencies, whose major function was to reestablish and maintain coordination among USDA agencies in matters regarding biological control. The NPL for Biological Control was once again vacated at the end of 1992 when Soper assumed the duties of Assistant Administrator for the Office of International Research Programs in ARS. In January 1993, the NPS biological control position vacated by Soper was filled by J. L. Krysan, as National Program Leader for Pest Management Systems. And in September, another major reorganization of the USDA was announced. One of the proposed actions was the consolidation of the ARS, CSRS, Extension Service, and National Agricultural Library into a new agency to be called the Agricultural Research and Education Service (ARES). The new USDA reorganization was approved by Congress in October 1994; however, ARS was retained as a separate agency.

The increased concerns from public and private sectors about environmental contamination and the need for increased use of nonchemical methods of pest control resulted in a recognition that regulations concerning these methods, particularly those regarding importation of exotic organisms for biological control purposes, needed to be examined and improved. Two major USDA workshops were held in 1991 on the subject of guidelines and regulations impacting biological control. These were organized in an attempt on the part of research scientists to provide some guidance for regulatory agencies involved (primarily APHIS and EPA) in assessing pertinent regulations to prevent the development of regulations that would have a severe, negative impact on biological control research and development. (Coulson and Soper 1989; Coulson et al. 1991; Charudattan and Browning 1992; Kauffman and Nechols 1992). Increasing public scrutiny of USDA biological control programs has led to considerable activity in APHIS, USDA's regulatory agency, regarding an overhaul of pertinent regulations and procedures dealing with these programs; see Chapter VI, and Epilogue.

B. BIOLOGICAL CONTROL OF ARTHROPODS (INSECTS, MITES, AND TICKS)

1. Arthropod Biological Control Agents

a. Classical biological control (introduction of biological control agents). By J. R. Coulson

Of all areas of ARS biological control research, classical biological control felt the effects of the 1972 ARS reorganization the most severely, because, within ARS, this type of biological control involved sequential activities carried out by many people at widely distant locations. The previous centralized and effective coordination and direction of these activities, from the overseas biological control facilities to the biological control quarantine receiving facilities and other Insect Identification and Parasite Introduction Research Branch (IIPI) domestic facilities scattered in various regions and areas of the new ARS structure, was destroyed or fragmented. Subsequent attempts to reestablish such tight coordination have been largely unsuccessful. One immediate effect of the reorganization was the cessation of quarterly and annual reports of many of the old IIPI laboratories, in favor of new, less detailed reporting systems, with narrower distribution of reports than under IIPI and the Entomology Research Division.

For a short period after the reorganization in 1972, the administrative offices of the now defunct IIPI, together with the Branch's Systematic Entomology Laboratory, became the Systematic Entomology and Beneficial Insect Introduction Laboratory (SEBIIL) of the Plant Protection Institute. The SEBIIL was one of nine newly created Institutes at the Beltsville Agricultural Research Center (BARC) at Beltsville, MD.

In a memorandum to the ARS Administrator dated August 14, 1972, R. I. Sailer, former IIPI Branch Chief and at the time Laboratory Leader of SEBIIL, presented his ideas on "organizational requirements of an operationally effective biological control program" in ARS. In this memorandum, Sailer proposed the eventual development of a "National Institute of Biological Control and Beneficial Insect Research," and presented a list of its proposed responsibilities. These included line administrative authority for overseas biological control research and domestic quarantine receiving activities within each of the four ARS Regions, with the help of a Committee chaired by a National Program Staff (NPS) specialist for program supervision and budget development purposes. Such proposed centralized direction did not fit well into the new regionalized structure of ARS, and met with resistance. As a result, a second memorandum, prepared by A. A. Hanson, BARC Area Director, with Sailer's assistance, presenting revised ideas on the "proposed organization for coordination of ARS research on natural enemies of insects and weeds," was sent to the ARS Administrator September 22, 1972. These proposals included 1) establishment of an ARS Committee to Coordinate Research on Natural Enemies of Pests, 2) establishment of the Insect Identification and

Beneficial Insect Introduction Institute (IIBIII) at Beltsville (the Institute Chair to serve as Vice Chair of the Coordinating Committee), and 3) "maintaining close coordination between all units engaged in the introduction, colonization, evaluation and management of beneficial insects." Specific organizations and functions of the proposed Coordinating Committee and Institute were outlined in the memorandum.

These proposals, and other proposals from the ARS Western Region, concerning overall coordination and national planning for research programs on natural enemies of insects and weeds were discussed by the ARS Board of Directors at various times. Though initially rejected, revised proposals eventually resulted in the approval in May 1973 of "A Plan for Coordination and Leadership of Biological Control Research in the Agricultural Research Service" and the creation of the Working Group on Natural Enemies of Insects, Weeds and Other Pests (WGNE) (see section A above, and the WGNE Charter in Appendix I.A). The IIBIII, with Sailer as Chair, was established at Beltsville in September 1972.

Believing the lack of close centralized direction to be a fatal flaw in the ARS biological control program, Sailer retired in 1973 and moved to the University of Florida as a Distinguished Professor of Biological Control. A similar loss of a key USDA biological control specialist, C. P. Clausen to the University of California, occurred 20 years earlier under similar circumstances (weakening of strong centralized direction of USDA classical biological control research as a result of events culminating in the 1953 reorganization, see Chapter III). Sailer's views on the optimal organization of a strong classical biological control program later appeared in print (Sailer 1974, 1976b, 1981b; Beirne 1985).

The new Institute (IIBIII) at Beltsville consisted of the Systematic Entomology Laboratory (SEL) and the newly created Beneficial Insect Introduction Laboratory (BIIL). At its inception, BIIL consisted of one entomologist (J. R. Coulson) and two clerical assistants, with responsibility for maintenance of the extensive files of IIPI, for providing information on classical biological control of arthropods and weeds as needed by scientists and administrators, and for otherwise assisting the Institute Chairman, Dr. Sailer, in working with the NPS to coordinate the ARS classical biological control programs. L. Knutson became Institute Chair following Sailer's retirement in 1973, and matters concerning coordination of ARS biological control programs were placed with the new WGNE, with BIIL providing significant support.

Line administrative authority for the overseas biological control laboratories was placed in the newly formed International Programs Division (IPD), and for the domestic quarantine facilities, line authority remained with the various areas and regions in which the facilities were located. Three Technical Advisors (TAs) were appointed in 1973 to assist IPD in managing the technical details of the research programs of the three overseas biological control facilities, and to assist in providing some coordination of the overseas programs with quarantine and other domestic research facilities. The TAs were J. R. Coulson (of BIIL) for the European Parasite Laboratory (and later for the new Asian Parasite Laboratory), and L. A. Andres (ARS, Albany, CA) and C. J. DeLoach (ARS, Temple, TX) for the Biological Control of Weeds Laboratories in Italy and Argentina, respectively (see section C below). These roles were abolished in 1981 when line authority for the overseas facilities was placed in the newly created International Activities office, now the Office of International Research Programs (see section A above).

In its information and coordination roles, BIIL also retained a special relationship with the biological control quarantine facilities and other domestic research facilities. A uniform system and set of forms for recording information on importation, domestic shipment, release and recolonization of beneficial invertebrates, which are used by most ARS facilities and some state and university facilities in the U.S., were developed by 1976 and improved in 1984, as a result of an extensive user survey (Coulson

1987a; 1992b). Biological control information documents were produced by BIIL, which contained rosters of U.S. and Canadian biological control workers, with brief description of their research areas, and other information of interest to biological control, the last of which was produced in 1985 (Coulson and Hagan 1986). A number of historical surveys and evaluations of recent ARS classical biological control programs have been produced by BIIL (Coulson 1977, 1987b; Coulson in Doane and McManus 1981; Coulson et al. 1986). Also, BIIL was much involved in developing procedures or guidelines for importation of exotic beneficial organisms into the U.S. (Klingman and Coulson 1982-83; Nickle et al. 1988; Coulson and Soper 1989; Coulson et al. 1991), and in assisting in biological control exchange programs, particularly with the USSR and PRC (Coulson 1981a; Coulson et al. 1982). The information activities of BIIL, which received special funding in 1981, were formally recognized in 1982 by the establishment in BIIL of the ARS Biological Control Documentation Center, in which a number of computerized databases of importance to biological control were to be developed and maintained (see section A, and Epilogue, and Coulson 1987a, 1988, 1992 b and c; Coulson et al. 1988; Knutson et al. 1990).

In addition to these non-research functions, BIIL developed a research program, with the addition of research entomologists for biological control of insect pests (1973), for biological control of weeds (1974), for biosystematics of beneficial insects (1978), and for research on genetics of insects of importance to biological control (1984). Notes on BIIL's weed research program are included in section C below. Research on parasites and predators at BIIL (and after 1985 at BIL and IBL, see below) included studies on the gypsy moth, Mexican bean beetle, Colorado potato beetle, corn rootworms, asparagus beetles, and euonymus and other armored scales, and on biosystematics of *Trichogramma* parasites. (Schroder 1981, 1982; Nickle et al. 1984; Schroder and Athanas 1985; Hung and Huo 1985; Hung at al. 1985; Vincent and Goodpasture 1986; Drea and Carlson 1987, 1988; Hendrickson and Drea 1988; Nalepa et al. 1993; Schroder et al. 1993.)

In November 1985, BIIL was combined with the Bioenvironmental Bee Laboratory at Beltsville, and the combined laboratory became the Beneficial Insects Laboratory (BIL), headed by H. Shimanuki (1985-87) and J. J. Drea (1988-1990). At the same time, IIBIII became the Biosystematics and Beneficial Insects Institute (BBII), with three laboratories: SEL, BIL, and a new laboratory, the Systematic Botany, Mycology, and Nematology Laboratory (SBMNL), created from three taxonomic units in the Plant Protection Institute. One unfortunate result of this "mini-reorganization" was to begin the process of obscuring the identity of classical biological control introduction activities among the many research units at Beltsville. Also, support personnel for the ARS Biological Control Documentation Center were drastically reduced in the course of this reorganization, causing a corresponding reduction in BCDC's documentation activities. Then, in a larger reorganization at Beltsville in January 1988, BBII was abolished altogether, after 16 years of existence; SEL, BIL, and SBMNL became laboratories of a newly organized Plant Sciences Institute (PSI). The research and reduced documentation activities of BIL continued under the new organizational structure.

There was a further reorganization in June 1990, in which the biological control personnel of BIL were incorporated with the insect pathologists of the Insect Pathology Laboratory (see later in this section) to form an Insect Biocontrol Laboratory (IBL) within the PSI, under the leadership of J. L. Vaughn. A Bee Research Laboratory was reconstituted, and BIL abolished.

Before discussing the programs of other ARS units involved in classical biological control research from 1972-93, mention must be made of several other general events impacting upon this area of the ARS biological control program. The lack of a biological control specialist on the National Program Staff from 1972-76 and 1982-88, the development of National Research Programs (NRPs) and other research management systems from 1976-87, and the establishment, organization and activities of the ARS Working Group on Natural Enemies of Insects, Weeds and Other Pests (WGNE), have all been discussed in section A above. The establishment of Research Teams and Coordinating Subgroups to

assist in the coordination of research programs crossing ARS area and regional boundaries was one of the functions of the WGNE. No Research Teams and only one Coordinating Subgroup were actually established by the WGNE.

A Coordinating Subgroup on Biological Control of *Lygus* spp. and Other Plant Bug Pests in the U.S. was established in June 1980, its first of a series of meetings being held in July 1980. Subgroup members included representatives from five domestic ARS laboratories, the European Parasite Laboratory, Texas A & M University locations at College Station and Dallas, and eventually the University of Oregon and two research stations in Canada, all locations conducting biological control or taxonomic research on plant bugs or their parasites. The Subgroup's objectives were: 1) to provide joint planning for exploration for and quarantine receipt of natural enemies; 2) to expedite research on testing and propagation of the natural enemies and to facilitate their dissemination to federal and state agencies for laboratory studies and field releases; 3) to provide for an adequate exchange of information among all involved locations; and 4) to coordinate the evaluation of field releases and the reporting of results of establishment of natural enemies and of their effectiveness. The Subgroup produced a bibliography (Graham et al. 1984) and a publication of their activities (Hedlund and Graham 1987), and met biennially on an ad-hoc basis through 1991.

The WGNE was instrumental in creating, for a short period during the late 1970s, a foreign exploration fund consisting of $40,000 annually from the ARS Administrator's funds. Proposals for explorations were reviewed and prioritized by the WGNE. Beginning in 1989, ARS funds for foreign explorations, mostly involving specific pests, again became available, and ARS began to solicit proposals annually from both federal and state scientists for explorations. These proposals were evaluated and ranked by the ARS Biocontrol Working Group on Classical Biological Control, the ARS Biological Control Matrix Team, and the Interagency Biological Control Coordinating Committee; see section A.

The establishment, organization, and activities of the interdepartmental USDA Work Group on Biological Pest Control Agents (WGBCA) was also discussed in section A above, and its charter is presented in Appendix I.B. One of the several interdepartmental subcommittees established by the WGBCA was the Subgroup on Introduction of Biological Control Agents (SIBCA) (Coulson and Soper 1989). SIBCA was established in November 1976 with members from ARS, APHIS, CSRS, and FS, with the responsibility of responding to requests from APHIS concerning the propriety of certain intended introductions of entomophagous insects and nematodes, insect pathogens, antagonists of plant pathogens and nematodes, or other biological control agents, except those intended for control of weeds (which were evaluated by another interagency group; see Chapter III, section B, above). Only "controversial" cases involving permit applications for introduction of exotic biological control agents were submitted for SIBCA review by APHIS. SIBCA became defunct with the WGBCA in 1981.

Also discussed in section A above, are the various task forces, conferences, and workshops from 1978-87 in which concerns were expressed and recommendations made concerning the need for strengthening biological control research, including improvement in the effective coordination of such programs in the United States. For the most part, it was classical biological control that was perceived to be in most need of strengthening and improved coordination. This area of research in the U.S. had long been conducted largely by the USDA, the University of California, and the Hawaiian Department of Agriculture, all of which maintained biological control quarantine facilities, and adequate program coordination was relatively simple. As mentioned previously, the classical biological control program of the University of California operated under a Memorandum of Agreement between the State of California, the University and USDA (Appendix I.C).

In the early 1970s, other university and state agencies began to develop classical biological control programs. These new programs included quarantine receiving facilities, beginning with the approval of that of the Virginia Polytechnic Institute and State University (VPI) in 1970, and the Florida Department of Agriculture and Consumer Services facility in 1973. The latter facility operated cooperatively with the University of Florida and USDA-ARS at Gainesville. Quarantine facilities and importation programs were established by Texas A & M University at College Station in 1981, by the North Carolina Department of Agriculture at Raleigh in 1984, and by Montana State University at Bozeman in 1988. Other state/university and federal quarantine facilities have since been opened, or are under construction or planned (Coulson et al. 1991). In order to operate, all quarantine facilities must be initially (and periodically thereafter) inspected and approved by APHIS-PPQ. ARS draft guidelines for importation of exotic natural enemies were prepared, which included guidelines for quarantine facility operation (Coulson et al., 1991), and contained provisions requiring the establishment of MOA's for all federal/state/university quarantine facilities similar to that for the University of California facilities; but no such MOA's were ever established for any of the new facilities. The proliferation of biological control quarantine facilities and importation programs has made information exchange between them, documentation of importation and release of exotic organisms, and coordination of classical biological control programs much more difficult.

In a 1979 report by the Office of Technology Assessment of the U.S. Congress on Pest Management Strategies in Crop Protection (OTA 1979), it was recommended that "the classical biological approach on insect and mites, especially exotic species, is one to be stressed," and increased funding for this purpose was recommended. But the report also recommended a reorganization of biological control efforts, including modification of the "present Federal horizontal structure" to a "centrally organized, vertically structured unit," and the formation of a national biological control planning body with more even representation among ARS, APHIS, FS, CSRS, the Extension Service (ES), and the states, than existed on the ARS-WGNE. Also in 1979, a proposal for establishing a National Program for Biological Control was presented at the annual Entomological Society of America meeting that year (Gilstrap and Cate 1979). The authors noted their reason for devising the plan was a perception that biological control was struggling because of inadequate organization, support, and leadership. The plan, which was preliminary and never published, identified needs for more support for taxonomic research and identification services, improved guidelines and support for quarantine facilities, and functional regional and national records systems. Parts of the recommendations of the 1978 USDA report (USDA 1978) and of the 1979 OTA report (OTA 1979) were addressed by the proposal (R. L. Ridgway in litt. 1979). Recommendations for improving communication, coordination, and cooperation between the many USDA and state/university biological control programs were included among the many recommendations of the 1983, 1984, and 1987 conferences (Battenfield 1983; USDA 1984a; King et al. 1988).

The development of the APHIS-PPQ biological control implementation program from its initiation in ARS with the cereal leaf beetle (CLB) program (see Chapter III, section A) is discussed in Chapter VI. The need for an agency that would handle the large-scale distribution of established effective natural enemies was recognized during the ARS alfalfa weevil program. USDA research scientists at the ARS quarantine facility in New Jersey (later Delaware) were heavily involved in dissemination of established alfalfa weevil parasites. The biological control program of the New Jersey Department of Agriculture joined in this effort and combined efforts had soon established the parasites throughout New Jersey. But ARS research scientists still were involved in distributing the parasites to other states, at the expense of research time. The highly successful CLB parasite distribution program of the APHIS-PPQ laboratory in Niles, MI, gave evidence as to the benefits of such an implementation program. Therefore, ARS scientists at Newark, DE, and Beltsville, MD, were highly supportive of the development of the PPQ biological control implementation program (Coulson 1976; Sailer 1976b), which was initiated in 1980. The program has been highly successful, and a 1985 team reviewing the program recommended that APHIS-PPQ "continue as a leader in biological

control by assisting research and implementing action projects." As recommended by the review team, a biological control specialist was added to APHIS-PPQ to assist in the development and coordination of the program. In 1988, the APHIS program embarked on a new initiative which was designed to expedite natural enemy importation, quarantine screening, and mass rearing and release efforts. The APHIS initiatives in foreign explorations and collections, importation, and quarantine screening seemingly conflicted with ARS efforts in these areas. Attempts were renewed in 1989 to establish a joint APHIS-ARS biological control committee to coordinate efforts in these areas. As noted in section A above, these efforts culminated in formation of the Interagency Biological Control Coordinating Committee (IBC^3) in the USDA.

During 1973-93, ARS biological control research continued at the three overseas laboratories, and at a fourth laboratory, the Asian Parasite Laboratory, which was reestablished in 1975. Projects at the laboratories in Italy and in Argentina continued to be almost exclusively devoted to biological control of weeds (see section C). However, at the Biological Control of Weeds Laboratory at Hurlingham, Argentina, there were also projects on pathogens and other natural enemies of grasshoppers, pickleworm, and on dung beetles for control of dung-breeding flies, for the ARS laboratories at Bozeman, MT, Charleston, SC, and College Station, TX, respectively. In addition, the Argentine laboratory provided strong logistical and other support for visiting U.S. explorers seeking natural enemies of insect pests in South America of potential use in U.S. biological control programs; such explorations included several groups of university and ARS scientists studying natural enemies of soybean insects (velvetbean caterpillar, soybean looper, etc.) in the early 1980s (see Jones et al. 1983; Boethel and Orr 1990), and ARS scientists studying enemies of corn rootworms (*Diabrotica*), in 1988 and 1991. However, by the end of 1993, the mission of the Argentine laboratory, renamed the South American Biological Control Laboratory, was changed drastically to concentrate almost exclusively on insect target pests, including the *Heliothis/Helicoverpa* moth complex, *Diabrotica* beetles, sugarcane borer, pickleworm, and fire ant, with only one target weed remaining (H. A. Cordo, pers. commun., 1993).

Research at the European Parasite Laboratory (EPL) in France from 1973-91, and later at the consolidated European Biological Control Laboratory (EBCL) (see below) in 1991-93, concerned natural enemies of the following insect pests: alfalfa blotch leafminer (1973-80); lygus and other plant bugs (1973-88); gypsy moth (1973-92); alfalfa snout beetle (1973-74); grasshoppers (1973-77); elm leaf beetle (1973, 1981-82); European corn borer (1974); Eurasian pine adelgid, for Hawaii (1975-77); *Sitona* weevils (1975-79, 1982-84); greenbug and other grain aphids, for Oklahoma, Texas, Chile, and Brazil (1975-82); alfalfa weevil, for APHIS, California, and Canada (1976, 1979-82); bark beetles (1977-81); birch leafminer (1979-82); green peach aphid (1979); horn fly and other dung-breeding flies (1979-91); anthomyiid maggots (1979-80); euonymus scale (1981); pear psylla (1981-83); asparagus beetles and asparagus aphid (1982-87); noctuid pests (*Heliothis*, *Autographa*, and *Spodoptera*) (1982-86); *Empoasca* leafhoppers (1984-86); nitidulid sap beetles (1985); cockroaches (1986-88); southern green stink bug (1986-87); "apple ermine moth" (1988-92); Russian wheat aphid (1988-92); codling moth (1990-92); and sweetpotato whitefly (1991-93). Explorations and collections were made by EPL and EBCL personnel throughout Europe, and in North Africa, Iran, Turkey, the USSR and countries of the later Commonwealth of Independent States, China and Japan. EPL and EBCL Directors during this period were J. J. Drea (1969-80), R. C. Hedlund (1980-81), B. D. Perkins (1981-86), R. F. Moore (1986-89), and L. Knutson (1990-93). (Drea 1981; Hoyer 1981, 1986; Hérard 1985, 1986; Blanchot 1992; Lacey et al. 1993; Gruber et al. 1994; and other references listed below under significant accomplishments of the period.)

Beginning in the mid-1960s, considerable effort was expended by ARS to consolidate the two ARS European biological control laboratories, at that time both in unsuitable rented facilities. In the 1970s, plans were made for constructing a modern ARS research facility at a location near the biological control laboratory of the French Institut Nationale de Recherche Agronomique (INRA)

near Antibes in southern France. These efforts failed in 1980, and in late 1983, the EPL moved into purchased facilities at Béhoust, about 40 kilometers west of Paris. (The Rome laboratory moved into better rented facilities in 1981.) Efforts to consolidate the two laboratories resumed in 1988, and by the end of that year, consideration was being made for the location of a consolidated laboratory at Montpellier in southern France. The two laboratories were finally united in temporary facilities at Montpellier in September 1991, as the European Biological Control Laboratory (EBCL), under the leadership of L. Knutson. Unfortunately, accompanying the consolidation was a loss of several long term employees of both laboratories. Construction of facilities for the EBCL was scheduled to begin in 1998. One-man substations of the EBCL were retained in Italy and Greece, and their programs broadened to included research on insect pests as well as weeds.

In 1981, an insect pathology research program was initiated at the EPL under cooperative agreements, and was formalized at the 1983 EPL program review (see below); this became an official part of the EBCL program in 1991. Pathogens from the various EPL/EBCL target pests under study have been isolated at EPL/EBCL and many have been shipped to the ARS Insect Pathology Research Unit at Ithaca, NY, and the Insect Pathology Laboratory (Insect Biocontrol Laboratory since 1990) at Beltsville, MD, from 1981 to the present. See Appendix II for more details of the European pathology program.

In October 1983, the programs of the EPL and the Rome laboratory underwent a high level review by ARS and many other scientists and administrators, the first major review ever held for the ARS overseas laboratories. Among many recommended changes in administration and research resulting from the review, that can be noted in the proceedings of the review, was a controversial recommendation that EPL markedly increase the percentage of publishable "basic research" at the expense of "service work" (i.e., the search for, collection, and shipment of natural enemies); these services, which are essential to a successful biological control program, are often viewed as non-research activities by administrators and peer reviewers, and promotions for overseas personnel have lagged behind those of their domestic colleagues. In recent years, a better balance between research and service has been sought in the European program.

In May 1975, an ARS Asian Parasite Laboratory (APL) was reestablished by P. W. Schaefer, with the help of special funds made available for ARS biological control research on the gypsy moth (Coulson 1981b; Schaefer 1981; Pemberton et al. 1993). (See Chapters I and II for information regarding the earlier Asian Parasite Laboratory.) The reestablished APL was first located at Sapporo, Hokkaido, northern Japan, which was near known populations of the gypsy moth, the major target pest for the laboratory. In 1982, the APL was relocated to Seoul, South Korea, as a result of the need to conduct research on additional target pests. Research at the APL in Japan and South Korea concerned natural enemies primarily of the gypsy moth (1975-93), but also of the following additional insect pests: larch casebearer (1976); "oriental chestnut gall wasp" (1977-79, 1984-89); *Fiorinia* scales (1977); Japanese beetle (1978, 1982, 1987-88); "Asian corn borer" (1978-79, 1985-87); epilachnine beetles (1979-88); pear psylla (1979-80); red pine scale (1979-80, 1983-84); southern green stink bug (1979-85); green peach aphid (1979); euonymus and other armored scales (1982-86); imported cabbageworm (1988); and "apple ermine moth" (1988-91). Studies by APL personnel were also conducted in China, on the "apple ermine moth" (1990-91) and "Asian gypsy moth" (1991-92), and in Russian Far East, on the latter in 1992. Research on biological control of weeds was also begun by APL personnel, in 1991 (see section C). ARS scientists in charge of the new APL were P. W. Schaefer (1975-79), R. W. Carlson (1980-85), D. K. Reed (1985-88), and R. W. Pemberton (1989-93). (Schaefer 1981; Schaefer and Ikebe 1982; Drea and Carlson 1987, 1988; Schaefer et al. 1988; Pemberton et al. 1993.) An administrative decision was made by ARS in 1993 to close this laboratory at the end of the fiscal year, and the long history of the USDA Asian Parasite Laboratory, which first opened in the 1920s, ceased.

In the past, foreign explorations could generally be carried out over many parts of the world from ARS overseas laboratories. Research on exotic natural enemies in some areas of the world could also be carried out under the SFC or PL-480 program, which has been continued under OICD administration. There have been three large geographical areas of the world where such explorations and research have been more difficult or impossible: the area of the former Union of Soviet Socialist Republics (USSR), the People's Republic of China (PRC), and Australia and the South Pacific. As a result of a 1972 US-USSR agreement in the area of environmental protection, U.S. and Soviet specialists began exchanging biological control agents in 1972, and there were several ARS exploration trips in the USSR under this agreement (Coulson 1981a). From the U.S. viewpoint, results were somewhat disappointing. An agricultural agreement was also signed with the PRC, in 1978, and exchanges of biological control agents and personnel were begun in 1979 between Chinese and American specialists (Coulson et al. 1982; Knutson and Gordon 1982). These, too, were largely unsatisfactory, though some materials were exchanged. Negotiations conducted by ARS (R. S. Soper and others) and the Chinese Academy of Agricultural Sciences in 1988 have resulted in the establishment of a Sino-American Collaborative Biological Control Laboratory in Beijing, PRC, in November 1988, greatly improving the situation in regard to obtaining biological control agents in the PRC. By the end of 1988, similar agreements with the Zoological Institute of the USSR Academy of Science in Leningrad, and the All-Union Institute for Biological Methods of Plant Protection in Kishinev, Moldavian SSR, also greatly improved cooperative US-USSR efforts in biological control. The breakup of the Soviet Union in 1991 caused problems with these arrangements, and efforts are being made to reestablish cooperative linkages. And finally, in 1989, an ARS laboratory was established in Australia, primarily for study of natural enemies of aquatic and wetland weeds, but with potential to expand into other areas of biological control; see section C.1 below.

Special relationships were maintained between the principal domestic ARS quarantine facility for parasites and predators at Newark, DE, (having moved from Moorestown, NJ, in 1973; see also Ertle and Day 1978) and the European and Asian Parasite Laboratories. Similar relationships were maintained by the ARS quarantine facilities for natural enemies of weeds at Albany, CA, and at Temple, TX, with the weeds laboratories at Rome, Italy, and Hurlingham, Argentina, respectively; see section C, below. In addition to a large quarantine clearance service for imported parasites and predators destined for many state and other federal biological control programs, the Beneficial Insects Research Laboratory (BIRL) at Newark, DE, maintained a research program during 1973-93, based primarily on material received from the programs of the EPL/EBCL and APL. Imported natural enemies were released, and their establishment, dispersal, and impact evaluated. These included natural enemies of: alfalfa weevil (1973-88); gypsy moth (1973-93); cereal leaf beetle (1973-77); alfalfa blotch leafminer (1973-82); pea aphid and other aphids (1973-88); lygus and other plant bugs (1976-93); European corn borer (1974-77); birch leafminer (1974, 1978-88); *Sitona* weevils (1975-86); asparagus aphid (1975); Mexican bean beetle (1975-76, 1979-88); spider mites in greenhouses (1980, 1985); Colorado potato beetle (1981-84); larch casebearer (1980-86, 1991-92); European wheat stem sawfly (1982-83); asparagus beetles (1983-87); potato leafhopper (1983-87); and euonymus and other armored scales (1986-88). (See pertinent references cited below under significant accomplishments of the period.) BIRL's alfalfa weevil program and the support given by BIRL scientists in the development of the APHIS-PPQ biological control implementation program, have been discussed in section A. The APHIS program has relieved BIRL scientists of the large task of disseminating established, effective alfalfa weevil parasites to new areas. Research Leaders at BIRL (renamed BIIR, Beneficial Insects Introduction Research, in 1989) during this period have been W. H. Day (1971-78), R. J. Dysart (1978-87), and R. W. Fuester (1987-present).

The research program of the Biological Control of Insects Research Laboratory (BCIRL) at Columbia, MO, during 1973-93 largely concerned parasite/predator augmentation and insect pathology (see sections B.1.b and B.3 for more information and list of research leaders for this Laboratory). However, BCIRL personnel (principally B. Puttler) were involved in release and

evaluation of both exotic insect parasites and predators, and exotic weed-feeding insects. Puttler also conducted three foreign explorations during this period that resulted in the discovery and introduction of two new and important parasites of insect pests. One of these, *Edovum puttleri*, is a species currently being studied at many locations for use in Colorado potato beetle parasite augmentation programs, and the other, *Euplectrus puttleri*, has been established in Florida as an effective parasite of the velvetbean caterpillar. (Waddill and Puttler 1980; Puttler and Long 1983; Puttler et al. 1980; Schroder et al. 1985.)

The ARS Stoneville Research Quarantine Facility (SRQF) at Stoneville, MS, which opened in 1973, had been planned and designed by IIPI as part of a special program on potential biological control of narcotic plants. The facility was also designed to serve as the major quarantine facility for classical biological control of weeds research in the eastern U.S., comparable to the facility at Albany, CA, for the western U.S. After the reorganization, an entomologist was stationed at the Southern Weed Science Laboratory (SWSL) at Stoneville for this purpose until the mid-1980's, but the classical program waned at the SWSL in favor of augmentative and pathology programs (see section C below). However, the WGNE recommended that the SRQF also serve as a major quarantine facility for insect parasites and predators for the southeastern U.S., to help lighten the heavy service load of the ARS quarantine facility at Newark, DE. Classical biological control of insects research began at the SRQF and the Bioenvironmental Insect Control Laboratory (Southern Field Crop Insect Management Laboratory, SFCIML, 1981-89, Southern Insect Management Laboratory, SIML, since 1989) at Stoneville in 1978; research leaders of this unit have been E. G. King, 1981-88, and D. D. Hardee, 1988-present. Projects there have included research on natural enemies of graminaceous stemborers, *Heliothis* (s. lat.), plant bugs, and other insect pests of cotton and soybean, and the southern green stink bug. During the early 1980s, the SRQF served as quarantine facility for the many explorations by state and federal entomologists involved in the EPA-supported Soybean Subproject of the Consortium for Integrated Pest Management. During this period, SRQF also served as the quarantine receiving facility for parasites of lygus bugs from Africa destined for release in southwestern U.S. The facility still serves as a quarantine receiving center, but on a reduced basis, briefly (1992) responsible for quarantine receipt of imported parasites of the sweetpotato whitefly. (Bailey and Kreasky 1978; Jones et al. 1983, 1985; Coulson 1987b; Schuster 1987; Snodgrass and Ertle 1987; Powell 1989; Parencia and Martin 1990; Tillman 1993.)

IIPI had also opened another station, at Gainesville, FL, just prior to the 1972 reorganization. The purpose of the station, located at the quarantine facilities of the Florida Biological Control Laboratory (FBCL) (Denmark 1978), was research on natural enemies of aquatic weeds, and research in this area has continued there (see section IC). During a short period in the 1970s, ARS personnel there (N. R. Spencer in charge) also began to engage in receipt and quarantine clearance of introduced insect parasites and predators, mostly scale insect parasites. The ARS station at Gainesville is now a satellite of the ARS Aquatic Plant Management Laboratory at Fort Lauderdale, FL.

Other ARS facilities, not originally IIPI locations, have also been involved in research involving introduced natural enemies of insect pests during 1973-93. These include work on lygus bug parasites at the ARS Biological Control of Insects Laboratory (later named the Honey Bee Research unit) at Tucson, AZ, and the SFCIML at Stoneville, MS (Hedlund and Graham 1987); work on pear psylla predators and parasites (Fye 1981; Unruh et al. 1995), and "apple ermine moth" parasites (Unruh et al. 1993; Unruh 1995), at the Yakima Agricultural Research Laboratory at Yakima, WA; work on various citrus pests at ARS locations at Weslaco, TX, and Riverside, CA (the latter research location being abolished in 1987); research on introduced natural enemies of pecan and other arboreal aphids at the Southeastern Fruit and Tree Nut Research Laboratory at Byron, GA (Tedders and Schaefer 1994); studies of pathogens and nematodes attacking corn rootworms collected in Argentina at the Northern Grain Insects Research Laboratory at Brookings, SD; and, most recently,

work on imported parasites and predators of the newly introduced Russian wheat aphid at ARS facilities at Stillwater, OK, and Brookings, SD. The laboratories in Arizona, Mississppi, Washington, Texas, and South Dakota have also been much involved in augmentation research; see section B.1.b below. Research on an imported parasite of rangeland grasshopper eggs was conducted under a cooperative ARS-APHIS program by R. J. Dysart at the ARS Northern Plains Soil and Water Management Research Center, Sidney, MT (Dysart 1991, 1992). These studies generated much controversy in the scientific press concerning the release of exotic natural enemies against native pests; see Lockwood 1993 a and b; Carruthers and Onsager 1993, and also section B.3 below. This research followed up much earlier research on grasshopper natural enemies conducted at the ARS Rangeland Insect Laboratory at Bozeman, MT, utilizing parasites received from the ARS European Parasite Laboratory (see Chapter III, section A.1.a). A compendium of known grasshopper parasites and predators in North America was published as an outgrowth of those early studies (Rees 1973).

Following the lead of the Hawaiian Department of Agriculture and University of California biological control programs, ARS began intensified research during this period on classical biological control of insect pests of livestock. The first importations of exotic dung beetles for control of dung-breeding flies were made in 1972 by personnel of the Veterinary Toxicology and Entomology Research Laboratory (name changed to Food Animal Protection Research Laboratory in 1991) at College Station, TX (Fincher 1986; Coulson and Soper 1989). Importations of several species of exotic histerid and staphylinid predators of dung-breeding flies were begun in 1985 at that Laboratory (G. T. Fincher, personal communication, 1992); the ARS importation of the staphylinid predator *Aleochara tristis* in the 1960s is noted in Chapter III. Importations of parasites of dung-breeding flies began in the early 1980s at the Insects Affecting Man and Animals Research Laboratory (name changed to Medical and Veterinary Entomology Research Laboratory in 1991) at Gainesville, FL, utilizing the FBCL quarantine facilities (Hoyer 1981, 1986; Morgan 1986). The Gainesville and other ARS facilities are also involved in considerable research on augmentation of natural enemies of livestock pests and on pathogens of insects affecting both livestock and man (see sections B.1.b. and 3, below).

Also during this period of classical biological control, apparently the first introductions of exotic insect-parasitic nematodes in the U.S. were made by ARS (Coulson 1981c; and section B.2 below), and, as noted above and in section B.3 below, ARS began importing exotic insect pathogens. By 1988, forms were developed by the ARS Biological Control Documentation Center for documenting the importation and release of exotic insect and weed pathogens and microbial antagonists of plant pathogens and nematodes (Coulson 1992b).

Significant accomplishments resulting from the USDA-ARS classical biological control program during 1973-93 include the control of the alfalfa blotch leafminer in the northeastern U.S. and of the Eurasian pine adelgid in Hawaii, and of grain aphids in some parts of South America, and the establishment of natural enemies of the gypsy moth, plant bugs, euonymus scale, birch leafminer, and arboreal aphids. Numerous exotic parasites, predators, and pathogens of the gypsy moth (see section A.3) and, since 1987, of the Russian wheat aphid and sweetpotato whitefly, have been collected and made available to many federal, state, and university research workers in the U.S. for study and release against these pests (Lacey et al. 1994). In addition, ARS research resulted in the importation of two exotic parasites that have been utilized in augmentation programs for control of the Mexican bean beetle and Colorado potato beetle during this period.

The alfalfa blotch leafminer was first found in the U.S. in 1968 and quickly spread extensively in northeastern U.S. and eastern Canada. Not only did it cause considerable loss in alfalfa yield, but insecticidal treatments used by farmers to combat it threatened to upset the successful alfalfa weevil biological control program by decimating the introduced alfalfa weevil parasites. Research conducted both at the European Parasite Laboratory (1973-79) and the ARS Beneficial Insects Research

Laboratory (BIRL) in New Jersey and Delaware (1970-82), resulted in the discovery and importation of 14 European leafminer parasites, three of which have become established in the U.S. These three parasites caused a remarkable degree of control of the pest by 1981 in Delaware, and rapidly dispersed throughout the range of the pest in northeastern U.S. and Canada, with the result that no further insecticidal treatments are required. An annual savings of about $13,200,000 ($17,200,000 in 1993 dollars) due to yield losses no longer encountered has been estimated; this does not take into account the cost of insecticides no longer applied. (Drea et al. 1982; Hendrickson and Plummer 1983; Drea and Hendrickson 1986; DeBach and Rosen 1991; and Chapter III, Table 1 above.)

The Eurasian pine adelgid was first found in Hawaii in 1970, and rapidly spread through the islands causing severe damage to pines. Chemical eradication attempts failed, and requests for natural enemies were made of the ARS European Parasite Laboratory. EPL personnel collected in France and shipped to Hawaii a predator of the adelgid, the establishment and spread of which has resulted in effective control of the pest in Hawaii. (Culliney et al. 1988.)

In connection with the greenbug program at the EPL, shipments of aphid parasites were sent to Chile, Brazil, and Argentina, to help combat the ravages of several species of grain aphids in those countries. Complete control of two of the aphids (*Metopolophium dirhodum* and *Sitobion avenae*) by the introduced parasites has been claimed in some areas of South America. (Rojas 1980; Zuñiga 1985; Gruber at al. 1994.) Releases of the European parasites in Oklahoma and Texas apparently were unsuccessful.

Explorations for gypsy moth parasites were conducted by personnel of both the European and the Asian Parasite Laboratories, and release and evaluation studies were conducted by personnel of BIRL in Delaware. BIRL was also much involved in quarantine clearance of imported gypsy moth natural enemies for study and release by the Forest Service and state biological control programs in New Jersey, Pennsylvania, Virginia, Maryland, West Virginia, and North Carolina. An APHIS Gypsy Moth Parasite Distribution Program was developed to help distribute the introduced parasites being cultured by the New Jersey Department of Agriculture. Only one species (*Coccygomimus disparis*) of the many introduced parasites has been successfully established so far from this program; it is too early to note whether the parasite will have an impact on gypsy moth populations. (Drea 1978; Coulson 1981 b and d; Fuester et al. 1981, 1988; Schaefer 1981; and other sections in Doane and McManus 1981; Schaefer et al. 1984, 1988, 1989; Coulson et al. 1986.)

Extensive research on natural enemies of lygus bugs and other plant bug pests has been conducted by personnel of the EPL and BIRL, and by some other ARS laboratories, during this period. Several European parasites have been introduced, and two species are firmly established in northeastern U.S. In 1987-88, one, *Peristenus digoneutis*, increased field parasitism of the tarnished plant bug to three times the previous rate by native parasites; the other, *P. conradi*, has raised field parasitism of the alfalfa plant bug by four times. Potential savings if adequate control of these two pests is eventually obtained ranges from $60 to $130 million per year (W. H. Day, personal communication, 1993). (Coulson 1987b; Day 1987; Hedlund 1987; Day et al. 1990, 1992.)

Beginning in 1980, research on the parasites and predators of the euonymus scale was conducted at the Asian Parasite Laboratory, and at BIRL in Delaware, and the Beneficial Insects Laboratory at Beltsville, MD. Several parasites and two predators, *Chilocorus kuwanae* and *Cybocephalus* sp. prob. *nipponicus*, were introduced, and the two beetle predators have become established. Results so far have been rather spectacular, the beetles being responsible for complete eradication of the scale in release sites in several States. A large program for the wide-scale dissemination of the established predators is being conducted by ARS, which is slated to become part of the APHIS-PPQ implementation program in the near future. (Drea and Carlson, 1987, 1988; Hendrickson and Drea 1988; Nalepa et al. 1993.)

Another pest of ornamentals, the birch leafminer, was first found in the U.S. in 1923, and has since dispersed throughout the northeastern U.S. and eastern Canada. European parasites were obtained from the Commonwealth Institute of Biological Control (CIBC) station in Europe and the ARS EPL and released by ARS personnel of the Delaware laboratory in Delaware, Maryland, Pennsylvania, and New Jersey in 1977-82, and two parasites became established (Fuester et al. 1984). The parasites are dispersing but it is still too early to assess their effect on birch leafminer populations.

An Asian coccinellid predator of arboreal aphids, *Harmonia axyridis*, was first introduced in 1978 for use against various pest aphid species and pear psylla. With releases made in Connecticut, District of Columbia, Delaware, Georgia, Louisiana, Maryland, Maine, Mississippi, Ohio, Pennsylvania, Washington, and in Canada during subsequent years, establishment was first confirmed in Louisiana in 1988 (Chapin and Brou 1991). This recovery was quite removed from intentional release sites and therefore may have resulted from accidental introduction. Nevertheless, in recent years its presence has been confirmed in Louisiana, Alabama, Mississippi, Georgia, North Carolina, Virginia and West Virginia, and most recently Washington. Its impact on arboreal aphid pests remains uncertain, but in some locations it is reportedly abundant. (P. W. Schaefer, BIRL, personal communication; Tedders and Schaefer 1994; see also Day et al. 1994, for comments on possible origin.)

Earlier research by personnel of the ARS laboratory in Moorestown, NJ (now BIIR, Newark, DE), on a parasite of epilachnine beetles imported from India, *Pediobius foveolatus*, for control of the Mexican bean beetle (MBB), established the fact that the species could not overwinter in the U.S. But because the parasite otherwise proved to be an effective parasite of MBB larvae, research at the University of Maryland, funded by ARS, showed that the parasite could be used effectively in an augmentation program. This concept was then carried further in a large-scale APHIS-PPQ demonstration project involving several mid-Atlantic states (see Chapter VI), and the parasite is still being used for Mexican bean beetle control by the New Jersey and Maryland Departments of Agriculture. Savings are estimated to be $1,000,000 per year in New Jersey, and $3.26/acre of fields treated with the parasite in Maryland (W. H. Day, personal communication, 1993). (Stevens et al. 1975; Reichelderfer 1979; Schroder 1981.) Other Asian and South American parasites and predators of the Mexican bean beetle have been under study at BIIR in more recent years.

Explorations in South America in 1980 by BCIRL reported above, resulted in the discovery and importation of *Edovum puttleri*, which, though originally from eggs of a related beetle, successfully attacks eggs of the Colorado potato beetle (CPB). ARS research showed that this species, too, could not successfully overwinter in the U.S., and the species has become the subject of several augmentation programs for control of the CPB in eggplant, tomatoes, and potatoes. It has been shown to be an effective and economic control agent for the beetle in eggplant. (Schroder and Athanas 1985, 1989; Schroder et al. 1985; Lashomb et al. 1987, 1988.)

b. Augmentation and conservation of parasites and predators. By D. A. Nordlund and E. G. King

Augmentation and conservation biological control received increased attention during the 1973-1993 period as environmental concerns, regulation of pesticides, and resistance to insecticides increased. Knipling (1979, 1992) even suggested, based on theoretical simulation models, that augmentation of host specific parasites and predators could provide a solution to some of the world's major insect pest problems. A number of reviews pertinent to augmentation and conservation were published during this period including: Chapman 1974; Rabb et al. 1976; Bay et al. 1976; Ridgway and Vinson 1977; Ables and Ridgway 1981; Stinner 1977; Nordlund et al. 1981; Rutz and Patterson 1990; Anderson and Leppla 1992; and Williams and Leppla 1992. Also pertinent is the widespread adoption of integrated pest management (IPM) programs during this period (Hoy and Herzog 1985). Though

many IPM programs were in practice basically pesticide management programs, they did contribute significantly to conservation.

Research by ARS scientists related to augmentation of entomophagous insects also increased during the 1973-93 period. Much of this research was basic in nature (influences of semiochemicals on host or prey selection; basic biology, physiology, and nutrition; development of mass production technology, etc.) There were, however, several pilot tests involving augmentation of specific biological control agents. Because of the large volume of material related to augmentation and conservation produced by ARS personnel during this period, an attempt to provide a comprehensive review will not be made here. Instead, discussions will focus on demonstrations of effectiveness and major new trends in basic research programs. It must be kept in mind that much of IPM research could be related to conservation of natural enemies.

Parasites (parasitoids) and predators of crop pests. *Lixophaga diatraeae*, a tachinid parasite native to several Caribbean islands, has been used in augmentation programs against the sugarcane borer in the Caribbean region and South America (King et al. 1981). Yet, the effectiveness of this parasite had not been conclusively demonstrated (Bennett 1969). Thus in 1973, the ARS began evaluating the technical feasibility of using *L. diatraeae* to suppress sugarcane borer populations in Louisiana and Florida. King et al. (1979) developed a mass production technique for this parasite using greater wax moth larvae, which cost about 1/5 as much as using sugarcane borer larvae. Field parasitism of sugarcane borer larvae increased significantly after augmentative releases of *L. diatraeae* in Louisiana and Florida and suppression was apparent in some fields (Summers et al. 1976; King et al. 1981). King et al. (1981) concluded that early-season releases of *L. diatraeae* may be useful against the sugarcane borer. Implementation of such a program, however, would require development of an inexpensive mass rearing technique, limiting parasite dispersal from release areas, establishing appropriate release rates, and an appropriate economic analysis.

The eulophid *Pediobius foveolatus* was imported from India during the late 1960s by personnel of the Beneficial Insects Research Laboratory then at Moorestown, NJ (Angalet et al. 1968). This parasite of epilachnine beetle larvae was imported to attack the native American Mexican bean beetle. The parasite cannot overwinter in the U.S. The parasite attacks beetle larvae and has no diapause, while the Mexican bean beetle overwinters as an adult. In the early 1970s, an area-wide suppression program for the Mexican bean beetle in Maryland using inoculative releases and nurse crops of snap bean resulted in nearly 100% parasitization of beetle larvae and a four-fold reduction in insecticide usage (Stevens et al. 1975). An economic analysis by Reichelderfer (1979) of the USDA, Economics, Statistics, and Cooperatives Service, demonstrated that inoculative releases of *P. foveolatus* yield greater returns than do insecticide treatments. This augmentation program became one of the initial demonstration programs of the APHIS biological control programs discussed in Chapter VI, and is continuing in the northeastern United States, particularly in New Jersey.

Edovum puttleri, another eulophid parasite, was imported from Colombia, South America in 1980 and found to parasitize successfully eggs of the Colorado potato beetle (Puttler and Long 1983). Like *P. foveolatus*, this parasite does not overwinter in the U.S. and, thus, must be released periodically. Though Schroder and Athanas (1985) reported significant rates of parasitization on potato plants, *E. puttleri* has not been found to be effective on potatoes, apparently because of the way potato leaves lay on each other. However, *E. puttleri* is being used effectively in New Jersey to control the Colorado potato beetle on eggplant (Lashomb 1989).

The genus *Chrysoperla* and other genera of the neuropteran family Chrysopidae includes a number of important insect predators, including *Chrysoperla carnea* and *C. rufilabris*. Both species are widely distributed in North America and *C. carnea* is found worldwide except for Australia. These two species are predaceous in the larval stage and attack a variety of pests including aphids, chinch bugs,

mealybugs, scales, whiteflies, leafhoppers, lepidopterous eggs and larvae, and mites (Hydorn 1971, and references therein). *Chrysoperla* species have a number of attributes that make them ideal candidates for periodic release programs: 1) they feed on numerous pests and occur in many different agroecosystems; 2) when released as eggs or young larvae, these predators are unable to leave the target area; 3) they have high searching rates; and 4) larvae are tolerant to some insecticides. In the late 1960s and early 1970s, considerable work on *C. carnea* was conducted by personnel of the ARS Cotton Insects Research Laboratory in College Station, TX. Field releases of *C. carnea* significantly reduced *Heliothis/Helicoverpa* populations and damage (Ridgway et al. 1973, 1974; Ridgway and Kinzer 1974; Kinzer 1976), though high release rates were required. Rearing techniques at the time could not economically produce the numbers of *Chrysoperla* needed for control of these pests. Thus, from the mid 1970s until the late 1980s, research on *Chrysoperla* in ARS was limited. In 1990, Nordlund and Morrison reported on the predation behavior of *C. rufilabris* larvae. These studies demonstrated that this predator exhibits some success-motivated searching, particularly when feeding on tobacco budworm eggs, but that handling time did not decrease with experience. Also, tobacco budworm larvae were the preferred prey, when compared to cotton aphid or tobacco budworm eggs. Nordlund et al. (1991) demonstrated that *C. rufilabris* larvae would feed on Colorado potato beetle eggs and larvae and could provide control of populations in field cages. With the rising concern about the sweetpotato whitefly, Breene et al. (1992) showed that *C. rufilabris* can also control this major pest on greenhouse *Hibiscus.*

Morrison and colleagues (Morrison et al. 1975; Morrison and Ridgway 1976; Morrison 1977; Elkarmi et al. 1987) worked on improving rearing techniques for these predators. The status of *Chrysoperla* mass rearing technology was reviewed by Nordlund and Morrison (1992). A number of commercial insectaries are currently producing *C. carnea* and *C. rufilabris* for use against a variety of pests using the basic technology developed at the Cotton Insects Research Laboratory. Efforts are currently underway at the Biological Control of Pests Research Unit in Weslaco, TX, to automate this rearing process (Nordlund and Morrison 1992).

In 1981, the ARS initiated a pilot test "to evaluate on a large scale, in replicated field experiments, current technology for augmenting and manipulating *Trichogramma* populations to manage *Heliothis* [s. lat.] spp. in cotton." This project involved personnel from the Cotton Insects Research Laboratory, and the Pest Control Equipment and Methods Research Unit, College Station, TX; Southern Grain Insects Research Laboratory (now the Insect Biology and Population Management Research Laboratory), Tifton, GA; Southern Field Crop Insect Management Laboratory (SFCIML), Stoneville, MS; the Boll Weevil Eradication Research Unit, Raleigh, NC; Beneficial Insect Introduction Laboratory, Beltsville, MD; the University of Arkansas; and North Carolina State University. This pilot test provided an opportunity to test a number of the components including mass production and aerial release of a *Trichogramma* augmentation program. The studies conducted during this pilot test did demonstrate the ability to mass-produce *Trichogramma*, transport them to the field, release them, and increase rates of parasitization significantly. Unfortunately, boll weevil outbreaks in the study area resulted in the extensive use of insecticides, which had a negative impact on both the released *Trichogramma* and naturally-occurring predators and parasites. Thus, the results were not conclusive (King et al. 1985). This study did demonstrate, however, that high levels of parasitization can be produced with augmentative releases of *Trichogramma.*

A number of other parasites for control of *Heliothis/Helicoverpa* spp. have been studied by ARS scientists. H. R. Gross, at the Insect Biology and Population Management Research Laboratory, Tifton, GA, did considerable work with the tachinid *Archytas marmoratus* for control of the corn earworm in corn (Gross 1988, 1990; Gross and Johnson 1985; Gross and Young 1984). This work demonstrated that significant increases in parasitization could be obtained with applications of mechanically extracted maggots or releases of adult insects. The braconid *Microplitis croceipes* also received considerable research attention. Workers from SFCIML, Stoneville, MS; Insect Biology and

Population Management Research Laboratory, Tifton, GA; Insect Attractants, Behavior, and Basic Biology Research Laboratory, Gainesville, FL; Biological Control of Insects Research Laboratory, Columbia, MO; and the Veterinary Toxicology and Entomology Research Laboratory, College Station, TX, cooperated in various aspects of this research (Powell et al. 1989). The inability to mass-produce these parasites economically is the major impediment to their utilization. (For *Heliothis/Helicoverpa* studies, see also King et al. 1989, and Tillman 1993.)

Workers at the Biological Control of Insects Laboratory (later the Honey Bee and Insect Biological Control Research Unit) in Tucson, AZ, studied parasites for use in augmentation programs against lygus bugs. This work involved studies of the biology and ecology of *Anaphes iole* (=*ovijentatus*), an egg parasite, and *Leiophron uniformis*, which attacks nymphs (Debolt 1981, 1987, 1989; Jackson 1982, 1986, 1987; Jackson and Graham, 1983; Graham and Jackson 1982; Graham et al. 1986; Jones and Jackson 1990; Norton et al. 1992). Here, too, the inability to mass-produce these parasites economically proved to be a major impediment to their use (Debolt 1987).

In the late 1980s, workers at the Subtropical Agricultural Research Laboratory, Weslaco, TX, building on the previous work by J. R. Cate while he was at Texas A&M University, began working on augmentation programs against the boll weevil. The Lower Rio Grande Valley of Texas had an effective cotton stalk destruction program that generally held boll weevil populations to relatively low levels. Also, the Valley is a fairly small and isolated cotton growing region. The boll weevil, of course, is an exotic pest, originating in southern Mexico, where it is attacked by numerous parasites (Cross and Mitchell 1969; Cate 1985; Cate et al. 1990). Though research on classical biological control of the boll weevil has a long history, all attempts to establish exotic boll weevil parasites in the U.S. have been unsuccessful. Yet, Johnson et al. (1973) and Cate et al. (1990) reported significant increases in boll weevil mortality following releases of the pteromalid parasite *Catolaccus grandis*, indicating the possibility of using this exotic parasite in an augmentation program against the exotic boll weevil. Summy et al. (1991) and Morales-Ramos and King (1991) reported that such an approach is technically feasible, though work will be required to develop adequate mass production and efficient release techniques.

Workers at the Tropical Fruit and Vegetable Research Laboratory in Honolulu, HI, have recently begun research on the possibility of augmenting parasites of fruit flies in Hawaii (Wong et al. 1991). They have been releasing over a million wasps per week of three braconid species, *Diachasmimorpha longicaudata*, *D. tryoni*, and *Psyttalia fletcheri*, against three tephritid pests, oriental fruit fly, Mediterranan fruit fly, and melon fly (Wong and Ramadan 1992). Also, work on the braconid parasite *Biosteres arisanus*, an egg-larval parasite, which can develop in at least seven species of tephritid pests, and on other parasites, is continuing (Ramadan et al. 1991, 1992).

Parasites and predators in stored products. The stored product environment, in which losses due to insects amount to about 4 million tons of grain per year in the United States (Nilakhe and Parker 1989), provides an ideal situation for augmentation. A number of parasites and predators that may be useful in stored products have been studied by personnel of the Stored Products Insects Research and Development Laboratory in Savannah, GA, and the Stored Products Insects Research Unit, Madison, WI. These include: *Trichogramma pretiosum*, *Habrocytus cerealella*, *Anisopteromalus calandrae*, *Xylocoris flavipes*, *Bracon hebetor*, and *Pyemotes tritici* (Arbogast 1979, 1984; Brower and Cogburn 1989; Brower 1984 a and b; Brower and Press 1988, 1992; Burkholder 1981; Hagstrum and Smittle 1977, 1978; Keever et al. 1986; LeCato et al. 1977; Press et al. 1975, 1977). Experiments in the laboratory and small scale warehouse studies have shown that the pteromalid parasite *A. calandrae* can effectively suppress populations of "grain weevils" (*Sitophilus* spp.), the parasites *B. hebetor* and *T. pretiosum* can be effective against lepidopterous pests in grain, and that *X. flavipes*, a generalist predator, can likewise be effective. Studies show that over 90% control can be achieved in single parasite-host or predator-prey systems (Brower and Cogburn 1989; Brower and Press 1992).

Commercial production and use of these biological control agents had begun and apparently was proving effective. Then in 1988, Food and Drug Administration (FDA) regulations relating to the addition of insects, even parasitic and predaceous insects, to food came into play; U.S. Marshalls "arrested" a bin of combine-run rye in Texas that had been treated with biological control agents (Maedgen 1989). This effectively put an end to the commercialization of this technology, at least temporarily. The regulations that mandated FDA's position have since undergone review and newly proposed regulations (Environmental Protection Agency, 1991) will, if adopted, permit use of parasitic and predaceous arthropods for biological control in stored products. Thus, research in this important area is continuing.

Parasites and predators of insects affecting man and animals. Biological control of insect pests of man and livestock is an important component of the ARS research program. Weidhaas and Morgan (1977) of the Insects Affecting Man and Animals Research Laboratory (now the Medical and Veterinary Entomology Research Laboratory), Gainesville, FL, reviewed biological control of muscoid flies and selected species of mosquitoes. The house fly costs U.S. farmers approximately $100 million annually (Anonymous 1980), annual losses caused by the horn fly are $730 million, and for the face fly losses are in excess of $53 million (Drummond et al. 1981).

Blume (1985) listed 43 species of parasitic Hymenoptera and Fincher (1990) listed 81 species of predators associated with insect pests in cattle dung in the U.S. Yet these important pests are seldom effectively controlled. One important factor contributing to this lack of control is that the parasitic and predaceous insects do not appear early in the season when fly populations begin to build up. This provides an opportunity for augmentation programs, and research is continuing (Summerlin et al. 1984, 1990, 1991 a, b and c).

The pteromalid *Spalangia endius* has advantages in augmentation programs over a number of other parasites that attack muscoid flies. For one thing, females search all levels of the manure, the major fly breeding site. The development time for *S. endius* is approximately twice that for house flies. While this long development time is probably one reason *S. endius* does not provide satisfactory control of house flies in nature, it makes the mass production, packaging, storage, and transportation activities associated with a periodic release program much easier. For example, Weidhaas and Morgan (1977) reported that parasitized fly pupae of different ages could be packaged together to give sustained release of parasites over a period of up to a week. Morgan et al. (1975a) conducted a preliminary experiment involving releases of *S. endius* in an enclosed building and eliminated a population of house fly. Morgan et al. (1975b) tested *S. endius* in a commercial poultry installation and 100% parasitism was observed after four weeks, and house flies were completely suppressed within 35 days. Morgan et al. (1976) released *S. endius* three times per week for five weeks (a total of 90,000 parasites) at a commercial dairy and reduced fly populations by 93%. This parasite is now available from a number of commercial sources.

Work on *S. endius* and *Muscidifurax zaraptor*, a pteromalid wasp that attacks house fly pupae, was also conducted at the Midwest Livestock Insects Research Unit in Lincoln, NE, with particular emphasis on infield propagation (Pawson and Petersen 1989; Petersen 1989; Petersen et al. 1991, 1992 a and b; Petersen and Watson 1992).

There was also some additional work on dung beetle competitors of livestock pests during this period at the Veterinary Toxicology and Entomology Research Laboratory, College Station, TX (Fincher and Hunter 1986, 1989; Fincher et al. 1986; Hunter et al. 1991). However, ARS efforts in this area have declined.

Recent research by ARS and other U.S. scientists on the use of parasites, predators, and competitors for the control of livestock pests has been discussed in several comprehensive reviews (Science and

Education Administration 1981; Patterson and Rutz 1986; Drummond et al. 1988; Rutz and Patterson 1990).

Advances in rearing parasites and predators. Augmentation of entomophagous arthropods in the form of inoculative and particularly inundative releases is dependent on an ability to produce large numbers of high quality biological control agents at a relatively low cost (King and Morrison 1984). Rearing on natural or factitious hosts or prey can be very expensive. Thus, considerable interest in the development of artificial diets for predators and *in vitro* rearing techniques for parasites exists. Efforts by ARS in this area began at the Biological Control of Insects Research Laboratory at Columbia, MO, with *in vitro* rearing of *Pteromalus puparum* (Hoffman and Ignoffo 1974; Hoffman et al. 1973, 1975). Efforts to develop *in vitro* rearing techniques for *Cotesia* (=*Apanteles*) *marginiventris* and *Microplitis croceipes* were undertaken at the Insects Attractants, Behavior and Basic Biology Research Laboratory in Gainesville, FL (Greany 1980, 1981, 1986). At the Cotton Insects Research Unit in College Station, TX, work was begun by W. C. Nettles, Jr. on development of *in vitro* rearing techniques for the tachinids *Eucelatoria bryani* and *Palexorista laxa*, and for *Trichogramma* spp. (Nettles 1990) and is continuing at the Biological Control of Pests Research Unit in Weslaco, TX. Nettles has achieved 50% yield of adults with *Eucelatoria*. To date, at least 33 species of parasites have been reared with varying degrees of success on artificial diets (Nettles 1990).

In regard to predators, artificial diets for *Chrysoperla* spp. were developed by Vanderzant at the Cotton Insects Research Laboratory at College Station, TX (Vanderzant 1969, 1973; Martin et al. 1978). Research on development of artificial diets for *Geocoris punctipes*, a predaceous heteropteran, and other predators has been conducted at the Honey Bee and Insect Biological Control Research Laboratory at Tucson, AZ. This work is reviewed by Cohen (1992) and Cohen and Staten (1993). Guerra (1992) of the Subtropical Agricultural Research Laboratory, Weslaco, TX, reported on the development of diets for *Bracon mellitor* and *Catolaccus grandis*, parasites of the boll weevil, which are based on hemolymph of non-host insects. Adult yields were low, however; high larval mortality was attributed to non-dietary factors in the rearing process. Work to improve the diets and rearing system is continuing. (Anderson and Leppla 1992.)

Semiochemicals to manipulate parasites and predators. One of the major new research efforts and one which developed considerable momentum during the 1973-93 period was on the use of semiochemicals to manipulate the host and prey selection behavior of entomophagous insects (Nordlund et al. 1981). Many entomophagous insects are dependent on semiochemicals to locate suitable habitats in which to search or to locate hosts or prey within the habitat (Vinson 1981; Weseloh 1981; Greany and Hagen 1981). Use of semiochemicals to increase the effectiveness of naturally occurring or released parasites or predators is environmental manipulation.

Researchers had known for some time that *Trichogramma evanescens* females responded to chemical stimuli associated with the oviposition site of their hosts. Scientists at the Southern Grain Insects Research Laboratory (now the Insect Biology and Population Management Research Laboratory) in Tifton, GA, reported that *T. evanescens* females responded to kairomones in the scales of corn earworm moths (Lewis et al. 1972). As the research program developed, a number of *Trichogramma* species, including *T. achaeae* and *T. pretiosum*, were studied. This work initially demonstrated that the kairomone(s) in the moth scales could elicit increased rates of parasitization when applied to plots in the field (Lewis et al. 1975a). Lewis et al. (1975b) also demonstrated that this increase in parasitization was due to the inducement and continuous reinforcement of an intensive search behavior rather than attraction. This work continued and other parasites and predators, including *Chrysoperla carnea*, *Microplitis croceipes*, *Cotesia marginiventris*, and *Telenomus remus*, and the roles plant-produced compounds play in host selection have been studied (Dmoch et al. 1985; Lewis

et al. 1977, 1988, 1990; Nordlund and Lewis 1985; Nordlund et al. 1977, 1983, 1985, 1987, 1989; Tumlinson et al. 1993).

ARS scientists at other locations also began working on semiochemicals influencing the behavior of entomophagous insects. Greany et al. (1977), of the Insect Attractants and Basic Biology Research Laboratory, at Gainesville, FL, found that *Diachasmimorpha longicaudata*, a parasite of fruit fly larvae, is attracted to acetaldehyde, a chemical produced by a fungus in rotting fruit. Personnel at the Cotton Insects Physiology Laboratory in Baton Rouge, LA, reported that *Eucelatoria* spp. are stimulated to larviposit by a kairomone found in tobacco budworm cuticles (Nettles and Burks 1977; Burks and Nettles 1978). The importance of semiochemicals in the host and prey selection behavior of parasites and predators was demonstrated and considerable insight into how they function was gained. However, to date, there has been no practical utilization of semiochemicals in applied biological control programs.

Gross et al. (1975) found that prerelease stimulation of *Trichogramma* spp. and *Microplitis croceipes* resulted in significant increased retention of parasites in the release area and increases in parasitization. Use of prerelease stimulation could improve the effectiveness of release programs and is likely to be the first applied use of semiochemicals in biological control programs.

Significant achievements in ARS's biological control augmentation/ conservation programs during 1973-93. During this period, the technical feasibility of augmenting several parasites and predators was demonstrated. While this was being accomplished, some improved techniques for rearing, storing, transporting, and releasing several organisms were developed. Knowledge of the basic biology and ecology of numerous parasites and predators and of the mechanisms of host and prey selection was increased.

It became abundantly clear that before augmentation in the form of inundative releases could be widely adopted, some major advances in the development of economical mass rearing systems were needed. Toward that end, ARS has increased the amount of research effort on the development of mass rearing techniques for entomophagous insects.

2. Arthropod-Parasitic Nematodes. By W. R. Nickle, J. R. Coulson, P. V. Vail, J. E. Lindegren, and W. J. Schroeder.

By 1972, personnel in the Nematology Investigations of ARS had increased to 28 SYs nationwide. Of these 27 conducted research on plant nematodes, and only one worked on insect nematodes; there were, however, several ARS entomologists also working with insect nematodes. After the 1972 reorganization, the single insect nematologist, W. R. Nickle, became part of the new Nematology Laboratory of the Plant Protection Institute at the Beltsville Agricultural Research Center in Maryland. In November 1985, the nematode taxonomists of this Laboratory were administratively merged with other taxonomists to form the newly organized Systematic Botany, Mycology, and Nematology Laboratory (SBMNL) within an expanded Biosystematics and Beneficial Insects Institute (BBII) at Beltsville. In 1988, the BBII was disbanded, and in January 1989, the SBMNL became the Systematic Botany and Mycology Laboratory with the return of the nematode taxonomists to the Nematology Laboratory, both laboratories being part of the new Plant Sciences Institute at Beltsville organized in 1988. (See also section D below.)

Nickle's work on the classification of mermithid nematodes (Nickle 1972), in which he described the infective stage of the mosquito nematode now known as *Romanomermis culicivorax*, enabled ARS entomologists studying control of mosquitoes at Lake Charles, LA, to develop techniques for mass-rearing the nematode. Research by ARS insect pathologists and entomologists, and Nickle's pilot test project in 1974, resulted in the commercialization of this nematode as a mosquito control

product, and the nematode is still used for mosquito control in some third world countries. In 1976 and again in 1981, the Environmental Protection Agency determined that nematodes were classified as macroorganisms, exempting them from regulation as pesticides under the Federal Insecticide, Fungicide, and Rodenticide Act (FIFRA). (Ignoffo et al. 1973, 1974; Petersen 1975, 1980, 1984; Nickle 1976; Petersen and Chapman 1979; Nickle and Welch 1984.)

A *Hexamermis*-type mermithid, known to kill up to 30% of gypsy moth caterpillars in the USSR, was imported from Europe and Japan in 1974-76 from the European and Asian Parasite Laboratories' gypsy moth exploration programs, and the US-USSR biological control exchange program, and some were released in New Jersey (by Nickle and the New Jersey Department of Agriculture) and Pennsylvania (by the Pennsylvania Bureau of Forestry). This mermithid was apparently the first exotic insect-parasitic nematode purposely introduced into the U.S. (Drea et al. 1977; Coulson 1981c; Schaefer and Ikebe 1982; Coulson and Soper 1989).

High rates of parasitization by *Hexamermis*-type nematodes of the Colorado potato beetle were found in studies in the early 1980s by foreign scientists in Austria, and in explorations for parasites of corn rootworms by ARS scientists in Peru. These nematodes were studied by Nickle and were shown to have too wide a coleopteran host range, which included beneficial lady beetles, for introduction into the U.S., and the foreign material was destroyed. (Nickle and Kaiser 1984; Nickle et al. 1984; Kaiser and Nickle 1985.)

Recent work by Nickle includes the description of a nematode parasitizing fire ants in Brazil (Nickle and Jouvenaz 1987) and joint studies at Beltsville with *Steinernema*-type nematodes for control of "mushroom flies" (Nickle and Cantelo, 1991). The fire ant nematode was discovered by scientists of the ARS Insects Affecting Man and Animals Research Laboratory at Gainesville, FL (now the Medical and Veterinary Entomology Research Laboratory), during explorations in Brazil, where it destroyed 25% of fire ant colonies there; plans include possible introduction of this nematode into fire ant-infested areas of the U.S. There are 88 CRIS projects that include work on *Steinernema* nematodes, of which about ten strains are known, and several other ARS nematologists are studying their use against various insect pests.

Studies of insect-parasitic nematodes by other ARS scientists (entomologists) also included the discovery of a new species of nematode found attacking the tobacco flea beetle in North Carolina (Elsey and Pitts 1976; Elsey 1977), studies of nematodes attacking *Spodoptera* armyworms and wireworms in Washington (Howell 1979; Toba et al. 1983) and cucumber beetles in South Carolina (Creighton and Fassuliotis 1980, 1982; Elsey 1989, 1991; Schalk and Creighton, 1989), and work in Georgia with a nematode discovered in French Guiana parasitizing *Spodoptera* adults (Remillet and Silvain 1988).

Some recent events important to the development of the use of insect-parasitic nematodes for biological control of insects include: 1) publication of several important reference works on the subject by University of California and ARS nematologists (Poinar 1979; Nickle 1984); 2) the Symposium on Entomogenous Nematodes held in 1980 at the annual meeting of the Society of Nematologists in New Orleans, the proceedings of which (Society of Nematologists, 1981) include papers by ARS scientists W. R. Nickle and J. J. Petersen; 3) the ARS Nematology Workshop held in 1984 at Beltsville to discuss the status and future direction of ARS nematology research (USDA 1984b); and 4) the joint development by ARS nematologists and entomologists of suggested guidelines for the importation and release of foreign insect-parasitic nematodes into the U.S. (Nickle et al. 1988).

By 1989, ARS had an increased emphasis on biological control due to contamination of ground water by chemical pesticides. ARS now (1993) has about five SYs working on insect-parasitic nematodes,

mainly on steinernematids. J. E. Lindegren is working with nematodes for control of fruit flies and the pink bollworm, a cooperative California-Arizona project (Lindegren et al. 1990, 1992). M. G. Klein has studied nematodes on Japanese beetle grubs in Ohio. W. J. Schroeder has been in the process of developing nematodes for control of *Diaprepes abbreviatus* and other weevils (*Pachnaeus* spp.) affecting citrus roots in Florida since 1980; following a pilot test during 1989-91 (Schroeder 1992), the commercial nematode product BioVector™ was released by Biosys, and the product was added to the citrus spray guide in Florida. G. Fassuliotis and C. S. Creighton continued work on nematodes of *Diabrotica* beetles in South Carolina, and C. E. Rogers and others continued studies on the new aphelenchid on *Spodoptera* in Georgia (Rogers et al. 1990). J. J. Jackson continued research on *Steinernema* and *Heterorhabditis* nematodes, including laboratory study of a species introduced from Argentina, on the western corn rootworm in South Dakota (Jackson and Brooks 1989). Nickle and W. W. Cantelo continued study of these nematodes on "mushroom flies" and Colorado potato beetles in Maryland (Nickle and Cantelo 1991; Cantelo and Nickle 1992). Nickle also worked on nematode delivery systems, taxonomy, and nematodes of corn rootworms (Nickle and Shapiro 1992; Connick et al. 1993).

Additional recent research dealing with insect-parasitic nematodes by ARS scientists was identified in preparation of the following section on arthropod pathogens, and is summarized briefly here and in Appendix II.

Much of the developmental work, such as on life cycles, taxonomy and rearing, had been completed by 1974 when research on this novel approach to insect control was undertaken by Lindegren. Further advancement toward commercial use did, however, require development of new or improved methods for nematode production, storage, application, selection for virulence, and quality control monitoring systems (Lindegren et al. 1979, 1993b; Hara et al. 1981). Some of the accomplishments include the development of application and monitoring techniques for the first commercial application of nematodes for control of carpenterworm in commercial fig orchards in California (Lindegren et al. 1981a; Lindegren and Barnett 1982); help in the establishment of the first commercial nematode production company in the United States, and similar consultation with subsequent companies; successful field applications of nematodes for control of the Colorado potato beetle, sugarbeet wireworm, "medfly", oriental fruit fly, and melon fly, with ongoing research on the Caribbean fruit fly, Fuller rose beetle, and pink bollworm (Toba et al. 1983; Lindegren and Vail 1986; Lindegren et al. 1990, 1992); the development of a genetically selected, more virulent nematode called "Kapow" (Agudelo-Silva et al. 1987); and the development of a simple, dependable *in vivo* production method for laboratory and small scale testing (Lindegren et al. 1993b).

Cooperative tests with the University of California Cooperative Extension Service and industry provided data on control of navel orangeworm with an entomogenous nematode (Agudelo-Silva et al. 1987; Lindegren et al. 1978, 1981b, 1987). A nematode larvicidal soil drench was developed for reduction of Hawaiian fruit flies (Lindegren and Vail 1986; Lindegren 1990; Lindegren et al. 1990). Soil applications of the nematode *Steinernema feltiae* in field cages reduced larval populations of Colorado potato beetle and sugar beet wireworm by 71 and 29%, respectively (Toba et al. 1983). Searches in Brazil provided a nematode capable of invading fire ant queens that is highly destructive to its host and has the potential for eliminating established colonies (Nickle and Jouvenaz 1987). A sand barrier bioassay provided a measurement of host searching ability of various insect-parasitic nematodes, and showed a significant difference in host searching ability for three of the six nematodes tested; when evaluated at lower nematode concentrations, a new species of *Steinernema* from Texas and Mexico was the most effective host searching nematode (Lindegren et al. 1992, 1993a). This new species (*S. riobravis*) shows great promise for controlling the corn earworm (Cabanillas and Raulston 1994 a and b; Cabanillas et al. 1994). And finally, as noted above, based on the findings of a joint ARS-University-Industry effort, the U.S. Environmental Protection Agency

exempted entomopathogenic nematodes from setting of a tolerance (exempt from registration) which promoted the testing, commercial production and sale of these organisms for insect control.

3. Arthropod Pathogens. By P. V. Vail, R. A. Humber and J. R. Coulson

After the reorganization of 1972, insect pathology research became the responsibility of the National Program Leader (NPL) in charge of Biological Control. However, most of the insect pathology/microbial control research was still conducted in commodity or problem area oriented laboratories. Exceptions included the Insect Pathology Laboratory at Beltsville, MD, and the Biological Control of Insects Research Laboratory at Columbia, MO. Thus, many of the pathology programs were within research units headed by other NPS members (i.e., cotton, grains, etc.) and the NPL for biological control had little input into these programs. Prior to the reorganization, ARS insect pathologists/microbial control scientists had annual research workshops which provided for information exchange between scientists as well as a mechanism for development of cooperative research projects. The last of these workshops was held in 1984 and thus a major coordination activity was lost. The opportunity for interaction between all insect pathologists and microbial control specialists to meet with interested NPLs as related to program goals was also lost. This forum has now been "taken over" by the Southern Regional Project 240 on developing insect pathology and microbial control agents. In the 1980s, the Insect Pathology Laboratory was placed into the new Plant Protection Institute at Beltsville, and was later renamed Insect Biocontrol Laboratory, with the addition of biological control entomologists from other laboratories at Beltsville (see section IVA). As with other disciplines, the number of insect pathologists has decreased due to program and budget constraints. However, it is believed that with the current concerns about misuse of chemical insecticides, emphasis on the development of microbial control agents should significantly increase both for production and postharvest pests.

During the years 1973-93, significant advances were made in insect pathology/microbial control in both basic and applied areas. These are discussed in detail in Appendix II, with notes on administrative developments at the various involved locations. Only a summary of the more significant research advances is given here.

Diseases and anomalies of the honey bee under continuous production and with different diets and amounts of pollen were investigated (Gilliam and Tabor 1973; Prest et al. 1974). This included one of the first reports of chalkbrood caused by *Ascosphaera apis* in honey bees in the U.S. Only larvae and prepupae would support the pathogen (Gilliam et al. 1978). Large variability in susceptibility was found between individual colonies and stressors were defined (Gilliam 1986). The alfalfa looper NPV host range continued to expand and its use in *in vitro* systems increased significantly. Genetic engineering of this virus for both agricultural and medical uses has made it one of the most thoroughly studied of all viruses. As one result of continuing studies at the Fresno, CA, location, a pathogen of nitidulid beetles was found to infect 15 species from six families and three insect orders and three species of mites (Kellen and Lindegren 1973, 1974). Osmotic studies of insect hemolymph (Adams and Wilcox 1973) aided in the development of new insect tissue fixatives and improvement of insect cell culture media. A granulosis virus was shown to control the imported cabbageworm (Hostetter et al. 1973). Pathogen autodissemination experiments were conducted with *Trogoderma glabram* using pheromone contamination sources, a method later recommended for population reduction (Burkholder and Boush 1974). Similar studies were conducted with Indianmeal moth and a granulosis virus (Kellen and Hoffmann 1987; Vail et al. 1993).

Cooperative studies between Brazil and the United States led to the discovery of a fire ant pathogen which further stimulated interest in biological control for this important organism (Knell et al. 1977). The first reports of spiroplasmas led to their isolation from a number of insects including bees, wasps, beetles, flies and butterflies (Clark 1982). A non-occluded virus of *Culicoides cavaticus*

caused mortality rates of 70-90% in field collected larvae (Clark and O'Grady 1975). Based on research at Manhattan, KS, *Bacillus thuringiensis* was registered as a protectant for stored grains (McGaughey 1975b, 1976, 1978, 1980, 1982). Similar results were obtained with a granulosis virus (Kinsinger and McGaughey 1976; McGaughey 1975a, 1983). During these studies McGaughey discovered the potential for resistance to *Bacillus thuringiensis* in stored product pests (McGaughey 1985, McGaughey and Beeman 1988).

Research on formulations and adjuvants continued to extend the field activity of *Bacillus thuringiensis* and viruses (Hostetter et al. 1975, 1982; Bell and Kanavel 1978; Bell and Romine 1980; Dunkle and Shasha 1988; Bartlett et al. 1990; McGuire et al. 1990; McGuire and Shasha 1990). A large research program on the use of *Nomuraea rileyi* showed that this pathogen could be used as a prophylactic agent when directed towards early instars (Ignoffo 1981; Ignoffo and Garcia 1985). Significant reduction of grasshoppers resulted from the treatment of 37,312 ha of rangeland with *Nosema locustae* (Henry and Onsager 1982). In early experiments to determine the feasibility of area wide suppression methods, it was found that control of cabbage looper on cotton with a baculovirus could influence future population levels on lettuce (Vail et al. 1976). Bell and Kanavel (1976) conducted important investigations on methods of transmission of cytoplasmic polyhedrosis virus of the pink bollworm which led to large increases in production at the APHIS Pink Bollworm Mass Rearing Facility in Phoenix, AZ. An entomopathogenic fungal collection started by R. S. Soper and continued by R. A. Humber led to the world's foremost collection of these organisms ("ARSEF"), which is located at Ithaca, NY. As of 1991, over 3,200 isolates of over 250 species are in the collection (Humber 1992). The importance of timing and adequate volume in the use of *Bacillus thuringiensis* for navel orangeworm control was demonstrated by Kellen et al. (1977). The first virus from fire ant was discovered in collections from Brazil by Avery et al. (1977). Additional pathogens from this insect were described by Banks et al. (1985) and Jouvenaz et al. (1980). Two forms of virions were recognized in baculoviruses which had important implications in understanding the pathology, cell culture and use of these organisms (Adams et al. 1977; Adams and McClintock 1991).

Research on comparative susceptibility of tobacco budworm/corn earworm showed the latter to be about ten times less susceptible to the alfalfa looper *M*NPV regardless of the inoculation method (Vail et al. 1978, 1982; Vail and Collier 1982). These studies pointed to the importance of knowing which of these species or proportions thereof were infesting fields. A large field test in El Salvador with microbial agents resulted in the near eradication of an anopheline mosquito malarial vector (Petersen et al. 1978a, 1978b; Willis et al. 1980). More simplified and efficient rearing procedures for gypsy moth led to a large scale production plant which produced over 1.5 million insects in a 100-day period, yielding 50,000 ac equivalents of the gypsy moth NPV. Costs were reduced at least 10-fold in the process (Shapiro and Bell 1981; Podgwaite et al. 1983). In 1980, *Nosema locustae* became the first protozoan registered as a microbial insecticide in the U.S. by the Environmental Protection Agency (Henry 1981). *Bacillus thuringiensis* was the first microbial registered for use on stored grain as a result of many of the studies conducted at the ARS Manhattan, KS, laboratory (McGaughey 1986). ARS, together with the Australian Commonwealth Scientific and Industrial Research Organization (CSIRO), played a key role in successfully introducing a pathogenic fungus of the spotted alfalfa aphid in Australia (Milner and Soper 1980; Milner et al. 1982). The first serum free insect cell culture medium (gypsy moth) that supported serial replication cycles of a baculovirus was developed (Goodwin and Adams 1980). *Ascosphaera aggregata* was shown to be the causative agent of chalkbrood of the alfalfa leafcutting bee and the epizootiology of the disease was established (Vandenberg and Stephen 1982; Stephen et al. 1981). In cooperation with the University of California, Berkeley, the first known occurrence of a calicivirus in an insect was reported (Kellen and Hoffmann 1982; Hillman et al. 1982). Two forms of the virus were described (Hoffmann and Hillman 1984). Later studies (Kellen and Hoffmann 1982) described the symptoms of the virus and described it as the "chronic stunt virus." Various adjuvants were discovered to increase the field

persistence or activity of baculoviruses such as sun screens, microencapsulation and boric acid (Tompkins et al. 1988; Shapiro and Bell, 1982).

During the 1970s and 1980s, insect cell culture became a useful tool in the study of insect pathogens (baculoviruses). Scientists at ARS laboratories, primarily at Beltsville, MD, Gainesville, FL, Columbia, MO, and Fargo, ND, developed cell lines for this purpose from several major agricultural pests. Among the many lepidopterous pests from which cell lines were developed are fall armyworm (Vaughn et al. 1977; Lynn and Oberlander 1983), bollworm (Goodwin et al. 1982; McIntosh and Ignoffo 1983; McIntosh et al. 1983), tobacco budworm (McIntosh et al. 1981), cabbage looper (Goodwin et al. 1973; Lynn et al. 1982; Rochford et al. 1984), and tobacco hornworm (Eide et al. 1975). Cell lines have also been developed from southern corn rootworm (Lynn and Stoppleworth 1984), boll weevil (Stiles et al. 1992), Indianmeal moth (Lynn and Oberlander 1983), diamondback moth (Quhou et al. 1983), and navel orangeworm (Hoffman et al. 1990).

The feasibility of applying entomopathogens in irrigation water was demonstrated (Hamm and Hare 1982). Genetically controlled hygienic behavior of worker bees was shown to aid in control of chalkbrood in the honey bee (Gilliam et al. 1983). Quality control procedures were developed to preclude contamination of alfalfa looper NPV preparations by a calici-like virus (Morris et al. 1981; Vail et al. 1983). Formulation, treatment parameters and a method for disbursing *Bacillus thuringiensis israelensis* were developed for control of black flies. A UV tolerant gypsy moth NPV biotype was selected (Shapiro and Bell 1984). The first report of *Bacillus thuringiensis* crystal proteins toxic to muscid flies was reported by Temeyer (1984). Studies continued on the use of fungicides to control chalkbrood of alfalfa leafcutting bees; captan was shown to be effective as a dust in nest shelters (Parker 1984, 1985, 1987, 1988; Mayer et al. 1990). Researchers in Florida discovered that a copepod was an intermediate host for a protozoan pathogen of mosquitoes (Sweeney et al. 1985). This finding finally completed the known life cycle of one of the most common microsporidian in mosquitoes and other biting flies. A new group of viruses (ascoviruses) was found in fall armyworm, corn earworm and tobacco budworm, which was readily transmitted by a parasite but only moderately infective *per os* (Hamm et al. 1985, 1986). McCabe and Soper (1985) developed and patented a widely used process to dry mycelial mats for application of fungi as microbial control agents. A new production/formulation of the Indianmeal moth virus was developed (Cowan et al. 1986) and later patented (Vail 1991) which could reduce damage in raisins to the point of being of no economic consequence. Hamm et al. (1988) reported the first baculovirus infectious to a parasite which pointed out the need to diagnose imported or mass-produced beneficials when used for field release or research. During studies of introduced *Entomophaga* (as *Entomophthora*) *grylli*, it was discovered that sun-basking by grasshoppers may raise their body temperature above that required for development of pathogens (Carruthers et al. 1988b). Larkin et al. (1988) developed a program for the rapid construction of simulation models which was instrumental in guiding and evaluation of epizootiological studies on grasshopper pathogenic fungi (Carruthers et al. 1988a).

A cooperative ARS-APHIS biological control of rangeland grasshoppers program utilizing an introduced *Entomophaga* fungus was conducted beginning in 1989 (Hostetter et al. 1993). This program and the successful establishment of the Australian fungus in North Dakota generated considerable controversy over the ecological significance of introducing exotic natural enemies against native pests in the U.S. (Lockwood 1993 a and b; Carruthers and Onsager 1993).

In 1990, a large scale pilot test was initiated to determine the feasibility of using a nuclear polyhedrosis virus for control of early season populations of *Heliothis/Helicoverpa* over large areas of the Mississippi Delta (Bell 1990a, 1990b, 1991; Bell and Scott 1989; Bell et al. 1992). Granulosis virus infections were shown to influence hormonal titers in an insect host (Dougherty et al. 1989). A theoretical paper described the biophysical/biochemical basis for the process of germination in protozoa (Undeen 1990). An endophytic relationship was described between the corn plant and an

entomopathogenic fungus, *Beauveria bassiana*, in which the pathogen moves within the plant to control European corn borer (Bing 1990; Bing and Lewis 1991; Lewis and Bing 1991). A massive mortality of gypsy moths was inferred to have been caused by a fungus released 80 years earlier (Hajek et al. 1990).

A more virulent biotype of the gypsy moth NPV was obtained after serial passage through its host; this new biotype was patented by ARS and the scientists involved (Shapiro et al. 1992). Research on fluorescent brighteners as protectants for baculoviruses led to the granting of a U.S. Patent 05,124,149 (Shapiro et al. 1990). Both were licensed to private corporations for further development. Several pathogens including three fungi and a nematode were demonstrated to reduce sweetpotato weevil populations (Chalfant et al. 1990). *Beauveria bassiana* was shown to be effective against the boll weevil when used as a prophylactic treatment (Wright and Chandler 1990, 1991, 1992). Stephen and Fichter (1990a, 1990b) successfully selected for alfalfa leafcutting bee resistance, probably polygenic, to chalkbrood. McIntosh (1991) demonstrated that the celery looper NPV also had a wide host range *in vitro* and suggested that these systems could serve as rapid determinants of host range of natural viral isolates. Crystal protein genes of *Bacillus thuringiensis israelensis*, a pathogen of Diptera affecting man and animals, were cloned in *Escherichia coli* at Kerrville, TX, in 1991 (see Appendix II). Pink bollworm was demonstrated to be susceptible to several entomopathogenic nematodes (Lindegren et al. 1992). A rare protozoan, *Malpighamoeba mellificae*, was found to be causing severe population losses in the honey bee (Wilson and Collins 1992).

As noted in Chapter I (section A.3), a Japanese fungal pathogen of gypsy moth was introduced into Massachusetts in 1910-11 (Speare and Colley 1912), without apparent successful establishment. This fungus, later described as *Entomophaga maimaiga* (Soper et al. 1988), was nearly forgotten until R. S. Soper (then at the Insect Pathology Research Unit, ARS, Ithaca, NY) collected it in Japan in 1984 and began new studies of its potential to control gypsy moth (Shimazu and Soper 1986). It was released experimentally in the field in New York in 1985 and Virginia in 1986 (Reardon and Hajek 1993). A fungus causing considerable mortality of gypsy moth larvae across the northeastern U.S. during 1989-90 proved to be *E. maimaiga*. Because the causative fungus was biochemically indistinguishable from Japanese strains of *E. maimaiga*, and because no modern introductions of *E. maimaiga* were made in the specifically affected regions, it was inferred that the massive mortality of gypsy moth must have been caused by the fungus introduced 80 years earlier by Speare and Colley (Hajek et al. 1990). Though that is not altogether certain (Hajek et al. 1995), the Japanese fungus is proving to be an effective control agent for the gypsy moth in the northeastern U.S. See Appendix II, section on Ithaca, NY.

Another significant step in classical biological control occurred in 1981 with the establishment for the first time of an insect pathology component in the biological control exploration program at the ARS European Parasite Laboratory (EPL) in France. This began first by means of a cooperative agreement between the EPL and the French Institute Nationale de la Recherche Agronomique (INRA). The insect pathology program became an integral part of the ARS program by the time of the consolidation of the ARS European laboratories in Montpellier in 1991 with the assignment of L. A. Lacey. His principal duties are foreign exploration for entomopathogens of selected U.S. insect pests. Collections over a broad geographical area ranging from Spain to Nepal have been made. Many isolates have been obtained, but few have as yet been investigated for their potential as microbial control agents. See section B.1.a and Appendix II. The use of insect pathogens in classical biological control, though not new, increased in the U.S. in the latter part of this period (see Maddox et al. 1992).

In addition, ARS insect pathologists were involved in several exchange agreements between the United States and the Soviet Union and People's Republic of China, some of which are noted in section B.1 of this chapter. These involved exchange of scientists, research information, and

microbial cultures (Ignoffo 1979; Ignoffo et al. [1980]; Wong [1982]; Soper et al. 1992). And, an ARS insect pathologist also performed research in regard to microbial control of the Japanese beetle in the Azores, after the discovery of that pest in those islands (see Appendix II).

C. BIOLOGICAL CONTROL OF WEEDS

1. Invertebrate Natural Enemies of Weeds. By L. A. Andres, J. R. Coulson, T. D. Center, C. E. Turner, and C. J. DeLoach

The period 1973-93 saw first the addition of new ARS laboratories and personnel devoted to classical biological control of weeds by introduction of insects and mites (Andres and Kok 1981), but toward the end of the period this trend was reversed. The expanded interest in the use of plant pathogens for weed control that also occurred during this period, is discussed in the following section (C.2). Though an active program for introduction and release of arthropod natural enemies continued, the work was severely hampered by several administrative changes plus questions of conflicting ecological interests. Most of these problems and questions also affected programs dealing with weed pathogens.

A major problem concerned the coordination of research activities. The ARS classical biological control of weeds program was adversely affected by the 1972 ARS reorganization as was the ARS classical biological control of insects program. Discussions of the effects of this reorganization in regard to abolishment of the Insect Identification and Parasite Introduction Research Branch (IIPI) and thus the end of centralized leadership and coordination of ARS classical biological control research, the development of National Research Programs (NRPs) and National Program Leaders (NPLs), the formation of Working Groups, Technical Advisors, the International Activities office, and NPS matrix teams to attempt to coordinate ARS classical biological control programs for both insects and weeds, are included in sections A and B.1 in this chapter.

Although the impact on the biological control of weeds program was not immediately apparent due to a number of newly released or promising agents in the introduction pipeline, the 1972 dissolution of the IIPI had a severe ongoing effect on the coordination of the study and importation of exotic natural enemies of weeds. This is perhaps even more severe than in the biological control of insects program. Weed projects often continue for ten or more years, which necessarily entails long-term coordination of the exploratory and research activities of the overseas laboratories with the domestic locations. This involves joint development of project plans and assignment of responsibilities; joint preparation of petitions and proposals for the importation and release of new candidate agents; the interchange of domestic and foreign stocks of the targeted weed to verify identification and acceptance by the foreign natural enemies; interchange of overseas and domestic researchers to facilitate pooling of information and skills; collecting and supplying to the overseas and North American cooperating laboratories native or rare and endangered test plants for host specificity tests; and coauthoring of reports and publications; etc.

The IIPI formed a single administrative/technical unit for coordinating and directing the domestic and overseas research and importation program and apportioning and optimizing resources. Following the split of administrative and technical direction into two separate lines of responsibility, considerable effort was spent to devise ways of coordinating these two aspects to maintain national program coordination, as well as of addressing other problems noted below. The responsibility for day-to-day administration of ARS domestic biological control of weeds programs became scattered among those line managers in whose areas of responsibility the pertinent domestic laboratories were located. The administration of the foreign program, on the other hand, shifted to the international arm of ARS, i.e., the International Program Division until 1981, and since then the International Activities Office (now Office of International Research Programs). Since 1973, technical direction of

the overall national ARS biological control of weeds program was totally apart from the administrative elements, and rested with the ARS National Program Staff (NPS), and, until 1981, with Technical Advisors. This responsibility was shared by the incumbent NPLs for biological control, when one existed (see sections above), and the NPLs for weed research, which presented an opportunity for conflicting views concerning program needs, etc. As noted above, Technical Advisors (TAs) were appointed to assist the NPS in program coordination, from 1973-81; L. A. Andres, Research Leader of the Albany, CA, laboratory, was TA with primary advisory responsibility for the overseas program in Europe (the Rome laboratory), and C. J. DeLoach, Research Entomologist, Temple, TX, was TA with advisory responsibility for the program in South America (the Argentine laboratory); both also served as Technical Advisors for pertinent domestic aspects of the research program. In 1981, an NPS Biological Control Matrix Team was established and assumed responsibility for the technical planning and coordination of the ARS biological control program.

As discussed in above sections, the ARS Working Group on Natural Enemies of Insects, Weeds and Other Pests (WGNE) was formed in 1973 in an effort to maintain national coordination of ARS biological control programs, including those devoted to weed control, but this group ceased to function after 1979. Other coordination efforts included the various workshops and meetings mentioned in previous sections. Although the Technical Advisors and the WGNE could prioritize research needs, the implementation of their recommendations, as well as those generated at these workshops and meetings were quite limited. The administration and coordination of classical biological control of weeds research processes and associated protocols remained cumbersome at best.

Research on new biological control agents and their clearance for introduction into the United States continued to require close cooperation between domestic and overseas researchers. This included quarantine studies and handling of exotic natural enemies, release clearance by state and federal authorities, and finally, distribution, field release, and follow up evaluation studies. The success of the ARS biological control of weeds program led to the addition of new state and university biological control personnel to handle the cleared control agents. Unfortunately, the demand by these new state/university personnel and by the public for ever increasing numbers of organisms to release against their rangeland weeds led to federal-state coordination difficulties. ARS research efforts were in part diluted by efforts to collect, clear, and distribute agents to meet this rising demand (Andres and Kok 1981). APHIS' interest in biological weed control and establishment of laboratories at Mission, TX, and Bozeman, MT, (see Chapter VI), for the importation and distribution of new and established weed control agents in the 1980s, provided relief in regard to the weeds of interest to APHIS; some funding for ARS overseas studies on those weeds was provided by APHIS. However, this added a second federal agency to the weed program, further compounding coordination problems. Retirements and relocations of research personnel, and changing NPS personnel of varying backgrounds and interests directing the technical aspects of the program, brought the former closely coordinated U.S. and Canadian biological control of weeds programs to a state of disarray (Harris 1990).

Another problem facing the weed program lay in the area of setting target weed priorities. Although several attempts were made to establish logical priorities in the weed program, much depends on funding sources and factors outside the scientists' realm (e.g., political factors). Weed priorities in the Northeastern Region were established in the early 1970s by a regional biological control working group, and an attempt to establish national priorities was made at the 1984 ARS Research Planning Conference (USDA 1984a). Although these and earlier priorities were established without the benefit of much pertinent economic information, they did earmark principal weeds of regional and national importance. To assure that limited ARS resources were focused on projects of national interest as more ARS personnel became involved in biological control of weeds during the late 1970s and the

1980s, the assembling of data on economic losses due to specific weeds was encouraged to justify the selection of target weeds for new research projects. However, the difficulty in obtaining this information, which was extremely limited in regard to the weeds most amenable to biological control such as many pasture and rangeland weeds, and the general absence of strong user group support for many weeds, slowed the targeting of new projects. The lack of economic data also hampered ongoing projects when potential economic versus ecological questions arose in conjunction with the introduction of control agents. In the 1970s, a priority request for studies of the arthropod fauna associated with several narcotic plant species diluted overseas research efforts on biological control of rangeland weeds, and further interfered with the technical direction of the foreign program. On the other hand, the influx of narcotics program funds resulted in establishment of a new quarantine laboratory in Stoneville, MS (see below), which, however, by 1993, was non-functional for classical biological control of weeds, and strengthened the overall biological control of weeds program, at least temporarily (see Epilogue, section A).

Other problems concerned potential conflicts of interest associated with targeted weeds and clearance of new biological agents for release in North America. The passage of the National Environmental Policy Act of 1969, and the Endangered Species Act of 1973, and subsequent regulations, severely impacted the biological control of weeds program. The often conflicting factors contributing to a slowdown of the program were: 1) differing views among the public and scientific community over the potential economic benefits and losses caused by specific weeds; and 2) increased concerns of environmentalists, ecologists, and weed researchers themselves that introduced weed control agents might impact native, non-target plants closely related to the target weed (Andres 1981). These concerns translated into increased care in selecting plants for host specificity testing of proposed agents and, more importantly, increased the test time and logistical problems encountered in locating and culturing native plant species for the tests (Pemberton 1986; Turner 1986; Coulson and Soper 1989; Coulson et al. 1991). Eventually a testing strategy was developed that recognized these concerns and permitted a balanced assessment of the candidate agent's host range potential, allowing the introduction of the safest agent first. The testing of closely related native plant species became routine protocol (Pemberton 1986; Turner 1986).

The interagency Working Group on Biological Control of Weeds established in 1957 (see Chapter III, section B) proved ineffective in resolving conflicts of interest regarding weeds targeted for research and in dealing with the questions raised regarding potential impacts on native plants of agents proposed for introduction. In an attempt to improve upon this situation, the interagency Working Group was disbanded and a Technical Advisory Group (TAG) on Biological Control of Weeds was created in 1987 to make recommendations directly to APHIS-PPQ, the agency responsible for issuance of U.S. importation and release permits; an official of the APHIS-PPQ permit office served as Executive Secretary of the TAG (Coulson and Soper 1989; Coulson 1992a). Unfortunately, due to implementation and coordination problems in the review process, TAG's responses to petitions were not always provided on a timely basis, and questions remained as to means of handling conflicts of interest, differences in Canadian and U.S. release standards, etc.

The TAG, and the interagency Working Group before it, reviewed pre-release study data for adequacy and safety, and also reviewed background data on natural enemies proposed for release in Canada. Recommendations on Canadian proposals were advisory only. This led to confusion when concurrence was granted for release in Canada but denied in the U.S. until additional tests were carried out. Representatives of states bordering Canada and infested with the same weed species questioned those procedures, as did ARS researchers who felt some of the agents released in Canada might pose a threat to plants of ecological importance in the U.S.

In 1993 efforts were begun in APHIS to reconstitute this advisory group, including the drafting of a new charter, to help make the group more effective in assisting in the evaluation of proposed

introductions of exotic weed control agents in the U.S.; this was part of a larger effort in APHIS to revamp all pertinent regulations and procedures for approving introductions of all exotic biological control agents.

Since 1973, research at the ARS Biological Control of Weeds Laboratory in Italy focused on the following target weeds: field bindweed (1973-88); musk thistle and yellow starthistle (1973-present); Dalmatian toadflax (1974-79); leafy spurge (1974-present); diffuse knapweed (1975-present), curly dock (1977-83), and smooth bedstraw (1982-83), in addition to miscellaneous studies and collections of natural enemies of Eurasian watermilfoil, rush skeletonweed, Canada and Italian thistles, velvetleaf, Russian knapweed, spotted knapweed, and tansy ragwort. As noted above, during the years 1973-77, the laboratory was also directed to study the natural enemies of opium poppy (Rizza et al. 1980; Buckingham et al. 1983b). Research Leaders of the laboratory during this period have been G. R. Buckingham (1973-77), N. R. Spencer (1977-81), P. H. Dunn (1981-88), and L. Knutson (1988-91). The field bindweed and yellow starthistle projects were the focus of University of California scientists, but when these same scientists were hired as federal employees, the projects shifted to ARS. A substation was established in Greece in 1980 for study of the natural enemies of yellow starthistle, and studies of additional weeds were added later to the substation's program. And in 1981, the Rome laboratory was moved from its originally established location to expanded quarters outside of the city.

As discussed in section B.1.a, several efforts were made during this period to consolidate the Rome and Paris laboratories at a single European location. This was finally accomplished in 1991, with the establishment of the European Biological Control Laboratory (EBCL) at Montpellier, France, under the direction of L. Knutson. Satellite locations were retained in Italy and Greece. Explorations by Rome and Montpellier personnel have ranged from locations in Europe and the former Soviet Union to China. Weed research at the EBCL and satellites continued to concentrate on leafy spurge, yellow starthistle and knapweeds in 1991-93, and studies of saltcedar were begun in cooperation with the ARS laboratory in Temple, TX (see below). Most of the natural enemy studies at the European laboratories were done in close cooperation with personnel at the Albany, CA, laboratory, and the agents were eventually shipped to that laboratory. However, since 1988, importations have also gone to the ARS locations at Temple, TX, and Bozeman, MT, for further study and release, and to APHIS personnel at Mission, TX, Albany, CA (1988-90 only), and Bozeman, MT, and to Montana State University scientists at Bozeman; see discussion of the ARS locations below. Several species were also sent to cooperators at Virginia Polytechnic Institute and State University, Blacksburg, VA, and the Maryland and New Jersey Departments of Agriculture (musk thistle insects). Natural enemies of curly dock and smooth bedstraw were studied briefly for the ARS laboratories at Stoneville, MS, and Beltsville, MD, respectively (see below). A high level review of the Rome laboratory program was held near Paris in October, 1983 (see also section B.1 above), which resulted in limiting the number of the laboratory's target weeds to one per scientist, all of which were to be deemed of **national** importance; see discussion above regarding establishing priorities for target weeds. The important reference/voucher collection of weed insects collected and studied during the Rome research program (1959-91) was recently organized, and records computerized. A plant pathology research program was initiated at the Rome laboratory in 1989, assisted by the temporary placement there of a scientist funded by the ARS laboratory at Frederick, MD (see section C.2 below). For references to some of the studies on weeds during this period at the Rome and Montpellier laboratories and substations, see: Dunn and Rizza 1977; Frick 1977; Boldt and Campobasso 1978; Kok et al. 1979; Pecora and Rizza 1980; Pemberton and Hoover 1980; Rosenthal 1981; Spencer 1981; Rosenthal and Buckingham 1982; Rizza and Pecora 1984; Sobhian and Zwölfer 1985; Maddox and Sobhian 1987; Clement et al. 1988; Dunn and Knutson 1989; Clement 1990, 1994; Fornasari and Knutson 1990; Castagnoli and Sobhian 1992; Pecora et al. 1992 a and b; Sobhian et al. 1992 a and b; Sobhian 1993 a and b; Boldt and Sobhian 1993; Fornasari 1993; Fornasari and Pemberton 1993; Fornasari and Sobhian 1993; Fornasari et al. 1994.

During 1973-93, research at the ARS Biological Control of Weeds Laboratory in Argentina, under the leadership of C. J. DeLoach (1973-74) and H. A. Cordo (1974-present), focused on the following target aquatic weeds: waterhyacinth (1973-81), waterlettuce (1973-78), and waterprimroses and other aquatic weeds (1973-79); natural enemies resulting from these studies were designated for further study by the ARS laboratories in Florida (see below). As noted above, C. J. DeLoach was appointed Technical Advisor for this laboratory in 1974, and research in Argentina was subsequently begun on some of the target weeds of the new Temple, TX, laboratory, to which DeLoach was reassigned (see below); these included the native shrubs: mesquites, broomweeds and snakeweeds, creosotebush, *Baccharis* spp., "bitterweeds", Texas whitebrush, and other southwestern range weeds and brush pests, from 1976 to 1993. A few studies were also conducted during this period on natural enemies of pasture and row crop weeds (prickly sida, cockleburs, hemp sesbania, and smallflower galinsoga) for ARS laboratories in Mississippi and Maryland, as well as of a few insect pests (see section B.1.a above). In a striking example of cooperation that exists between ARS overseas scientists and local scientists, ARS and Argentine scientists cooperated in the introduction of insects already tested and established in the U.S. into Argentina for musk thistle and rush skeletonweed, and in the publication of a book on the potential of biological control of weeds in Argentina; the latter study analyzed the biological control potential of all the major Argentine weeds, discussed theory and methodology, work done in other countries, and the availability of natural enemies (DeLoach et al. 1989). For some other references to work at the Argentine station during this period, see DeLoach and Cordo 1976, 1978, 1983; DeLoach et al. 1976, 1980; Cordo et al. 1978, 1981 1984; Cordo 1986; Cordo and DeLoach, 1975, 1982, 1987, 1992, 1993; see also references cited in the discussions below of the Temple, TX, laboratory, and significant accomplishments during this period. By the end of 1993, the mission of this laboratory, renamed the South American Biological Control Laboratory, was altered to target primarily insect pests (see section B.1.a above), with snakeweeds (*Gutierrezia* spp.) remaining the only target weed for the station (H. A. Cordo, pers. commun., 1993).

In 1989, a third overseas biological control of weeds laboratory was established, in Queensland, Australia, by J. K. Balciunas (University of Florida collaborator, first employed by ARS in 1989), for the study of invertebrate natural enemies of aquatic and wetland weeds. This facility, called the Australian Biological Control Laboratory from 1989, originated as a University of Florida laboratory in 1985, and was initially made a satellite location of the ARS Fort Lauderdale, FL, laboratory (see below). In 1991, it was placed under the administration of the ARS International Activities office (now the Office of International Research Programs, OIRP) in Beltsville, MD, together with all other ARS overseas laboratories. Targets of research there have been the aquatic and wetland weeds hydrilla and melaleuca, but were restricted to the latter in 1992. (Balciunas and Purcell 1991; Balciunas and Burrows 1993; Balciunas and Chen 1993; Balciunas et al. 1993 a and b.)

In an effort to develop a flow of effective weed natural enemies from the Ukraine, Caucasus, and central and eastern Asia, surveys for, and exchanges of natural enemies were carried out in the USSR and China, the native areas of many introduced U.S. weeds (Coulson 1981a; Coulson et al. 1982); beginning in 1988, as a result of new agreements between the U.S. and the USSR and PRC (see section B.1.a above), increased field studies in these areas were conducted by personnel of the ARS laboratories in Italy and South Korea (Fornasari and Pemberton 1993), Australia (Balciunas and Chen 1993), Frederick, MD, Bozeman, MT, Gainesville, FL, and Temple, TX, and have included surveys for weed pathogens (see section C.1, below).

The first exploration in China was actually conducted in 1987, targeting leafy spurge (Fornasari and Pemberton 1993), and biological control of weeds research was soon begun at the Asian Parasite Laboratory (APL) in South Korea with work on *Tamarix* spp. (1991) and "water caltrop" (or water-chestnut) (1992). This work was terminated upon closing of the APL in 1993.

During 1973-85, the research program of the Biological Control of Weeds Research Laboratory at Albany, CA, shifted from programs on aquatic weeds (i.e., alligatorweed and waterhyacinth) and back to research on biological control of rangeland weeds, including tansy ragwort (1959-78), Scotch broom (1960-75), puncturevine (1961-65, 1976-80), halogeton (1964-66, 1975), alligatorweed (1964-74), Mediterranean sage (1966-76), Russian thistle (1968-80), milk and Italian thistles (1969-78), spotted and diffuse knapweeds (1973-87), rush skeletonweed (1974-82), leafy spurge (1974-87), and yellow starthistle (1976-78, 1982-present). New personnel (S. S. Rosenthal and R. W. Pemberton) joined the Albany staff in 1980-81 to replace persons retiring (R. B. Hawkes) or transferring (P. H. Dunn). A plant pathologist (J. M. Klisiewizc, ARS-Davis, CA) was assigned to the program during 1981-86 and conducted studies of indigenous pathogens of yellow starthistle and common purslane. Botanist C. E. Turner was added to the staff in 1984; S. L. Clement joined the staff briefly in the early 1980s, but transferred to the Rome laboratory. Some of the research by personnel of the California laboratory during this period has been reported in the following papers: Hawkes and Mayfield 1976; Andres 1978; Dunn 1978; Hawkes and Johnson 1978; Sobhian and Andres 1978; Maddox and Andres 1979; Maddox 1982; Klisiewicz et al. 1983; Klisiewicz 1985; Rosenthal 1985; Pemberton 1986; Maddox and Sobhian 1987; DeLoach 1991a; Rosenthal et al. 1994; and 12 papers by ARS and university colleagues on 12 target rangeland weeds in Nechols et al. 1995. (See also references cited in the section on significant accomplishments, below.)

A new, expanded research quarantine facility for the laboratory was designed and constructed specifically for biological control, and the unit moved into new quarters at the Western Regional Research Center at Albany in 1986. In 1985, the biological control of weeds research unit was administratively shifted from the office of the ARS CA-NV-HI Area Director in Fresno, CA, to the Western Regional Research Center at Albany, where the unit became one of several "projects" under the Center's Plant Protection Research Unit following a Center reconsolidation program. L. A. Andres served as Research Leader of the biological control unit at Albany from 1964 until the 1985 consolidation, at which time he became Project Leader until his retirement in September, 1988. C. E. Turner served as Project Leader from 1988 to present. As a result of reviews of the biological control of weeds program in 1985-86, decisions were made by the National Program Staff (in the absence of a NPL for biological control) that resulted in the downgrading of the spurge and knapweed projects at Albany and the reassignment of these projects, plus three biological control scientists, from Albany to Bozeman, MT, in 1987, to emphasize introduction and evaluation studies on the control of these weeds, both of importance to that area. The newly constructed non-quarantine plant growth facilities, which had been designed for biological control research, were temporarily released to other, biotechnologically-oriented research at Albany. Montana State University at Bozeman was in the process of strengthening its biological control of weeds program and new quarantine facilities were constructed by the university at Bozeman to accomodate the transferred ARS personnel as well as university needs. The quarantine facility became operational during 1988; see additional comments on the ARS Bozeman location below. Also, the APHIS-PPQ biological control implementation program initiated a biological control of weeds project on leafy spurge and knapweeds, and stationed several persons at the Bozeman location; see Chapter VI. Following several retirements, only one ARS scientist (C. E. Turner) remained at Albany by 1988 to continue biological control research on yellow starthistle and other weeds. In 1989, a second scientist (B. D. Perkins) was added to the Albany facility (though administratively under the ARS Bozeman laboratory) for testing and release of agents on gorse and Dalmatian toadflax, but he retired in 1992. During 1988-90, the Albany quarantine facility was shared with APHIS-PPQ biological control personnel importing natural enemies of leafy spurge provided by the ARS laboratory in Rome and other cooperators.

The research program on rangeland weeds formerly headed and coordinated by the Albany unit from 1958-87 involved many ARS and state cooperators in many western states (Andres and Kok 1981): ARS cooperators were located at ARS facilities at BCIRL, Columbia, MO; BIIL, Beltsville, MD; the

Forage and Range Research Unit, Lincoln, NE; and the Rangeland Insect Laboratory, Bozeman, MT (Puttler et al. 1978; McCarty and Lamp 1982; Rees 1977, 1982; and the section below on BIIL). The ARS Aquatic Weed Control Research Laboratory at Davis, CA, also cooperated with the Albany laboratory in the release of waterhyacinth bioagents in California. ARS cooperators with the current program remain at all locations except Beltsville, MD.

The new ARS biological control of weeds unit, the Rangeland Weeds Laboratory at Bozeman, MT, with its access to Montana State University quarantine facilities, and the APHIS-PPQ biological control program, assumed the role of coordinating activities in regard to the rangeland weeds of the northern states. Of the three ARS scientists reassigned to Bozeman from Albany in 1987, one retired (D. M. Maddox) and one (R. W. Pemberton) was later reassigned to the Asian Parasite Laboratory (see section B.1.a). The latter was replaced by P. C. Quimby, who transferred from Stoneville in 1989 to serve as Research Leader for the newly designated ARS Rangeland Weeds Laboratory at Bozeman. The biological control of weeds group at Bozeman consisted of S. S. Rosenthal (who retired in 1993) and N. E. Rees (who transferred to the unit from the ARS Rangeland Insect Laboratory at Bozeman, where he had conducted release studies of introduced insects on thistles and leafy spurge). A plant pathologist, A. J. Caesar, was added to the unit in 1991 (see section C.2 below). Satellite locations were established at Sidney, MT (see below), and Albany, CA (for gorse and Dalmatian toadflax research; see above). Research directed from the Bozeman location focused primarily on study and release of introduced natural enemies of leafy and cypress spurges and spotted, diffuse and squarrose knapweeds, in cooperation with scientists of Montana State University, and other western universities, and with Canadian and APHIS biological control of weeds programs. Coordination between the two latter programs and the ARS program, initially a problem, has improved significantly since the ARS Research Leader position at Bozeman was filled in 1989. Much of the ARS research has been funded in part by USDI's Bureau of Land Management and Bureau of Indian Affairs. Some of the resulting research at Bozeman dealing with introduced invertebrates (including a nematode, *Subanguina picridis*, for Russian knapweed) is reported in the following papers: Rees 1990, 1991 (thistles); Pemberton and Rees 1990, Rees and Spencer 1991, and Rees 1992 (spurges); Rees and Story 1991, Rosenthal et al. 1991, and Rosenthal and Piper 1995 (knapweeds); Quimby et al. 1991 and DeLoach 1991a (general); and Caesar (T.) et al. 1993 (nematode).

An additional ARS unit joined the rangeland weed program, with the transfer in 1987 of N. R. Spencer from Stoneville, MS, to conduct biological control research at the ARS Northern Plains Soil and Water Management Research Laboratory, Sidney, MT, under the technical supervision of the Bozeman laboratory. Studies at Sidney have concentrated on the collection of introduced natural enemies of leafy spurge and Canada thistle from their U.S. and Canadian areas of establishment and their recolonization in North Dakota and eastern Montana.

During 1973-93, research on biological control of aquatic weeds continued at the old IIPI locations at Gainesville and Fort Lauderdale, FL (see Chapter III, section B). ARS researchers at the Gainesville quarantine facility have been N. R. Spencer (1970-77) and G. R. Buckingham (1977-present). The research at this location during this period has been on imported natural enemies of alligatorweed (1973-74, 1979-80), waterhyacinth (1973-84), Eurasian watermilfoil (1974-present), hydrilla (1976-present), and melaleuca (1992-present). In addition, research on waterlettuce (1986-90) was conducted at this facility by D. H. Habeck (University of Florida) under a cooperative agreement with the ARS Fort Lauderdale laboratory. Much of this research, including overseas surveys, was made possible via cooperative agreements between the ARS Fort Lauderdale laboratory and the University of Florida (J. K. Balciunas, now with ARS), and was supported by the U.S. Army Corps of Engineers and the former Florida Department of Natural Resources (consolidated with the Florida Department of Environmental Regulation in 1992 to become the Florida Department of Environmental Protection). Quarantine service activities in regard to introduced insect parasites also

was conducted at Gainesville, until 1973 (see section B.1.a). The Gainesville location was administratively linked with the Fort Lauderdale laboratory beginning in 1985. (Spencer 1973; Spencer and Lekic 1974; Spencer and Coulson 1976; Center and Spencer 1981; Buckingham and Ross 1981; Buckingham and Bennett 1981, 1989; Buckingham and Buckingham 1981; Buckingham et al. 1983a, 1989, 1992; Buckingham 1984, 1988, 1994; Balciunas and Minno 1985; Bennett and Buckingham 1991; Balciunas and Purcell 1991.)

The biological control of aquatic weeds program benefited greatly from the special foreign currency program (PL-480) during the 1960s and 1970s. This program provided foreign exploration for biological control agents of waterhyacinth in Uruguay, hydrilla in Pakistan, Eurasian watermilfoil in Yugoslavia, and several weed species in India. (Silveira-Guido 1965; Ghani 1976; Rao and Sankaran 1974; and Lekic and Mihajlovic 1970.)

Biological control of aquatic weeds research initiated by IIPI in 1972 at the ARS Aquatic Plant Management Laboratory at Fort Lauderdale has been directed by B. D. Perkins (1972-76) and T. D. Center (1978-present). This research has been supported by the Aquatic Plant Control Research Program and the Jacksonville District of the U.S. Army Corps of Engineers, the Florida Department of Environmental Protection, the Southwest Florida Water Management District, and the National Park Service of the U.S. Department of the Interior. Studies there have consisted of release and field evaluations of imported natural enemies of alligatorweed, waterhyacinth, hydrilla, and waterlettuce, following quarantine research and clearance procedures conducted first at the Albany quarantine facility and, from 1977, at the Gainesville location. A hiatus in natural enemy introductions occurred in the aquatic weed program from 1977 until the first releases of natural enemies of hydrilla and waterlettuce in 1987. This was due to the lack of a coordinated foreign exploration program between 1974 and 1982, and unresolved questions on the specificity of agents for submersed weeds. This program gap was filled by the development of a cooperative agreement with the University of Florida in 1981. This agreement provided a university research associate position, subsequently filled by J. K. Balciunas, that was intended specifically for foreign exploration for biological control agents for hydrilla. Several new weeds are targeted for research at Fort Lauderdale, including the wetland tree melaleuca, for which research on natural enemies was initiated at the new Australian laboratory in 1988 (see this section above). (Center and Durden 1981, 1986; Balciunas and Center 1981, 1991; Center et al. 1982a, 1982b, 1990; Center 1982a, 1984, 1987, 1992a, 1994; Haag and Center 1988; Dray et al. 1990, 1993; Center and Kipker 1991; Center and Wright 1991; Center and Dray 1992; Dray and Center 1992 a and b.)

The results of much of the research on biological control of aquatic weeds conducted at both Gainesville and Fort Lauderdale are contained in many of the reports and miscellaneous papers of the U.S. Army Corps of Engineers' Aquatic Plant Control Research Program published by the Corps' Waterways Experiment Station, Vicksburg, MS. (Pemberton 1980; Buckingham et al. 1981; Center 1981, 1982b, 1983, 1992b; Center and Durden 1984; Center et al. 1984; Balciunas and Minno 1984; Balciunas 1985; Markham 1986; Dray et al. 1988; Center and Dray 1991; Dray and Center 1992 a and b; Buckingham and Okrah 1993.)

Research on the biological control of aquatic weeds has also been conducted at the ARS Aquatic Weed Control Research Laboratory at Davis, CA. Research on competitive plants and the diploid grass carp (*Ctenopharyngodon idella*) initiated in the early 1970s by R. Yeo was resumed during the mid-1980s, the latter by L. W. J. Anderson and R. T. Pine, focusing on the sterile triploid fish. The Davis laboratory collaborated with the Corps of Engineers and the California Department of Food and Agriculture (CDFA) on the release of waterhyacinth insects in the Sacramento Delta. The quarantine facility at Albany, CA, under the direction of L. A. Andres, also collaborated in this effort. In 1990, the Davis laboratory, under the direction of L. W. J. Anderson and enabled with funding from CDFA, began an effort to establish the "hydrilla weevil" *Bagous affinis* in California.

Plans include similar effort with the "hydrilla leaf-mining fly" *Hydrellia pakistanae*. Quarantine and field evaluation support for these studies is being provided by C. E. Turner of the Albany laboratory. (Yeo and Holm 1981; Stewart et al. 1988; and Pine and Anderson 1989, 1991.)

Two new ARS biological control of weeds units, planned prior to 1973 by IIPI, and both with associated quarantine facilities (Bailey and Kreasky 1978; Boldt 1982), were established during this period. The one located at the Jamie Whitten Delta States Research Center, Stoneville, MS, initially focused on the study of the arthropod fauna of narcotic plants, under the leadership of J. C. Bailey (1972-77), in association with the research at the ARS laboratory at Rome (see above). The Quarantine Laboratory for Plant-Feeding Insects at Stoneville was constructed specifically for the quarantine testing and production of narcotic plant-feeding arthropods, and for use as a biological control of weeds quarantine receiving center after cessation of the narcotics program (Bailey and Kreasky 1978). Following the closing of the narcotics program in 1977, the quarantine facilities became the Stoneville Research Quarantine Facility (SRQF), first under the ARS Southern Weed Science Laboratory (SWSL) and later transferred to the Bioenvironmental Insect Control Laboratory (later the Southern Field Crop Insects Management Laboratory [SFCIML] and now Southern Insect Management Laboratory [SIML]) at Stoneville. The facility was used extensively for quarantine receipt of insect parasites and predators (see section B.1.a), and to a lesser extent by research workers assigned to the SWSL at Stoneville (Jones et al. 1985). Studies on the biological control of pasture, row crop, and aquatic weeds of the Southeast by use of arthropods at the SWSL from 1972-86, and subsequent research on pathogens, were conducted under SWSL Directors C. R. Swanson (until 1974), C. G. McWhorter (1974-87), and S. O. Duke (1987-present). Leaders of the biological control research unit (combined with the weed management research unit in 1987) within the SWSL were K. E. Frick (1972-77), P. C. Quimby (1978-87), and G. H. Egley (1987-93). Biological control research, which actually began in 1971 with the transfer of Frick from California to Stoneville that year by IIPI, included: study of imported and/or native insect enemies of puncturevine, velvetleaf, and curly dock by Frick, Quimby (from 1972), and N. R. Spencer (from 1982); study of the potential control of purple nutsedge by augmentation of the native moth *Bactra verutana* by Frick, Quimby and J. M. Chandler (1971-81); and study of the impact of natural enemies of alligatorweed and waterhyacinth by G. B. Vogt and Quimby (1973-86). A research program on control of weeds by use of indigenous weed pathogens was initiated by the SWSL in 1973 (see section C.2, below), and after the retirements of Vogt and Frick and transfer of Spencer to the SFCIML in 1986, research on the use of arthropods for weed control was phased out. Biological control of weeds research at Stoneville is now focused on use of indigenous pathogens. (Frick and Garcia 1975; Garcia and Frick 1975; Spencer 1984, 1988, 1990; Vogt et al. 1979, 1992.)

Research at the second ARS biological control laboratory planned by IIPI prior to 1973, is located at the Grassland, Soil and Water Research Laboratory at Temple, TX. The research has been directed by C. J. DeLoach since his return from the Argentine laboratory in 1974, and with the addition of P. E. Boldt after his return from the Rome laboratory in 1982. Research at Temple has addressed biological control of native and introduced weeds and brush of the southwestern rangelands by the introduction of foreign control agents. The emphasis on native weeds was because of the ca. 20 southwestern rangeland weeds and brush with biological control potential, of which all but two are native. This has been the only project anywhere in the world devoted to classical biological control of native weeds in a continental area.

Native weeds investigated have been honey mesquite, broom and threadleaf snakeweeds, common and "Texas" broomweed, creosotebush, seepwillow and other *Baccharis* spp., Texas whitebrush, bitter rubberweed, "tarbush", and others, all of which have related species native in Argentina, and for which close ties with the Argentine laboratory were essential (DeLoach 1981a). All of these native plants, which occurred in restricted areas or at low or moderate densities when European settlers first arrrived, have increased enormously in density during the last 150 years, and now cause

serious losses in rangelands over wide areas of the Southwest. Two projects were also initiated to control native plants that are primary pests of crops and secondarily of pastures and ranges; these were common cocklebur and hemp sesbania. Conflicts of interest over the harmfulness versus benefits of these targeted weeds have been addressed, and approval was granted by the TAG to proceed with biological control projects for snakeweeds and broomweeds, seepwillow, whitebrush and bitter rubberweed, provided that suitable natural enemies could be found.

Much has been accomplished in the development of theory and application that demonstrates that biological control of native weeds is both possible and feasible if the target weeds and biological control agents are carefully selected (DeLoach 1978, 1981). Much information has been obtained on the host range, ecology, life history and impact of native U.S. natural enemies of the target weeds, and of South American natural enemies of related species, regarding the following: 1) honey mesquite (DeLoach 1981b, 1982, 1983 a and b; Cordo and DeLoach 1987; Cuda et al. 1990), which was eventually discarded as a target because of significant beneficial qualities (DeLoach 1986); 2) snakeweeds and broomweeds (Foster et al. 1981; DeLoach and Psencik 1982 a and b; DeLoach, 1991b; Cordo and DeLoach, 1992), for which studies in Temple quarantine of two Argentine species were conducted, one of which, a weevil (*Heilipodus ventralis*), was released in Texas; 3) *Baccharis* spp. (Boldt 1987, 1989 a, b and c; Boldt and Robbins 1987, 1990, 1992; Boldt et al. 1988, 1991; Gagné and Boldt 1989; Boldt and White 1992; Boldt and Staines 1993), for which two insects were tested in quarantine at Temple, but neither was released, and *Baccharis* spp. have been discarded as targets, at least temporarily; and 4) creosotebush (Cordo and DeLoach 1993).

In practice, control has not yet been achieved for any of the target native weeds. The primary difficulties have been 1) conflicts of interest for certain weeds (the weed has substantial beneficial values), 2) few insects overseas that are sufficiently host specific, and 3) the overseas insects do not feed and develop well on certain of the target U.S. weed species.

Only a few introduced weeds are of much importance in southwestern rangelands. The most important of these is saltcedar, although Russian-olive is rapidly invading riparian sites in more northern areas, and the poisonous African rue, which occurs sporadically, is spreading along highways.

Saltcedar, first proposed as a candidate for biological control in the early 1970s by L. A. Andres, was studied under PL480 programs in Pakistan and Israel, during which numerous promising candidate insects in both areas were identified. However, further research was postponed until there could be a resolution of the conflicting economic interests concerning this weed. Beginning in 1987, an extensive review of the literature and analysis of the harmful and beneficial values of saltcedar and of its potential for biological control was conducted at Temple, and the resulting petition to the TAG in 1989 resulted in the resolution of the conflict and allowed the testing of insects for introduction to begin. Additional surveys for natural enemies have recently been conducted by ARS European laboratory scientists in southern Europe and North Africa and in the People's Republic of China and by the Asian Parasite Laboratory in 1991. More extensive surveys were conducted there by C. J. DeLoach and staff of the Sino-American Biological Control Laboratory (SABCL) in 1992-93. Preliminary surveys began in Turkmenistan during the summer of 1993 by EBCL scientists. Host range testing of candidate agents began in 1991 by EBCL and Israeli cooperators, and two insect species are currently undergoing quarantine testing at Temple. See DeLoach 1990.

Also, follow up studies on projects to control introduced weeds initiated by other ARS laboratories have been undertaken at Temple, to establish those natural enemies in Texas that already were tested overseas or in some cases already released and established in other areas of the U.S. These projects included Russian thistle, milk and musk thistles (Boldt and DeLoach 1986, and Boldt and Jackman 1993), and field bindweed (Ciomperlik et al. 1992, and Boldt and Sobhian 1993). Natural enemies of

these weeds were established in Texas, and the introduced mite *Aceria malherbe* appears to be dispersing and shows promise of substantially reducing the growth of field bindweed.

In 1974, research on biological control of weeds was initiated by the Beneficial Insect Introduction Laboratory (BIIL), at Beltsville, MD, with the hiring of S. W. T. Batra, in order to take advantage of previous research and the clearance and release of insect enemies of weeds elsewhere in the U.S. against weeds also common in the northeastern region. Investigation of the potential for the biological control of other weeds of northeastern pastures was also initiated. The BIIL (later BIL, see section B.1.a) biological control of weeds research program was hampered by the lack of nearby quarantine facilities. Nevertheless, natural enemies of thistles, knapweeds, and spurges, provided by the Albany laboratory, state cooperators, and Canadian sources, were established in the Northeast. A number of northeastern pasture weeds were identified as having potential for classical biological control, including bedstraws, hawkweeds, smallflower galinsoga, and others; see Batra 1979, 1980, 1981, 1983, 1984. Unfortunately, economic data sufficient to justify a sustained biological control program at the ARS laboratory in Rome was not obtained for any of the potential targets (see discussion above concerning establishing priorities). As a result of BIIL's initial research efforts on *Carduus* and other thistles, funded in part by the Maryland Department of Transportation, the Maryland Department of Agriculture later instituted a biological control of weeds program, with emphasis on thistles, and in 1989 established a quarantine facility at Annapolis (Tipping and Hight 1989). The last targeted weed for the BIL program was purple loosestrife (Batra et al. 1986; Hight 1990; Kok et al. 1992 a and b; Malecki et al. 1993); overseas and quarantine research on the biological control of this wetland weed was funded by the U.S. Fish and Wildlife Service; the overseas studies were conducted under contract by the International Institute of Biological Control (IIBC) and the quarantine studies by VPI scientists. Three European beetles (*Hylobius transversovittatus*, *Galerucella calmariensis*, and *G. pusilla*) were imported and released in 1992 in several sites throughout the U.S., and in Canada, and at least two were found to have overwintered and begun oviposition in 1993 (Malecki et al. 1993). The biological control of weeds program in the northeastern region lost much of its funding with the departure in 1985 of the research scientist (Batra) assigned to the program (studies continued by the support scientist S. D. Hight), and was never thereafter adequately supported by ARS. Consequently, the program was terminated by the National Program Staff at the end of Fiscal Year 1993.

During this period, ARS also contracted with university workers in Virginia (VPI) to speed clearance of insects attacking musk and related thistles (see also Chapter III, section B and section B.1.a of this Chapter), and at the University of Idaho to facilitate the development of an integrated pest management program against yellow starthistle utilizing chemicals, plant competition, and biological control strategies. The successful VPI program led to the redistribution of two introduced musk thistle natural enemies that became established in Virginia, and as such provided reciprocal support for the ARS thistle program at Beltsville, MD.

Significant accomplishments of ARS programs utilizing invertebrate agents for biological control of weeds during 1973-93 include the introduction and establishment of 33 new exotic weed-feeding invertebrates (including a nematode) into the United States, only some of which are listed by Julien (1992). Several of these projects have resulted in control of the weeds in portions of their ranges. (Two foreign pathogens were also established during this period; see section C.2 below for accomplishments of the ARS programs utilizing foreign and endemic pathogens for control of weeds.)

Evaluation of the tansy ragwort program was conducted during the period. The dramatic control of tansy ragwort, a poisonous pasture and range weed, throughout its range in California, Oregon, and parts of Washington matched the levels of control achieved in the early common St.-Johnswort program. The improved control was primarily due to the feeding of an earlier introduced small

chrysomelid beetle, *Longitarsus jacobaeae*, that attacks the leaves, crowns, and roots of the plant (Hawkes and Johnson 1978; Pemberton and Turner 1990). See also the discussion of the economic results of this program in Chapter III, section B. The Oregon Department of Agriculture has been instrumental in distributing the introduced ragwort insects throughout the state to the extent that they now pay some farmers to maintain ragwort to serve as a source of future beetle collections. This project demonstrated the need for such distribution programs, leading to the development of such a program in APHIS; see Chapter VI. The Colorado and New Jersey Departments of Agriculture have been similarly involved in distributing introduced weed natural enemies, for thistles and other weeds, in their states.

Rush skeletonweed, a tough-stemmed composite that has the potential to spread into grain areas of the West and reduce production as well as hamper harvesting, has been curbed by the introduced rust (*Puccinia chondrillina*), leaf- and stem-galling midge (*Cystiphora schmidti*), and stem-tip-galling eriophyid mite (*Eriophyes chondrillae*). The rust has reduced stem height in California, while the eriophyid mite has been credited with reducing plant abundance in Washington (Piper 1986).

Eleven new agents have been introduced against leafy spurge, a weed toxic to cattle in the northern great plains, 12 against diffuse and spotted knapweed, one (a nematode) against Russian knapweed in the northern and northwestern states, and five species against yellow starthistle in the West and Northwest. At least five insect species have been established on the aquatic weeds waterhyacinth, waterlettuce, and hydrilla (discussed below). And at least two, and probably three, European species of beetles are provisionally established on purple loosestrife in the Northeast. Some of these natural enemies have not had time to fully demonstrate their control potential.

Yellow starthistle is an annual weed from southern Eurasia that is highly invasive on rangelands and other environments in the far western states. The weed displaces native plants, is poisonous to horses, and the spiny heads deter grazing by cattle as well as human enjoyment of infested recreational lands. Early work by ARS and the University of California, initiated in 1959 and the early 1960s, did not directly result in the establishment of any biological control agents. The yellow starthistle project was rejuvenated in the 1980s when ARS made it a high priority project at the Albany and Rome laboratories. R. Sobhian was stationed in Greece for work on this weed, and D. M. Maddox from the Albany laboratory went to Greece one summer to help run a field-plot, host-specificity experiment on *Bangasternus* spp. Progress has been very rapid since then, thanks in great part to simultaneous host-specificity experiments carried out in the field in Greece by Sobhian and others, at the Rome laboratory by S. L. Clement and L. Fornasari, and at the Albany laboratory by D. M. Maddox and C. E. Turner. Since the mid-1980s, five insects have been introduced from Greece and have successfully established in the U.S.: the tephritid flies *Urophora sirunaseva* and *Chaetorellia australis,* and the weevils *Bangasternus orientalis*, *Eustenopus villosus*, and *Larinus curtus*. All five species attack the flowerheads and reduce seed production, the only means of reproduction by this weed. These insect species feed on different parts of the flowerhead and attack the heads at different stages of development. Among the five species, the flowerhead is attacked at all stages of development, from the earliest closed bud stage to full flowering. It is too soon to know the impact of these insects, but they almost certainly should slow the rate of invasiveness of the weed over the short and long term. (Maddox and Mayfield 1985; Maddox et al. 1985, 1990; Sobhian and Zwölfer 1985; Maddox and Sobhian 1987; Clement 1990, 1994; Groppe et al. 1990; Clement and Sobhian 1991; Fornasari et al. 1991; Sobhian 1993b; Turner 1994; Turner et al. 1994, 1995; Fornasari and Turner 1995.)

Leafy spurge is an extensively rooted perennial herb from Eurasia that is weedy on rangelands in the northcentral states and adjacent areas of Canada. The weed can dominate rangeland vegetation, and produces a latex that causes dermatitis in cattle and humans. A biological control program against spurges was initiated by Agriculture Canada and CIBC/IIBC in the 1960s. ARS joined this research

effort in the 1970s through work carried on at the Albany (P. H. Dunn, R. W. Pemberton) and Rome (P. H. Dunn, P. Pecora) laboratories. The domestic program shifted to Bozeman with the transfer there of R. W. Pemberton from Albany in 1987. APHIS has carried out a high level of implementation activity on this weed since the late 1980s.

A total of 11 insects has been imported from Eurasia and released in the U.S. against leafy spurge. Establishment is confirmed for eight of these. These insects and the years of their first U.S. release are as follows: the hawk moth *Hyles euphorbiae* (1964), the clearwing moth *Chamaesphecia tenthrediniformis* (1975), the long-horned beetle *Oberea erythrocephala* (1980), the gall midge *Spurgia esulae* (1985), the flea beetles *Aphthona flava* (1985), *A. cyparissiae* (1986), *A. czwalinae* (1987), *A. nigriscutis* (1989), *A. abdominalis* (1993), and *A. lacertosa* (1993; an accidental release of this species was apparently made in 1988), and the clearwing moth *Chamaesphecia hungarica* (1993). Through 1993, establishment is confirmed for all but *C. tenthrediniformis* and the two insects first officially released in 1993. In terms of specific research efforts by ARS, the agency has carried out U.S. releases of all these insects except the second clearwing moth, *C. hungarica*. ARS has performed the host specificity studies on four of the *Aphthona* species and *S. esulae*, as well as on the gall midge *Dasineura* sp. nr. *capsulae*, and the moths *Oxicesta geographica*, *Simyra dentinosa*, and *Chamaesphecia crassicornis*.

The most promising biological control agents for leafy spurge appear to be the *Aphthona* flea beetles, due to their relatively high level of host specificity and effectiveness. Most of the damage is done by the larvae, which feed on the roots of the weed. Substantial reductions of leafy spurge are becoming evident in areas following the release of these flea beetles, especially with *A. flava* and *A. nigriscutis*. Following his transfer to the Asian Parasite Laboratory in 1989, R. W. Pemberton discovered *Aphthona* flea beetles on leafy spurge in China (Inner Mongolia). Two of these Chinese species, *A. chinchihi* and *A. seriata*, have undergone host-specificity assessment in Europe and Bozeman, MT. (Dunn 1979; Pemberton 1986; Rees et al. 1986; Pemberton and Wang 1989; Pemberton and Rees 1990; Pemberton 1995.)

Diffuse knapweed and spotted knapweed are biennial and perennial herbs, respectively, that are native to Eurasia and weedy on rangelands in the northwestern United States and southwestern Canada. Historically, biological control research on these weeds was begun in 1961 by Canada and CIBC/IIBC, and their strong activity on these weeds has been ongoing. Since the late 1980s, Montana State University has had a high level of domestic activity on knapweeds, particularly spotted knapweed. Since the late 1980s, APHIS has carried out a high level of implementation work on knapweed insects. ARS has contributed a greater research effort to diffuse knapweed than to spotted knapweed. The biological control agents released have been European insects that attack the heads or roots of knapweeds. A total of 12 insects have been intentionally introduced into the United States against these two knapweeds, and another species spontaneously colonized the United States from Canada. Of these 13 knapweed insects, ten are confirmed established through 1993. Some of these insects attack both knapweed species, while others preferentially attack one or the other knapweed. Some of these knapweed insects also attack another weedy knapweed, squarrose knapweed. The earlier ARS research was done by the Albany laboratory (D. M. Maddox, S. S. Rosenthal) and the Rome lab (P. H. Dunn, R. Sobhian), with the domestic effort transferring to the Bozeman laboratory with the transfer of S. S. Rosenthal there in 1987. As there have been many recent releases of new agents, it is too soon to know their control impact. However, due to the combined impact of head and root insects, the biological control potential appears to be excellent.

The knapweed insects and the years of their first releases into the U.S. are as follows: the fly *Urophora affinis* (1973), the moth *Metzneria paucipunctella* (1980), the beetle *Sphenoptera jugoslavica* (1980), the moths *Agapeta zoegana* (1984), *Pelochrista medullana* (1984), and *Pterolonche inspersa* (1986), the weevils *Cyphocleonus achates* (1988), *Bangasternus fausti* (1989),

and *Larinus minutus* (1991), the flies *Chaetorellia acrolophi* and *Terellia virens* (1992), and the weevil *Larinus obtusus* (1993). The fly *Urophora quadrifasciata* spontaneously spread to the U.S. from Canada in 1980. Establishment is confirmed for all of these except *P. medullana*, *P. inspersa*, and *L. obtusus*. ARS has specifically performed host specificity studies on *P. inspersa*, *B. fausti*, *L. minutus*, and *U. quadrifasciata*; and has carried out field releases of most of the others listed. (Maddox 1982; Maddox and Sobhian 1987; Dunn et al. 1989; Groppe et al. 1990; Rees and Story 1991; Sobhian et al. 1992a; Piper and Rosenthal 1995; Story 1995.)

Though much basic information has been gathered in connection with the unique research program at Temple, TX, on native weeds and brush of southwestern rangelands (see discussion above), which has been a difficult and controversial program because of major conflicts of interest, control has not yet been achieved for any of the targeted native species. Only one foreign natural enemy has been released in the U.S. to date, the weevil *Heilipodus ventralis* against snakeweeds, but it has so far failed to establish. Research on introduced weeds in Texas has resulted in the establishment of a promising natural enemy of field bindweed, as a result of previous research by the Albany laboratory (Rosenthal and Platts 1990). And prospects for control of saltcedar are promising. See discussion of the Texas program above.

Waterhyacinth, a floating aquatic weed that covers the surface of lakes and slowly moving water, has been reduced to one-third of its former abundance in the Gulf Coast states (Cofrancesco et al. 1986; Center et al. 1990). This reduction has resulted not from removal of biomass by introduced insects, but rather reduced regrowth following annual winter die-back. Two weevils and a moth introduced from Argentina (1972-77) tunnel the leaf petioles and plant crown, destroying meristematic tissue in the process. Having lost the ability to replace senescent tissue as a result of this damage, the plants sometimes lose bouyance and sink. More often, they merely stop growing. In recent experiments, for example, standard-sized plots inoculated with the weevils expanded during the growing season to cover only two to three times the initial area, whereas uninoculated controls expanded nearly six-fold. Hence, the success of this project seems to stem from the regulation of plant growth rather than from the wholesale destruction of plant populations (Center et al. 1990).

Two Asian natural enemies of hydrilla were released in 1987 in Florida -- an ephydrid fly, *Hydrellia pakistanae*, and a tuber weevil, *Bagous affinis*. The fly is now well established throughout the Southeast and has overwintered as far north as northern Alabama. Hydrilla beds have either partially or completely degenerated at several release sites, but cause and effect have not yet been proven. There are plans to release this fly in California in 1994. The weevil, which requires prolonged dry periods, failed to establish in Florida from lack of suitable habitat. Promising results have been obtained in California by K. E. Godfrey of the Davis laboratory, however, so this insect may prove useful in areas with pronounced dry summers. An Australian ephydrid fly, *H. balciunasi*, was released in Florida in 1989 and Texas in 1991. Although it initially seemed to establish at early release sites in Florida, populations failed to persist. This may be partially attributable to site invasions by expanding populations of *H. pakistanae*. The releases in Texas by the U.S. Army Corps of Engineers (USACE) resulted in establishment of at least one population, which has grown and survived for over a year, despite the inadvertent release of *H. pakistanae* as a contaminant in the stock cultures. A stem weevil, *Bagous hydrillae*, also from Australia, was first released in Florida in 1991, but establishment has not yet been verified. A strain of *H. pakistanae* from the north temperate region of China was first released in 1992, but may have been absorbed by the rapidly expanding populations of the Indian/Pakistani strains before a discrete population could establish.

Under an ARS/University of Florida cooperative project on the biological control of waterlettuce sponsored by the USACE Jacksonville District, a South American weevil, *Neohydronomus affinis*, was obtained from the Australian Commonwealth Scientific and Industrial Research Organization (CSIRO), and released in 1987 in Florida. Although the weevil had been discovered and tested by

ARS scientists in Argentina (DeLoach et al. 1976), it was first successfully utilized as a biological control agent by the Australians. Complete control of waterlettuce was realized at two of three initial release sites within two years of the first release, and the species spread widely in Florida, both by natural dispersal and by means of a redistribution program by the Florida Department of Natural Resources (now Department of Environmental Protection). The USACE also released this species in Texas, and it has been found to be established in Louisiana (Grodowitz 1991). See also Thompson and Habeck 1989, and Dray et al. 1990.

Some of the agents studied and introduced to the U.S. have also been exported to other countries. Consequently, successful efforts at biological control of waterhyacinth have been reported from the Sudan, India, Argentina, and Australia (Beshir and Bennett 1985; Jayanth 1987; DeLoach and Cordo 1983; Wright 1981). Australia has also had good success with alligatorweed insects (Julien 1981).

Much of the work in the rapidly expanding field of weed biological control is coordinated through an ongoing series of international symposia held quadriennially, and informal, annual meetings of European-stationed biological control of weeds specialists. The first of the symposia was held in 1969 in Delémont, Switzerland, and was attended by 20 scientists from eight countries, resulting in a 110-page published proceedings (Simmonds 1970). The sixth symposium was held in Vancouver, Canada, in 1984, and was attended by 135 scientists from 16 countries, and resulted in a 885-page published proceedings (Delfosse 1986). The seventh symposium was held in 1988, was attended by 110 scientists, and was sponsored by the ARS laboratory in Rome and the Istituto Superiore di Santidad Vegetale (Delfosse 1990); the ARS laboratory had also sponsored the second symposium (Dunn 1973). The eighth symposium was held in Canterbury, New Zealand, in 1992, the proceedings of which (Delfosse & Hill, 1994) was not available by the end of 1993 for a comparison with the Vancouver and Rome symposia.

Based on the difference in attendance between the 1969 and 1984/1988 symposia, there was an apparent 5- to 6-fold increase in the number of scientists addressing the biological control of weeds over those 20 years; this includes an increasing number of plant pathologists. Unfortunately, the number of ARS scientists addressing classical biological control of weeds by use of invertebrates has declined in recent years. In the early 1980s, about 19 ARS scientists were working full time in this field; today only 12 remain, and five are near retirement.

2. Weed Pathogens. By W. L. Bruckart and J. R. Coulson

Introduction. The period 1973-93 saw the organization of formal research on plant pathogens for biological control of weeds. Prior to this time, research in this area was tentative and random, without clear focus or major support (Wilson 1969). Research activities described in Wilson's paper and the success of entomologists in classical application of insects for weed control provided the necessary visibility and demonstrated potential to justify organization of a formal effort by the USDA-ARS in this area. Currently, plant pathogens are deployed in two ways. They can be introduced as classical agents like the foreign invertebrates, or they can be used like herbicides. Generally, the classical approach involves foreign pathogens for rangeland weed control and the bioherbicide approach involves endemic pathogens for control of weeds in row crops. Each of these approaches resulted from research prior to the period encompassed by this section.

The earliest USDA involvement with a plant pathogen for biological weed control was sponsorship of R. I. Inman in 1965 by the ARS Crops Protection Research Branch to investigate the potential of the rust fungus, *Uromyces rumicis*, for control of curly dock (Inman 1971). This research was conducted in Rome, Italy, with a foreign pathogen intended for classical control of a U.S. weed. Results of this research were encouraging, but the pathogen has not been introduced into the U.S. to date, because *U. rumicis* is heteroecious and the host range determination with plants related to the

alternate host, "lesser celandine" (*Ranunculus ficaria*), was not accomplished until recently. This research initiated the concept of using foreign plant pathogens in a manner similar to the use of insects as classical biological control agents.

The discovery of *Colletotrichum gloeosporioides* f. sp. *aeschynomene* (CGA) in 1969 at the University of Arkansas Rice Research and Extension Center initiated the concept that plant pathogens could be used in ways similar to herbicides, now known as the bioherbicide or mycoherbicide approach. Development of CGA involved cooperation between University of Arkansas and ARS (Stuttgart, AR) scientists (Daniel et al. 1973, 1974; Smith et al. 1973 a and b; Smith 1986). In 1974, CGA became the first pathogen patented for use as a mycoherbicide (Daniel et al. 1974), and in 1982 it was commercially registered for weed control (Bowers 1986; Smith 1986; Templeton 1988).

Problems associated with 1) coordination of research activities (particularly in regard to a focused national program on classical biological control), 2) setting target weed priorities, and 3) conflicts of interest, that were described for development of insect biological control agents in the previous section (C.1 above), have also affected progress in development of plant pathogens as biological control agents. Also, regulations specific to microorganisms (and not to invertebrates) have been reevaluated by the Animal and Plant Health Inspection Service (APHIS) and Environmental Protection Agency (EPA) since 1973 because of the development and proposed use of plant pathogens for weed control; utilization of plant pathogens as weed control agents was slowed as a result of this review and reinterpretation of the regulations for microbes.

Foreign pathogens. A research program on foreign pathogens for biological control of weeds was initiated in 1974 at the recommendation of the ARS Working Group on Natural Enemies of Insects, Weeds and Other Pests (WGNE). The ARS Plant Disease Research Laboratory (now the Foreign Disease-Weed Science Research Unit) at Frederick, MD, was designated for this effort. The Frederick Laboratory had an established facility designed for study of quarantine and containment of plant pathogens (Melching et al. 1983). This facility was designated as the ARS containment facility for receipt and study of exotic weed pathogens. ARS scientists involved in the biological control program at the Frederick facility have been R. G. Emge and C. H. Kingsolver (1974-80), W. L. Bruckart (1981-present), S. M. Yang (1987-present), A. R. Bennett (1987-1992), and D. G. Luster and N. W. Schaad (1993-present).

The rust *Puccinia chondrillina* was the first foreign pathogen introduced into the United States for weed biological control. A strain of this fungus had been introduced previously from Europe into Australia for control of rush skeletonweed. Evaluation of European acquisitions of *P. chondrillina* were made in containment at Frederick in cooperation with Australian scientists at the Commonwealth Scientific and Industrial Research Organization's (CSIRO) laboratory in Montpellier, France (Emge et al. 1981). The pathogen was very host specific and aggressive on the most common form of rush skeletonweed in the U.S. Releases were made between 1976 and 1978 at locations in California, Idaho, Oregon, and Washington (Adams and Line 1984; Supkoff et al. 1988). The rust became established and spread throughout stands of susceptible biotypes of the target weed. In California, stand reduction varied from 55 to 87%, and *P. chondrillina* appeared to be the organism most damaging to rush skeletonweed over a 10-year period (Supkoff et al. 1985, 1988), which agreed with reports on the effects of the rust in Australia.

Other fungi studied at the Frederick facility as candidates for biological control include the autoecious *Uromyces* spp., *Alternaria* spp. and *Myrothecium verrucaria* for leafy spurge control, *Puccinia carduorum* for *Carduus* thistle control, and *Puccinia jaceae* for control of *Centaurea* species (Bennett et al. 1991; Bruckart 1989; Shishkoff and Bruckart 1993; Yang et al. 1990, 1991, 1993a). Nearly all risk assessment research on plant pathogens have been conducted in a containment

greenhouse at Frederick, unlike the study of invertebrate agents which involves preliminary investigations at overseas locations. Philosophy and protocols for development of these pathogens were modelled after those used by entomologists (Bruckart and Dowler 1986), but certain modifications have been incorporated that suit the development of plant pathogens (Bruckart and Shishkoff 1993). The primary reliance on greenhouse data for risk assessments necessitated incorporation of side-by-side greenhouse comparisons of candidate foreign pathogens with endogenous (endemic) fungi from North America for perspective about field performance (Bruckart and Shishkoff 1993).

The most progress to date has been with *Puccinia carduorum*, a rust fungus proposed for use against musk thistle. Although pustules developed on some native North American thistles (*Cirsium* spp.) and artichokes under optimal greenhouse conditions for infection, reactions on non-target species were resistant and *P. carduorum* could not be maintained on these species, even in the greenhouse (Politis et al. 1984; Bruckart et al. 1985; Politis and Bruckart 1986; Bruckart and Shiskoff 1993). Phenotypic characterization using isozyme analysis and pathogen morphology related to differences between strains from different *Carduus* species noted in host plant inoculation studies (Bruckart and Peterson 1991). Similar results were found in field evaluations in Switzerland and Virginia (Baudoin et al. 1993; Bruckart et al. 1993). At the end of 1993, a proposal for general use of the pathogen in the U.S. was under review by APHIS and the U. S. Fish and Wildlife Service.

Leafy spurge received considerable attention from plant pathologists during the period 1973-93. Collecting trips were made from the Frederick laboratory to Europe by S. K. Turner (1983, in cooperation with Montana State University) and A. R. Bennett (assigned to temporary summer duty at the ARS facilities in Italy and France between 1989-91). Also, G. Defago of the Institut für Spezielle Botanik in Switzerland, was funded by ARS between 1980 and 1985 to study the autoecious rust fungi in the genus *Uromyces* that attack leafy spurge (Defago et al. 1985). Additional trips to the former Soviet Union were made by A. J. Caesar (ARS, Bozeman, MT) in 1992 and 1993. Those explorations emphasized collection of soilborne pathogens, particularly *Rhizoctonia* spp., that may be related to a pathogen causing leafy spurge stand reductions in Montana (Caesar et al 1993b; Caesar 1994a). S. M. Yang made collecting trips to the People's Republic of China between 1989 and 1993 as part of the Sino-American biological control collaborative program (Yang et al. 1991, 1993a). Although leafy spurge has been the principle target, pathogens from *Centaurea* spp. (particularly yellow starthistle) and other thistles were sought.

Endemic pathogens. Several contributions to the discovery, development, and evaluation of plant pathogens for use as mycoherbicides have been made through research at the ARS Southern Weed Science Laboratory in Stoneville, MS, begun in 1974. ARS plant pathologists at this location have been H. D. Ohr (1974-77), H. L. Walker (1974-85), and C. D. Boyette (1985-present). (See section C.1 above for other biological control of weeds research at Stoneville.) Among the fungi discovered and evaluated were *Alternaria cassiae* from sicklepod, *Fusarium lateritium* from velvetleaf, *A. crassa* from jimsonweed, *Colletotrichum truncatum* from hemp sesbania, and *A. helianthi* from sunflower for common cocklebur (Walker 1980, 1981, 1982; Boyette and Walker 1985; Boyette 1986, 1988, 1991 a and b; Quimby 1989; Boyette et al. 1991, 1993). Subsequent evaluation of *A. cassiae* was made on a regional basis through the S-136 Regional Research Committee and with involvement from federal, state, and private sectors (Charudattan et al 1986; Bannon 1988). The ARS contributions to the *A. cassiae* research also included development of procedures for mass-production and financial support for regional evaluation (Walker 1980, Walker and Riley 1982). Commercial use of *A. cassiae* is pending EPA registration of a product through a commercial enterprise.

Once a pathogen has been identified and found promising for application as a mycoherbicide, there are other, major hurdles to overcome in its development. The most significant of these obstacles are

scaling-up and formulation. ARS scientists have provided innovative advances in each of these areas that increases the potential for these pathogens to be utilized in weed management. Perspectives about both the process of and advances in mass production and formulation have been written by Quimby and Boyette (1987) and Daigle and Connick (1990). Innovations in carrier or formulation include the use of sodium alginate (Walker and Connick 1983), water-in-oil invert emulsions (Quimby et al. 1988; patented by Quimby 1990; later modified or improved by Boyette et al. 1993; Yang et al. 1993b), and a wheat gluten matrix called 'Pesta' (Connick et al. 1991, 1993).

Recently, the expertise of scientists at the ARS Fermentation Biology Research Unit in Peoria, IL, was enlisted to investigate large-scale, liquid fermentation of fungi for use as mycoherbicides. Factors such as the C:N ratio in liquid media affects the yield and virulence of *Colletotrichum truncatum* conidiophores, and such must be considered in the large-scale, economic production of fungi for use in biological weed control (Schisler et al. 1991b, 1992; Jackson et al. 1992). Potential of *Puccinia canaliculata*, an obligate pathogen, as a mycoherbicide was evaluated at the Frederick location in cooperation with state and ARS scientists in Georgia and Maryland (Phatak et al. 1983; Bruckart et al. 1988).

Study of endemic pathogens of leafy spurge and other rangeland weeds was initiated by A. J. Caesar and his colleagues at the Rangeland Weeds Laboratory in Bozeman, MT (Caesar 1994 a and b; Caesar et al. 1993 a and b). Caesar et al. (1993a) found a reduction in the density of rangeland weeds, and particularly leafy spurge, associated with "fairy ring-like" patches in the Montana rangelands. Pathogenic isolates of a *Rhizoctonia* sp. have been isolated from diseased leafy spurge in these areas (Caesar et al. 1993b; Caesar 1994a).

Innovative research into use of endemic bacteria has been pursued by ARS scientists more recently. Crown gall, caused by *Agrobacterium tumefaciens*, was described recently on leafy spurge, Russian knapweed, and both spotted and diffuse knapweeds (Caesar 1994b). Rhizobacteria have been screened and field tested for potential to control downy brome and jointed goatgrass at Pullman, WA (Kennedy et al. 1991, 1992), and other weeds at Columbia, MO (Kremer 1987, 1993; Kremer et al. 1990). Bacteria also were found to enhance symptom development caused by *Colletotrichum truncatum* on hemp sesbania (Schisler et al. 1991a), suggesting that an understanding of phyllosphere ecology may be valuable in optimal use of mycoherbicidal agents.

Finally, experiments with a registered biological control agent transformed with a gene for herbicide resistance are being conducted at Beltsville, MD, and in containment at Frederick, MD (Brooker et al. 1993).

ARS and other plant pathologists engaged in research on biological control of weeds with plant pathogens have been regular attendees at conferences and workshops on biological control and related issues (Battenfield 1983; USDA 1984a; Delfosse 1986, 1990; King et al. 1988; Coulson et al. 1991; Lumsden and Vaughan 1993; Delfosse and Scott 1995), and several important international annual workshops organized under the Southern Regional Research Projects S-136 and S-234 (Charudattan and Walker 1982).

Significant accomplishments. During this period, the first foreign pathogens were purposely introduced and established in the field in the United States for biological control of weeds. Of the two pathogens introduced, one (*Puccinia chondrillina*) had previously been studied and introduced in Australia, and approval was obtained for its introduction into the United States after limited additional study. The rust is providing significant control of its targeted weed, rush skeletonweed, in western U.S. Research on the second exotic pathogen, *Puccinia carduorum* for musk thistle control, was conducted from start to finish by USDA-ARS. The research was conducted during a period when procedures for introducing biological control agents in the U.S. were undergoing increasing scrutiny

and change, which caused undue delay in obtaining approval for its release. Approval for experimental release of *P. carduorum* was recommended by the Working Group on Biological Control of Weeds in 1986, but final approval by the USDA for general use of the pathogen has not yet been received, after a period of over seven years. Once such final approval has been obtained, if such is obtained, the regulatory procedures developed during the approval process, and the research conducted to meet resulting regulatory requirements, will provide important precedents to guide future development of foreign pathogens for weed control. A third pathogen, a strain of *Puccinia jaceae* for yellowstar thistle control, is available for testing these new regulatory procedures. The Technical Advisory Group on Biological Control of Weeds gave a positive recommendation for field tests of this rust in 1990. Additional tests are to be conducted before final application for a release permit is made.

Much progress also has been made by ARS scientists for use of endemic pathogens for weed control. This is best exemplified by references cited above, and the following U.S. patents issued: Patent No. 3,849,104 - Control of northern jointvetch with *Colletotrichum gloeosporides* f. sp. *aeschynomene* (Daniel at al. 1974); Patent No. 4,390,360 (Int. CI AO1N 63/04) - Control of sicklepod, showy crotalaria, and coffee senna with a fungal pathogen (Walker 1983); Patent No. 4,178,935 - Method for the preparation of mycoherbicide- containing pellets (Walker et al. 1988); Patent No. 4,902,333 - Patent on the concept of the invert emulsion (Quimby 1990); Patent No. 5,034,328 - Control of hemp sesbania with a fungal pathogen (Boyette 1991b); Patent No. 5,074,902 - Granular products containing fungi encapsulated in a wheat gluten matrix for biological control of weeds (Connick and Boyette 1991); and Patent No. 5,163,991 - Biocontrol of jointed goatgrass (Kennedy et al. 1992).

D. BIOLOGICAL CONTROL OF PLANT NEMATODES. By R. M. Sayre

In 1973, as a result of the agency wide reorganization of ARS mentioned in sections A and B.2, the Nematology Investigations unit ceased to be national in scope and its personnel of 28 scientists then located nationwide were reassigned to their respective regional and area management units. The single largest group of six scientists formed the Nematology Laboratory within the Plant Protection Institute (now Plant Sciences Institute) in the Beltsville Agricultural Research Center in Maryland. Leaders of this Laboratory have been R. Rebois (1974-85), R. N. Huettel (1985-1992), and D. J. Chitwood (1992-present).

Early in this period, several nematicides were deregistered by action of the Environmental Protection Agency (EPA) and not allowed to be used on any crops. Consequently, nematologists were left with only five broad-use nematicides, four preplant fumigants, and six limited-use materials for making pest control recommendations (Feldmesser et al. 1985). Some nematode pest problems were not amenable to control by the remaining few materials as they were either ineffective or too costly for use on low value crops. As a consequence, control measures for nematodes were inadequate.

Fortuitously, during this period B. R. Kerry of the Rothamsted Experiment Station in England, demonstrated that naturally-occurring fungi (i.e., four different fungal species) controlled the cereal cyst nematode (Kerry 1975, 1981). This was the first instance where soil microorganisms were found to be naturally suppressive to a population of pest nematodes. His discovery gave new impetus to research on soil fungi that attack eggs and other life stages of nematodes as possible biological control agents. Also this same year, a spore-forming bacterial pathogen was found to be an effective control agent for root-knot nematodes (Mankau 1975). These two discoveries set in motion renewed interest in using natural enemies of pest nematodes as control agents.

R. M. Sayre of the Beltsville Nematology Laboratory has continued studies on the bacteria that parasitize nematodes, and in collaboration with M. P. Starr (University of California, Davis) in a series of studies on the spore-forming bacterial pathogens of nematodes, established the generic

designation *Pasteuria* for five bacterial species (Sayre 1980 a and b, 1988, 1993; Sayre and Starr 1988, 1989; Sayre et al. 1991 a and b). These studies offered the means to others for identification of new isolates of the bacteria. In collaboration with N. A. Minton (ARS, Tifton, GA), it was determined through bioassays that endospores of *Pasteuria penetrans* were primarily responsible for a natural decline of the peanut root-knot nematode observed in field soils (Minton and Sayre 1989). While field observations indicated the potential of the bacterial group as control agents of pest nematodes, the inability to cultivate *Pasteuria in vitro* has prevented its commercial utilization.

S. F. Meyer and colleagues of the Nematology Laboratory have isolated fungal parasites of the soybean cyst nematode (Meyer 1992; Meyer and Huettel 1993; Meyer et al. 1990). In particular, an isolate of *Verticillium lecanii* showing enhanced virulence to the nematodes has become the test organism in a technology transfer project with Crop Genetics International of Columbia, MD (Huettel and Meyer 1992). In August, 1992, Meyer and R. N. Huettel spent two weeks in China collecting fungal isolates found colonizing the life stages of soybean cyst nematode. These fungi were test organisms in a joint Sino-American Biological Control Laboratory project to find and utilize fungi as control agents for this pest nematode.

In 1985, the Nematology Laboratory was divided, its taxonomists being transferred to a systematics laboratory (see also section B.2), leaving only three full-time nematologists in the Laboratory. The mission of the reduced laboratory was the development of new technologies to better manage plant-parasitic nematode pests by the use of safe, environmentally acceptable, control measures. This research effort included biological and bioregulatory control strategies as well as biochemical and molecular genetics, population dynamics, simulation modeling, and ultrastructure studies that provide a basic understanding of nematode biology. In 1989, the nematode taxonomists were returned to the Nematology Laboratory and the Laboratory mission once again included research on nematode taxonomy and insect-parasitic nematodes.

Three ARS workshops have been held during this period to provide a forum to discuss relevant topics and a means of input into the planning process for future efforts in the area of biological control of soil pests. As a result, the Nematology Laboratory has a major commitment and defined mission in biological control of plant-parasitic nematodes.

E. BIOLOGICAL CONTROL OF PLANT PATHOGENS. By R. J Cook, G. C. Papavizas, H. W. Spurr, C. L. Wilson, R. D. Lumsden, and C. R. Howell

ARS research on biological control of plant pathogens during this last period has been conducted primarily at five locations: Work continued at the Beltsville, MD, and Pullman, WA, locations, and biological control studies on foliar pathogens and soilborne pathogens were begun at Oxford, NC, and College Station, TX, respectively, and three other locations, and on postharvest pathogens at Kearneysville, WV. Progress at each of these locations is discussed separately below.

Beltsville, Maryland. At the time of the ARS reorganization in 1972, the Microbiology Group was separated from the Mushroom Group, and was renamed Soilborne Diseases Laboratory (SBDL), which was placed in the newly created Plant Protection Institute at the Beltsville Agricultural Research Center. G. C. Papavizas was named Chief of the new research unit, serving as leader of the unit from 1972-92.

The next 21-year period could easily be divided into two periods, 1973-78 and 1979-93. The first of the two periods was characterized by the reintroduction of the "Mass Introduction and Augmentation" concept in plant pathology. As noted in sections above, the concepts of deliberate mass introduction and augmentation of beneficial organisms to control plant diseases was not very popular among plant pathologists, including those in USDA, because of early failures and because of

S. D. Garrett's first book (Garrett 1956). According to Garrett, a British plant pathologist, the attempt to increase the population of beneficial organisms in the soil was believed contrary to the ecological principle that the population reflects the habitat and that introduced changes are only transient. Although this concept is largely true, notable exceptions began to appear in plant pathology in the early 1970s. H. D. Wells, ARS plant pathologist at Tifton, GA, working with two Georgia scientists, was among the first to report use of *Trichoderma* preparations for field control of Sclerotium blight on peanuts (Wells et al. 1972). Their system was based on the introduction of the beneficial fungus to soil together with large amounts of organic matter to sustain augmentation of the antagonist.

During the 1973-78 period, scientists of the SBDL at Beltsville obtained biological control of black root rot of bean (*Thielaviopsis*) by adding to soil industrial by-products (soybean cake, castor pomace, cotton seed cake) high in unsaturated fatty acids. They also isolated unsaturated fatty acids from the plant rhizosphere. These acids stimulate spore germination of the pathogen followed by lysis and destruction of propagules before infection can take place (Papavizas and Kovacs 1973). Concurrently, the SBDL developed a control system for Aphanomyces root rot of peas with cruciferous amendments added to soil and unravelled the mechanism of action which involved the decomposing action of soil microbes (Lewis and Papavizas 1973).

An IPM breakthrough in the control of fruit rot of cucumber and root rot of bean caused by *Rhizoctonia* was also achieved in the SBDL at the same time. The IPM approach involved normal plowing (8-9 inches deep) instead of disking, use of the biological control agents *Trichoderma* and *Corticium*, and very small amounts of registered fungicides (Lewis and Papavizas 1980).

Impressive advancements in the biological control of plant diseases in the Beltsville unit occurred from 1979-93. The unit's name was changed from Soilborne Diseases Laboratory to Biocontrol of Plant Diseases Laboratory (BPDL) in 1987, and was placed in the Plant Sciences Institute (PSI), created in 1985. Upon retirement of Papavizas in 1992, R. D. Lumsden was appointed Research Leader of the BPDL. At the establishment of the BPDL in 1987, most importantly, all scientific and material resources of the laboratory were redirected towards one goal only, viz., biological control of plant diseases with emphasis on soilborne diseases.

During this last 15 year period, unit scientists discovered two unusual beneficial fungi, *Sporidesmium sclerotivorum* and *Teratosperma oligocladum*, on sclerotia of the soilborne plant pathogen *Sclerotinia* in soil at Beltsville. *Sporidesmium* parasitizes and destroys the survival structures (sclerotia) of *Sclerotinia* and can control this pathogen in the field for three consecutive years with a single application to soil (Adams and Ayers 1981; Ayers and Adams 1979, 1981; Uecker et al. 1978, 1980). The BPDL received a U.S. Patent (No. 4,246,258, 1982) on *Sporidesmium* and is now in the process of transferring the biological control technology to industry. At the same time, other BPDL scientists developed for the first time in plant pathology new genetic variants of the biological control agents *Trichoderma harzianum*, *T. viride*, *Gliocladium virens*, and *Talaromyces flavus* (U.S. Patent No. 4,489,161, 1984) that possess enhanced abilities to control plant diseases and resistance to MBC fungicides, a major group of commonly used pesticides (Papavizas et al. 1982; Papavizas and Lewis 1983). Also, the BPDL developed liquid fermentation technology and an innovative encapsulation system for slow release of biological control agents and for field delivery (U.S. Patent Nos. 4,668,512, 1987, and 4,724,147, 1988) (Fravel et al. 1985; Lewis and Papavzas 1987b; Lewis et al. 1985; Papavizas et al. 1984).

It was during this period that BPDL scientists established the importance of the chlamydospore of *Trichoderma* and *Gliocladium* in survival of these biocontrol agents in soil and in the eventual formulation of the biomass produced during liquid fermentation (Lewis and Papavizas 1984a; Papavizas et al. 1984). In 1984, the effectiveness of applying bran preparations containing young, actively-growing hyphae (3-day-old) of *Trichoderma* species and *G. virens* to reduce the pathogens

Rhizoctonia, *Pythium*, and *Sclerotium* was reported (Lewis and Papavizas 1984b, 1987a). For the first time, it was shown that these young hyphae (germlings) of the biocontrol fungi significantly reduced pathogen inoculum with a decrease in disease, whereas conidial preparations were ineffective.

In addition to these outstanding discoveries, BPDL scientists described potential commercial biological control systems for Sclerotium blight of bean (Papavizas and Lewis 1989b), Verticillium wilt of potato and eggplant (Marois et al. 1982), Rhizoctonia scurf of potato (Beagle-Ristaino and Papavizas 1985), Fusarium wilt of chrysanthemum (Locke et al. 1985), and Rhizoctonia and Pythium damping-off of ornamental plants (Lumsden and Locke 1989). In biocontrol studies of more basic nature, the mechanisms were elucidated by which the antagonists *Talaromyces* attacks *Verticillium* (Kim et al. 1988), *Sporidesmium* attacks *Sclerotinia* (Adams et al. 1985), *Trichoderma* and *Gliocladium* attack *Rhizoctonia* (Lewis and Papavizas 1987c; Lewis et al. 1991), and *Gliocladium* attacks *Pythium ultimum* (Lumsden et al. 1992; Roberts and Lumsden 1990). Also, research has been initiated to determine the genetic basis for biocontrol and for antagonist resistance to pesticides (Ossanna and Mischke 1990) as well as on the application of rhizosphere bacteria for biocontrol (Roberts et al. 1992). Considerable effort has also been given to the development of potential biocontrol fungi in the genera *Laetisaria*, *Stilbella*, and *Cladorrhinum* which have not previously been studied to any great extent (Lewis and Papavizas 1988, 1992, 1993).

In the culmination of several years of research effort on the part of BPDL scientists in cooperation with W. R. Grace Company, the first fungal biocontrol formulation developed in the United States against plant pathogens received registration by the Environmental Protection Agency (EPA) in 1991 (Lumsden et al. 1991). The formulation is an alginate prill (pellet) containing a food base (wheat bran) and biomass of *G. virens* (Gl-21) which is registered for use against Pythium and Rhizoctonia damping-off of vegetables and ornamental seedlings grown in commercial greenhouses (Lumsden and Locke 1989). The prill is produced by an industrial process and, in 1992, was test-marketed in several states. The use of the prill formulation on high-value field crops may eventually be feasible, since beneficial effects of the Gl-21 prill (GlioGard™) on diseases of tomato and pepper in the field caused by *Sclerotium rolfsii* were observed (Ristaino et al. 1991). A novel formulation consisting of vermiculite/bran and activated biomass of various isolates of *Trichoderma* spp. and *G. virens* has been patented recently by the BPDL (U.S. Patent No. 5,068,105, 1991) and shows potential against diseases caused by *Rhizoctonia solani* (Lewis et al. 1991).

Results of these and other biological control research activities of the Beltsville Laboratory also appear in various reviews and book chapters, some of which are: Adams and Ayers 1981; Fravel 1988; Harman and Lumsden 1990; Lewis 1991; Lumsden 1992; Lumsden and Lewis 1989; Lumsden and Papavizas 1988; Papavizas 1984, 1985, 1987; Papavizas and Lewis 1981, 1989a; Papavizas and Loper 1986; Papavizas and Lumsden 1980; and in the proceedings of Beltsville Symposium XVIII (Lumsden and Vaughn 1993).

Pullman, WA. A landmark event in biological control of plant pathogens occurred in 1974, with the publication of the first book wholly devoted to the subject. This book was coauthored by K. F. Baker, a retired University of California professor and ARS collaborator, and R. J. Cook, an ARS plant pathologist at the ARS Regional Cereal Disease Research Laboratory at Washington State University, Pullman (Baker and Cook 1974). A second book on the subject by the same two authors was published nine years later (Cook and Baker 1983).

Using the two-step approach outlined in the 1974 book, i.e., 1) to find effective antagonists, look where the disease does not occur but should, and 2) then isolate candidates from plant parts where protection is needed, scientists from the Pullman unit, working cooperatively with scientists from England and Australia, obtained evidence that the biological factor responsible for take-all decline in

wheat was transferable from soil to soil, and was active in the rhizosphere or possibly within the roots of the protected wheat. They isolated several flourescent *Pseudomonas* strains from the protected roots and showed the potential of these bacteria to duplicate the suppressive effect typical of soil from fields where take-all had declined (Cook and Rovira 1976). The Pullman scientists then showed that the soils change microbiologically, both quantitatively and qualitatively, toward higher populations of fluorescent *Pseudomonas* species inhibitory to the take-all fungus as the soil converts from conducive to suppressive during take-all decline (Weller and Cook 1983). They obtained the first experimental evidence in the field that take-all of wheat could be suppressed by simply treating the wheat seeds with one or more strains of inhibitory pseudomonads (U.S. Patent No. 4,456,684). They then demonstrated that Pythium root rot of wheat could also be suppressed to a significant degree by treatment of wheat seeds at planting with one or more strains selected for ability to inhibit this pathogen (U.S. Patent No. 4,647,533).

In 1987, Pullman scientists presented proof based on both genetic evidence and direct isolation from rhizosphere soil that the protection afforded wheat roots by at least two fluorescent *Pseudomonas* species resulted from ability of these species to produce phenazine-type antibiotics (Thomashow and Weller 1988). Soil microbiologists and plant pathologists had debated since the 1940s and earlier whether antibiotics played any role in the ecology of soil microorganisms or in biological control of root pathogens by antagonists. Pullman scientists used Tn5 mutagenesis to produce mutant strains identical to the parental (wild-type) strain but unable to produce phenazine because of the inactivization of a single gene (Thomashow and Weller 1988). These strains retained some residual biological control activity against take-all when introduced into the rhizosphere of wheat by seed inoculation (indicating more than one mechanism of inhibition), but they were markedly less active than their parents. Restoration of antibiotic production by complementing the inactivated DNA sequence with DNA introduced from a library of parental DNA coordinately and fully restored biological control activity. The Pullman workers then demonstrated by use of analytic chemical techniques that both the parent and complemented strains, but not the mutant strain, produced phenazine in the rhizosphere of wheat growing in natural soil (Thomashow et al. 1988).

The ARS group at Pullman in cooperation with scientists at the Monsanto Company, St. Louis, MO, have subsequently demonstrated a role of the antibiotic phloroglucinol in the biological control of wheat take-all by other strains of fluorescent pseudomonads (Vincent et al. 1991). Again, the tools of recombinant DNA (rDNA) technology were used to produce antibiotic-negative mutants, restore antibiotic producing ability, and prove the role of antibiotic production in biological control.

The demonstrations by the ARS unit at Pullman that wheat root diseases can be controlled by microorganisms introduced into the rhizosphere parallels several similar studies by workers in other federal (see College Station, TX, paragraphs below) and state experiment station laboratories, private companies, and in other countries on biological control of plant pathogens with plant-associated microorganisms. The first and still most successful example of this approach to biological control is work in Australia just previous to this period on control of crown gall caused by *Agrobacterium tumefaciens*, by prior establishment on the plant of populations of avirulent strains of *Agrobacterium radiobacter* K84 (New and Kerr 1972). These types of studies, and the new tools of rDNA technology, have ushered in approaches to "biological control" very different from the original approaches of C. V. Riley and other early entomologists. This in turn has reopened discussions of previous years over the definition of the term "biological control" (see Introduction to this history).

College Station, TX. Research on the biological control of cotton seedling diseases was initiated at the Cotton Pathology Research Unit (CPRU) of the Southern Plains Area in 1978 when C. R. Howell was relieved of work on Verticillium wilt and given responsibility for seedling disease research. By 1979, work was completed on the use of a strain (Pf-5) of *Pseudomonas fluorescens* to control cotton damping-off incited by *Rhizoctonia solani* (Howell and Stipanovic 1979). Control was ascribed to

production of the antibiotic pyrrolnitrin that was isolated and characterized from the bacterium. In 1980, strain Pf-5 of *P. fluorescens* was shown to suppress cotton seedling damping-off incited by *Pythium ultimum*, and control was ascribed to production of the antibiotic pyoluteorin by the bacterium (Howell and Stipanovic 1980). Also, in 1980-82, the use of the mycoparasitic fungus *Gliocladium virens* to control damping-off of cotton seedlings incited both by *R. solani* and *P. ultimum* was described (Howell 1980, 1982).

In 1983, an antibiotic strongly inhibitory to *P. ultimum* was isolated and described from a strain of *G. virens* (Howell and Stipanovic 1983). This newly discovered compound was named "glioviren," and its production was demonstrated to be a major factor in suppression of Pythium damping-off by *G. virens*. In 1984, a potent phytotoxin was isolated from cultures of *G. virens* and shown to cause necrosis of emerging seedling radicals (Howell and Stipanovic 1984). This compound was identified as viridiol, a reduced form of the antibiotic viridin, and preparations of *G. virens* containing this material were shown to be effective in controlling weed infestations in cotton field soil. (All identification and characterization of compounds isolated from bacteria and fungi were done in collaboration with R. D. Stipanovic, ARS, College Station.) In 1987, it was demonstrated, through the production of parasitic deficient mutants, that mycoparasitism was not an important mechanism in the control of *R. solani*-incited seedling disease by *G. virens*, and disease control was ascribed to antibiotic production by the antagonist (Howell 1987).

From 1988-90, collaborative research with Ciba-Geigy Corporation resulted in patent applications for use of six bacterial strains for control of seedling damping-off, the use of bacterial and fungicide combinations for seedling disease control, and for genes coding for or promoting antibiotic synthesis in bacteria. Also, the primary mechanism in the biocontrol of Pythium damping- off of cotton seedlings by *Enterobacter cloacae* was found to be the production of ammonia from seed exudates by the bacterium (Howell et al. 1988). In 1991, strains of *G. virens* were separated into two distinct groups on the basis of their antibiotic production *in vitro*; Q strains were found to produce gliotoxin, while P strains produced only gliovirin (Howell and Stipanovic 1991). Also, a seed treatment method was developed to control Pythium damping-off of cotton seedlings with *G. virens* (Howell 1991); biocontrol efficacy depended on the strain of the fungus and the substrate on which it was grown. A method was developed to suppress phytotoxin (viridiol) production in cultures of *G. virens* by the addition of low concentrations of sterol-inhibiting fungicides to the growth medium and to the air dried preparations to prevent subsequent production (Howell and Stipanovic 1993); this does not suppress the fungal growth rate or production of antibiotics.

Oxford, NC, and other locations. Research on the biological control of foliar plant pathogens has been conducted at four locations during this period. Research at the ARS Crops Research Laboratory (prior to 1987 the Tobacco Research Laboratory) at Oxford, NC, under the leadership of H. W. Spurr, was conducted 1970-present. One of the primary objectives of this research has been to develop practical biological control methods or strategies for foliar diseases of tobacco and peanut. Research began in 1970 with the characterization of epi- and endophytic fungi in tobacco leaves in relation to the development of Alternaria leaf spot disease (Spurr and Welty 1975).

Inoculations of leaves with spores of nonpathogenic *Alternaria alternata* isolates decreased infections by pathogenic fungi (Spurr 1977). Various possible mechanisms for this biological control activity were considered, including toxin production, phytoalexin induction in the plant, and nutrient competition on or within the plant (Blakeman and Fokkema 1982). The mycelial growth of nonpathogenic *A. alternata* on the leaf surface was often colonized by bacteria which caused lysis. It was considered that these bacteria, in conjunction with the nonpathogenic *A. alternata*, controlled pathogenic *A. alternata*. Two investigations were then initiated.

In one test, a 70% ethanol treatment of leaf tissue was devised which decreased normal, resident, bacterial and fungal leaf microflora of greenhouse-grown tobacco leaf tissue by 91 and 100%, respectively (Spurr 1979). Protective biological control of Alternaria leaf spot resulting from application of nonpathogenic *A. alternata* spores was effective on both ethanol-treated and untreated leaf tissue, indicating nonpathogenic spores controlled leaf spot without interacting with other leaf surface microorganisms; but this does not mean that such interactions do not occur, thereby altering control efficacy.

In the second study, tobacco leaf surface bacteria were isolated and bioassayed for control of *A. alternata* (Fravel and Spurr 1977). One active isolate, identified as *Bacillus mycoides* (as *cereus* var. *mycoides*), prevented leaf spot disease in a controlled environment. After this discovery, bacterial strains, such as *Bacillus thuringiensis* (Bt), sold in commercial formulations to control insects, were tested. The Bt strain HD-1 was found to be equivalent to *B. mycoides*. A gram negative bacterium isolated from a pathogenic corn fungus in Ohio (Sleesman and Leben 1976), identified as *Pseudomonas cepacia* (Pc 742), was also active. The gram negative Pc 742 and the gram positive HD-1 strains were field tested for control of Alternaria leaf spot and peanut Cercospora leaf spot caused by *Cercospora arachidicola*. The tests in peanuts demontrated that this biological control approach was inconsistent, control varying from 20 to 70%, being more efficacious than some fungicides, but poorer than recommended fungicides (Knudsen and Spurr 1987). Bacterial numbers decreased dramatically following application to foliage.

Survival of antagonists introduced into the phylloplane is required to effect control, and equals the importance of the antagonistic potential of the biological control organism. It is suggested that the most effective method of foliar biological control is to begin with a bacterial epiphyte, one well-suited to the leaf surface environment and known to multiply (Leben 1974; Knudsen and Spurr 1988). Research on the phylloplane (Spurr 1990) is continuing at Oxford, which is the only ARS location where such research has been done (until recently; see below).

An important event for biological control of foliar pathogens occurred in 1984 with the Symposium entitled "Biological Control Strategies in the Phylloplane" held in conjunction with the annual meeting of the American Phytopathological Society in August of that year at Guelph, Ontario. Participants of this Symposium included ARS scientists from the Oxford laboratory and a number of scientists from several state agricultural experiment stations and U.S. and Canadian universities; the proceedings of the symposium were published in 1985 (Windels and Lindow 1985).

A second plant pathologist, V. J. Elliott, was recruited in 1990 at Oxford, the first plant pathologist employed by ARS to research biological control of foliar pathogens full time. The main thrust of research currently (1993) in progress is to develop an extensive description of epiphytic and endophytic microorganisms of foliage with emphasis on peanut and tobacco. The response of phyllosphere microfloral populations to environment and other dynamics must be understood prior to introducing microbes for control of foliar diseases.

There are several ARS projects on biological control of foliar pathogens that have been part of other research programs or are of recent origin. Research at Beltsville, MD, was conducted at the Fruit Laboratory by E. L. Civerolo from 1984 until 1988, when he became National Program Staff Leader responsible for plant pathology. He studied and characterized bacterial strains of *Xanthomonas campestris* pvs. *pruni* and *citri,* pathogens of fruit and foliage of peach and citrus trees, respectively. Bacteriophages, viruses which lyse bacterial cells, were isolated, identified and tested as biological control agents for these bacterial pathogens. The results demonstrate the feasibility of biological control using pruniphage as an alternative disease management strategy to chemical sprays (Randhawa and Civerolo 1986). Research at the Microbiology and Plant Pathology Laboratory at Beltsville resulted in the discovery and patenting of a strain of *Bacillus subtilis*, which when sprayed

on bean leaves controls rust (Baker and Stavely 1986). Various formulations were tested in field studies. Effective control was obtained only if the bacterial formulation was applied every other day. Studies of the mechanisms were also made but were unsuccessful. These discouraging events have led to a discontinuation of this research.

Cooperative research at the ARS U.S. Regional Pasture Research Laboratory at University Park, PA, and Pennsylvania State University, has resulted in the isolation of bacterial strains from ecosytems for testing as biological control agents for forage legume diseases. Emphasis is on control of alfalfa leaf spot caused by the fungal pathogen *Phoma medicaginis*, on survival of bacteria following introduction to leaf surfaces, and on evaluation of the impact of various formulation ingredients and combinations of bacterial strains (Jones et al. 1987).

Various wheat lines, resistant and susceptible to Septoria leaf blotch and Pyrenophora tan spot, are being evaluated for their potential to host leaf colonizing bacteria antagonistic to these fungal pathogens at the ARS Plant Science and Water Conservation Research Laboratory at Stillwater, OK. Of the leaf colonizing bacteria isolated, one strain of *Pseudomonas fluorescens* was inhibitory *in vitro* to the growth of the above fungal pathogens. Two toxic products were isolated from this bacterial strain (Gough and El-Nashaar 1989).

Kearneysville, WV. Research on the biological control of postharvest pathogens was conducted primarily at the ARS Appalachian Fruit Research Station (AFRS) at Kearneysville, WV, during this period. Chemical pesticides have been one of the major methods for controlling postharvest losses of food. Incidents in the 1980s involving food contamination with pesticides heightened public awareness of pesticide residues in food. In addition, a 1987 National Academy of Sciences report on food safety (NRC, 1987) indicated that fungicides used to preserve food posed more of an oncogenic risk than other pesticides. Also, resistance of microorganisms to fungicides applied after harvest has occurred rather frequently. Thus a critical need developed for alternatives to synthetic fungicides for the control of postharvest diseases of fruits and vegetables. The biological control research program of the AFRS has been directed toward addressing this need. The pathology group at the AFRS, under the initial leadership of C. L. Wilson, has since 1984, accelerated and expanded its research program on the biological control of postharvest diseases and fire blight. The program has involved the use of: 1) antagonistic microorganisms; 2) natural fungicides; and 3) induced resistance as alternatives to synthetic fungicides. Some results of this research are summarized below.

In a 1982-84 postdoctoral study by P. L. Pusey in association with the AFRS, an isolate of *Bacillus subtilis* was discovered that effectively controlled brown rot of peaches caused by *Monilinia fructicola*. A patent was issued covering this process and a license has been issued to ISK Technologies to develop a marketable product. (Pusey and Wilson 1984; Pusey et al. 1986, 1988). This was the first patent of a microorganism to control postharvest diseases of fruits or vegetables.

In 1984, research was initiated on the biological control of pome fruit rots at Kearneysville by W. Janisiewicz. A number of antagonists were discovered that are effective against *Botrytis cinerea*, *Penicillium expansum*, and Mucor rots of apple and pear, and patents were issued on the use of the antagonists *Acremonium breve* and *Pseudomonas cepacia* against pome fruit rots (Janisiewicz 1987, 1988 a and b; Janisiewicz and Roitman 1988). The firm EcoScience has licensed these patents and is attempting to commercialize this technology.

In cooperative ARS-Israeli research under the Binational Agricultural Research and Development (BARD) program, a number of antagonistic yeasts active against postharvest rots of citrus and deciduous fruits have been discovered. Two of these, *Candida guilliermondii* (strain US-7) and *C. oliophila*, were found to have broad-spectrum activity against a number of rot fungi on a variety of fruit including citrus, pome fruit, grapes, persimmon, and tomatoes (Wilson and Chalutz 1989;

Wilson et al. 1993). Ecogen has licensed the patents on these organisms and is attempting to commercialize them.

In 1987, research was initiated at the ARS Blueberry and Cranberry Research Center at Chatsworth, NJ, to find antagonists that would control postharvest rots of cranberries and blueberries. One antagonist has been found that is effective against Alternaria rot of blueberries. In 1988, studies were begun by T. van der Zwet at the AFRS to find antagonists for biological control of the fire blight organism, *Erwinia amylovora*. The probability that streptomycin presently used to control fire blight may be withdrawn from the market makes this research particularly timely.

Other research at the AFRS includes studies by M. Wisniewski on the mode of action of various antagonists of fruit rot pathogens. Cooperative research has shown that an antagonist of Rhizopus rot of peaches, *Enterobacter cloacae*, and the broad-spectrum antagonist *Candida guilliermondii* (strain US-7) express their antagonism primarily through nutrient competition. It has also been shown that some yeast antagonists are able to attack rot pathogens directly and degrade their cell walls (Wisniewski et al. 1988, 1989, 1991 a and b; Droby et al. 1989).

AFRS researchers are conducting cooperative research with other U.S. and foreign investigators. A large scale test was conducted in cooperation with the ARS Southeastern Fruit and Tree Nut Research Laboratory at Byron, GA, to evaluate *Bacillus subtilis* for brown rot control under commercial conditions.

Cooperative research with Cornell University concerns cytological experiments on antagonist/host/pathogen interactions. Cooperators at the ARS Western Regional Research Center in Albany, CA, and the ARS Agricultural Research Center, Athens, GA, have helped characterize the antibiotics produced by two of the biological control agents found at the AFRS. Testing under storage conditions of some of the apple pathogen antagonists is underway at the ARS Tree Fruit Research Laboratory at Wenatchee, WA. The AFRS is also cooperating with the Volcani Institute in Israel and the Institute for Crop and Food Research, Levin, New Zealand. And research has been initiated at Kearneysville on the microecology of fruit surfaces as it relates to biological control, and on resistance in fruit that may be induced by antagonistic microorganisms and low-dose UV light.

In addition to the references noted above, results of the research discussed above and other biological control studies of the pathology unit at the AFRS can be found in many of its publications; see Chalutz et al. 1988 a and b; Chalutz and Wilson 1990; Wilson 1977, 1989; Wilson and Chalutz 1989; Wilson and Pusey 1985; Wilson et al. 1987 a and b; Wisniewski et al. 1988, 1989; see also Sanchez 1990. Several major reviews of the subject of biological control of postharvest diseases of fruits and vegetables have been authored by AFRS scientists (Janisiewicz 1988b, 1990; Wilson and Wisniewski 1989, 1992, 1994; Wisniewski and Wilson 1991; Wilson et al. 1991).

In September 1990, an international workshop sponsored by the BARD program was hosted by the AFRS on the "Biological Control of Postharvest Diseases of Fruits and Vegetables." This workshop brought together for the first time government and university reseachers with industry representatives who were interested in developing alternatives to synthetic fungicides for the control of postharvest diseases (Wilson and Chalutz 1991). A number of cooperative research projects and agreements resulted from this meeting.

CHAPTER V
1953-1993
FOREST SERVICE - OVERVIEW
By Mary Ellen Dix

The use of parasites, predators, and pathogens to control insect, disease-causing, and weed pests of trees is not a new idea in the United States. Natural enemies have been imported or manipulated to control tree pests for over 90 years. Prior to 1953, researchers of the U.S. Department of Agriculture's (USDA) Bureau of Entomology and Plant Quarantine (BEPQ) were responsible for biological control research and implementation on native and exotic forest pests. Their studies were designed to obtain information on the identities, distributions, and biologies of natural enemies of insects and pathogens of native trees, and of exotic pests in their home range whenever possible. Many parasites and predators were introduced and released for control of forest pests, especially pests of European origin (Clausen 1956, 1978; Schaffner 1959; Dowden 1962).

In 1954, the USDA was reorganized and the responsibility for biological control of forest pests was transferred from the BEPQ to the Forest Service. Many entomologists and pathologists, including P. B. Dowden, B. H. Kennedy, C. L. Massey, J. A. Beal, F. G. Hawksworth, and N. D. Wygant transferred from the Bureau to the Forest Service where they continued their biological control research and implementation activities. However, many research papers, reports, and parasite releases during the late 1950s and early 1960s were the result of initial work by the Bureau (Clausen 1956; Schaffner 1959; Dowden 1962; see Chapters I and II).

This overview and Appendix III summarize biological control research and application efforts in the Forest Service from 1953 to present. The overview briefly describes the trends and directions of biological control; however, it is not all inclusive. Appendix III contains detailed information on biological control activities, arranged by pest, and includes literature references to the studies briefly reported in this overview.

Organization of the Forest Service. In 1954, the Forest Service was divided into three branches: Research, State and Private Forestry, and the National Forest Administration. All insect and disease research and survey activities were administered by the Research branch. Forest Insect Research and Forest Disease Research staffs in the Washington Office (WO) were separate staffs with their own directors, but were administered by the Assistant Chief for Research. In about 1960, Forest Pest Control (survey) was split from Research and placed in State and Private Forestry, Forest Insect and Disease Management (FIDM). The Insect and Disease Research staffs were later combined into Forest Insect and Disease Research (FIDR). The Director of FIDR reported to the Associate Deputy Chief for Research who in turn reported to the Deputy Chief for Research. During the 1960s, the number of Forest Experiment Stations decreased from nine to eight in addition to a Forest Products Laboratory. During this same period the number of Regions decreased from ten to nine. Each Experiment Station contained numerous research laboratories, and each Region had several field offices (Steen 1976).

State and Private Forestry (Forest Health) was and remains responsible for providing leadership and assistance for the protection, management, and effective use of 574 million acres of non-federal forests and grasslands (Rietveld 1993). In 1975, Forest Insect and Disease Research (FIDR) became a separate organization under the Associate Deputy Chief in the Office of the Deputy Chief for State and Private Forestry (Steen 1976). The name was shortened to Forest Pest Management (FPM) during the 1980s and changed to Forest Health in 1993.

The Forest Service is currently divided into six Branches: Research, State and Private Forestry, National Forests, International Forestry, Administration, and Programs and Legislation. Responsibility for biological control of forest pests falls within the missions of both the Research and State and Private Forestry (Forest Health) Branches. International Forestry facilitates and helps coordinate foreign activities of these two branches.

Before 1980, the WO staffs strongly influenced the direction of biological control research and implementation activities in all Experiment Stations and Regions. After 1980, the WO staffs served in an advisory role, while the Station Directors and Regional Foresters were responsible for formulating program directions.

Biological Control Activities, 1954-1969. The overall mission of FIDR from 1954 to 1970 was the "development of safer and more economical methods of direct and preventive control of forest pests" (USDA Forest Service 1962). This mission included completion and publication of results of studies and surveys initiated under the BEPQ. Such studies centered on identifying forest pests, determining their distribution and documenting aspects of their biologies and that of their natural enemies. For example, J. V. Schaffner, Jr., published information on the identity, distribution, and biology of parasites reared from microlepidoptera in the northeastern United States between 1915 and 1959 (Schaffner 1959; Clausen 1978). The passage of the Forestry Research, State Plans, and Assistance Act (McIntire-Stennis) in 1962 facilitated these kinds of efforts by authorizing federal support for forestry research on the biological control of forest pests at land grant universities.

Public Law 480 (PL-480) projects also were used to help identify exotic parasites of introduced forest pests in their native land. In 1960, ten PL-480 projects were funded in five countries. By 1965, there were 27 projects in nine countries (Finland, Poland, Spain, Pakistan, India, Yugoslavia, Brazil, Colombia, and Uruguay). Through these projects, parasites, predators, and pathogens were identified for gypsy moth, European pine shoot moth, "tip moths" (*Rhyacionia* spp.), balsam woolly adelgid, smaller European elm bark beetle, and various sawflies. (Scientific names and orders and families of organisms mentioned in this Chapter are listed in the Index.) In addition, Agricultural Research Service (ARS) scientists at overseas laboratories collected natural enemies that were subsequently identified at their Systematic Entomology Laboratory, headquartered at Beltsville, Maryland. Candidate natural enemies were shipped to the ARS quarantine facilities in Moorestown, NJ (Newark, DE, after 1973), for initial clearance and biological evaluations before being sent to the appropriate Forest Service facility for further biological evaluations and impact studies.

Most of the insect pests and pathogens targeted for biological control within the different Experiment Stations and Regions caused localized problems; however, a few were of regional, national or international importance (Table 3). In the Pacific Northwest, including Alaska, parasites were released for control of the Douglas-fir beetle and larch casebearer. Concurrently, natural enemies were identified for the western blackheaded budworm, western spruce budworm, hemlock looper, Douglas-fir tussock moth, and the pine tip moths (*Rhyacionia* spp.). In California and the Pacific Islands, scientists identified hymenopterous and nematode parasites, and avian predators of seed and cone insects and beetle borers. Scientists also evaluated the impact of *Bacillus thuringiensis* (*Bt*) on populations of the "Great Basin tent caterpillar". Parasites, birds, nematodes and other natural enemies of spruce budworms, spruce beetle, Engelmann spruce weevil, and Douglas-fir beetle were

identified by scientists in the Intermountain and Pacific Northwest Regions. Scientists working within the Stations and Regions now within the Rocky Mountain Station identified nematodes, mites, and arthropod parasites and predators of the western spruce budworm, spruce beetle, and various pine bark beetles.

In the eastern United States, natural enemies were released for control of the smaller European elm bark beetle, balsam woolly adelgid, larch sawfly, red pine scale, European pine shoot moth, European pine sawfly and elm spanworm. *Bt* strains were evaluated for control of the "eastern" spruce budworm and gypsy moth, as were other pathogens. Predators and parasites were identified for cankerworms, gypsy moth, "forest budworms", southern pine beetle and other bark beetles. Southern biological control efforts were primarily concerned with identifying natural controls of the black turpentine beetle, southern pine beetle, hardwood borers, and *Cydia* (=*Laspeyresia*) spp. See Appendix III for details of these programs, and of those noted below.

Biological Control Activities, 1970-1979. Biological control efforts in the 1970s were shaped by several events. During the early 1970s, severe outbreaks of the gypsy moth, southern pine beetle, and Douglas-fir tussock moth resulted in a public and congressional call for their suppression. In 1972, EPA banned the use of DDT, a commonly used and potent insecticide, because it was hazardous to the environment. The publication of "Silent Spring" (Carson 1962) and other environmental publications, increased public concern about the environment and its pollution, particularly by chemical pesticides. Conversely, the adverse impacts of imported pests, and potential adverse impacts of imported natural enemies, also became of concern. During the 1970s, the Forest Service approached pest control in a more systematic manner than previously in the 1950s and 1960s. However, only a few serious pests were targeted. The concept of integrated pest management (IPM) gained popularity in forestry. A variety of methods and a highly flexible planning base were used to cope with pests on a long-term basis. IPM enabled forest resource managers and pest control specialists to manage trees for specific objectives (Miller et al. 1975).

Also, during the 1970s, biological control research was slowly deemphasized as research efforts increased on pheromones, impacts, biologies, and chemical controls of major insect pests and pathogens (Table 3). Identification of natural enemies of many forest insects continued, but usually as a secondary endeavor. Most biological control research was targeted toward understanding the impacts of natural enemies on pest population dynamics, modelling natural enemy-pest interactions, or developing techniques for suppressing pest populations with microbials. Nuclear polyhedrosis viruses (NPVs) were successfully used against several sawflies and the Douglas-fir tussock moth, whereas *Bt* preparations gave encouraging results in experimental studies against gypsy moth, spruce budworms, forest tent caterpillar, and other defoliators (Abrahamson and Harper 1973). Natural enemies or potential enemies were identified for mountain pine beetle, dwarf mistletoes, Armillaria root rot, southern pine beetle, Douglas-fir tussock moth, Douglas-fir beetle, spruce budworm, gypsy moth, seed and cone insects, *Fusarium* spp., sawflies and a few minor pests. Control programs with parasites were implemented for the smaller European elm bark beetle and spruce budworm and with pathogens for southern pine beetle, gypsy moth, and Douglas-fir tussock moth.

The 1970s are best known for the accelerated research and development programs ("big bug programs") to control severe outbreaks of the gypsy moth in the Northeast, the southern pine beetle in the South, and the Douglas-fir tussock moth in the Pacific Northwest. Between 1970 and 1973, outbreaks of these three pests severely damaged forests, causing huge losses in forest revenues. In the fall of 1973, the USDA Assistant Secretary of Agriculture for Conservation, Research and Education requested that the Forest Service (FS), Cooperative State Research Service (CSRS), Agricultural Research Service (ARS), and Animal and Plant Health Inspection Service (APHIS) all coordinate short-term programs to reduce damage caused by these three forest pests (Bayley 1981). In the fall of 1974, Congress appropriated over $6 million above existing funds for major forest insect and disease

programs on these three pests. Research and development emphasis and objectives were slightly different for each accelerated regional program (Shea 1985).

The Expanded Southern Pine Beetle Research and Application Program focused on understanding the population dynamics of the beetle; using beetle-killed trees, silvicultural techniques for prevention, and cut and leave techniques; developing integrated models for predicting impacts, population levels and forest susceptibility; and developing survey and suppression techniques with pheromones and insecticides. Research on potential biological control agents was not immediately addressed unless program management viewed the biological agents as critical to understanding the population dynamics of the pest, or to predict population trends (Thatcher 1981). Consequently, in-depth research on natural enemies was limited to a few species of predators and parasites.

The Gypsy Moth Expanded Research and Application Program called for use of broad-based pesticides to control the moth; increased foreign exploration for parasites and predators; developmental research on microbial control; and increased research to analyze and predict changes in pest populations. In cooperation with ARS, a nuclear polyhedrosis virus (NPV) was produced *in vivo*. Eventually the virus was tested for environmental persistence, epidemiology, and efficacy, and later aerially applied to outbreaks. After completing safety evaluations per EPA regulations on safety testing of insect viruses, the gypsy moth NPV product (Gypchek™) was approved by EPA in 1978. During the 1970s, a few exotic parasites of gypsy moth were imported for evaluation and released by Forest Service scientists. None of these are at this time considered established. However, intensive field and laboratory trials collected data on the behavior, host selection, site preferences, and other information needed to evaluate impact and management of the parasites: *Brachymeria intermedia*, *Cotesia* (=*Apanteles*) *melanoscelus*, *Blepharipa pratensis*, and *Compsilura concinnata*. Augmentative release of these parasites in the Northeast also showed mixed results. Releases of other parasite species in combination with *Bt* or NPV applications also had mixed results. In one study, where *Bt* was used in combination with *C. melanoscelus*, gypsy moth populations were lower and foliage protection was higher than when *Bt* was used alone. This parasite also has been implicated in the transmission of NPV (Doane and McManus 1981). Following the releases, research was accelerated on selection and evaluation of strains, formulations, and application techniques for *Bt*, NPV, and other pathogens.

The Douglas-fir Tussock Moth Accelerated Research and Development Program focused on developing effective suppression techniques with NPV and *Bt*; obtaining information on natural enemies needed to predict population levels; and impacts of the pest. Intensive research by the insect pathology project personnel at Corvallis, OR, focused on virus strain identification, virus potency trials, and assessment of impacts on non-target organisms. Large-scale forest tests obtained data to optimize viral dosage, develop application strategies, and receive EPA approval for the registration of the NPV BioControl-1™ in 1976. Parasites and predators of Douglas-fir tussock moth were identified and their impacts on pest populations were assessed at high and low host population levels (Torgersen 1977, 1981; Mason and Overton 1983; Mason and Torgersen 1983; Mason et al 1983). Both the Douglas-fir tussock moth and gypsy moth programs were redirected into the spruce budworm program after the former terminated in the late 1970s.

In 1977, the Canada/United States Spruce Budworms Program (CANUSA) was established similar to the Douglas-fir tussock moth and gypsy moth programs. This six-year research, development, and application program actively explored the identity and role of natural enemies in regulating pest populations. Methods were developed for suppressing "eastern" and western spruce budworm populations with natural enemies (Winget 1985).

Biological Control Activities, 1980-1986. Funding for Forest Service insect and disease research (FIDR) increased slightly during the 1980s. However, FIDR funding in terms of constant dollars

decreased by over 20% (Sesco 1992). FIDR was extensively reorganized and biological control research in the Forest Service came upon hard times. Research work units were merged and some programs were consolidated into centers while others were eliminated. As a consequence of such program reorganization, there were significant losses of qualified scientists working in biological control. F. B. Lewis and A. T. Drooz retired and other positions were lost. Many scientists were assigned to positions that did not include biological control. Such scientists had not only been instrumental in the development of biological control research within the Forest Service, but they also were pioneers in biological control of specific insects and diseases. Because of these changes, biological control research was reduced by the mid-1980s, and consequently limited to only a few locations and projects. Studies to identify and evaluate natural enemies diminished to secondary priority among other research areas.

In 1980, a five-year Integrated Pest Management Program for Bark Beetles and Diseases of Southern Pines was initiated to complete research and transfer technical information from the Expanded Southern Pine Beetle Research and Application Program. This program also began developing an integrated southern pine pest management system for several species of bark beetles (southern pine beetle, black turpentine beetle, and *Ips* spp. "engraver beetles") and disease complexes (fusiform rust, annosus root rot, and littleleaf disease) of southern pines. Information on natural enemies was collected and summarized to improve the accuracy of population dynamics models (Shea 1985; Branham and Thatcher 1985). Findings and activities of these "big bug programs" are summarized by Sanders et al. (1985), Thatcher et al. (1981), and Doane and McManus (1981). These publications also listed research needs for improving methods of coping and controlling these insects.

By 1982, 264 species and strains of parasites and predators were imported and released against 60 species of introduced and native tree pests. In 1981, coccinellids were released in young cottonwood plantations in Mississippi to control the cottonwood leaf beetle (Solomon and Neel 1985; Neel and Solomon 1985). During the 1980s, Forest Service entomologists visited the People's Republic of China to identify natural enemies of "Asian" gypsy moth. They conducted preintroduction evaluations and developed a long-term project with Chinese scientists to identify alternate host requirements for maintaining parasite populations. Although parasite species from the China were sent to the United States, none were released. During this same period, a research program on natural enemies of exotic forest weeds in Hawaii was initiated and several foreign natural enemies were identified and released. Parasites of the larch casebearer continued to be released in the Northwest and survival was monitored for released parasites of both the larch casebearer in the Northwest and larch sawfly in the Northeast. Research was well underway to determine the effect of parasites and predators on the population dynamics of gypsy moth, Douglas-fir tussock moth, "eastern" and western spruce budworms, mountain pine beetle, and southern pine beetle.

By the mid-1980s, nuclear polyhedrosis virus (NPV) sprays were developed in Canada for use against the European pine sawfly, Virginia pine sawfly, and Swaine jack pine sawfly, redheaded pine sawfly, forest tent caterpillar, European spruce sawfly, and other pests (Drooz 1985). A baculovirus production facility was established at the Forest Service Laboratory in Corvallis, OR, and used to produce viral insecticide for the Douglas-fir tussock moth.

After termination of the accelerated gypsy moth research program, biological control research continued at the Northeastern Forest Experiment Station's research laboratories at Hamden, CT, Morgantown, WV, and Delaware, OH. Northeastern Area and Southern Region offices of Forest Health in West Virginia, New Hampshire, and North Carolina were responsible for the transferring of research technology through demonstrations and other applications of research. Southern pine beetle research continued at Pineville, LA. Spruce budworms research was conducted by units located in New England and the Pacific Northwest.

Between 1980 and 1985, Forest Service CANUSA research on the "eastern" and western spruce budworms concentrated on the role of parasites, predators, antagonists, and pathogens in the population dynamics of the pests. In these studies, avian, arachnid, and formicid predators were found to be influential in regulating budworm populations. Inundative release of parasites were unsuccessful because the parasites failed to become established. Cooperators refined the application techniques and formulations of *Bt*. A 1984 international symposium held in Bangor, ME, resulted in a summarization of the research results of Forest Service, state, and Canadian scientists. This information was used to develop management strategies for the budworms that integrated biological, chemical, and silvicultural control techniques (Sandors et al. 1985).

Research on biological control of forest diseases focused on: 1) evaluating fungal interactions of *Trichoderma* spp. with *Phellinus weirii* and *Armillaria* spp.; 2) assessing the ability of hypovirulent isolates to control chestnut blight and other virulent cankers; and 3) the ability of *Streptomyces* spp. to control Dutch elm disease. Mycorrhizal fungi were identified and their host ranges, physiologies, and ecological diversities were assessed. Scientists at the Forest Products Laboratory evaluated Polyoxin D™ for control of wood-staining mold and decay fungi.

Biological Control Activities, 1987-1993. By 1986, approximately 13% of the FIDR research budget was devoted to biological control research. This research effort was concentrated on insect pests (75%), tree diseases and wood decay (17%), and weed control (8%) (Stewart 1989). In October 1987, Forest Service project leaders met with the FIDR staff in Washington to discuss current and planned programs, and to identify priority areas for research. This information was used to develop a ten-year plan to guide FIDR into the twenty-first century, ensure that management decisions during the 1990s were consistent with national needs and priorities, and provide a framework for future planning. The plan released in August 1989 called for research focus on pests of national concern and on new research technologies. Centers would be developed for concentrated research to develop new technologies. This plan called for: 1) fundamental research to determine how interactions among hosts, pests, natural enemies, and the environment affected the frequency and severity of pest outbreaks; 2) operational research to develop effective and environmentally safe microbial agents for non-chemical control of insect and disease pests; and 3) the development of control tactics using parasites and predators either through inundative or augmentative releases.

Research on interactions among plant hosts, pests, natural enemies, and the environment was located in Lincoln, NE (Rocky Mountain Forest and Range Experiment Station (RM)), Pineville, LA (Southern Forest Experiment Station (SO)), and Corvallis, OR (Pacific Northwest Forest and Range Experiment Station (PNW)). Development of effective and environmentally safe microbial agents was concentrated at Hamden, CT (Northeastern Forest Experiment Station (NE)), Delaware, OH (NE), East Lansing, MI (North Central Forest Experiment Station (NC)), and Corvallis, OR (PNW). Research to develop suppression tactics with parasites was concentrated in Hamden, CT (NE), Pineville, LA (SO), Corvallis, OR (PNW), and Hawaii (Pacific Southwest Forest and Range Experiment Station (PSW)).

In 1988, a strategic plan on "Forest Health Through Silvicultural and Integrated Pest Management" was developed by WO staffs in response to congressional concern about the continued impacts of gypsy moth, southern pine beetle, mountain pine beetle, spruce budworms, root diseases, and atmospheric deposition on forest health. Congress also was concerned about the balance between short-term, commodity-oriented pest suppression projects and long-term investment in prevention and research. This plan decentralized Forest Pest Management Regional Offices, increased the number of regional offices (8 to 18) and established 27 new permanent positions nationwide. A cooperative Forest Health Monitoring Program was established by the Forest Service and the Environmental Protection Agency. WO Forest Pest Management also allowed the Forest Service to

continue production of Gypchek™, a biological insecticide for gypsy moth, until it could be produced commercially.

In 1990, Congress amended the Cooperative Forestry Assistance Act of 1978 and strengthened the Forest Service programs concerned with forest health monitoring, technology development, and promotion of management measures to protect forest health. The strategic plan, "Healthy Forests for America's Future", was developed by the Forest Service in 1993 to further strengthen Forest Service policies and direction for responding to forest health problems. This plan updated and superseded the 1988 plan. The strategic plan emphasized ecosystem management in the National Forests and integration of forest pest management into ecosystem management. It addressed congressional concern about forests where ecological conditions have been altered, resulting in increased susceptibility to drought, pest epidemics, wildfire, and introduced pests (USDA Forest Service 1993a). The plan called for increases in biological control research: 1) to understand impacts of natural enemies on the population dynamics of pests in order to develop pest models and decision support systems needed to assist land managers in making management decisions; 2) to fill gaps in environmental data for *Bt*, increase research on the development of other key microbes, and assess the impacts of pesticides and microbes on non-target insects in the ecosystem; 3) to explore the use of classical biological control and conservation and enhancement of native controls and resistant varieties of trees in cooperation with other USDA agencies; and 4) to understand the ecological roles of forest insect pests, their natural controls, and other associated arthropods and microorganisms.

In 1992, the USDA Forest Service Quarantine Laboratory was established in Ansonia, CT, to facilitate and accelerate research and development in biological control. This 3100 ft^2 facility is certified to confine and colonize entomophagous and phytophagous arthropods and entomopathogens for biological control research. From 1992-93, research has focused on biological control of exotic pests. The facility management is designed for cooperative research with state, federal and international biological control projects.

A "National Center for Forest Health Management" was established in Morgantown, WV, in April, 1993, to: 1) facilitate the promotion, development, and use of technologies to sustain or enhance forest health, and 2) advance understanding of forest health and effects of forest health technologies on forest ecosystems management goals (USDA Forest Service 1993 b and c). Biological control efforts could include the introduction of exotic predators, parasites or pathogens, and/or augmentation of natural enemies; conservation or enhancement of native species; and evaluation of impacts of microbials and other pesticides on non-target species such as parasites, predators, or their alternative hosts. In 1993, the National Center for Forest Health funded research to evaluate the impacts of *Bt*, Dimilin™ and defoliation on non-targets, spread of the gypsy moth fungus, *Entomophaga maimaiga*, in the southern Appalachians, and formulation of the Gypchek™ virus for control of gypsy moth (USDA Forest Service 1993d).

As the world economy becomes more global with goods and products traded among countries, the opportunities for the introduction of exotic pests increase. For example, concern about the importation of exotic pests has increased following the importation of gypsy moths in 1990 on birch logs imported from Russia, and the introduction in 1991, 1992 and 1993 via Germany to North Carolina of the "Asian" gypsy moth, "common pine shoot beetle", and an Eurasian poplar leaf rust. The spread of previously introduced European gypsy moth and white pine blister rust has increased this concern. Future research and survey efforts will focus on identification of biological control agents for these pests, and the development of biological control technologies needed to suppress and manage pest populations.

In 1990, Forest Pest Management (Forest Health), International Forestry's Tropical Forestry Program, the International Institute of Biological Control (IIBC) in Great Britian, World Bank, United Nations

Development Program (UNDP) and the United Nations' Food and Agriculture Organization (FAO) initiated a cooperative project with Kenya's Forestry Department to identify potential parasites and predators of the "cypress aphid", *Cinara cupressi*, an aphid pest of tropical cypress in East Africa. This aphid was discovered in Malawi in 1986 and was found doing damage in Kenya in 1991.

Biological control research and application highlights (Table 3) between 1986 and 1993 include: 1) completing research on the biological control of larch casebearer, one of the most successful and well documented cases of biological control in the Forest Service; 2) releasing of an exotic beetle predator (*Rhizophagus grandis*) of black turpentine beetle in the south; 3) release of natural enemies of several exotic weeds in Hawaii; 4) identifying potential predators of forest pests in forests, plantations, agroforestry systems and other plantings; 5) developing models that explain the role of natural enemies in regulating abundance of the spruce budworms, larch casebearer, and gypsy moth; 6) commercially producing the microbials Gypchek™ (for gypsy moth) and BioControl-1™ (for Douglas-fir tussock moth); and 7) identifying new microbials and evaluating their effects on pest populations. Forest disease activities include: 1) assessing commercial *Trichoderma* spp. preparations against wood decay; and 2) evaluating *Ophiostoma* sp. for control of oak wilt, and *Fusarium* spp. for control of pitch canker on Virginia pine, and *Steptomyces* spp. to control poplar leaf spot and canker pathogens.

Summary. Biological control activities within the Forest Service have increased as concern over chemical pesticide contamination of the environment and pest resistance to these chemicals has increased. Prior to the early 1970s, efforts were directed toward identification and release of parasites and application of chemical pesticides. During the 1970s and 1980s, research and application efforts focused on specific pests and were usually directed toward nonbiological control methods and the use of *Bt* and NPV. Biological efforts focused on use of these microbials and understanding the role of natural enemies in regulating abundance of gypsy moth, spruce budworms, and Douglas-fir tussock moth. During this time, research on biological control of forest diseases was minimal. Since 1986, public and administrative interest in biological control have increased, particularly during the 1990s. Research and application activities have focused on: 1) understanding the role of natural enemies in the ecosystem and development of methods to manipulate the ecosystems to enhance natural enemy effectiveness and survival; 2) developing more effective microbial insecticides and delivery systems and understanding their impacts on non-target organisms; and 3) identifying and releasing natural enemies that can be used to control exotic and native pests within the United States and other countries. Future development and implementation of biological control techniques will depend upon public acceptance of the long-term manipulation of ecosystems, concern over pesticide contaminants, and the availability of adequate levels of long-term funding needed to develop and implement biological control techniques.

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Table 3. USDA, Forest Service Research and Application Activities in Biological Control (1953-1993)

[See Appendix III for additional information.]

Pest	Years	Activities
BARK BEETLES		
Black Turpentine Beetle	1953-1959	---
	1960-1969	---
	1970-1979	* Identification of nematodes, clerids, mites and other natural enemies in the South. * Evaluation of their impacts.
	1980-1986	* Identification of exotic predators.
	1987-1993	* Release of the beetle predator, *Rhizophagus grandis*, in Louisiana.
Douglas-fir Beetle	1953-1959	* Identification of nematodes and parasites in the Northwest. * Documentation of the biology and embryology of *Coeloides brunneri*.
	1960-1969	* Identification of arthropod parasites and nematodes, and avian predators. * Assessment of the impact of woodpeckers.
	1970-1979	* Assessment of the impacts of woodpeckers.
	1980-1986	---
	1987-1993	---
Spruce Beetle	1953-1959	---
	1960-1969	* Identification of parasites in Colorado. * Identification, impact, and abundance of avian predators.
	1970-1979	* Evaluation of impacts of stand densities on woodpecker predation. * Identification of prey preference of woodpeckers.
	1980-1986	---
	1987-1993	---
Mountain Pine Beetle	1953-1959	* Identification and evaluation of avian predators.
	1960-1969	* Identification of avian predators, and arthropod parasites and predators.
	1970-1979	* Identification of predatory mites. * Assessment of relative abundance and effectiveness of parasites and predators. * Publication of a "Key to Common Parasites and Predators." * Assessment of natural enemies' responses to pheromones.

Table 3. USDA, Forest Service Research and Application Activities in Biological Control (1953-1993)

[See Appendix III for additional information.]

Pest	Years	Activities
	1980-1986	* Assessment of relative abundance and effectiveness of predators. * Assessment of natural enemies responses to pheromones.
	1987-1993	---
Smaller European Elm Bark Beetle	1953-1959	---
	1960-1969	* Importation of parasites from France. * Mass production and release of the parasite *Dendrosoter protuberans*.
	1970-1979	* Refinement of rearing techniques, and mass production and release of *D. protuberans*. * Evaluation of the population dynamics of *D. protuberans*.
	1980-1986	---
	1987-1993	---
Southern Pine Beetle	1953-1959	* Nematodes sprayed on infested trees.
	1960-1969	* Identification of parasites, predators, and associates.
	1970-1979	* Congress approves funding for Expanded Southern Pine Beetle Research and Application Program. * Identification, and determination of biologies and impacts of parasites and predators.
	1980-1986	* Determination of effects of selected natural enemies on population dynamics. * Handbook published on "How to identify common insect associates of the southern pine beetle." * Techniques developed for identifying previous hosts of natural enemies.
	1987-1993	* Assessment of the relative abundance and effectiveness of predators. * Evaluation of abundance patterns of natural enemies during outbreaks.
Miscellaneous Bark Beetles	1953-1959	* Identification of nematode parasites and determination of their distributions.
	1960-1969	* Identification of nematode parasites, mites and avian predators of the mountain pine beetle and nematodes of other bark beetles.

Continued

Table 3. USDA, Forest Service Research and Application Activities in Biological Control (1953-1993)--Continued

[See Appendix III for additional information.]

Pest	Years	Activities
	1970-1979	* Identification of avian predators of spruce bark beetles and nematode parasites of bark beetles.
	1980-1986	---
	1987-1993	* Ecological studies on nematode parasites of *Ips* spp.
SHOOT BORERS	1953-1959	* Identification of native parasites of *Rhyacionia* spp. and exotic parasites of *R. buoliana*.
	1960-1969	* Identification of parasites of the egg, larvae and pupae of *R. frustrana* in the Southeast. * *Itoplectis quadricingulata*, an exotic parasite of *R. buoliana* reared by scientists at Corvallis, OR.
	1970-1979	* Identification of parasites reared from *Rhyacionia* spp., needleminers and other Tortricidae throughout the U.S. * *I. quadricingulata* released against *R. buoliana* in Oregon.
	1980-1986	* Identification of parasites of *Retinia metallica* in the Great Plains and *Rhyacionia zozana* in the West and determination of their relative abundance.
	1987-1993	* Identification of parasites and predators of *R. metallica* in the Great Plains. * Determination of the impact of natural enemies on the population dynamics of *R. metallica* in Nebraska.
HARDWOOD DEFOLIATORS		
Cottonwood Leaf Beetle	1953-1959	---
and Other Chrysomelid	1960-1969	---
Beetles	1970-1979	* Augmentative release of *Coleomegilla maculata* in Mississippi.
	1980-1986	* Augmentative release of *C. maculata* in Mississippi.
	1987-1993	* Assessment of activity of *Bt* isolates and their physiological interactions with cottonwood leaf beetles. * Research initiated to understand mechanism of resistance of the beetles to *Bt*.
Elm Spanworm	1953-1959	---
	1960-1969	* Egg parasites cause the collapse of an outbreak in Southeast.
	1970-1979	* Identification of additional egg parasites and development of techniques for mass rearing them.

Table 3. USDA, Forest Service Research and Application Activities in Biological Control (1953-1993)

[See Appendix III for additional information.]

Pest	Years	Activities
	1980-1986	---
	1987-1993	---
Fall Cankerworm	1953-1959	---
	1960-1969	* Survey of egg masses for parasites.
	1970-1979	* Survey of egg masses for parasites. * Identification of alternate hosts of *Telenomus alsophilae* and characterization of its biology. * Development of techniques for storage of host eggs and mass production of *T. alsophilae*. * Release of *T. alsophilae* in Colombia to control *Oxydia trychiata* on *Cupressus lusitanica* and its successful establishment on *O. trychiata*.
	1980-1986	---
	1987-1993	---
Gypsy Moth	1953-1959	* Determination of parasite biologies and impacts.
	1960-1969	* Inundative release of *Cotesia melanoscelus*. * Cooperating P.L. 480 scientists in Spain, Yugoslavia, and India survey for natural enemies. * Evaluation of effectiveness of arthropod natural enemies, a nuclear polyhedrosis virus (NPV), and *Bt*.
	1970-1979	* Congress approves funding for the Expanded Gypsy Moth Research and Application Program. * Evaluation of effectiveness of parasites with Intensive Plot System. * Laboratory and field evaluation of *Blepharipa pratensis*. * Augmentative release of *B. pratensis* and inundative releases of 3 parasites with *Bt*. * Demonstration that *C. melanoscelus* can transmit gypsy moth NPV. * Pre-introduction evaluations of potential exotic parasites. * Scientists visit the USSR to identify parasites and understand IPM practices. * Registration of Gypchek™. * Evaluation of *Bt* strains, formulations, dosages and physical properties. * Evaluation of spray droplet size and coverage for aerial and ground application.

Continued

Table 3. USDA, Forest Service Research and Application Activities in Biological Control (1953-1993)--Continued

[See Appendix III for additional information.]

Pest	Years	Activities
	1980-1986	* Scientists visit the Peoples' Republic of China to identify natural enemies and conduct pre-introduction evaluations. * Development of joint long-term research projects with China on significance of alternative hosts for maintaining parasite populations. * Establishment of Gypsy Moth Research and Development Program and an extramural research program to develop methods to evaluate impact of parasites on gypsy moth population dynamics. * Research to develop an easy-to-use formulation of Gypchek™.
	1987-1993	* Initiation of research to quantify interactions between NPV and *Nosema* spp. and *Vairimorpha* spp. * Transfer of *Entomophaga maimaiga* into Michigan and the Southeast and initiation of *E. maimaiga* impact study on non-target insects. * Development of life system model with a predator/parasite submodel. * Development of methods to produce NPV in cell culture. * Evaluation of *Bt* formulations, dosages and impacts on non-target arthropods.
Miscellaneous Hardwood Defoliators	1953-1959	---
	1960-1969	* Demonstration of effectivenesss of aerial application of *Bt* for cankerworm control in North Dakota.
	1970-1979	* Identification and documentation of aspects of the biology of *Malachius ulkei*, an egg predator of spring cankerworm in the northern Great Plains.
	1980-1986	* Assessment of impact of natural enemies on the abundance of a sawfly (*Pontania* sp. nr. *pacifica*) on willow in Arizona. * Assessment of effectiveness of *Bt* against large aspen tortrix in Alaska.
	1987-1993	---

Table 3. USDA, Forest Service Research and Application Activities in Biological Control (1953-1993)

[See Appendix III for additional information.]

Pest	Years	Activities
CONIFER DEFOLIATORS		
Blackheaded Pine Sawfly	1953-1959	---
	1960-1969	---
	1970-1979	* Identification and evaluation of the impact of parasites along the Gulf Coast. * Identification of parasites and fungi in Belize.
	1980-1986	---
	1987-1993	---
Douglas-fir Tussock Moth	1953-1959	* Identification of viruses.
	1969-1969	* Identification of viruses. * Pilot tests on control with viruses. * Control trials with NPV and *Bt*. * Use of parasite abundance in egg masses to predict subsequent defoliation.
	1970-1979	* Congress approves funding for the Expanded Douglas-fir Tussock Moth Research and Application Program. * Identification and impacts of predators and parasites. * Keys to parasites and predators. * Distribution, impact, behavior of *Telenomus californicus*, an egg parasite. * Development of a viral insecticide by identifying and characterizing strains, testing potency, standardization and formulation trials, mammalian and fish toxicity and pathogenicity tests, etc., and propagation of the virus. * Registration of BioControl-1™ in 1976, the first virus registered in the U.S. for forest insects. * Pilot control study with NPV and *Bt*. * Evaluation of *Bt* strains, formulations, dosages, and physical properties. * Evaluation of spray equipment, droplet size, and coverage for aerial and ground application.
	1980-1986	* Identification of hymenopterous parasites and avian, arachnid, and insect predators. * Assessment of natural enemy impact on the moth. * Baculovirus production facility established at Corvallis, OR.
	1987-1993	---

Continued

Table 3. USDA, Forest Service Research and Application Activities in Biological Control (1953-1993)--Continued

[See Appendix III for additional information.]

Pest	Years	Activities
Introduced Pine Sawfly	1953-1959	---
	1960-1969	---
	1970-1979	* Survey for parasites in North Carolina. * Release of *Monodontomerus dentipes*, *Exenterus amictorius*, and *Dahlbominus fuscipennis* for control.
	1980-1986	* Release of *M. dentipes* for control. * Release of the egg parasites *Dipriocampe diprioni*, *Chrysonotomyia ruforum* and *C. formosa* in North Carolina in 1982.
	1987-1993	* *M. dentipes* continues to control the sawfly.
Larch Casebearer	1953-1959	* Canadian scientists develop life tables for parasites.
	1960-1969	* Collection of *Agathis pumila* in northeastern U.S., and rearing and release of the parasite in the Northwest.
	1970-1979	* Release of four species of parasites found in northeastern U.S. and two European parasites in the Pacific Northwest. * Evaluation of single-species vs. multi-species releases.
	1980-1986	* Releases of parasites in Pacific Northwest. * Evaluation of impacts of parasites on population dynamics.
	1987-1993	* Evaluation of impacts of parasites on populations.
Larch Sawfly	1953-1959	* Evaluation of distribution and impact of parasites in Minnesota.
	1960-1969	---
	1970-1979	* Release and establishment of *Olesicampe benefactor* in Pennsylvania.
	1980-1986	* Evaluation of *0. benefactor* survival in Pennsylvania.
	1987-1993	---
Virginia Pine Sawfly	1953-1959	---
	1960-1969	---
	1970-1979	* Release of *Monodontomerus dentipes*, *Exenterus amictorius*, and *Dahlbominus fuscipennis* in Virginia.
	1980-1986	---
	1987-1993	---

Table 3. USDA, Forest Service Research and Application Activities in Biological Control (1953-1993)

[See Appendix III for additional information.]

Pest	Years	Activities
Redheaded Pine Sawfly	1953-1959	---
	1960-1969	* Release of *Exenterus amictorius* and *Dahlbominus fuscipennis* in North Carolina in 1969.
	1970-1979	* NPV used to control the sawfly.
	1980-1986	---
	1987-1993	---
Spruce Budworms and Jack Pine Budworm	1953-1959	* Identification of natural enemies of spruce budworms in the northeastern and northwestern U.S.
	1960-1969	* Identification of predators, parasites, and pathogens of spruce budworms. * Documentation of spruce budworm biologies. * Assessment of avian predator impact on jack pine budworm abundance in Minnesota.
	1970-1979	* Identification of natural control agents and evaluation of their impacts and abundance. * CANUSA approved by Congress in 1977. * Evaluation of the effects of parasites and predators on the population dynamics of spruce budworm. * Pilot study evaluating spruce budworm control with *Bt* and NPV. * Evaluation of *Bt* strains, formulations, dosages, and physical properties. * Evaluation of spray equipment, droplet size, and coverage for aerial and ground application.
	1980-1986	* Evaluation of the impact of *Nosema fumiferanae* on population dynamics of spruce budworm. * Evaluation of the effects of parasites and predators on the population dynamics of spruce budworm. * Pilot tests evaluating the efficacy of *Bt*. * Successful rearing of five generations of the parasite *Glypta fumiferanae* in California. * Release of the egg parasite *Trichogramma minutum*. * Assessment of parasite distribution. * Efficacy and field persistance of *Bt* after ground and aerial application on fir in Wisconsin.
	1987-1993	* Continuation of research to evaluate the impact of *N. fumiferanae* on budworms.

Continued

Table 3. USDA, Forest Service Research and Application Activities in Biological Control (1953-1993)--Continued

[See Appendix III for additional information.]

Pest	Years	Activities
Miscellaneous Conifer Defoliators	1953-1959	---
	1960-1969	* Evaluation of western hemlock looper control with *Bt*.
	1970-1979	* Assessment of effectiveness of aerial application of *Bt* against the pine butterfly.
	1980-1986	---
	1987-1993	---
SAP SUCKING INSECTS		
Balsam Woolly Adelgid	1953-1959	* Identification of natural enemies in Japan, India, and Pakistan. * Introduction of invertebrate predators.
	1960-1969	* Identification of predators in India and China (P.L. 480). * Introduction of predators from India, Pakistan, England, Australia, Germany, Austria into New England, North Carolina, Washington, and Oregon.
	1970-1979	---
	1980-1986	---
	1987-1993	---
MISCELLANEOUS INSECT PESTS	1953-1959	* Publication of list identifying and describing the biologies of parasites reared from microlepidoptera between 1915 and 1959.
	1960-1969	---
	1970-1979	* Identification of spiders found in forest ecosystems, plantations, and other plantings.
	1980-1986	* Identification of parasites and predators of "striped pine scale" and "loblolly pine mealybug." * Identification of spiders found in forest ecosystems, plantations and other plantings.
	1987-1993	* Identification of spiders found in forests, plantations, and other plantings. * Identification of pathogens and parasites of stored products pests.
FOREST DISEASES		
Root and Butt Rots	1953-1959	---
	1960-1969	* Development of methods for assaying soil for antagonistic organisms.
	1970-1979	* Evaluation of nematodes for control of *Armillaria* spp.

Table 3. USDA, Forest Service Research and Application Activities in Biological Control (1953-1993)

[See Appendix III for additional information.]

Pest	Years	Activities
	1980-1986	* Evaluation of interactions of *Trichoderma* spp. with *Phellinus weirii* and *Armillaria* spp.
	1987-1993	* Evaluation of interactions of *Trichoderma* spp. with *Phellinus weirii* and *Armillaria* spp. * Evaluation of seed treatments with beneficials and antagonistic organisms for control of damping off and root rots of pines.
Stem Cankers and Other Canker Diseases	1953-1959	---
	1960-1969	---
	1970-1979	* Impact of hypovirulent strains of *Cryphonectria parasitica* on chestnut blight. * Identification and impact of hyperparasite.
	1980-1986	* Impact of hypovirulence of *C. parasitica* on chestnut blight. * Evaluation of the ability of hypovirulent isolates to control virulent cankers.
	1987-1993	* Evaluation of *Arthrobacter* sp. and *Fusarium* sp. for control of pitch canker on Virginia and slash pine. * Evaluation of *Streptomyces* spp. for control of poplar leaf spot and canker pathogens.
Mycorrhizal Symbiosis	1953-1959	* Identification and isolation of ectomycorrhizal fungi. * Description of ectomycorrhizae of Douglas-fir and pine seedlings.
	1960-1969	* Identification and isolation of ectomycorrhizal fungi. * Host/fungus index developed for ectomycorrhizal fungi.
	1970-1979	* Development of practical inoculation procedures for nursery seedlings. * Development of a commercial source of *Pisolithus tinctorius* inoculum. * Isolation and confirmation of ectomycorrhizal host range. * Publication of a Monograph on Endogonaceae. * Evaluation of the influences of soil factors and natural disturbances on ectomycorrhizal fungi development on Douglas-fir, larch, and pines. * Evaluation of physiology and ecological diversity.

Continued

Table 3. USDA, Forest Service Research and Application Activities in Biological Control (1953-1993)--Continued

[See Appendix III for additional information.]

Pest	Years	Activities
	1980-1986	* Isolation and confirmation of ectomycorrhizal host range. * Inoculation program with basidiospores. * Evaluation of physiology and ecological diversity.
	1987-1993	---
Vascular Wilts agents.	1953-1959	* Identification of potential biological control
	1960-1969	---
	1970-1979	---
	1980-1986	* Assessment of *Streptomyces* spp. for control of Dutch elm disease. * Evaluation of interactions of xylem-colonizing *Bacillus* spp. with verticillium wilt of maples.
	1987-1993	* Identification of bacterial and fungal endophytes of American elm. * Evaluation of *Bacillus* spp. and *Pseudomonas* spp. as biological controls of oak wilt. * Evaluation of colonization by *Ophiostoma* sp. for control of oak wilt.
Wood Products	1953-1959	* Evaluation of enhancement of *Trichoderma*, growth, and reduced decay by treating pulpwood with fluoride.
	1960-1969	* Assessment of the impact of isolates of *Trichoderma viride* on *Gloeophyllum sepiarium*, and *G. trabeum*.
	1970-1979	---
	1980-1986	* Evaluation of Polyoxin D™ for control of wood-staining mold and decay fungi.
	1987-1993	* Evaluation of antagonistic abilities of *Gliocladium virens* and various *Trichoderma* spp. against white and brown rot. * Assessment of potential *Trichoderma* spp. preparations and application of commercial *Trichoderma* spp. preparations against wood decay fungi. * Evaluation of interactive effect and persistence of *Trichoderma* spp. strains against wood decay. * Identification of additional antagonistic fungi. * Evaluation of the efficacy of bacteria against wood decay.

Table 3. USDA, Forest Service Research and Application Activities in Biological Control (1953-1993)

[See Appendix III for additional information.]

Pest	Years	Activities
WEEDS	1953-1959	---
	1960-1969	* Identification of fungi and insects associated with dwarf mistletoes and documentation of their biologies. * Evaluation of fungal distribution, host preferences, and impact.
	1970-1979	* Identification of fungi and insects associated with dwarf mistletoes and documentation of their biologies. * Evaluation of fungal distribution, host preferences, and impact.
	1980-1986	* Identification and release of exotic natural enemies of weeds in Hawaii.
	1987-1993	* Identification and release of eight exotic natural enemies of weeds in Hawaii.

CHAPTER VI
1971-1993
ANIMAL AND PLANT HEALTH INSPECTION SERVICE.
Edited by W. C. Kauffman

Biological control activities in the Animal and Plant Health Inspection Service (APHIS) are conducted in three work units: 1) Biological Control Operations, Plant Protection and Quarantine (PPQ); 2) Methods Development, PPQ; and 3) the National Biological Control Institute. Many of the biological control projects are conducted cooperatively between Biological Control Operations and Methods Development. Some of the projects discussed in this chapter will continue beyond the 1993 cutoff date of this history. (As elsewhere in this history, full scientific names of all organisms mentioned in this chapter are given, and are cross-referenced, in the Appendix.)

A. BIOLOGICAL CONTROL OPERATIONS, PLANT PROTECTION AND QUARANTINE. By D. E. Meyerdirk, G. L. Cunningham, T. L. Burger, and L. E. Wendel

The Biological Control Operations (BCO) within the U. S. Department of Agriculture (USDA), Animal and Plant Health Inspection Service, had its origin in 1966 with the initiation of an operational program addressing the biological control of the cereal leaf beetle under the North Central Region of Plant Protection and Quarantine. Throughout the 1970s, biological control activities within APHIS were generally restricted to major quarantine pests such as cereal leaf beetle, gypsy moth, and citrus blackfly. Some of these activities were conducted, prior to the formation of APHIS, by the ARS Plant Protection Division (PPD), which was to become PPQ of APHIS, as discussed in Chapter IV, Section B.1.a. These programs were centered around production and large-scale redistribution of natural enemies. Viewed as highly successful and necessary (USDA 1976b), these implementation procedures were suggested for use against additional pests. Practical application of biological control agents on a large-scale basis was recognized as a proper function of action agencies such as APHIS. APHIS, in cooperation with state departments of agriculture, provided leadership to exploit and expedite the use of proven natural enemies.

The present goal of BCO within APHIS is "to implement biological control technologies to control agricultural pests of economic importance in a cooperative effort with federal and state agencies." The principal objective of the program is to mass produce and release native and exotic biological control agents for the control of selected arthropod and weed pests of agriculture. The effects of natural enemies on target pests is fostered through various activities, including: foreign collection, importation, quarantine screening, rearing, establishment, augmentative releases, and domestic collection and redistribution of the natural enemies. The first two tasks are generally conducted in close association with the Agricultural Research Service (ARS) and other research units. Surveys are conducted to confirm establishment and geographic distribution of selected natural enemies. Detailed evaluations of the effects of natural enemies on their target pests are conducted. Economic evaluations are conducted to determine the cost:benefit of each project, when possible.

1. Gypsy Moth (1963-1979) and Cereal Leaf Beetle (1966-1979) Programs

Personnel at Otis Air Force Base, MA, have been involved in the collection, culture, and release of imported gypsy moth parasites since 1963 (see Chapter IV). In late 1971, these activities at Otis (now under PPQ) were discontinued and PPQ initiated the Gypsy Moth Parasite Distribution Program. Through cooperative agreements with the New Jersey Department of Agriculture, the University of Maryland, and later the Maryland Department of Agriculture, gypsy moth parasite rearing activities were continued. Parasites imported by ARS were mass-reared and made available for release in states which were newly infested or threatened by invasion by the gypsy moth. (Reardon et al. 1973; Reardon 1981; Reardon and Coulson 1981; Coulson 1981d.)

The program against the cereal leaf beetle (CLB) was one of the most successful examples of classical biological control in the United States (Anonymous 1978; Graham 1984; DeBach and Rosen 1991). The beetle was first discovered in Michigan in 1962 and became a major pest of small grain crops, such as wheat, oats, and barley. The pest reduced yield up to 50% in some instances (Pierce 1982). A foreign exploration and importation program against the CLB was conducted by the Entomology Research Division of ARS. This was closely followed by a large-scale production and distribution program conducted by the Plant Protection Division (PPD) of ARS, in cooperation with Purdue and Michigan State Universities (see Chapter III, Section A.1.a). A laboratory was established by PPD for this program in Niles, MI; this became a PPQ facility after PPQ's creation in 1971, now called the Niles Biological Control Laboratory. Four species of parasites (see Table 4) were imported from Europe. An egg parasite, *Anaphes flavipes*, proved very effective, along with three other species, which were larval parasites. An economic evaluation of the CLB program showed benefits ranged from $7 to $105 million annually (Moffitt et al. 1993). Total benefits (above costs) of the program were estimated at about $170 million, with benefit to cost ratio of 12:1. The program ended in 1979 after 13 years of cooperative efforts with state departments of agriculture, ARS, and many universities. Distribution of CLB during the 1970-1979 period was confined to the northeastern region of the U.S. Later, as the beetle invaded new areas, the program was resumed (see below).

2. Initiation and Development of the PPQ Biological Control Implementation Program (1980-1993)

APHIS-PPQ biological control implementation activities began in 1980, when PPQ significantly expanded its activities in biological control. The publication "Guidelines for PPQ Action Programs in Biological Control" was issued to define PPQ's roles and responsibilities (USDA 1980b). APHIS initiated biological control implementation projects by following the identification of specific agricultural pests on which sufficient research had been conducted to allow implementation of the research results. G. L. Cunningham was named Biological Control Staff Officer on PPQ's National Program Planning Staff, a position he occupied until 1990. During those ten years, a variety of actions were taken in support of biological control. A four-state, cooperative demonstration program for biological control of the Mexican bean beetle was conducted. A biological control implementation program against the alfalfa weevil was initiated in midwestern U.S. Construction was initiated for a biological control laboratory at Moore Field in Mission, TX (1980), now called the Mission Biological Control Laboratory. A satellite laboratory to the Mission facility was established in Bozeman, MT, in 1986 to provide assistance to a biological control of rangeland weeds program.

A major revision of the BCO Program took place as a result of a review in 1985, and agency "guidelines" were revised. In 1986, D. E. Meyerdirk, joined the PPQ Operational Support Staff as a biological control technical specialist to implement the recommendations of the 1985 review. Since 1990, he has served as the Chief of BCO in PPQ. A second BCO program review occurred in 1987. This review suggested that APHIS increase its leadership in biological control within the federal government. Specific responsibilities for APHIS-PPQ biological control were identified, as well as

other responsibilities shared jointly by APHIS and ARS. Basic functions in biological control programs were identified and the agency (APHIS or ARS) that was to have the lead role in each function was specified. The need to coordinate biological control research and implementation among USDA agencies led to the formation of the USDA Interagency Biological Control Coordinating Committee (IBC^3) in 1988. This committee initially consisted of representatives from ARS and APHIS, but later included members from USDA's Forest Service, Extension Service, and Cooperative State Research Service as well (see also Chapter IV, Section A).

In 1989, the National Biological Control Institute (NBCI) was established within APHIS, one purpose of which was to further coordination. This Institute is headed by E. S. Delfosse (see this Chapter, Section C).

Following are brief summaries of biological control implementation programs targeting agricultural pests by APHIS-PPQ from 1980 to 1994. The natural enemies employed in these programs are listed in Table 4.

Mexican bean beetle (1980-1984). The Mexican bean beetle program was a state/federal project to demonstrate the augmentative use of parasites. Building on previous activities against this pest in New Jersey, Maryland, Delaware, and Virginia, the project used the Indian eulophid parasite, *Pediobius foveolatus*, in the four-state area to demonstrate the effect of properly timed releases of parasites for control of the Mexican bean beetle (MBB). Since *P. foveolatus* does not overwinter in the U.S., laboratory-reared parasites were released in "nurse" plots, which consisted of plantings of early season snap beans, a preferred host of MBB. These nurse plots provided an early-season release and breeding site for parasites, which promoted establishment and increase in parasite numbers. As beetle populations increased in adjacent soybean fields, the parasites spread from the nurse plots to the soybeans. In soybeans, the parasites provided good control of the MBB and often eliminated the need for insecticides. The results of a large-scale biological and economic study of the project are available for use by other interested states and farm communities as an alternative control technology (Reichelderfer 1979; Dively 1985). (For early ARS involvement in the MBB program, see Chapters III and IV, above.)

Alfalfa weevil (1980-1991). The alfalfa weevil biological control project was directed by the Niles, MI, laboratory, under the leadership of T. L. Burger. This program was an outstanding example of what can be accomplished when research and action agencies work together. Ten species of natural enemies were involved in the combined USDA program, as listed in Table 4 (Bryan et al. 1993). Five of these parasites (*Bathyplectes anurus*, *B. curculionis*, *Microctonus aethiopoides*, *M. colesi*, and *Oomyzus* [previously *Tetrastichus*] *incertus*) were shown by ARS and APHIS to be effective against the weevil (Dysart and Day 1976; Day 1981; Kingsley et al. 1993). In the 1950s and 1960s, these parasites were introduced and established by ARS in the northeastern U.S. (see Chapters III and IV). Weevil numbers were reduced and application of chemical insecticides for control of the weevil decreased by 73% by 1980. This saved alfalfa producers an average of $8 million a year in pesticide and application costs. In New Jersey alone, ARS estimated that the percentage of alfalfa fields treated for the pest decreased from 96% before parasite introductions to only 7% subsequently.

Continued distribution of parasites to other states was considered by ARS to be beyond their primary mission. Consequently, in 1980, APHIS assumed responsibility for parasite distribution to new areas. Under APHIS direction, the program expanded from 17 northeastern states to all remaining portions of the continental U.S. Not all species became established in all states. Problems were encountered because additional U.S. strains of the alfalfa weevil and other species of related weevils were found in the western U.S.

During this program, more than 16 million parasites were released at 41,200 sites throughout the U.S. Seventy-three new state and 11,330 new county parasite-occurrence records were established as part of the program's biological evaluation studies (Bryan et al. 1993). The net social benefits of biological control of the alfalfa weevil has been estimated at $2.2 billion (Moffitt et al. 1990); see Section B of this Chapter for more detailed explanation of this economic analysis.

Citrus whitefly (1981-1985). Biological control of citrus whitefly was begun in 1981 as a regional implementation project, and was directed by the new APHIS-PPQ Biological Control Laboratory at Mission, TX, under the leadership of L. E. Wendel. The objective of the project was to redistribute an introduced parasite, *Encarsia lahorensis*, throughout the southeastern states. This Asian parasite of citrus whitefly had been successfully established by university researchers in California and Florida, where it had successfully reduced citrus whitefly populations on citrus and ornamental plants (Nguyen et al. 1983). Nursery stock was infested with parasitized citrus whitefly produced in the laboratory at Mission and distributed to locations from Texas throughout the southeastern U.S. It is believed that the parasite has effected some control of citrus whitefly in the new areas where parasites are now established. The project has not yet undergone a detailed evaluation.

Silverleaf nightshade (1982-1986). In 1982, the agency began a 5-year pilot project directed against the perennial weed silverleaf nightshade. This is an important weed in the southwestern U.S., infesting pastures, cotton, and other crops. An alternative to cultivation and application of herbicides is the use of a leaf-galling nematode, *Ditylenchus* (previously *Orrina*) *phyllobius*. The biological control of silverleaf nightshade project developed technology for large-scale augmentative use of the nematode. This native nematode causes extensive galling to the leaves, stems, and flowers of silverleaf nightshade. Infected plants are severely stunted and weakened. Techniques were developed to mass rear the nematode in field plots and to apply the inoculum at desired rates over broad infestations. Although effective in reducing silverleaf nightshade populations, the cost of producing the nematode was not competitive with use of herbicides.

Colorado potato beetle (1985-1993). In 1985, APHIS began a project against the Colorado potato beetle (CPB). The goal of the project was to demonstrate the use of biological control agents as a component of an integrated pest management system for CPB. To accomplish this, APHIS collaborated with university, state, and federal (Methods Development Centers and ARS) cooperators. The Mission Biological Control Laboratory provided biological control agents and participated in laboratory and field studies, including studies on optimum release strategies for the agents, development of synthetic CPB diet, improvement of parasite and predator rearing methods, quality assessment of the natural enemies, economic evaluation, and development of public awareness programs for CPB biological control. APHIS also supported foreign exploration to search for new exotic agents. Natural enemies involved in this program are listed in Table 4.

Diffuse and spotted knapweeds (1985-1993). In 1985, the agency initiated cooperative biological control projects on diffuse and spotted knapweeds. This project was conducted by the APHIS laboratory at Mission, TX, and satellite facility at Bozeman, MT, in cooperation with ARS and university researchers in the northwestern U.S. The Bozeman facility was under the direction of R. D. Richard. Eight European insect species that had been approved for introduction into North America by U.S. and Canadian authorities were obtained for distribution either from North American establishment sites or directly from overseas laboratories of ARS and the International Institute of Biological Control (IIBC) (Table 4). Some of these agents have become established and are spreading. Weed biological control offers ranchers solutions that are long-term and considerably more cost effective when compared to other means of control. (For ARS research on the biological control agents for these weeds, see Chapter IV, Section C.)

European corn borer (1986-1993). The European corn borer (ECB) has a host range which includes over 200 plants, among which are corn, snap beans, sorghum, cotton, peppers, and apples. A cooperative survey was initiated in 1986 to identify existing natural enemies attacking ECB eggs or larvae in the U.S. A specific objective was to determine the distribution of *Lydella thompsoni*, a European dipterous parasite, reintroduced from Delaware to additional areas. A total of 73,192 ECB larvae from 1,337 collection sites in 28 states were processed at the APHIS laboratory in Mission, TX. Two additional, previously-introduced European parasites were recovered during the collections (*Eriborus terebrans* and *Macrocentrus grandii*) as well as three pathogens (*Bacillus thuringiensis*, *Beauveria bassiana*, and *Nosema pyrausta*). Collaborators have also provided exotic egg parasites from China (*Trichogramma dendrolimi* and *T. ostriniae*) and a larval parasite from Egypt (*Habrobracon brevicornis*). Some of the natural enemies listed in Table 4 were used to develop integrated pest management programs for ECB and/or released for establishment purposes.

Aphids (1987-1988). Biological control of aphids began as a project in 1987 with the redistribution of the sevenspotted lady beetle, *Coccinella septempunctata*, throughout the U.S. This European lady beetle was first found in New Jersey long after initial introduction attempts by ARS (see Chapters III and IV), and soon became the dominant aphid predator in portions of the eastern U.S. APHIS and state cooperators determined the U.S. distribution of the beetle, established field collection sites, and collected and redistributed the species across the western third of the country. This program was later redirected toward a newly introduced aphid pest, the Russian wheat aphid (see below).

Leafy spurge (1988-present). Leafy spurge is a major rangeland weed infesting millions of acres of grazing land in the western U.S. and Canada. In 1988, Congress directed APHIS to implement biological control of leafy spurge as part of a pest management approach. The work was done together with state, ARS, and Canadian scientists who had previously identified, studied, and obtained release authorization for several exotic natural enemies of the weed (see Chapter IV, Section C). The APHIS laboratory in Mission, TX, and its satellite facility at Bozeman, MT, determined the extent of leafy spurge infestations, supported foreign collection of the natural enemies, and assisted in their quarantine screening, establishment, and redistribution. In addition, economic and biological evaluations were conducted. Initial efforts concentrated on releasing four chrysomelid flea beetles, *Aphthona cyparissiae*, *A. nigriscutus*, *A. czwalinae*, *A. flava*; a cecidomyiid midge, *Spurgia esulae*; and a cerambycid beetle, *Oberea erythrocephala* (Table 4).

Russian wheat aphid (1988-1993). Using funds previously devoted to the aphid biological control program, APHIS developed a comprehensive biological control program against the Russian wheat aphid (RWA). This pest invaded the U.S. from Mexico in 1986 and has caused up to a 70% reduction in yield in small grains. This aphid is a major problem to grain growers in the western half of the U.S. The project initially focused on importing exotic parasites and predators by ARS and university reseachers. Parasite rearing facilities to support the project were developed at the Biological Control Laboratory in Mission, TX, in association with Texas A & M University. Exotic predators and parasites (Table 4) were reared at APHIS laboratories at Mission, TX, and Niles, MI, with overall project leadership at the Niles laboratory.

Biological control was one of several components in a RWA integrated pest management system. APHIS worked with the National Association of State Departments of Agriculture and other interest groups to coordinate their biological control efforts with other control efforts (Anonymous 1989, 1990, 1991).

Euonymus scale (1991-1993). The euonymus scale occurs throughout most of the U.S. attacking ornamental species of euonymus. It is a serious economic pest to the nursery industry, affecting landscape plants in both commercial and residential areas. ARS imported several natural enemies from South Korea (see Chapter IV), including the predators *Chilocorus kuwanae* and *Cybocephalus*

sp. prob. *nipponicus* (Table 4). These were established and found to control the euonymus scale effectively. In addition, two parasite species were introduced from China by university cooperators (see Table 4). In 1991, BCO began implementation of the euonymus scale biological control project. Through cooperative efforts, the success of the project is being measured by the reduction of scale on euonymus by these exotic natural enemies.

Sweetpotato whitefly (1991-1993). The sweetpotato whitefly was recognized as a serious economic threat to agriculture in the U.S. in 1981, when the whitefly was found attacking field and vegetable crops in the farming areas of the desert Southwest (Arizona and southern California) (Meyerdirk et al. 1986). In the late 1980s, a new "biotype" or "strain" of the whitefly was found severely attacking poinsettias and vegetables across the southern U.S. This new pest was causing silverleaf disease of squash and irregular ripening of tomatoes. Through an USDA Interagency Cooperative Agreement, APHIS began the development of a biological control program against this pest as part of an integrated pest management program. The APHIS Mission, TX, laboratory is conducting quarantine screening of exotic natural enemies from Europe, the Middle East, and Asia, that have been collected by ARS, IIBC, and university scientists. Most of the parasites were species of *Encarsia* or *Eretmocerus* (see Table 4).

Cereal leaf beetle (1993). In 1993, APHIS reestablished a cereal leaf beetle (CLB) biological control program, which was originally begun in 1966 (see above). This action was taken because the CLB expanded its geographical distribution after 1979 from the northeastern and midwestern U.S. into Utah, Montana, and Idaho. The natural enemy complex that successfully controlled the CLB in the Northeast and Midwest did not move naturally with the pest to these new areas. In addition, the CLB in the southeastern portion of its range (North and South Carolina, Georgia, and Alabama) was not effectively controlled by the existing natural enemy complex. The latter may have been the result of the failure of the previously imported natural enemies to acclimatize in the Southeast. ARS is presently (1994) conducting foreign collection of known and new CLB natural enemies from more southern climatic zones of Europe for the APHIS program. These will be released in the southeastern and western U.S. Previously established CLB parasites will also be collected in the northeastern and midwestern U.S. for redistribution in the West.

B. METHODS DEVELOPMENT, PLANT PROTECTION AND QUARANTINE. By W. C. Kauffman and P. C. Kingsley

1. History of Methods Development

Methods Development, as a specific activity identified in the U.S. Department of Agriculture (USDA), began in the 1930s as part of the Bureau of Entomology and Plant Quarantine. Much of the early work was carried out by the Aircraft and Special Equipment Center in Greenfield, MA, which provided technical support (i.e., services and aerial application activities) to USDA projects. In the mid-1940s, a laboratory was established at Hoboken, NJ, to develop commodity treatment schedules for the use of methyl bromide, ethylene dibromide, and cold treatments. During the 1950s and 1960s, other laboratories were created to investigate control techniques for various pests such as boll weevil, gypsy moth, cereal leaf beetle, imported fire ants, pink bollworm, and witchweed. These laboratories were under the administrative control of the USDA regions in which they were located. In 1969, the Plant Protection Division of the USDA Agricultural Research Service (ARS) was reorganized, and a new Branch, called Methods Development, was created. The mission of this Branch was to fulfill the growing need for a specific group to work with the research community to develop practical pest control by transferring small-scale tests into pilot programs and full-scale operational technologies. Specific responsibilities of these Methods Development facilities were: 1) involvement in cooperative efforts with research agencies to ensure that plant pest control needs were addressed, and 2) development of large-scale eradication programs in pilot trials. A Chief Staff Officer was assigned

to supervise the activities of the following Methods Development facilities and one Equipment Center:

Boll Weevil Methods Development Laboratory, Gulfport, MS;
Cereal Leaf Beetle Methods Development Laboratory, Niles, MI;
Cereal Leaf Beetle Parasite Rearing Laboratory, Niles, MI;
Gypsy Moth Methods Development Laboratory, Otis Air Force Base, MA;
Hoboken Methods Development Laboratory, Hoboken, NJ;
Imported Fire Ant Methods Development Laboratory, Gulfport, MS;
Pink Bollworm Methods Development Laboratory, Brownsville, TX;
Pink Bollworm Moth Rearing Facility, Phoenix, AZ;
Witchweed Methods Development Laboratory, Whiteville, NC; and
Methods Development Equipment Center, Beltsville, MD.

In 1971, the Animal and Plant Health Inspection service (APHIS) was established as a separate agency of the USDA with responsibility for Plant Protection and Quarantine (PPQ) operational programs. Methods Development Centers were placed in APHIS and their mission was to provide the agency with scientific and technological capabilities for protecting and improving American agriculture and public health. Methods Development continues to support APHIS programs primarily by optimizing existing pest control practices and by developing new technologies for pest exclusion, detection, and control. This is accomplished by developing and refining methods for controlling plant pests, evaluating new biological and chemical materials, adapting or inventing equipment, providing technical consultation and training, collecting and disseminating pertinent information, participating in strategic and tactical planning, serving as a liaison between APHIS and the research community, and integrating technological advancements into pest management systems.

These activities are performed at the following five centers:

Hoboken Methods Development Center, Hoboken, NJ;
Mission Methods Development Center, Edinburgh, TX (moved in 1983 from the Brownsville Methods Development Center, Brownsville, TX. Field Stations: Gainesville, FL; Guatemala City, Guatemala; State College, MS; Waimanalo, HI);
Otis Methods Development Center, Otis Air Force Base, MA;
Phoenix Methods Development Center, Phoenix, AZ (established 1989. Field Station: Brawley, California);
Whiteville Methods Development Center, Whiteville, NC (Field Stations: Little Rock [Dillon], SC; Gulfport, MS).

2. Biological Control Activities

Methods Development Centers have contributed significantly to the development and success of many biological control activities of APHIS, as described below. Many of these projects involved close cooperation between the Centers and the Biological Control Operations (BCO) laboratories (Niles, MI, and Mission, TX). Further details on implementation of these biological control projects are described in Section A of this Chapter.

Gypsy Moth Biological Control (1963-1993) - Otis Methods Development Center. The early work with gypsy moth parasites at Otis AFB under ARS' Plant Protection Division is noted in Section A.1. Work on other gypsy moth natural enemies was also conducted at Otis and continued after establishment of APHIS-PPQ in 1971.

a) *Bacillus thuringiensis* Strains and Formulations (1963-1993). Work conducted at the Otis Center has been instrumental in the testing, development and registration of *B. thuringiensis* (*Bt*) for use as an effective material to control gypsy moth. For the past 30 years, *Bt* strains and formulations have

been tested in the laboratory and effective strains and formulations have been tested in the field using aerial application. These tests led to the registration of most of the *Bt* formulations presently used for gypsy moth control. Field testing led to the development of a higher dosage, single application technique now used, compared to previous double applications at low dosage. Also, the majority of data on weather effects on *Bt* efficacy, including the first field testing, was developed at the Otis Center. "Stickers" were tested and recommended for use with each *Bt* formulation. Otis personnel continue to test new strains and formulations of *Bt* in laboratory bioassays on oak seedlings and to conduct field studies with *Bt* for improvement of its efficacy and safety to the environment.

b) Nuclear Polyhedrosis Virus (1963-1993). From 1963-1965, personnel at the Otis Center first collected, purified, and applied nuclear polyhedrosis virus (NPV) from field-collected gypsy moth larvae. In the 1970s, following development of gypsy moth mass rearing techniques and an artificial diet, Otis personnel provided gypsy moth eggs and larvae to the Forest Service for the production of NPV (Podgwaite 1981). From 1977-1982, a pilot production team of ARS and APHIS scientists harvested NPV from cadavers of infected larvae reared at Otis (Shapiro 1981). On several occasions, egg masses were supplied to private industry in attempts to produce virus for purification by the Forest Service. Since these attempts were unsuccessful, the Otis Center has continued to collaborate with the Forest Service to produce cadavers (up to 7.5 million per year) for NPV production (1987-1993). Efforts continue to transfer NPV rearing technology to private industry in North America.

c) *Ceranthia samarensis* (1992-1993). Improvements for the rearing of this European tachinid parasite are underway in collaboration with Forestry Canada. This parasite is associated with low-density populations of gypsy moth larvae in Europe. This effort involves improvements to Forestry Canada's rearing method. The feasibility of artificially implanting parasite maggots onto host larvae is being tested. Preliminary results indicate that artificial implantation can be used to propagate the parasite in the laboratory; however only maggots with highly developed mandibles successfully parasitize gypsy moth larvae. Further refinements of both methods are needed to increase rearing efficiency to assist a cooperative USDA and Forestry Canada project of *C. samarensis* release and establishment in North America.

Citrus Blackfly (1973-1980) - Mission Methods Development Center. In 1974, parasites of the citrus blackfly were taken from Mexico to Brownville, TX, where colonization methods were developed. Subsequently, these parasites were released in south Texas and were monitored for establishment. Surveys in Texas later recovered four parasite species: *Encarsia opulenta*, *E. clypealis*, *E. smithi* and *Amitus hesperidum*. From 1976-1980, *E. opulenta* and *A. hesperidum* were mass reared using hydroponically-fed, potted, rough-lemon plants as hosts for the citrus blackfly, and were released in south Texas by Mission Center personnel and in south Florida by the Florida Division of Plant Industry. These two parasites became established in 1980 in south Florida where they dramatically reduced citrus blackfly populations (Nguyen et al. 1983). The State of Florida continues to rear these parasites for release.

Mexican Bean Beetle (1979-1984) - Mission and Otis Method Development Centers, with Niles BCO. Beginning in 1979, procedures were developed for mass rearing the Mexican bean beetle, a pest of green beans and soybeans, and its parasite *Pediobius foveolatus*. This parasite was released by BCO in several eastern and midwestern states. Methods Development personnel worked in Maryland to determine optimal parasite release rates for production in nurse plots, parasite dispersal from these plots, and level of control in green beans and soybeans (Mellors et al. 1983). By 1984, results from field studies in Maryland and Indiana indicated reductions in Mexican bean beetle populations.

Alfalfa Weevil (1981-1991) - Otis Method Development Center, with Niles BCO. An alfalfa weevil biological control evaluation survey (1981-1989) was designed by ARS, APHIS, and Economic Research Service to document changes in alfalfa weevil populations due to the establishment of new

parasite species (Kingsley et al. 1993). This project was coordinated by the Otis Center in cooperation with the Niles BCO Laboratory. Biological and economic data were collected by APHIS-PPQ personnel from cooperating alfalfa growers in 180 alfalfa fields sampled in nine states for up to eight years. Results from this survey indicated that biological control was an important factor in maintaining alfalfa weevil populations below economic injury levels. Analysis of the economic data with an econometric model suggested that net social benefits to producers and consumers from the Alfalfa Weevil Biological Control Program were $2.2 billion for the duration of the project (White 1989; Moffitt et al. 1990). This amount is equivalent to a perpetual stream of net social benefits of $88 million per year measured in 1987 dollars. Net social benefit refers to the difference between estimated market benefit and government expenditures. The expected cost:benefit ratio associated with the biological program against the alfalfa weevil is 1:87.

Hydrilla (1981-1993) - Whiteville Methods Development Center. When hydrilla was discovered in the All-American Canal in the Imperial Valley of California in 1979, this invasive alien aquatic weed was deemed to be a catastrophic threat to this irrigation system. Since APHIS is the agency that administers the Federal Noxious Weed Act, Methods Development joined in an interagency task force to examine potential controls. White amur, commonly referred to as the grass carp, provided efficient hydrilla control in the Imperial Valley. Mechanically-induced triploidy in this fish induced sterility, providing a non-reproducing biological control agent that has virtually eliminated hydrilla and other troublesome weeds from this irrigation system. The triploid white amur is now (1993) extensively used nationwide for aquatic weed management.

Citrus Whitefly (1982-1983) - Mission Methods Development Center, with Mission BCO. Initial work was done on mass rearing the citrus whitefly and its parasite, *Encarsia lahorensis*. Improvements in whitefly rearing included the use of a non-citrus host (viburnum). These improvements in rearing enabled BCO to produce adequate numbers of parasites for field release.

Silverleaf Nightshade (1982-1984) - Mission Methods Development Center, with Mission BCO. A method was developed to disinfect seeds of silverleaf nightshade and other *Solanum* species for tissue culture studies. A method to extract and count the leaf-galling nematode, *Ditylenchus* (as *Orrina*) *pyllobius*, was also developed. Although *D. pyllobius* inoculum was effective against silverleaf nightshade, this project was terminated by BCO in 1986 due to the high cost of producing the inoculum.

Sugarcane Borer and Mexican Rice Borer (1981-1991) - Mission Methods Development Center. Mass-rearing techniques were developed, at the request of the Rio Grande Valley Sugar Growers Association, for the sugarcane borer and the Mexican rice borer as hosts for the parasites *Cotesia flavipes*, *Allorhogas pyralophagus* and *Rhaconotus roslinensis*. Improvements in rearing included egg-disinfecting and antimicrobial agents, and the publication of a Standard Operating Procedure Manual (Martinez et al. 1988). This technology was transferred to the Texas A & M University Experiment Station for continued experimental work.

Colorado Potato Beetle (1985-1993) - Otis and Mission Method Development Centers, with Mission BCO. An artificial diet was developed for Colorado potato beetle (CPB) adults as a host for the egg parasite *Edovum puttleri*. Adults were reared on the improved diet for up to eight generations with no loss in quality compared to beetles reared on potato foliage. The parasite completed its life cycle on eggs from diet-reared beetles. New methods were developed to increase the efficiency of rearing the parasite in the laboratory for release. The use of CPB eggs killed by irradiation eliminated cannibalism by larvae from unparasitized eggs. Methods were also developed for mass producing the coccinellid *Coleomegilla maculata*, an egg predator, on a diet of air-dried Mexican fruit fly eggs. Fecundity, larval survival, and developmental time were improved compared to the standard raw

pork liver diet. The BCO project using natural enemies in integrated pest management of the Colorado potato beetle is ongoing (1993).

Aphid Biological Control (1987-1988) - Otis Methods Development Center, with Niles BCO. Beginning in 1987, APHIS-PPQ-BCO redistributed the introduced aphid predator *Coccinella septempunctata* in the U.S. in an effort to suppress pest aphids in agricultural habitats. Methods Development contributed to this rearing and release effort by improving mass rearing techniques. The nutritional suitability of several aphids for the predator's larvae and adults was determined through laboratory life table analysis, and it was recommended that pea aphid, rather than greenbug, be used as prey in mass rearing.

The results of two field studies in Massachusetts demonstrated the ability of *C. septempunctata* to reduce field populations of aphids in small field cages and open field plots (Kauffman and Schwalbe 1991). These studies indicated that field evaluations of natural enemies should strive to quantify plant growth and crop yield responses to reduced pest herbivory under biological control.

The Otis Center, in cooperation with BCO and research cooperators in Arkansas, Kansas, and Texas, evaluated the ability of *C. septempunctata* and *Hippodamia convergens*, a native coccinellid, to suppress aphids in small grains and alfalfa. Despite apparent visual differences, high variability of aphid populations and small numbers of replications prevented any demonstration of statistically lower aphid densities in cages with coccinellids compared to controls. The two predators reduced aphids to a similar degree and had no obvious incompatibility with each other.

Russian Wheat Aphid (1988-1993) - Otis Methods Development Center, with Niles and Mission BCO. With the assistance of APHIS-PPQ field personnel and BCO, a field sampling method was developed for a national survey of Russian wheat aphid (RWA) and its natural enemies in the U.S. This sampling method employed visual sampling of plant tillers and sweep netting and was used to evaluate the impact of beneficial species on RWA populations. In addition, other techniques for evaluating the effects of natural enemies on RWA were developed during two years (1990-1992) of cooperative agreements between Otis Center and state cooperators in California, Colorado, Idaho, Kansas, and Texas. These included: 1) sampling techniques for RWA and its natural enemies, 2) insecticidal exclusion, 3) exclusion cages, 4) inclusion cages, 5) host exposure on single-plant exclusion cages, and 6) host plant assessments in surrounding non-agricultural habitats. These evaluation techniques included a standardized impact and economic evaluation work plan, coordinated by Methods Development and BCO with cooperators, for implementation in selected sites throughout the RWA distribution in the U.S. beginning in 1994.

Because RWA usually feeds inside the sheaths of rolled leaves of susceptible grasses, a laboratory study determined to what extent coccinellids collected from RWA homelands were adapted to search for RWA prey inside rolled leaves. Among the predators, *Scymnus frontalis* was found to be better adapted than *Hippodamia variegata*, *H. tredecimpunctata*, and *Propylea quatuordecimpunctata* to exploit this "prey-protecting niche," and appeared to offer the greatest promise for RWA biological control in the U.S. (Kauffman and LaRoche 1994).

Improved rearing techniques were developed for another aphidophagous predator, *Leucopis ninae*, which was reared and released by BCO against RWA. Findings from laboratory studies and from field studies done in cooperation with ARS suggested that RWA concealment in rolled leaves limited the effectiveness of *L. ninae* against RWA.

Mexican Fruit Fly (1990-1993) - Mission Methods Development Center. Techniques were developed for mass rearing the larval parasite *Diachasmimorpha longicaudata* using irradiated Mexican fruit fly, i.e., larvae that pupate but do not produce adult flies. Releases were made into commercial citrus

and wild hosts in northern Mexico, and a recommendation was made to include the release of parasites as part of the future development of fly-free zones in that area.

Investigations were conducted in 1993 to determine the effect of *Bacillus thuringiensis* isolates on Mexican fruit fly adults. Four active isolates were identified, and soil samples from Guatemala were collected to identify and culture additional *Bt* strains.

Euonymus Scale (1991-1993) - Otis Methods Development Center, with Niles BCO. The objectives of this project were to determine the impact of the euonymus scale on its host and to determine how the establishment of natural enemies affects scale populations and the survival of the euonymus host. A survey to estimate the economic benefits of the Euonymus Scale Biological Control Program was developed in collaboration with BCO and the University of Massachusetts. The survey was implemented in eleven states in 1993 and is to continue through 1996.

Sweetpotato Whitefly (1991-1993) - Phoenix Methods Development Center, with Mission BCO. Phoenix Center personnel have collaborated with ARS researchers at the Western Cotton Research Laboratory, Phoenix, AZ, in enhancing a method of mass rearing the native predator *Geocoris punctipes* using artificial diet (Cohen and Staten 1994). Trial releases were conducted in southeastern California and Arizona in early 1993. Preliminary data show that the predator feeds extensively on sweetpotato whitefly. Collaborative studies have also been initiated to devise rearing methods and study the feeding behavior of *Catana parcesetosa*, an exotic coccinellid predator of whiteflies. The Phoenix Center provided support for areawide whitefly management trials on cotton in three locations in southern Arizona and California in 1993. These trials incorporated inundative releases of *Chrysoperla* species to supplement naturally occurring biological control.

Methods Development also stationed an entomologist in Brawley, CA, to evaluate exotic natural enemies released against the whitefly. Exotic parasites for the releases were produced at the Mission BCO Laboratory. This program involved: 1) pre-release surveys to document the indigenous natural enemies, 2) releasing and establishing exotic natural enemies, 3) surveys to demonstrate natural enemy recovery and dispersal, 4) population studies of whitefly and its enemies on major crops throughout the year, 5) field and laboratory evaluations of the efficacy of exotic and indigenous natural enemies and their impact on whitefly populations, and 6) providing voucher specimens for morphological and molecular taxonomic studies.

Beauveria bassiana for Rangeland Grasshoppers (1991-1993) - Phoenix Methods Development Center. Formulations of this fungal pathogen were developed and tested in laboratory and small field tests against the complex of rangeland grasshoppers. Work in 1993 included a large-scale field test and examination of effects of the fungus on non-target organisms.

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C. THE NATIONAL BIOLOGICAL CONTROL INSTITUTE. By E. S. Delfosse

The National Biological Control Institute (NBCI) was established in 1990 by the Animal and Plant Health Inspection Service (APHIS) "to promote, facilitate, and provide leadership for biological

control". It is thus a unique group in the history of biological control in the United States. NBCI had a relatively short, but very intense, ontogeny. Some of the important steps in the formation of NBCI, as well as recent changes in its activities, are discussed below.

1. Establishment of NBCI

A chronology of significant events in establishment of NBCI is presented in Table 5. Several reviews of biological control policy and implementation in APHIS preceded establishment of NBCI. In October 1985, a Review Team headed by W. W. Metterhouse of the New Jersey Department of Agriculture submitted a "Biological Control Program Evaluation Report" (APHIS, PPQ 1985) to Harvey L. Ford, then Deputy Administrator of the Plant Protection and Quarantine (PPQ) unit. The terms of reference of this report are directly relevant to establishment of NBCI:

> "A. Review the established [PPQ] biological control goals, objectives, and guidelines, to update or modify them based on current needs.
> B. Review current procedures for selecting, developing, and implementing biological control projects. Determine if existing procedures are appropriate and, if not, modify them to improve program results.
> C. Review program activities at the Mission, Texas, and Niles, Michigan, laboratories to assess activities and accomplishments. Make recommendations on resource needs and other areas of concern.
> D. Review the existing organizational structure of biological control and the interrelationships between laboratory/staff personnel with the field organization. Make recommendations for increasing organizational effectiveness which will benefit PPQ and further the accomplishment of biological control objectives.
> E. Make recommendations on the future of the PPQ biological control program specifically addressing such items as funding, personnel, additional rearing facilities, etc.
> F. Determine whether an ARS employee should be stationed at the Mission Laboratory."

There were 18 recommendations from the "Metterhouse Report," four of which are relevant to this discussion of NBCI:

> "4. Increase national visibility of the biological control program through aggressive public relations.
> 6. Take the lead in establishing an interagency biological control advisory group within the USDA.
> 11. Establish a Program Manager position at Hyattsville, Maryland, reporting to the Assistant Deputy Administrator for National Programs, to direct the overall biological control program.
> 12. Establish a Biological Control Specialist position to provide technical and scientific expertise in program operation and development."

Recommendations 4 and 6 were implemented by APHIS; 11 and 12 were deferred pending review of the National Program Planning Staff by a private contractor.

The next pivotal document in the formation of NBCI is called the "Thomas Report" (APHIS 1987). It was commissioned by William F. Helms, Deputy Administrator, PPQ, in May 1987, and had the following terms of reference:

> "[Mr. Helms] asked PPDS to propose for top management consideration, the roles PPQ should play in the future to develop, implement and evaluate biological control projects. The new roles proposed should contribute to: (1) increasing the impact of biological control projects; and (2) increasing the involvement of other organizational entities."

The recommendations of the Thomas Report were as follows:

> "This Committee recommends that PPQ take the leadership role in the United States for all aspects of biological control of pests of interest and high priority to the Agency and to American Agriculture. By doing so, the Agency will fill a void not currently addressed by any other organization. We recommend that PPQ take the leadership role by implementing and managing the 'Holistic Approach to Biological Control.' ... In taking the lead, PPQ would identify and prioritize its own projects of interest; become involved in foreign exploration, quarantine operations, screening natural enemies, importation, colonization and establishment, evaluating effectiveness of natural enemies; and distributing natural enemies in large-scale implementation projects. In addition, PPQ would expand its role in developing augmentative biological control projects which could also complement Integrated Pest Management (IPM) programs conducted by the Agency."

These recommendations were also accepted in principle by the then-Administrator, Donald L. Houston (Houston 1987), who, on December 21, 1987, suggested that the APHIS biological control activities should be developed in a "world recognized center of excellence for biological control". This is the first reference to developing NBCI as a center of excellence with a mandate beyond the USDA.

Several drafts of a plan for a "National Biological Control Service Institute (NBCSI) within APHIS" were developed and discussed from 1987-89. Dr. Houston's successor, James W. Glosser, announced on March 22, 1989, at the Biological Control Centennial Celebration in Washington that there would be a new APHIS initiative: the NBCSI. The aims of the NBCSI would be (Glosser 1989):

> "... to provide an expansion of implementation services, improved coordination, and a greater leadership role for APHIS in biological control. This initiative has been taken as a key strategy in protecting American agriculture through the use of environmentally sound methods. The initiative and the concept of the Institute is the result of an intensive series of meetings and reports involving APHIS staff and line managers over the past two years."

In fact, there were prolonged and often spirited discussions between interested parties from 1986-88 as to the NBCI location, mission, stakeholders, and related matters. Many locations within APHIS (an existing unit, or the Office of the Administrator), and outside APHIS (to somewhere in the Department of Agriculture, or becoming "independent"), were discussed. This culminated in an important Decision Paper in 1989 that concluded that the two most appropriate locations were PPQ and Science and Technology (S&T), and recommended that PPQ would be the most appropriate location.

However, in the ensuing discussions, this position was reversed, and it was decided that S&T was the most appropriate initial location for NBCI. It was felt that an "institute" must be scientifically-based, and strategically-oriented. At least initially, NBCI would have a policy role, rather than a program role, and would be given a global orientation. This "noble" vision of NBCI was approved formally by

Dr. Glosser in 1990, and a "National Biological Control Institute Implementation Plan" (APHIS 1990) was released on February 15, 1990.

Thus, the formative period of NBCI, during which critical philosophical issues were examined in extreme detail, can be considered to be 1985-90. NBCI rose out of the perceived need for a biological control group that would be capable of interacting at all administrative and scientific levels, and would have a global focus.

2. The Initial Mission, Functions and Staffing of NBCI

The mission of NBCI is "to promote, facilitate, and provide leadership for biological control" (APHIS 1990). The initial NBCI functions (APHIS 1990) were to:

- ensure national leadership for the development and implementation of biological control;
- develop an effective network of federal, state, and private organizations committed to biological control;
- solicit input from cooperating institutions in identifying potential biological control projects;
- identify and support the technical needs of cooperators and clients; collect, analyze, and disseminate general and technical information on biological control activities;
- expedite acquisition, development, and implementation of biological control agents;
- coordinate technical education and training programs; and
- integrate biological control with other pest management technologies.

Other functions were to be added as biological control customers identified them.

Six positions were approved initially for NBCI: Director, Secretary, Technical Coordinator, Technical Consultant, Database Manager, and Computer Operator. NBCI was committed to facilitating the use of the scientific and other expertise in the global community to the fullest extent in its operations.

Additionally, a Visiting Scientist position was established, which was to be filled for relatively short periods of time by world-class scientists or other specialists. These individuals advise and consult on a relevant biological control problem, perform a specific function such as a review or a survey, etc. There have been two NBCI Visiting Scientists to date (1993): Dan Girling (University of Israel), who advised on biological control of whiteflies, and V. C. Moran (Dean of Science at Cape Town University), who advised on the international role of NBCI.

The Director was to be "a world-class biological control scientist who must be capable of operating at all scientific, technical, social, environmental, media, legal and political levels." Entrepreneurial policy, media and educational campaigns would be necessary. It is essential that the Director maintain scientific credibility. The Director was to manage the budget and staff, and was to provide consultation to APHIS units and to the Administrator on biological control and related environmental, sustainable agriculture, and integrated pest management issues.

To ensure that NBCI would continue to receive current, complete, and accurate details on operational and scientific needs, critical issues, and feedback on NBCI activities, a Customer Advisory Panel (CAP; formerly "User Advisory Panel") was established. On this Panel (Table 6) were 16 outstanding individuals from federal and state governments, universities, and the private sector. CAP members serve three-year terms, and three members are replaced each year. CSRS Regional Biological Control Projects recommend their representative. The NBCI CAP is the only cross-cutting customer group in the U.S. to give consistent direction to a biological control/integrated pest management policy group, and has contributed significantly to the early success of NBCI.

In 1989, NBCI was formally named one of the three APHIS "Centers of Excellence." NBCI reported, for an interim period of February-March 1990, to the Director of S&T through the Director of Methods Development, and in March 1991, NBCI reported directly to the Director of S&T. In late 1991, APHIS was reorganized, and S&T was disbanded. All locations in APHIS (and some outside of APHIS) were considered for NBCI. From this examination it was concluded that it would be inappropriate to place the NBCI in any APHIS Unit, because two insurmountable problems would be created: 1) a perception that the NBCI is less important to APHIS, and 2) a structural incompatibility. In regard to 1) the clear message to customers would be that NBCI was not considered as important to APHIS as it was when it was first established. This would make it difficult, if not impossible, for NBCI to achieve its mission. And in regard to 2), since all APHIS Units are important NBCI customers, it is clearly inappropriate for NBCI to be located in any of them.

After considering all possible locations for NBCI, the Administrator decided in January 1992 to elevate NBCI to the Office of the APHIS Administrator. There are several benefits to this level of reporting, and no obvious disadvantages to NBCI. Some of the significant advantages are:

- higher visibility within APHIS, which will lead naturally to higher visibility outside of APHIS;
- a strong show of support for NBCI and its environmental activities;
- easier access to and by the decision- and policy-makers;
- ability to interact more easily with the Administrator and the APHIS Management Team (AMT) on critical issues facing biological control and integrated pest management.

3. The Current Role of NBCI

It was recognized from the outset that NBCI would be a special, "noble" effort by APHIS. It was to be a scientifically and philosophically based policy group, rather than an operationally oriented group, but would still have to operate effectively with line programs. Identifying customers, determining collaboratively their needs, and providing services is an important NBCI mandate.

In effect, NBCI was established to be an entrepreneurial policy group for biological control, encouraged to interact freely within APHIS and other USDA agencies, universities, the National Plant Board, state departments of agriculture and similar bodies, special interest groups, the environmental community, industry, politicians, the media, the international community, etc.

It was obvious that there was a need in the U.S. for such a group to act for biological control and integrated pest management, and that it could only do so if it were given an unusual amount of freedom, responsibility and accountability. This was particularly important because the NBCI was located within APHIS, and there was criticism that several of its key customers (in particular, Biotechnology, Biologics and Environmental Protection [BBEP], Biological Control Operations [BCO], and Biological Assessment and Taxonomic Support [BATS]) were also in APHIS. Despite having no line responsibilities for programs or regulations, it was important for NBCI to interact with these customers.

NBCI currently (1993) has lead roles in biological control and integrated pest management policy, training and education, and facilitating biological control. For example, in early 1992, NBCI was charged by the APHIS Administrator with reviewing the APHIS biological control policy. This was undertaken in six steps: Examine APHIS legislative authority; develop a philosophy; confirm lines of authority; document current regulatory procedures; develop, with customers, new regulations and procedures; and enter into a process of renewing regulations and procedures regularly, with significant input from customers.

This process took a year to complete. A highlight is the APHIS Biological Control Philosophy, approved by the then-Administrator, Robert B. Melland, on August 7, 1992. This philosophy states:

"APHIS believes that modern biological control, appropriately applied and monitored, is an environmentally safe and desirable form of long-term management of pest species. It is neither a panacea nor a solution for all pest problems. APHIS believes that biological control is preferable when applicable; however, we also recognize that biological control has limited application to emergency eradication programs. Whenever possible, biological control should replace chemical control as the base strategy for integrated pest management.

"In support of this philosophy, APHIS will develop regulations that facilitate the release of safe biological control agents, while maintaining adequate protection for American agriculture and the environment. The regulations will give clear and appropriate guidance to permit applicants, including specific types of data needed for review and environmental analysis and specific time limits for Agency review. They will be updated as the science progresses. APHIS believes that public input on procedures to approve the release of biological control agents is a desirable and necessary step, and will strive to gather input from scientists, industry, and the public."

Existing procedures for approval of biological control agents were examined, with input from APHIS (BATS and BBEP, primarily), and customers (scientists, environmental groups, commercial groups, and international groups). Input was also sought from these same groups for the elements needed to improve the procedures, and drafts of a new process were prepared. The final draft is currently being reviewed internally, and will be distributed for external comment via the *Federal Register*.

NBCI is developing a training and education plan to help meet the needs of biological control. For example, NBCI is developing with collaborators a series of written and video materials that discuss biological control in a non-technical manner. Each 3-year age class from pre-school to university level will be covered. The first video, which addresses the mature, but scientifically-unsophisticated customer group, was (1993) in final production. An extensive computerized NBCI Bulletin Board System has been established and is used by the biological control community. A cooperative arrangement with the ARS Biological Control Documentation Center has been established to maximize the effectiveness of each group in delivering biological control information.

NBCI's facilitation efforts have resulted in granting over $1 million since 1990 in funds for implementation evaluation of biological control, including support for meetings and publications. To address the critical shortage of systematists in groups of importance to biological control, NBCI has awarded three, 2-year Post-Doctoral Positions in Systematics. Two major Focus Group Workshops have been facilitated by NBCI: Scientific Considerations in Release of Transgenic Arthropod Biological Control Agents (with Marjorie A. Hoy of the University of Florida), November, 1993, and New Directions in Biological Control of the Gypsy Moth (with other USDA agencies, universities, and states), early January, 1994. Workshops on quarantine issues, documentation, host specificity, commercial biological control, and other issues are planned.

4. Future of NBCI

In three years, NBCI completed the primary goals for which it was established. A strategic planning process has continued. One outcome of this process is development of an NBCI Program Logic Model, philosophy, and vision for biological control. With customer input, these documents help frame the future activities of NBCI.

Clearly, biological control is becoming the method of choice for pest management around the world (for example, the current U.S. Administration is committed to increasing biological control as part of sustainable agriculture and integrated pest management). These sentiments mirror those of NBCI.

However, biological control faces many critical scientific, legal, political and social issues, which are hindering severely the objective conception, development, and implementation of programs. The historical structure of science in general and biological control in particular in the U.S. has been incapable of addressing these issues effectively. Most university and government scientists are neither trained nor willing to deal with difficult legal, political, or social conundra. NBCI is a unique government body which was formed to deal with these difficult issues. NBCI is capable of continuing to serve agriculture and the environment in the United States and internationally, and with continued support, will meet this goal.

Table 4. Pests and Associated Natural Enemies for USDA Programs Coordinated by the Biological Control Laboratories of the Animal and Plant Health Inspection Service, Plant Protection and Quarantine

Pest Species (Common Name) Order:Family	Natural Enemy Order:Family Species
ARTHROPOD PESTS	
Bemisia tabaci (Gennadius) (Sweetpotato whitefly) Homoptera: Aleyrodidae	Hymenoptera: Aphelinidae *Encarsia formosa* Gahan *Encarsia lutea* (Masi) *Encarsia nigricephala* Dozier *Encarsia pergandiella* Howard *Encarsia transvena* (Timberlake) *Encarsia* sp. nr. *strenua* (Silvestri) *Encarsia* spp. *Eretmocerus mundus* (Mercet) *Eretmocerus* spp. Coleoptera: Coccinellidae *Catana parcesetosa* (Sicard) Fungi **Beauveria bassiana* (Bals.) **Paecilomyces* spp.
Dialeurodes citri (Ashmead) (Citrus whitefly) Homoptera: Aleyrodidae	Hymenoptera: Aphelinidae *Encarsia lahorensis* (Howard)
Diuraphis noxia (Mordvilko) (Russian wheat aphid) Homoptera: Aphididae	Coleoptera: Coccinellidae *Adalia bipunctata* (L.) *Coccinella septempunctata* L. *Coccinella transversoguttata graminum* Mader *Coccinellina ancoralis* (Germar) *Coleomegilla quadrifasciata* (Schoenherr) *Eriopis connexa* Mulsant *Hippodamia tredecimpunctata* (L.) *Hippodamia variegata* (Goeze) *Oenopia conglobata* (L.) *Propylea quatuordecimpunctata* (L.) *Scymnus frontalis* Fabricius *Semiadalia undecimnotata* (Schneider)

Continued

Table 4. Pests and Associated Natural Enemies for USDA Programs Coordinated by the Biological Control Laboratories of the Animal and Plant Health Inspection Service, Plant Protection and Quarantine--Continued

Pest Species (Common Name) Order:Family	Natural Enemy Order:Family Species
Diuraphis noxia (Continued)	Diptera: Chamaemyiidae *Leucopis ninae* (Tanasijtshuk) Diptera: Syrphidae *Eupeodes nuda* (L.) *Sphaerophoria scripta* (L.) Hymenoptera: Aphelinidae *Aphelinus albipodus* Hayat & Fatima *Aphelinus asychis* Walker *Aphelinus varipes* (Förster) *Aphidius colemani* Viereck *Aphidius matricariae* Haliday *Aphidius picipes* (Nees) *Aphidius rhopalosiphi* DeStefani-Perez **Aphidius uzbekistanicus* Lushetzki *Diaretiella rapae* (M'Intosh) *Ephedrus plagiator* (Nees) *Praon gallicum* Starý
Epilachna varivestis Mulsant (Mexican bean beetle) Coleoptera: Coccinellidae	Hymenoptera: Eulophidae *Pediobius foveolatus* (Crawford)
Hypera postica (Gyllenhal) (Alfalfa weevil) Coleoptera: Curculionidae	Hymenoptera: Ichneumonidae *Bathyplectes anurus* (Thomson) *Bathyplectes curculionis* (Thomson) *Bathyplectes stenostigma* (Thomson) Hymenoptera: Pteromalidae *Dibrachoides dynastes* (Förster) *Peridesmia discus* (Walker) **Trichomalus inops* (Walker) Hymenoptera: Braconidae *Microctonus aethiopoides* Loan *Microctonus colesi* Drea *Microctonus stelleri* Loan Hymenoptera: Eulophidae *Necremnus leucarthros* (Nees) *Oomyzus incertus* (Ratzeburg)

Table 4. Pests and Associated Natural Enemies for USDA Programs Coordinated by the Biological Control Laboratories of the Animal and Plant Health Inspection Service, Plant Protection and Quarantine

Pest Species (Common Name) Order:Family	Natural Enemy Order:Family Species
Hypera postica (Continued)	Hymenoptera: Mymaridae **Patasson luna* (Girault)
Leptinotarsa decemlineata (Say) (Colorado potato beetle) Coleoptera: Chrysomelidae	Hymenoptera: Eulophidae *Edovum puttleri* Grissell Diptera: Tachinidae *Myiopharus doryphorae* (Riley) *Myiopharus* sp. Coleoptera: Coccinellidae *Coleomegilla maculata* (DeGeer) Heteroptera: Pentatomidae *Perillus bioculatus* (Fabricius) Neuroptera: Chrysopidae **Chrysoperla rufilabris* (Burmeister) Nematoda: Enoplida: Mermithidae *Hexamermis* sp. Nematoda: Rhabditida: Steinernematidae *Steinernema feltiae* (Filipjev, 1934) Bacteria **Bacillus thuringiensis sandiego*
Ostrinia nubilalis (Hübner) (European corn borer) Lepidoptera: Pyralidae	Diptera: Tachinidae *Lydella thompsoni* Herting Hymenoptera: Braconidae *Macrocentrus grandii* Goidanich *Macrocentrus linearis* (Nees) *Habrobracon brevicornis* (Wesmael) Hymenoptera: Ichneumonidae *Eriborus terebrans* (Gravenhorst) Hymenoptera: Trichogrammatidae **Trichogramma chilonis* Ishii **Trichogramma dendrolimi* Matsumura *Trichogramma nubilale* Ertle & Davis *Trichogramma ostriniae* Pang & Chen Bacteria **Bacillus thuringiensis* Berliner Fungi **Beauveria bassiana* (Bals.)

Continued

Table 4. Pests and Associated Natural Enemies for USDA Programs Coordinated by the Biological Control Laboratories of the Animal and Plant Health Inspection Service, Plant Protection and Quarantine--Continued

Pest Species (Common Name) Order:Family	Natural Enemy Order:Family Species
Ostrinia nubilalis (Continued)	Protozoa *Nosema pyrausta* (Paillot)
Oulema melanopus (L.) (Cereal leaf beetle) Coleoptera: Chrysomelidae	Hymenoptera: Mymaridae *Anaphes flavipes* (Förster) Hymenoptera: Ichneumonidae *Diaparsis temporalis* Horstmann *Lemophagus curtus* Townes Hymenoptera: Eulophidae *Tetrastichus julis* (Walker)
Unaspis euonymi (Comstock) (Euonymus scale) Homoptera: Diaspididae	Coleoptera: Coccinellidae *Chilocorus kuwanae* (Silvestri) Coleoptera: Nitidulidae *Cybocephalus* sp. prob. *nipponicus* Endrödy-Yonga Hymenoptera: Aphelinidae *Coccobius* sp. nr. *fulvus* (Compere & Annecke) *Encarsia* sp. nr. *diaspidicola* (Silvestri)
	WEED PESTS
Centaurea diffusa Lam. (Diffuse knapweed) *Centaurea maculosa* Lam. (Spotted knapweed) Asterales: Asteraceae	Coleoptera: Curculionidae *Bangasternus fausti* (Reitter) *Cyphocleonus achates* (Fåhraeus) *Larinus minutus* Gyllenhal Coleoptera: Buprestidae *Sphenoptera jugoslavica* Obenberger Diptera: Tephritidae *Chaetorellia acrolophi* White & Marquart *Terellia virens* (Loew) *Urophora affinis* Frauenfeld *Urophora quadrifasciata* Meigen Lepidoptera: Gelechiidae *Metzneria paucipunctella* Zeller Lepidoptera: Pterolonchidae *Pterolonche inspersa* Staudinger

Table 4. Pests and Associated Natural Enemies for USDA Programs Coordinated by the Biological Control Laboratories of the Animal and Plant Health Inspection Service, Plant Protection and Quarantine

Pest Species (Common Name) Order:Family	Natural Enemy Order:Family Species
Centaurea spp. *(Continued)*	Lepidoptera: Tortricidae *Pelochrista medullana* (Staudinger) Lepidoptera: Cochylidae *Agapeta zoegana* L. Acari: Acariformes: Eriophyidae **Aceria centaureae* (Nalepa)
Euphorbia esula L. (Leafy spurge) Euphorbiales: Euphorbiaceae	Coleoptera:Chrysomelidae *Aphthona cyparissiae* (Koch) *Aphthona czwalinae* Weise *Aphthona flava* Guillebeau *Aphthona lacertosa* Rosenheim *Aphthona nigriscutis* Foudras Coleoptera: Cerambycidae *Oberea erythrocephala* (Schrank) Coleoptera: Curculionidae **Oxicesta geographica* (Fabricius) Diptera: Cecidomyiidae *Dasineura* sp. nr. *capsulae* Kieffer **Spurgia capitigena* (Bremi) *Spurgia esulae* Gagné Diptera: Anthomyiidae *Pegomya curticornis* (Stein) *Pegomya euphorbiae* (Kieffer) *Pegomya transversaloides* Schnabel Hymenoptera: Eurytomidae **Eurytoma* sp. *Hyles euphorbiae* (L.) Lepidoptera: Sesiidae *Chamaesphecia crassicornis* Bartel *Chamaesphecia hungarica* (Tomala) Lepidoptera: Noctuidae **Simyra dentinosa* Freyer Fungi **Uromyces scutellatus* (Pers.) Ler. **Uromyces striatus* Schroet.
Solanum elaeagnifolium Cav. (Silverleaf nightshade) Solanales: Solanaceae	Nematoda: Tylenchida: Anguinidae *Ditylenchus phyllobius* (Thorne) Filipjev

* Natural enemies associated with cooperators, but not a direct responsibility of APHIS-PPQ-BCO.

Table 5. Chronology of events leading to the establishment of the National Biological Control Institute in APHIS

Date	Item
October 1985	Dr. Harvey Ford, APHIS Administrator, established a review team, headed by Mr. William Metterhouse, to review APHIS biological control. A report entitled APHIS, PPQ Biological Control Evaluation Report was submitted, and circulated widely for comment.
May 1987	Mr. William Helms asked Program Planning and Development Staff (PPDS), PPQ, to determine if the roles being played by PPQ in biological control program were appropriate and what role PPQ should play in the future to develop, implement, and evaluate biological control projects. The "Thomas Committee," headed by Mr. Ed Thomas, established for this review.
October 1987	A Biological Control Review Report submitted by the Thomas Committee.
November 1987	Briefing paper submitted to the Administrator Office entitled Biological Control: A Recommendation, 1987.
December 1987	Biological Control Program Orientation and Recommendation made to Dr. Donald Houston, APHIS Administrator, which discussed the Thomas Report.
December 1987	Dr. Houston states that APHIS should upgrade its activities in biological control and should establish a "world recognized center of excellence," which became NBCI.
February 1988	Briefing paper Status of the New Biological Control Initiative in the Animal and Plant Health Inspection Service (APHIS) submitted to the Administrator, Dr. Jim Glosser.
February 1988	D. E. Meyerdirk presented APHIS' New Biological Control Initiative to the USDA, ARS Biological Control Matrix Team, and Delfosse. D. L. Husnik wrote E. B. Knipling, ARS, about the initiative. These efforts helped obtain intraagency support for NBCI.
April 1988	Position paper submitted to the Administrator's Office Proposed Animal and Plant Health Inspection Service (APHIS) Initiative in Biological Control.
August 1988	The New APHIS Biological Control Initiative and Task Element Matrix presented to Dr. Dean Plowman, ARS, by Dr. James Glosser.

Table 5. Chronology of events leading to the establishment of the National Biological Control Institute in APHIS

Date	Item
October 1988	APHIS Reorganization, creating a new Unit called Science and Technology.
January-April 1989	Intense planning activities by APHIS, during which the formation of NBCI was debated.
March 1989	Dr. Glosser announced of the New APHIS Biological Control Initiative and the Biological Control Institute presented during the Biological Control Centennial Celebration on the Patio of the Administration Building.
March 1989	NBCI named as one of three APHIS "Centers of Excellence."
April 1989	NBCI "Organizational Decisions" were identified: 1) What is the structure of the institute; 2) How would the institute be staffed; 3) To whom should the institute report.
February 1990	National Biological Control Institute Implementation Plan released, and the search for the first Director begun.
September 1991	Organizational Review by the APHIS Management Team decisions released. Decision Number 6 was: "Scientific support for line delivery units will be enhanced through re-integrating the Science and Technology unit's functions into the operational units with which they are primarily aligned. A Transition Team chaired by Dr. Charles Schwalbe has been charged to develop a comprehensive action plan for the orderly transfer of functions."
January 1993	APHIS Administrator, Robert Melland, elevated NBCI to the Office of the Administrator.

Table 6. NBCI Customer Advisory Panel Members, 1990-92

Name	Organization (Also Representing)	Location	Dates
Dr. W.L. Bruckart	USDA, ARS, NAA	Frederick, MD	1992-95
Dr. G. Buckingham	USDA, ARS	Gainesville, FL	1993-96
Dr. J.R. Cate	USDA, CSRS	Washington, DC	1990-94
Dr. J.H. Frank	Entomology & Nematology Dept. University of Florida	Gainesville, FL	1990-92
Mr. R.C. Frey	Arizona Biological Control, Inc. (Assoc.of Natural Bio-Control Producers)	Tucson, AZ	1990-92
Mr. R. Gaskalla	Florida Div. of Plant Industry (National Plant Board; States)	Gainesville, FL	1992-96
Dr. T.J. Kring	University of Arkansas	Fayetteville, AR	1990-92
Dr. J.L. Krysan	USDA, ARS, Natl. Progr. Staff	Beltsville, MD	1993-96
Dr. N.C. Leppla	USDA, APHIS, PPQ, Methods Devel.	Hyattsville, MD	1990-94
Dr. R.F. Luck	University of California	Riverside, CA	1990-93
Dr. J.V. Maddox	Illinois Natural History Survey	Champaign, IL	1992-96
Dr. D.L. Mahr	University of Wisconsin	Madison, WI	1990-93
Mr. W. Metterhouse	New Jersey Dept. of Agr. (National Plant Board; States)	Trenton, NJ	1990-92
Dr. D.E. Meyerdirk	USDA, APHIS, PPQ, BCO	Hyattsville, MD	1990-94
Mr. G. Scriven	Biotactics (Assoc. of Natural Biocontrol Producers)	Grand Terrace, CA	1992-96
Dr. R.S. Soper	USDA, ARS, OIRP	Beltsville, MD	1990-92

EPILOGUE

A. ACCOMPLISHMENTS AND CURRENT STATUS OF ARS RESEARCH ON CLASSICAL BIOLOGICAL CONTROL OF ARTHROPODS AND WEEDS. By J. R. Coulson, C. J. DeLoach, R. I. Carruthers, and K. J. Hackett

As noted in Chapters III and IV, the Agricultural Research Service (ARS) classical biological control (CBC) programs, and the CBC programs of its predecessor Bureau of Entomology and Plant Quarantine (BEPQ; see Chapters I and II) have produced some very significant accomplishments, in terms of both research results and successful pest control over the past 110 years. This Epilogue does not purport to provide updated information on USDA biological control programs beyond the history's cutoff date of December 1993. However, a number of important general biological control publications, in addition to those referenced above, can be reported here and are included in the Reference Cited section: National Research Council (1996); Van Driesche and Bellows (1996); Barbosa (1998); and Bellows and Fisher (1999). Also, a reference overlooked in preparing the history, Sawyer (1990), provides interesting information concerning USDA's biological control programs from 1888 to 1951.

However, in addition to these added references and a general discussion of the ARS CBC programs, a number of important events during the last six years (1994-1999) that have affected ARS programs are noted in this Epilogue. The National Program Leaders (NPLs) for Biological Control during this period were R. I. Carruthers and K. J. Hackett. E. S. Delfosse joined ARS in 1997 as NPL for Weed Science.

Program Successes: The arthropod and weed pests for which complete or substantial economic control has been achieved by CBC, or, in the case of recent programs, for which there is ample potential for success, are listed in Table 7. The terms "complete" and "substantial" control are those traditionally used in regard to CBC programs (DeBach and Rosen 1991), in which "complete economic control" indicates that other control measures are rarely if ever required on a sustained basis. In this regard, CBC entomologists are fond of noting that these programs appear to be the only such examples in which USDA research has in fact resulted in actual long-lasting economic control of a pest. Many examples in which "partial" control of a pest has been achieved by means of establishment of one or more exotic natural enemies are not listed in the table. Though footnoted in the table, it must be stressed that many other organizations besides ARS have been involved in most of the programs listed, for which credit is richly deserved but which are not herein specifically indicated. Likewise, ARS has played a role in many projects that were led by state, university, and other federal agencies.

Benefits in terms of annual savings have only been estimated for a few of the classical biological control importation programs conducted by the USDA-ARS from 1953 to 1993. This is primarily because economists have rarely been included in ARS research programs, and most entomologists have little expertise or time to conduct benefit:cost analyses. As noted in Chapters III and IV, the ARS programs for which some benefit:cost figures do exist include successful programs against the cereal leaf beetle, alfalfa weevil, Rhodesgrass mealybug, pea aphid, and alfalfa blotch leafminer, for

which a conservatively estimated combined annual savings totals about $150,000,000, in terms of 1993 dollars, plus increased crop yields. The few extant examples of estimated benefits from biological control of weeds projects from 1944 to the present (common St. Johnswort, alligatorweed, tansy ragwort, and puncturevine projects) total at least $30,000,000 annually. The resulting total of estimated annual benefits from CBC is therefore well over $180,000,000, eight times the estimated $21,500,000 spent on all aspects of biological control by ARS in 1987 (Table 8), and represents a total grower savings from CBC during the past decade of more than $2 billion (Hays 1992). The highly positive benefit:cost ratio of CBC is clearly demonstrated by comparing these savings with the estimated total cost ($20 million) of federal and state research on CBC from 1888 to 1976, and the estimated $420 million spent annually on insecticides in the 1960s (see Chapter III, and Sailer 1973, 1976b). (Use of pesticides in the United States in 1995 was estimated to be 1.2 billion pounds valued at over $10 billion [Benbroke et al. 1996].) It must be emphasized that most of these estimated figures are savings resulting from cessation of pesticide treatments no longer required because of permanent biological control of the pests, and do not include the additional (and incalculable) environmental benefits.

Costs of the alfalfa weevil and alligatorweed programs are estimated to have been $1 million each (Chapter III). The relatively small costs of CBC result in the highly favorable and often cited 30:1 benefit:cost ratio for CBC (DeBach and Rosen 1991); the benefit:cost ratio of the alfalfa weevil program alone is estimated at 87:1 (Kingsley et al. 1993). CBC is often unfairly criticized for being too slow a method of pest control; it often takes five to ten years before populations of introduced natural enemies increase sufficiently for adequate control to be realized, although spectacular control is sometimes achieved much earlier. However, both costs and control time for CBC compare quite favorably with research on pesticide development. It has been estimated that it takes six to 13 years and $30-50 million to develop a pesticide from its discovery to registration and marketing (Weil 1988; Menn and Christy 1992; Hutchins and Gehring 1993).

Successful augmentative biological control programs have also resulted from CBC research. The identification and introduction of the exotic natural enemies *Pediobius foveolatus* and *Edovum puttleri* were accomplished during CBC explorations. These parasites were found to be incapable of establishment in the U.S., but have been successfully utilized in augmentative programs against Mexican bean beetle and Colorado potato beetle, respectively (see Chapter IV, section B.1.b).

In addition to the many positive ARS CBC programs and trends over the past 110 years documented in the previous chapters of this history, this history has also documented several negative trends, one of which included a sharp decline in the number of scientists, facilities, and programs of the ARS biological control effort during the two decades prior to the original drafting of this Epilogue (1993). By 1999, however, this trend had reversed dramatically.

Personnel: Table 8 lists the number of ARS scientists at the end of December 1993 that devoted at least half time to CBC of arthropods and weeds, i.e., scientists exploring for, or working on the release, establishment and evaluation of exotic natural enemies. Six of the 28 SYs in 1993 were devoted to use of pathogens in CBC, an increase from zero in 1972. Five of the other SYs are foreign nationals stationed at ARS overseas stations in Europe and South America. Data obtained from the ARS Research Management Information System (RMIS) in December 1993 of CBC projects in ARS report a total of 31.7 SYs devoted to CBC. This included 13.7 SYs to weed control, and 16.3 SYs to arthropod control, and 1.7 SYs devoted to control of plant pathogens. The resulting total of 28 SYs in Table 8 is in agreement with the 30 CBC SYs from the RMIS report (excluding the 1.7 SYs for plant pathogens), when the RMIS figure is adjusted for loss of two CBC positions late in 1993.

Tables 9 and 10 show the estimated resources and SYs devoted to each biological control approach and research area (including taxonomic research related to biological control) by ARS in May 1987.

A total of an estimated 43.4 SYs are listed for CBC. The estimates are considered to be inflated due to the survey method in which as little as 10% of a scientist's time devoted to biological control was included in the tabulation, thus not presenting an accurate picture of the number of full-time ARS scientists devoted to biological control research. Because of this, comparisons among years are not entirely valid.

However, the total of 28 active SYs noted in Table 8 represented a significant reduction from the 43 SYs reported in 1972 (Sailer 1973; see Chapter III), and from those 1987 figures (Table 10).

Although the decline in number of biological control scientists within ARS caused some detrimental impacts to the success of the program, it represented not a specific reduction to the area of biological control research but a more widespread decline of available resources for many different types of agricultural research. This general decline was brought to the attention of USDA administrators by the current (1999) ARS Administrator, Dr. Floyd P. Horn. Dr. Horn documented that the number of ARS scientists has declined from an all time high of approximately 3,400 in the early 1970s to a low of 1,685 in the mid-1990s. This was over a 50% reduction in the number of scientists of all categories employed by ARS over an approximate 20 year period. Dr. Horn has made it an Agency-wide priority to reverse the downward trend and to again bolster the number of ARS scientists working on all types of agricultural research.

At the end of fiscal year 1999, ARS had expanded those numbers to over 1,900 Category 1 Research Scientists and had targeted a goal of 2,000 active Category 1 Scientists by the beginning of calendar year 2000. In working to accomplish this goal, biological control has been one of the disciplines that benefitted.

In 1999, records from 49 ARS locations where some biological control work was reported indicated a total of 188.4 SYs in all aspects of biological control research: 35.9 in CBC, 10 in conservation biological control, 38.9 in augmentation, 44 in microbial control, and an additional 59.6 conducting unspecified type of biological control research. Further, these SY figures can be considered to under represent ARS effort because foreign service nationals working at ARS overseas laboratories on CBC are not included in the tabulation. The total ARS biological control budget was reported to be $64,850,800: $12.5 million in CBC, $3.2 million in conservation, $14.0 million in augmentation, $16.1 million in microbial biological control, and the remaining $19.1 million in unspecified types of biological control.

Based on the leadership of Dr. Horn, additional new funds and over 20 new scientists were added to the ARS biological control program in several locations and included expansions primarily for classical and augmentation biological control. During this period, new positions were added: to Stoneville, MS, to address the biological control of tropical soda apple, termites, and general research on augmentation biological control diet development and engineering (4 positons); to Weslaco, TX, for augmentation biological control and insect pathology (2 positions); to Orlando (Ft. Pierce), FL, for biological control of vegetable and horticultural pests (2 positions); to Gainesville, FL, for natural enemy diet development (1 position); to Ft. Lauderdale, FL, for biological control of melaleuca (2 positions); to Newark, DE, for biological control of Asian longhorned beetle (1 position); to Beltsville, MD, for biological control of Colorado potato beetle and gypsy moth (2 positions plus additional technical support for the BCDC); to Ames, IA, for insect pathology and assessment of Bt resistance management (1 position); to Albany, CA, to enhance classical biological control of weeds, particularly yellow starthistle (2 positions plus additional resources for the quarantine operation); to Sidney, MT, for biological control and IPM of grasshoppers (2 positions); to Columbia, MO, for biological control of weeds and augmentation biological control diets (1 position); and to Montpellier, France, for the addition of a plant pathologist to study classical biological control of weeds (1 position). In addition, ARS has further partnered with USDA-APHIS

at several locations to enhance joint biological control activities and through this program has added a new position to the Albany biological control of weeds facility (quarantine officer and weed biological control scientist) in a new joint program.

While the general trend was therefore positive, some areas, e.g., systematics research, did not fare as well. There had been a severe loss of expertise in insect taxonomy in ARS, an area of research that is critical to biological control as noted by many authors (e.g., Sabrosky 1955; Knutson 1981). Since 1972, the number of research scientists in the ARS Systematic Entomology Laboratory (SEL) has fallen from a high of 32 (in 1972) to a total of 22 (and 18 in 1999) (M. B. Stoetzel, SEL, personal communication, 1993, [1999]). This included the loss of taxonomic expertise in the hymenopterous families Ichneumonidae (position lost in 1980) and Braconidae (position lost in 1993), families that contain the wasp parasites extensively used for biological control of arthropod pests. Taxonomic expertise in other families of importance to biological control (e.g., weeds, nematodes, microbial organisms) was also inadequate in ARS to meet current biological control research needs.

In the late 1990's, ARS did provide a new molecular systematics position to the Systematic Entomology Laboratory (1 position) and established a headquarters fund to assist in systematics issues linked to exotic pests and biological control (currently funding efforts on Asian longhorned beetle). Additional support for systematics was recognized as needed.

Facilities and Programs: Beginning with the loss of the West Coast Parasite Receiving Station at Riverside, CA, in 1968 (see Chapter III), CBC research at a number of other ARS facilities had been terminated or phased down by 1993. As indicated below, this trend was mostly reversed by 1999.

The Research Quarantine Facility at Stoneville, MS, planned by the Insect Identification and Parasite Introduction Research Branch (IIPI) prior to the 1972 ARS reorganization as a southeastern regional quarantine facility for receipt of exotic natural enemies for both arthropod pests and weeds, functioned as such until the mid-1980s (Jones et al. 1985). But until recently it was severely under-utilized with little or no CBC research at that location. A new Augmentation Biological Control Facility has now been designed and funded for construction in Stoneville, MS (construction scheduled for FY 2000). The Stoneville quarantine facility has also been brought back on-line, and quarantine studies for tropical soda apple have been initiated.

The CBC entomologist at Columbia, MO, who operated a small quarantine facility there, was not replaced after his retirement in 1989, leaving no ARS CBC research or ARS quarantine capability in the north central states. A scientist has recently been added there to conduct research on augmentation and biological control of weeds. CBC research at the ARS Plant Science and Water Conservation Laboratory at Stillwater, OK, involved in the Russian wheat aphid program, has also not been replaced following a retirement in 1993.

In 1996, the scientists conducting CBC research on weeds at the ARS Rangeland Weeds Laboratory in cooperation with Montana State University personnel and the quarantine facility at Bozeman were moved to Sidney, MT, where a small new quarantine facility is (1999) in the planning stage, and where several new biological control scientists have been hired following a local redirection of program activities.

The staff of the quarantine facility at Newark, DE, the primary ARS quarantine for exotic parasites and predators, was cut from five to three scientists by the end of 1993; but as noted above, the positions have been restored.

The staff of the quarantine facility at Albany, CA, once the primary ARS quarantine for exotic invertebrate natural enemies of weeds, was reduced from five SYs to one by 1993 (see Chapter IV,

section C; Goeden 1993). However, some of the recent additional funds have resulted in establishment of a new biological control program, the "Exotic and Invasive Weed Research Unit" at the Western Regional Research Center at Albany. This consolidated Research Unit includes the biological control of weeds personnel and quarantine facility at Albany, the rangeland weed program at Reno, NV, and the aquatic weed control unit at Davis. And the Albany quarantine facility has been significantly up-graded since 1997.

The former "Biological Control of Insects Laboratory" at Tucson, AZ, at which some CBC research was conducted, though research there was primarily related to augmentation, became the "Honey Bee Research Unit" as of 1993; biological control research there was transferred to the Western Cotton Research Laboratory at Phoenix.

Personnel of the former "Beneficial Insect Introduction Laboratory" (BIIL) at Beltsville, MD, were placed in 1990 in Beltsville's "Insect Biocontrol Laboratory," which consisted mainly of insect pathology research; the former northeastern biological control of weeds program of BIIL was terminated in 1993 (see Chapter IV).

By 1999, one of the two CBC scientists at the ARS quarantine facility at Temple, TX, had retired, leaving that facility in danger of termination upon the retirement of the second scientist.

By 1993, staffs of the ARS overseas biological control laboratories in Europe (EBCL) and South America (SABCL) had been trimmed; the new ARS facility in Australia (ABCL) was being supported only with "soft" funds (i.e., by non-ARS funds, in this case by temporary funds from a coalition of two other federal [U.S. Army Corps of Engineers and National Park Service] and six Florida state and county agencies); and the former Asian Parasite Laboratory in South Korea was closed in December 1993, despite the recent introductions of Asian pests (e.g., the "Asian" gypsy moth, brown citrus aphid, Asian longhorned beetle) (see Chapter IV). Program support by ARS for the cooperative Sino-American Biological Control Laboratory in Beijing, China, has recently been strengthened to help meet this need. By 1998, base ARS funds had been added to the Australian lab to support the SY there. It can also now be noted that the newly constructed facilities of the European Biological Control Laboratory at Montpellier, France, were completed and occupied in October 1999, and that a plant pathologist had been added to the staff there for biological control of weeds. And by 1999, ARS funding of the South American Biological Control Laboratory had been stabilized.

Some other reasons for the temporary decline in CBC research in ARS were noted in a paper entitled "Classical Biological Control: An Endangered Species" by J. J. Drea (1993), an ARS CBC retiree. Because of its nature, CBC research generally cannot be easily commercialized and thus is usually supported by public funds, both federal and state, rather than by private industry. Drea noted that there had been some conversion of positions to biotechnology (genetic engineering and molecular biology research, which require extremely expensive equipment and supplies and extensive support personnel; see also Freistadt 1988). Funding of CBC is also negatively affected by an expectation of instant gratification (CBC alone is not a suitable pest control tactic in all cases, but neither is any other single control method) and the long budget cycle (which, by long-term allocation of funds for specific purposes, limits flexibility to meet changing conditions and new target pests), as well as personnel in leadership positions. Many of these points have recently been addressed by ARS administrators, and benefits of CBC have again been realized and the negative trend in funding reversed.

Although the temporary shifts of personnel and programs to other disciplines reported above caused ARS CBC to decline for a number of years, the importance of the USDA CBC program and the demand expressed by stakeholders benefitting from the program caused an upsurge in ARS funding

and many new positions since 1993, as noted above. Not only have base-funded programs been increased, but ARS has now devoted several million dollars to an Area-wide IPM program for control of leafy spurge using CBC as the central control technology, and has taken steps to meet the influx of several new invasive weed and arthropod species, such as tropical soda apple, the Asian longhorned beetle, and pink hibiscus mealybug.

Program coordination: One important area not mentioned by Drea (1993) that seriously affects CBC in the United States is the lack of coordination of CBC research and implementation programs at all levels. As indicated in Chapter IV, sections A, B.1.a, and C, program coordination within the ARS was a serious problem by the end of 1993. The 1971-72 reorganizations of ARS destroyed the effective coordination of previous years, when CBC research in ARS, from overseas exploration and study, through quarantine research and clearance, to field release and evaluation, was administered and coordinated by a single ARS office. A similar loss of centralized direction of USDA's CBC activities occurred at the establishment of ARS in 1953, but was soon thereafter reestablished (except in regard to forest pests); see Chapters III and V. Frequent reorganizations within the USDA and ARS described in the above chapters certainly were of little help with regard to CBC in the U.S.

In addition, since 1972, nearly all ARS laboratories have ceased producing detailed periodic reports on their research, greatly reducing communication and coordination.

Attempts to reestablish effective coordination of ARS CBC research since 1972 to 1993 have included establishment of various Working Groups, Coordinating Subgroups, Technical Advisors, a "National Biological Control Program," and a "Biological Control Matrix Team" within the ARS National Program Staff (NPS), but problems still existed; see Chapter IV and Appendix I.A. A major difficulty has been that responsibilities for coordination of classical biological control research within ARS are severely diluted. Major coordination responsibility until recently was placed largely in the hands of one National Program Leader (NPL) for Biological Control in the NPS, whose responsibilities since 1993 include not only biological control and insect taxonomy, but also other pest management systems; recently CBC of weeds research projects were moved under the direction of the new NPL for Weed Science. On the other hand, all of ARS's overseas laboratories, including those conducting biological control research, were administered by the Office of International Research Programs (OIRP) (by 1999, administrative responsibility for a few of them were placed elsewhere); and within the NPS, other NPLs are responsible for coordination of ARS research on weeds, applied, and medical and veterinary entomology, and other related research areas that include biological control, but goals of which are often in competition with, or conflict with, those of CBC. It must be stressed that responsibilities of the position of NPL for Biological Control (no longer labeled "for Pest Management Systems", but includes insect taxonomy), are carried by a single staff scientist whose many duties require his time to be spread extremely thin, who has no full time technical assistance, and who may or may not have a broad background in biological control. Much the same responsibilities, but related specifically to biological control and taxonomy, were borne by three biological control/taxonomy specialists, each with technical and clerical staff, who administered the Insect Identification and Parasite Introduction Research Branch (IIPI) of ARS prior to the 1972 reorganization. Other current problems are many and include the fact that the NPS Biological Control Matrix Team did not function as an effective coordinating body (and was abolished), nor do the Biocontrol Working Groups function, as intended, as effective advisory bodies for the NPL. A fundamental problem is the quantity of paperwork and growing interagency coordinating responsibilities that hamper legitimate research coordination activities on the part of the NPLs.

Ideally, an effective CBC program needs to be centrally administered, with consequent avoidance of divided responsibilities among organizations for the various sequential activities involved. This has been pointed out by several authors (e.g., Beirne 1985; Sailer 1974, 1976b, 1981b). The three cited articles by R. I. Sailer, the last administrator of such a coordinated program in ARS, describe an

idealized program in detail. One major benefit of such a centralized organization (as existed prior to 1972) was the ability to move funds, other resources, and personnel quickly in response to emergencies and other program considerations. This included rotation of personnel from overseas to domestic locations and vice versa, and a close tie between the overseas laboratories and domestic program needs.

Coordination of CBC programs on a larger scale, i.e., USDA-wide and within the United States, is also badly needed (for weeds, see Goeden 1993). Broader coordination of CBC by the IIPI prior to 1972 was aided by Memoranda of Agreements between various other federal, state and university organizations, and the Special Foreign Currency (SFC, or PL480) program, and detailed reporting requirements; see Chapter III and Chapter IV, section B.1.a, and Appendix I.C. The development of CBC activities in other USDA agencies since 1980, particularly the Animal and Plant Health Inspection Service and Forest Service, requires better coordination than now exists. Attempts have been made to provide such coordination since 1972 by establishment of a Working Group on Biological Control Agents (WGBCA) and later by the Interagency Biological Control Coordinating Committee (IBC^3); see Chapter IV, section A, and Appendix I.B; these attempts were only partially successful.

As federal research on CBC diminished in the past 25 years, there has been a corresponding increase in CBC research and implementation at U.S. universities, with an increase in the number of biological control quarantine facilities, all of which has increased difficulties in providing overall coordination of CBC within the U.S. To assist in this regard, representatives of the Cooperative State Research Service (CSRS) and Extension Service, USDA's agencies administering federal funds for, and coordinating research and extension activities at State Agricultural Experiment Stations (SAES) at U.S. land-grant universities, were added to the WGBCA and IBC^3, but effective coordination between federal and SAES CBC research and implementation at the national level remains a problem; some regional coordination is effected by means of CSRS-sponsored Regional Research Projects, which include SAES and ARS scientists. CSRS and Extension Service were combined in 1993 as the Cooperative State Research, Education, and Extension Service (CSREES).

Also, the reduced federal CBC program has negatively impacted biological control implementation programs of some State Departments of Agriculture; representation of the interests of such state programs was added to the IBC^3 by means of liaison representation of the National Association of State Departments of Agriculture (NASDA), but coordination attempts were minimal.

Problems between state, federal and university scientists have existed almost from the beginning of CBC in the United States; see Chapter I. Conflicts arise over competition for funds, initiatives for basic versus applied research, and often the lack of formal training in CBC by ARS and other federal scientists involved in CBC research programs; the development of CBC implementation activities in APHIS and the states has complicated the situation (Goeden 1993). To meet those conflicting concerns, more funding for all aspects of CBC (including taxonomy) is required, more basic and theoretical research is needed (to help resolve some of the perceived problems in CBC [e.g., see Beirne 1985]), but not at the expense of applied research leading to control of serious introduced pests, and more highly trained CBC scientists are needed in the federal programs. Also, there are strong objections on the part of a few SAES scientists to perceived attempts to control (i.e., coordinate) biological control in the United States by ARS, or APHIS; coordination is needed at a higher level in USDA than from either agency. These current competitive attitudes among CBC scientists, whether in federal, state, and university programs, hamper good communication among workers and coordination of CBC throughout the country, and seem to require effective high level coordination to alleviate. A stronger relationship between all three areas, but particularly between USDA and SAES scientists, than exists today is needed. There has been recent improvement in this area through the CSREES Regional Projects, which involve both SAES and USDA scientists.

Coordination of a national biological control program has not yet been demonstrated, and a national policy in this regard is long overdue. Numerous recommendations to provide mechanisms for such coordination, within the USDA, have been proposed; see Chapter IV, and Ehler (1991), ESCOP [1989], and the many related recommendations made by the scientific community at a number of biological control conferences and workshops during the past 15 years (USDA 1978, 1984a; Battenfield 1983; King et al. 1988; Coulson et al. 1991). These many carefully considered recommendations, most made at great expense by groups of biological control scientists, have unfortunately been ignored.

Coordination efforts such as the IBC^3 could have conceivably been reorganized, with strong involvement of the SAES and all appropriate USDA agencies, to establish a "permanent biological control committee to coordinate a 'National Biological Control Program'". Such a structure was proposed by the Experiment Station Committee on Organization and Policy (ESCOP), Working Group on Biological Control (ESCOP [1989]; Ehler 1991a). The establishment of a national planning body for biological control was in fact proposed much earlier in a report by the Office of Technology Asssessment (OTA 1979); see Chapter IV, section B.1.a. A similar proposal, for different reasons, for establishment of a "Division of Biological Control" within USDA (or EPA) has been made (Miller and Aplet 1993); see sections on regulations and databases below. More recently, a "Directorate for Biological Control" (presumably within USDA) was proposed, under which a "National Biological Control Program", as proposed by the IBC^3 and ESCOP's Working Group on Biological Control, would be conducted (Cate and Hinkle 1993).

Since 1993, there has been some improvement in regard to coordination of CBC within the USDA. At the request of Richard Rominger, Deputy Secretary of Agriculture, the NPS (Drs. Carruthers and Delfosse) arranged for an "Invitational Workshop on USDA Activities in Biological Control", which was held in October 1996 in Riverdale, MD. This workshop brought together about 80 individuals from four USDA agencies (APHIS, ARS, CSREES and FS) and representatives from the EPA, State Departments of Agriculture, and Land Grant Universities to discuss biological control coordination, regulation and accountability. As far as coordination is concerned, this workshop resulted in the establishment of a USDA Biological Control Coordinating Council (BCCC) with the responsibility of developing an action plan to implement the Workshop's recommendations. The BCCC is composed of senior executive managers of APHIS, ARS, CSREES and FS with oversight responsibilities for biological control programs, biological control policy, and allocation of program resources within their respective agencies. Also established was an Inter-Agency Advisory and Action Team (IAAT) to serve as the operational arm of the BCCC to facilitate all elements of USDA's biological control programs. See Carruthers and Petroff (1997) and Carruthers and Delfosse (1998) for more information. It remains to be seen how effective the BCCC and IAAT will be in providing effective coordination of CBC on a national basis.

But coordination of a national program is not enough. There is also a need for international, particularly North American, coordination in biological control. Reestablishment of the communication and coordination between U.S. and Canadian biological control programs that existed prior to the 1972 reorganization of ARS is needed. Prior to the reorganization, annual meetings between IIPI and Canadian forestry and agricultural biological control administrators were arranged to discuss and coordinate the CBC programs of the two countries. Efforts to continue such coordination after the reorganization were largely unsuccessful. Some coordination of Canadian and U.S. exploration programs in Europe has been accomplished by annual meetings there involving not only ARS and Canadian programs carried out by the International Institute of Biological Control (IIBC), but also Australian program interests in Europe. The North American Plant Protection Organization (NAPPO), established in 1976, attempts to exchange information and provide some coordination of plant protection activities of Canada, the U.S., and Mexico. Country representatives on NAPPO are from Agriculture Canada's Plant Health Division, USDA's APHIS, and Mexico's

Dirección General de Sanidad y Protección Agropecuaria y Forestal. A Biological Control Panel exists within NAPPO, but there is no formal representation from ARS or other *research* organizations. Coordination of CBC activities with the developing programs in Mexico is becoming increasingly important. The lack of close coordination of such programs between the U.S. and Canada has been most troublesome in regard to biological control of weeds programs; see Chapter IV, section B, and below. Coordination of U.S. CBC programs on a broader international scale, involving potential cooperative programs of the IIBC, Australia, and various South and Central American, European, African, and Asian countries, is also highly desirable. Such international coordinative and cooperative activities in CBC does not seem to fit well in the role of the BCCC as presently organized.

Special Problems in ARS Classical Biological Control of Weeds Programs: The cost of a biological control program for a weed using foreign control agents, or of a testing program to clear one such agent for release in the U.S., is generally far greater than for a similar program to control an arthropod pest. This is because of the additional research necessitated by the generally acknowledged danger of attack by the introduced control agent on non-target plants, particularly beneficial plants that could include major crops. There has been increasing concern in this area in the CBC of invertebrate pests.

These problems are well understood and research protocols have been developed over the years that have produced excellent control of many weeds and have never resulted in significant, long-term damage to any beneficial plants. Since promulgation of the Endangered Species Act in 1973, concerns over endangered and threatened native plants has increased in ARS programs.

The incipient dangers involved in biological control of weeds demand extreme care in conducting host-specificity testing both overseas and in domestic quarantine, requiring three to five years before field releases are made. A large amount of time is spent 1) in the planning stage of a project (particularly in selection of appropriate target weeds and resolution of conflicts of interest between beneficial and harmful qualities of the weed), 2) in careful, long-term, coordinated explorations for natural enemies and selection of the best agent among many to test, 3) in the testing process itself (including both safety and efficacy testing) and in developing quarantine culture techniques, and 4) in obtaining approvals for field release, before the agent can be field released, and long before any results of the research can be demonstrated by any degree of weed control.

Fragmentation of the lines of communication under the present ARS organizational structure has often impeded progress in biological control of weeds programs, resulting in some delays in initiation and completion of programs, poor coordination between U.S., Canadian, and overseas researchers and state and federal (APHIS) "implementers" (Goeden 1993), and missed or delayed opportunities for successful projects. Although the NPS was established for program coordination, it has not in the past fully met the needs in regard to CBC of weeds, which had involved two NPLs -- one with responsibility for research on weed control and one with responsibility for research on biological control of pests, including weeds. Reasons, as discussed above and in previous chapters, include the often short duration that pertinent NPLs occupy their positions in NPS, significant periods during which one or the other NPL position is unoccupied, lack of in-depth knowledge peculiar to biological control of weeds by the incumbent NPL, and demands on the time of the NPLs to provide budgetary and other information to higher administrative levels which leaves little of their time for program planning and coordination with scientists in the field. Since 1993, there has been major improvement in this area. In particular, biological control of weeds has been placed under jurisdiction of the NPL for Weed Science. However, weed science encompasses a large area, and depending on the person occupying that NPL position, biological control of weeds could again be de-emphasized in the future.

One other problem that affects primarily weed programs is that a number of weed targets amenable to CBC are not "agricultural" problems, e.g., the several aquatic weeds that have been targeted, as well as the wetland weeds melaleuca, saltcedar, and purple loosestrife. As noted in previous chapters, in order for ARS researchers to address problems with such weeds, "soft" money, i.e., funds from other agencies, has generally been required, rather than regular ARS funds. This has caused some continuity problems in some of the research programs affected. One of the reasons for the termination of the ARS purple loosestrife program was the fact that the weed was not an "agricultural" weed; funding for the Australian laboratory, which provides ARS overseas research on melaleuca natural enemies, has also been in jeopardy. Recent public concerns over "invasive species", expressed first in the 1993 OTA report on non-indigenous species (OTA 1993), and more recently President Clinton's 1999 Executive Order on Invasive Species, has lessened the extent of this problem in ARS, though the Forest Service has begun to play a larger role in this area.

Regulations: Another development during the past 25 years that has had an impact on CBC in the United States is the gradually increasing strictness of safety evaluations and procedures inherent in the research process leading to the importation and release of exotic biological control agents, in response to scientific and societal environmental concerns (Coulson and Soper 1989; Lima 1990). A study by the congressional Office of Technology Assessment (OTA) identified CBC as one of a number of pathways for the introduction of harmful non-indigenous species (NIS) in the U.S., and noted that current regulations regarding the importation of all NIS were inadequate (OTA 1993). Some specific problems adding to environmental concerns directed at CBC include: perceived environmental damage caused by CBC in the past (e.g., see Howarth 1991; Miller and Aplet 1993); controversy over the use of exotic agents to control native pest organisms (e.g., see DeLoach 1978, 1995; Andres 1981; Hokkanen and Pimentel 1984; Goeden and Kok 1986; Ehler 1991b; Lockwood 1993 a and b, Carruthers and Onsager 1993); the potential hazard of overseas collections and introductions of exotic "biological control agents" by amateurs or non-specialists (Coulson and Soper 1989); and the recent increase in commercial shipments to the U.S. of biological control agents from foreign commercial suppliers, and shipments within the U.S. of many domestic and foreign natural enemy species by domestic commercial concerns (e.g., see OTA 1993; Frank and McCoy 1994).

The CBC scientific community has attempted to provide technical input for the use of regulatory agencies in considering development of specific regulations for CBC to address the environmental concerns (Coulson et al. 1991; Charudattan and Browning 1992; FAO 1992). There is concern among CBC scientists that regulations to be developed may become so strict that CBC research in the U.S., which has admirable success and safety records to date, could be brought to a near halt, and some aspects of recently published proposals have increased this concern (Howarth 1991; Miller and Aplet 1993). This concern would appear to be a real possibility, unless funding of CBC research were increased significantly to meet strict requirements for considerably more detailed pre- and post-introduction safety and environmental studies. For example, Miller and Aplet (1993) proposed that each biological control agent be subjected to public review as to potential effects on all "native organisms" in each new U.S. ecosystem into which the agent is proposed for release, "as well as [those in] neighboring ecosystems likely to be invaded [by the agent]." They also recommend passage of a U.S. Biological Control Act, establishing a Biological Control Division within the USDA (or EPA) with "authority to issue regulations governing the collection of required information about each biocontrol application, review all proposals, and ensure that follow-up studies assess the actual impact of biocontrols on both target and non-target organisms and on the ecosystem as a whole."

The OTA report on harmful non-indigenous species (NIS) (OTA, 1993) also made several recommendations pertinent to this discussion. Noting that the U.S. had suffered a loss of over $92 billion from only 43 of the many introduced insects from 1906-91, the report noted a need for a "real national policy" on harmful introductions and continued research and development on ways to

manage harmful NIS. Other needs mentioned were "solid databases (with information from foreign sources) and substantial taxonomic expertise," noting that "accurate and timely species identification is essential but sometimes not available." (In regard to CBC, such taxonomic expertise is needed for both pest and natural enemy taxa; see comments below regarding databases.) The OTA report went on to recommend "careful post-release monitoring" of planned releases (e.g., of biological control agents), i.e., follow up impact studies. These kinds of studies, which many scientists agree are highly desirable, will require significant additional funds for CBC research. (In fact, it is now [1999] ARS policy that all CBC for weeds program proposals must include provisions for follow up impact studies in order to be funded.)

Finalization of ARS guidelines and procedures for introduction and release of non-indigenous biological control agents has been held in abeyance pending finalization of pertinent procedural guidelines and regulations by APHIS (Coulson et al. 1991). No such proposed regulations or guidelines were published by APHIS by the end of 1993, leaving many scientists in a quandry as to standard procedures to be followed to obtain official clearance for field release of introduced biological control agents.

In 1999, problems still existed in this area. In 1996, APHIS published a Proposed Rule with the determination that natural enemies of invertebrates were not plant pests and thus were no longer to be regulated by APHIS (Carruthers and Petroff 1997). The regulation of natural enemies of weeds was still to be a responsibility of APHIS. Some of the increased ARS funds for biological control resulted in the establishment of a new position in the ARS Biological Control Documentation Center (BCDC) to serve as a liaison position to aid ARS scientists in meeting legal requirements for classical biological control introductions and other areas. The position was also charged with development of ARS biological control procedures to meet all legal requirements for classical and other types of biological control research, which became a priority necessity after the 1996 APHIS decision.

As of November, 1999, passages in the proposed consolidated statutes in the U.S. Congress can be interpreted to include placement of entomophagous agents under the jurisdiction of APHIS. This issue is likely to be an evolving one.

Databases: There are a number of technical databases developed by ARS that are of importance to classical and other types of biological control, and also to the "National Partnership for Biological Survey" of the nation's biological resources proposed by the U.S. Department of Interior (ESA 1993), and to the question of introductions of non-indigenous species (NIS) into the U.S. In February 1999, President Clinton signed an Executive Order on Invasive Species. One of the needs identified was for coordination of information on this subject, both nationally and internationally. In this regard, a Workshop on Invasive Species Databases was held in Las Vegas in November 1998, the Proceedings of which has been published (Ridgway et al. 1999). Some of the pertinent ARS databases were among those summarized in that document. These included several Systematic Entomology Laboratory databases on arthropods, the U.S. National Fungus Collections Database of the Systematic Botany and Mycology Laboratory, and the "Releases of Beneficial Organisms in the United States and Territories" (ROBO) database (Coulson 1992b). Not included in the 1999 publication were databases of ARS' Nematology Laboratory's USDA Nematology Collection and the Entomopathogenic Fungal Culture database (Humber 1992). All these databases are now (1999) available via the Internet. Lichtenfels et al. (1998) provide updated information on ARS systematic collections and databases. Because of limited resources, these and other databases have unfortunately received low priority among many agricultural research needs to be addressed by ARS.

ARS also developed the "North American Immigrant Arthropod Database" (NAIAD) (Knutson et al. 1990), but this was never adequately funded. Consequently, this database formed the basis of the "North American Nonindigenous Arthropod Database (NANIAD) developed by Pennsylvania State

University, listed in Ridgway et al. (1999). ROBO records the importation and release of non-indigenous beneficial invertebrate and microbial organisms into the U.S., whereas NANIAD records the establishment in the U.S. of non-indigenous arthropods, harmful, beneficial, or otherwise benign. Both databases meet the need stated in the OTA report (OTA 1993) to include extensive "information from foreign sources" regarding NIS, particularly NANIAD. ROBO currently resides in the ARS Biological Control Documentation Center (BCDC) together with extensive biological control files and a library; BCDC thus serves as an information source for biological control, one suggested function of the so-called "Division of Biological Control" recommended by Miller and Aplet (1993). ROBO, which was made available on the Internet in 1999, contains nearly 20,000 records of importations and releases of exotic biological control agents and pollinators from 1981 through 1985. A second position was added to the ARS Biological Control Documentation Center in 1999, which will aid in updating the database.

The Future for Federal Classical Biological Control Programs: The sections dealing with CBC of arthropods and weeds in previous chapters of this history, and earlier comments in this Epilogue, have indicated the benefits of a federal CBC program. They have also indicated a number of problems and drawbacks of the program, many of which have been addressed in recent years. It can be demonstrated that there is a compelling need for the continuation and augmentation of a strong, well-coordinated federal CBC program.

Introductions of harmful non-indigenous organisms into the U.S. will certainly continue and are expected to increase in number. This is due to increased international trade and tourism, the increase in containerized shipments of goods, and a possible change in APHIS pest exclusion policies leading toward elimination of "plant pest regulations as trade barriers". The latter may result in lessened detection and other actions designed to prevent plant pests from entering the U.S., which is perceived as eventually "an unrealistic goal" (OTA 1993; APHIS, PPQ 1993); although the 1999 Executive Order on Invasive Species may increase detection efforts. It can be expected that the numbers of potential targets for classical biological control are very likely to increase significantly. The list of exotic weeds in the U.S. that can be targeted for CBC research is already long and is growing (USDA 1984a; DeLoach 1991a; OTA 1993).

Some states, such as California, Hawaii, and Florida, have experienced an influx of an unusually high number of exotic pests specific to their particular ecosystems, climate, and agricultural and cultural history (Frank and McCoy 1992; OTA 1993). Because of this, these states have had a strong interest in, and have developed, CBC programs tailored to meet their specific needs. These programs have been highly successful (Clausen 1978; DeBach and Rosen 1991; Funasaki et al. 1988; Frank and McCoy 1993; Rosen et al. 1994) and have truly met the needs of those states. USDA CBC programs, on the other hand, have generally dealt with introduced pest problems that are of broader (regional or national) scope. It seems quite worthwhile to continue this "division of labor," although better coordination and communication between federal and state programs is highly desirable. However, a proliferation of probably under-utilized state quarantine facilities in each of the 50 states is certainly unnecessary, and would compound the problem of coordination and increase the hazard of unwise quarantine actions. Several CSREES Regional Research Projects have been designed to provide communication, but have not been particularly effective in providing coordination of national programs involving many agencies and people in many states in several regions.

For these several reasons, there is need for a strong nationally focused biological control policy, to include: 1) strengthened, well-coordinated and funded federal CBC research and implementation programs, in close partnership with state government and university biological control programs; 2) increased support for pertinent taxonomic research and identification services at both federal and state levels to support these programs; and 3) a national biological control information center to assist in communication and coordination, and to maintain a library and databases of importance to

classical and other types of biological control. Some suggestions regarding program coordination are included in comments in this Epilogue above, including the recent establishment of a Biological Control Coordinating Council (BCCC) within the USDA.

In regard to a strengthened federal CBC program, it has been proposed, in an unfinished and unpublished ARS Strategic Plan entitled "Biological Control for the 21st Century", that a federal CBC research capability be provided for most if not all major agroecosystems vulnerable to invasions by harmful non-indigenous organisms, again in close association with state, university, and other federal biological control programs. Needs for regional federal biological control quarantine facilities were discussed in a 1991 USDA workshop (Coulson et al. 1991). Such regional capability was absent when the cereal leaf beetle was first found in the Midwest in the 1960s (see Sailer 1976b), and is severely lacking in the present federal program. Furthermore, it would be well to expand such federal biological control capability beyond "agroecosystems" to include CBC targets in urban and "natural areas," the latter of which the USDA has been accused of neglecting in regard to effects of harmful non-indigenous species (OTA 1993).

The record of successful control of introduced pests by federal CBC programs representing savings of billions of dollars in control costs and immeasurable ecological benefits is noted above. The slow decline in the federal research program and its recent improvement has also been discussed above. Assuming a continuation of recruitment of trained CBC scientists, the pivotal problem remains a lack of a cohesive national CBC policy and coordinated federal research program. Whether current departmental coordination efforts, either by the BCCC, the National Biological Control Institute (NBCI; see Chapter VI, section C), or another USDA coodinating mechanism not yet in existence, can be of any assistance in establishing a real nationally coordinated classical biological control program remains to be seen.

B. SUMMARY OF ACCOMPLISHMENTS OF ARS ON INSECT CONTROL WITH MICROBIAL ORGANISMS. By P. V. Vail

The following pages present a brief summary of the research of the Agricultural Research Service reported in more detail in Chapters I-IV above, and particularly in Appendix II below.

The USDA received early recognition for its research on insect pathology/microbial control. In the early 1900s, extensive projects were begun on microbial control of the newly introduced Japanese beetle. Also, the impact of pathogens on honey bees was recognized and research began on ways to control bee diseases. These early projects emphasized surveys, epidemiology, pathology, and descriptions of relevant organisms, and provided important information bases for future basic and applied research for solving the problems. As mentioned by Steinhaus (1949), these Japanese beetle and honey bee projects provided the stimulus for modern-day programs and the acceptance of insect pathology and microbial control as distinct disciplines.

These developments led to the first extensive use of insect pathogens, “milky” disease organism(s), for control of the Japanese beetle. Steinhaus (1949), Clausen (1956), Fleming (1968), and Cameron (1973) discussed the importance of this achievement. The organism is still used for control of the Japanese beetle. The studies of honey bee diseases are also considered to be classics. Programs on both of these problems have expanded to include numerous target species and virtually every type of insect pathogen. The establishment of insect pathology as a discipline combined with the foresight of E. F. Knipling led to the establishment of insect pathology and microbial control programs at many ARS locations throughout the U.S., including the Insect Pathology Pioneering Research Laboratory at Beltsville, MD, beginning in the late 1950s. ARS programs developed during the 1960s and 1970s had more insect pathology/microbial control specialists than any other institution in the world, and

conducted diverse research on a variety of agricultural and man and animal pest species and their pathogens.

In the 1950s and 1960s, the adverse effects of a protozoan (Zimmack and Brindley 1957; Lewis et al. 1971) and a fungus (York 1958) on European corn borer were demonstrated. ARS scientists conducted early studies on the potential use of baculoviruses for insect control (Elmore 1961; Elmore and Howland 1964). Also in the 1960s research on all aspects of the production, efficacy, and safety of a baculovirus led to the first registration of a baculovirus for commercial use (Ignoffo and Couch 1981). ARS scientists were deeply involved in the development of *Bacillus thuringiensis* as a control agent by conducting basic and applied research on numerous insects and isolates (Dulmage and Beegle 1982). Critical to the use and commercialization of this organism was the development of standards for potency (Dulmage 1973 a and b). Strains and isolates of this organism are now used throughout the world to control many insect species. The development of application technologies was an important part of this program. Early studies on pathogens affecting insect pests of man and animals were initiated (e.g., Clark et al. 1968; Clark and O'Grady 1975; Hazard and Weiser 1968), and fungal and viral pathogens of mosquitoes were isolated (Chapman and Woodard 1966; Chapman et al. 1966).

In the late 1960s and 1970s, ARS research led to a more thorough understanding of insect pathogens and their interactions with their hosts. Significantly more knowledge about their use was developed. Two morphological types of nuclear polyhedrosis viruses (NPVs) were discovered (Heimpel and Adams 1966) which led later to the discovery of a baculovirus having a broad host range and thus the potential to control several insect species (Vail et al. 1971). Control of a number of economically important insect species by viruses was demonstrated including *Heliothis/Helicoverpa* spp. (Ignoffo and Couch 1981), fall armyworm (Young and Hamm 1966; Hamm and Young 1971), gypsy moth, codling moth, cabbage looper and others (see Chapters III and IV). Field trials for the control of anopheline mosquitoes with *Nosema algerae* were conducted in Panama (Anthony et al. 1978). In 1968, the ARS fire ant project began with a component for the development of microbial control agents (Knell et al. 1977; Avery et al. 1977; Jouvenaz et al. 1980; Banks et al. 1985). Significant reductions of grasshopper field populations by *N. locustae* were demonstrated (Henry 1971a). ARS scientists contributed significantly to the knowledge and development of *in vitro* cell cultures as related to entomogenous viruses, which greatly facilitated many studies on insect pathogens (Goodwin et al. 1970; Vaughn et al. 1977; see the additional references listed in Chapter IV, section B.3, and Appendix II). Numerous studies were conducted on the efficacy of *B. thuringiensis israelensis*. A number of UV screens were developed to reduce sunlight inactivation of microbial control agents (Ignoffo and Batzer 1971). This work continued into the 1990s with significant findings (Shapiro et al. 1992). Autodissemination of an insect pathogen was recommended for reduction of populations of khapra beetle (Burkholder and Boush 1974).

At the beginning of the 1900s, the USDA was involved in one of the first attempts to use insect pathogens as classical biological control agents, targeting grasshoppers (Carruthers et al. 1997). In 1919, the ARS European Parasite Laboratory was established in France. But it was not until 1981 that an insect pathology program was initiated there to provide microorganisms for potential control of exotic pests in the U.S. The program gradually evolved, and a permanent position for insect pathology research was established in 1991 for on-site research at the European Biological Control Laboratory. In concert with the Laboratory, a Japanese beetle control program in the Azores Islands, Portugal, was recently implemented by ARS. However, the most significant development in the use of pathogens for classical biological control purposes has been the introduction by the USDA of the fungus *Entomophaga maimaiga* from Japan in 1910-12 and again in 1984-86 against the gypsy moth, which is proving to be an effective control agent for that pest (Reardon and Hajek 1993; Hajek et al. 1995). Whether this can be claimed as a result of USDA's introduction of the fungus is a debated issue; see Hajek et al. 1995.

In the late 1970s through the 1990s, basic and applied research on insect pathogens continued. Studies of pathogens of insects affecting man and animals led to the isolation and development of many pathogens for population suppression (Hazard and Weiser 1968). In-depth studies of a protozoan infectious to mosquitoes led to the landmark discovery that *Thelohania* in larvae and *Nosema* in adults were portions of the life cycle of one species (Hazard and Weiser 1968). A copepod was determined to be an essential intermediate host for a protozoan pathogen of mosquitoes (Sweeney et al. 1985). A South American protozoan pathogen from fire ants was isolated and described (Knell et al. 1977). After discovery of spiroplasmas at Beltsville by R. F. Whitcomb and R. E. Davis (Davis et al. 1972), scientists there demonstrated for the first time that these cell wall-less bacteria occurred in a number of insects in the orders Homoptera, Coleoptera, Lepidoptera, Diptera, and Hymenoptera (Clark 1982; Hackett and Clark 1989).

As a result of ARS research, *B. thuringiensis* (*Bt*) was registered for use on stored grains and a granulosis virus also provided high levels of control (McGaughey 1983; Kinsinger and McGaughey 1976). The first documented case of resistance to *B. thuringiensis* was described by McGaughey (1985) at the Manhattan, KS, Laboratory. Following the isolation of *B. thuringiensis israelensis*, formulations and application methods were developed for dispensing and applying the organism for control of aquatic Diptera, and standardized assay methods were developed (McLaughlin 1983; McLaughlin et al. 1984). Considerable research was conducted on a novel use of *B. thuringiensis* as a food additive to provide control of livestock pests in feces (Gingrich 1984). Temeyer (1984) was the first to demonstrate toxicity of the crystal protein of *Bt* to muscid flies. Considerable research effort was expended in developing *Bacillus* spp. for control of black flies during the 1980s (Lacey and Undeen 1984).

As a result of increased databases, more microbial control agents were being field tested. Pressure to provide suitable alternatives to chemical insecticides was also a factor influencing increased field testing. Research was conducted with pathogens for area-wide suppression of multi-crop pests such as the cabbage looper (Vail et al. 1976) and *Heliothis/Helicoverpa* spp. (Bell 1988, 1990 a and b; Bell and Scott 1989; Bell et al. 1992). Adjuvants to increase the effectiveness of microbial pesticides were also developed (Bell and Kanavel 1978; Bell and Romine 1980; Hostetter et al. 1982; Dunkle and Shasha 1988; Bartell et al. 1990; McGuire et al. 1990; McGuire and Shasha 1990). Shapiro et al. (1992) discovered that high levels of synergism occurred between some of these compounds and baculoviruses. Gilliam et al. (1983) demonstrated that honey bees could be selected and bred for resistance to chalkbrood, and stressors were defined (Gilliam 1986). Captan was developed as an effective control for chalkbrood in leafcutting bees (Parker 1984, 1985, 1987, 1988; Mayer et al. 1990). The world's foremost collection of entomopathogenic fungi was started by R. S. Soper and continued by R. A. Humber; over 3,200 isolates of over 250 species are in the collection (Humber 1992). Intensive research on gypsy moth rearing and virus production resulted in the production of 1.5 million insects in 100 days which yielded 50,000 acre treatment equivalents with a 10-fold reduction in production costs (Shapiro and Bell 1981; Podgewaite 1983). *Nosema locustae* was the first protozoan registered by the U.S. EPA. It was found that insect damage to raisins and other dried fruits could be minimized by the use of a granulosis virus (Hunter et al. 1977, 1979; Vail 1991). Simulation models were shown to be instrumental in guiding and evaluating studies on fungi infectious to grasshoppers (Larkin et al. 1988). *Beauveria bassiana* was found to move within corn plants and provide control of the European corn borer (Bing 1990; Bing and Lewis 1991; Lewis and Bing 1991). Stephen and Fichter (1990 a and b) successfully selected for resistance to chalkbrood in the alfalfa leafcutting bee. A rare protozoan was found to cause severe population reductions in the honey bee (Wilson and Collins 1992).

Entomopathogens will likely be used even more in the future due to environmental and consumer concerns over chemical pesticides. ARS has been among the leaders in basic insect pathology and microbial control since the early 1900s. The strong research base provided by ARS and cooperating

research institutions should provide the basis to integrate insect pathogens into programs to manage insect pests in the future.

Table 7. Examples of Successful Classical Biological Control for which ARS and Predecessor Agencies Were Largely Responsible

[Many other federal, state and university organizations and personnel (particularly University of California and APHIS-PPQ) were involved in some of these programs. Many examples of "partial" economic control cited above and in literature are not listed here.]

Type Pest	Pest Species (Common Name)	Crop Affected & Area of Control	Chapter Reference
	Complete Economic Control		
Insects	Cottonycushion scale	Citrus - California	I
	Citrus blackfly	Citrus - Cuba	I
	Citrus blackfly	Citrus - Mexico	II
	Comstock mealybug	Fruits - Eastern U.S.	II
	European wheat stem sawfly	Wheat - Eastern U.S.	II
	Cereal leaf beetle	Small grain - Eastern U.S.	III
	Alfalfa weevil	Alfalfa - Eastern U.S.	III
	Rhodesgrass mealybug	Range grass - Texas	III
	Pea aphid	Alfalfa - U.S.	III
	Spotted alfalfa aphid	Alfalfa - U.S.	III
	Alfalfa blotch leafminer	Alfalfa - Eastern U.S.	IV
	Eurasian pine adelgid	Pine - Hawaii	IV
	English grain aphid & Metopolophium dirhodum	Small grains - Chile	IV
Weeds	Common St. Johnswort	Rangelands - Western U.S.	II
	Tansy ragwort	Rangelands - Western U.S.	III
	Alligatorweed	Rivers, lakes - Southeastern U.S.	III
	Substantial Economic Control		
Insects	Oriental, satin, gypsy, and browntail moths	Forest trees - New England	I
	Woolly apple aphid	Apple - Northwestern U.S.	I
	Alfalfa weevil	Alfalfa - Western U.S.	I
	Western pine tip moth	Pine - Nebraska	I
	Larch casebearer	Larch - New England	II
	Oriental fruit fly	Fruit - Hawaii	II
Weeds	Puncturevine	Rangelands - Western U.S.	III
	Musk thistle	Pastures & rangeland - U.S.	III
	Waterhyacinth	Rivers, lakes - Southeastern U.S.	IV

Continued

Table 7. Examples of Successful Classical Biological Control for which ARS and Predecessor Agencies Were Largely Responsible--Continued

[Many other federal, state and university organizations and personnel (particularly University of California and APHIS-PPQ) were involved in some of these programs. Many examples of "partial" economic control cited above and in literature are not listed here.]

Type Pest	Pest Species (Common Name)	Crop Affected & Area of Control	Chapter Reference
		Potential Economic Control[1]	
Insects	Plant bugs	Alfalfa - Northeastern U.S.	IV
	Birch leafminer	Birch - Northeastern U.S.	IV
	Euonymus scale	Ornamentals - U.S.	IV
Weeds	Yellow starthistle	Rangelands - Western U.S.	IV
	Leafy spurge[2]	Rangelands - Western U.S.	IV
	Purple loosestrife[3]	Wetlands - Northern U.S.	IV

[1] Programs are too recent to predict complete economic control, but preliminary results indicate at least substantial control will result.

[2] Agriculture Canada and International Institute for Biological Control are much involved in the potential success of this program.

[3] ARS involvement chiefly limited to initial stages of this program.

Table 8. ARS Scientists Devoted Full or Half Time to Classical Biological Control - December, 1993

[Based on personal count, not Research Management Information System (RMIS) accounting, for which, see text; does not include 1 SY in Biological Control Documentation Center, Beltsville, MD.]

Location	Target			
	Arthropod Pests		Weeds	
	Agent		Agent	
	Parasites and Predators	Pathogens	Pathogens	Invertebrates
Europe	3.5 SY	1.0 SY	3.5 SY	0
South America	0.5 SY	0	0.5 SY	0
Australia	0	0	1.0 SY[1]	0
Asia	0	0	0	0
NE U.S	3.5 SY[2]	0	0	3.5 SY[3]
SE U.S.	0.5 SY[4]	0	2.0 SY[5]	0
NC U.S	0	0	0	0
W U.S.	1.5 SY[6]	0	5.5 SY[7]	1.5 SY[8]
TOTALS	9.5 SY	1.0 SY	12.5 SY	5.0 SY

[1] Funded by "soft" funds (see text)
[2] Newark, DE (3); Beltsville, MD (0.5)
[3] Frederick, MD (only 2 full time)
[4] Stoneville, MS
[5] Gainesville, FL (1); Fort Lauderdale, FL (1)
[6] Sidney, MT (0.5; "soft" funds); Yakima, WA (0.5); Stillwater, OK (0.5)
[7] Bozeman, MT (1.5); Sidney, MT (1); Albany, CA (1); Temple, TX (2)
[8] Bozeman, MT

Table 9. Estimated Resources Devoted to all Types of Biological Control by the Agricultural Research Service, 1987

Scientist Years (SY) and $ (000's)

Biological Control Agent	SYs[1] Estimated	FY 1988[1] Estimated	FY 1989 Estimated
	Target: Arthropod Pests (Insects, Mites, and Ticks)		
Arthropod			
Parasites (Parasitoids)	41.2	$ 6,180	$ 6,180
Predators	17.5	2,625	2,625
Pathogens	31.5	4,725	4,725
Parasitic Nematodes	4.1	615	615
SUBTOTAL	94.3	14,145	14,145
	Target: Weed Pests		
Phytophagous Arthropods	15.8	2,370	2,370
Phytophagous Nematodes	0.0	0	0
Mycoherbicides	8.3	1,245	1,245
Plant Allelopaths	2.5	375	375
Herbivorous Fish	0.2	30	30
SUBTOTAL	26.8	4,020	4,020
	Target: Plant Pathogens and Nematodes		
Microbial Antagonists	21.6	3,240	3,240
Nematophages	1.0	150	150
SUBTOTAL	22.6	$ 3,390	$ 3,390
GRAND TOTAL	143.7	$21,555	$21,555

[1] Based on a survey conducted in May 1987, as reported in King et. al. 1988. Figures have not been updated.

Table 10. Estimated Scientist-Years Devoted to all Types of Biological Control in the Agricultural Research Service, 1987

Biological Control Research to Protect Selected Commodities/Areas from Pests

Commodity/Area	Control Approach (SYs)[1]			Total	
	Classical	Conservation	Augmentation	SYs	Scientists
Plants					
from Arthropods	18.0	14.2	41.8	74.0	120
from Weeds/Brush	15.9	1.3	6.8	24.0	40
from Disease	0.6	4.2	14.8	19.6	36
from Nematodes	0.1	0.3	0.7	1.1	2
Aquatic Resources					
from Weeds	2.1	0.0	0.1	2.2	3
Man/Animals					
from Arthropods	6.1	1.1	4.7	11.9	22
Post-Harvest Products					
from Arthropods	0.6	0.6	6.5	7.7	16
from Pathogens	0.0	0.3	1.8	2.1	5
TOTAL SYs	43.4	22.0	77.2	142.6	
TOTAL SCIENTISTS	84	74	148		[2] 218

[1] Based on a survey conducted in May 1987, as reported in King et. al. 1988. Figures have not been updated.

[2] Scientists often conduct research across several commodities/areas or control approaches, and thus total in this column exceeds 218.

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APPENDIX I
DOCUMENTS CITED IN CHAPTER IV

A. CHARTER OF THE ARS WORKING GROUP ON NATURAL ENEMIES OF INSECTS, WEEDS, AND OTHER PESTS (WGNE)

During the May 1973 meeting of the ARS Board of Directors, a Plan for the WGNE was approved, and its membership appointed. The following is a copy of this Plan as slightly revised following the first WGNE meeting in October 1973.

A PLAN
COORDINATION AND LEADERSHIP OF
BIOLOGICAL CONTROL RESEARCH
IN THE
AGRICULTURAL RESEARCH SERVICE

INTRODUCTION

The concept of biological control of pests involves the discovery, identification, evaluation, introduction and establishment of highly specific natural enemies (parasites, predators and pathogens) of target insects, weeds, nematodes, plant pathogens and other pests. It also involves the development of technology essential to manipulating such exotic and native enemies toward a balance which favors the plant, animal and beneficial organisms important to man's well-being and survival.

An effective and efficient program for biological control of pests is contingent on a manageable and productive multidiscipline research and development effort. The current program of ARS involves many scientists studying various aspects of biological control at foreign and domestic locations, as indicated in the attached appendix.

Since biological control studies encompass a complex network of research programs in several foreign centers and a widely diverse set of environmental conditions in the United States, a mechanism is hereby created to facilitate coordination and cooperation among the various locations and groups in ARS and with outside cooperators and interested agencies.

AGENCIES AND ORGANIZATIONS COOPERATING IN BIOLOGICAL CONTROL RESEARCH

The research on biological control of insects, weeds and other pests is of special interest to many other federal and state agencies. Some of these agencies support the cooperative ARS research program financially and utilize the biological agents in their insect, weed and other pest management programs.

Federal agencies concerned are the Departments of Defense, Interior, Agriculture, and Health, Education and Welfare, and the independent agencies -- Environmental Protection Agency and Tennessee Valley Authority. State Agricultural Experiment Stations, State Departments of Agriculture and state agencies responsible for water management are frequently cooperators in

biological control programs. In addition liaison is maintained with the Commonwealth Institute of Biological Control and counterpart agricultural agencies in Canada and Mexico. A high degree of coordination with these various agencies at the state, national and international levels is essential to the attainment of efficiency and effectiveness of the overall research program on biological control.

PLANNING AND COORDINATION OF RESEARCH

Authority for planning and coordinating a national program for biologcal control research is vested in the National Program Staff and the ARS Working Group on Natural Enemies of Insects, Weeds and Other Pests.

ARS Working Group on Natural Enemies of Insects, Weeds, and Other Pests (WGNE)

(a) Composition - The Assistant Administrator of ARS for Plant and Entomological Sciences shall appoint the Chairman and Cochairman to this Working Group. Both the Chairman and Cochairman will be members of the National Program Staff for Plant and Entomological Sciences. Other NPS members will participate as the situation requires. Appropriate members from each Region will be appointed by the Deputy Administrators. The Administrator will designate a member from the International Programs Division. Depending on the program under consideration, the Chairman can request participation by one or more biological control specialists who are not members of WGNE.

(b) Function

- To complete periodic reviews of both the domestic and foreign research on biological control within ARS in light of national needs and goals.

- To recommend the establishment of coordinating subgroups* and research teams* as appropriate to work on interregional biological control problems. The composition of subgroups and research teams will be identified together with special funding requirements. [* See below.]

- To prepare reports when needed for the Administrator on the priority needs and goals of biological control research. The reports will include: (a) proposals on major shifts in resources, both personnel and funds, to meet high priority needs, and (b) recommendations for the establishment of coordinating subgroups and research teams to facilitate interregional research needs, and (c) other recommendations as required.

(c) Procedures

A substantial portion of ongoing research will not require establishment of formal guidelines for cooperation within and between regions. However, coordinating subgroups and research teams will be organized to fulfill national needs for biological control investigations.

- Coordinating subgroups will be named and chairmen selected where there is an identifiable need for periodic planning and reporting sessions for specialists working on a common problem. Thus, subgroups would serve a useful role in the identification of target pests for biological control work within different Regions and coordinating the receipt, propagation, distribution, release and evaluation of effectiveness of the agents as components of balanced insect and weed management programs.

- Research teams will be named for high priority research projects that demand close coordination and direction. The team will assume a direct coordinating role for the life of the research project. In this capacity, it will exercise responsibility over the technical direction of personnel and the coordination of resources assigned to the project as mutually agreed upon by the parties concerned in advance.

- Chairmen of coordinating subgroups and research team leaders are responsible to their respective Area Directors. Reports will be prepared as needed. The WGNE evaluates progress, establishes priorities, recommends modification in plans and approves continuation of subgroups and research teams.

- The Adminstrator, ARS, will give final approval to the establishment of and appointment to coordinating subgroups and research teams.

[There followed an Appendix listing the major biological control units within ARS as determined at that time, with statements as to the major activities conducted by each, and whether quarantine facilities were available at that location. Because major changes have occurred since 1973, only the names of the units and their locations are listed here. For more up-to-date lists of ARS biological control units, see Coulson and Hagan 1986, and the "Profiles of ARS Biological Control Scientists" in King et al. 1988.]

MAJOR BIOLOGICAL CONTROL RESEARCH UNITS WITHIN ARS [in 1973]

A. Overseas Laboratories

1. Biological Control of Weeds Laboratory, Rome Italy
2. Biological Control of Weeds Laboratory, Buenos Aires, Argentina
3. European Parasite Laboratory, Sevres, France

B. Domestic Laboratories

Western Region

1. Cotton Insects Biological Control Laboratory, Tucson, AZ
2. Western Cotton Research Laboratory, Phoenix, AZ
3. Biological Control of Weeds Laboratory, Albany, CA*
4. Western Insects Affecting Man and Animals Laboratory, Fresno, CA
5. Stored Product Insects Research Laboratory, Fresno, CA
6. Grasshopper Laboratory, Bozeman, MT

Northeastern Region

1. Potato Insects Investigations, Orono, ME
2. Beneficial Insects Research Laboratory, Newark, DE*
3. Plant Disease Research Laboratory, Frederick, MD*
4. Systematic Entomology Laboratory, Beltsville, MD
5. Beneficial Insect Introduction Laboratory, Beltsville, MD
6. Insect Pathology Laboratory, Beltsville, MD
7. Nematology Laboratory, Beltsville, MD

North Central Region

1. Biological Control of Insects Research Laboratory, Columbia, MO

Southern Region

1. Cotton Insects Research Laboratory, College Station, TX
2. Entomology Research Center, Brownsville, TX
3. Gulf Coast Mosquito Research Laboratory, Lake Charles, LA
4. Special Plant Feeding Insect Quarantine Facility, Stoneville, MS*
5. Bioenvironmental Insect Control Laboratory, Stoneville, MS
6. Southern Weed Science Laboratory, Stoneville, MS
7. Southern Grain Insects Research Laboratory, Tifton, GA
8. Tobacco Research Laboratory, Oxford, NC
9. Aquatic Weed Control Laboratory, Fort Lauderdale, FL
10. Biological Control Laboratory, Gainesville, FL*
11. Insects Affecting Man Research Laboratory, Gainesville, FL
12. Insect Attractants, Behavior & Basic Biology Laboratory, Gainesville,FL

*Quarantine facility available

Initial 1973 membership of WGNE included the following persons:

W. B. Ennis, NPS, Chairman
M. D. Levin, NPS, Cochairman

Northeastern Region

J. R. Coulson
A. M. Heimpel

North Central Region

C. M. Ignoffo
L. A. Bulla

Southern Region

R. L. Ridgway
C. R. Swanson

Western Region

D. E. Bryan
L. A. Andres

International Programs Division
Not determined

B. CHARTER OF THE WORK GROUP ON BIOLOGICAL PEST CONTROL AGENTS (WGBCA)

OFFICE OF ENVIRONMENTAL QUALITY ACTIVITIES
Office of the Secretary
U.S. Department of Agriculture

WORK GROUP ON BIOLOGICAL PEST CONTROL AGENTS

Charter

BACKGROUND:

Biological pest control is a critical element in moving toward a total strategy for pest control. It involves the efficacious use of parasites, predators, and microorganisms, to control insects, nematodes, weeds, and pathogen pests on animal and plant hosts. The effectiveness of biological control can be assessed on the basis of economic as well as environmental benefits within the complex of pest control strategies.

At this time there is need for an improved understanding of adequate research and proper research balance, the development and implementation of effective biological control programs, and the establishment of legislative authority necessary for using certain types of biological controls. From the regulatory viewpoint, jurisdictional responsibilities need further clarification. It is appropriate for the Department to cooperate with the States and private organizations to utilize expertise on biological controls required to identify specific issues, assess the implications of these issues, and recommend possible courses of action that can contribute to development of sound programs and policy and regulatory requirements.

ORGANIZATION AND PURPOSE:

To provide for multi-agency and interdisciplinary participation in developing recommendations regarding programs and policies required to further promote biological pest control research and implement biological control programs, there is established a Work Group on Biological Pest Control Agents under authority of Secretary's Memorandum 1890, dated January 7, 1976. This effort is intended to assist in realizing the full potential of biological control to pest control activities. The roles of the Work Group include coordination and information exchange as contrasted to program leadership or management. The Work Group will provide background for Departmental situation assessment, problem identification, and identification of potential problem-solving approaches.

The Work Group will consist of a Chairman and appropriate representatives from involved USDA agencies. It will be responsible to the Office of Environmental Quality Activities. The membership is shown on Attachment #1 [not included here].

Member Agencies: ARS, APHIS, CSRS, ERS, ES, FS, OGC.

OBJECTIVES:

1. Evaluate the current status of biological control research and implementation activity, including an appraisal of past research implementation and success.

2. Coordinate the evaluation of emerging research and development needs.

3. Coordinate the evaluation of economic, biological, environmental and legislative implications of past and potential research and implementation programs.

4. Identify policy issues, implications of the policy issues and alternative courses of action to provide for further development and implementation of biological controls within a system of pest control strategies.

5. Recommend formation of task forces, as required, to develop in-depth analyses of specific subject-matter.

C. MEMORANDUM OF AGREEMENT BETWEEN USDA AND CALIFORNIA, 1974 REVISION

No. 3855
MEMORANDUM OF AGREEMENT
Among
THE REGENTS OF THE UNIVERSITY OF CALIFORNIA
THE CALIFORNIA STATE DEPARTMENT OF FOOD AND AGRICULTURE
And
THE UNITED STATES DEPARTMENT OF AGRICULTURE
AGRICULTURAL RESEARCH SERVICE
ANIMAL AND PLANT HEALTH INSPECTION SERVICE

THIS AGREEMENT is entered into by and among The Regent of the University of California, a California Corporation, hereinafter called "The Regents", the State of California acting by and through the California Department of Food and Agriculture, hereinafter called "The State", and the United States Department of Agriculture, Agricultural Research Service, hereinafter called ARS, and Animal and Plant Health Inspection Service, Plant Protection and Quarantine, hereinafter called the Service.

WHEREAS, the parties hereto desire to provide hereby an outline of a general procedure under which they will operate in a cooperative project whereby beneficial insects and other organisms are to be imported into the State of California from localities outside the continental United States as an aid in the biological control of pests affecting agriculture within the State; and

WHEREAS, the parties hereto desire that this agreement replace and be substituted in lieu of the Memorandum of Agreement among the parties, dated January 14, 1964, and covering the subject matter of this agreement.

NOW, THEREFORE, the parties hereto agree as follows:

A. The Regents Agree:

1. To provide and maintain a quarantine facility adequate to prevent the escape of any beneficial insect or other insects or organisms which may be imported by State or Regental agencies.

2. That prior to the use of any quarantine facility, it shall be approved in writing by duly authorized representatives of the Service; and if specifically requested, by duly accredited representatives of other contracting agencies.

3. That all shipments of beneficial insects and other organisms shall be opened only in a special room to be known as a "quarantine room"; this room shall be approved in the same manner as

provided above and shall be so screened or otherwise safeguarded to preclude the escape of insects or other organisms and shall be so constructed as to permit effective disinfection.

4. That all containers and packing material shall be destroyed after the insects or other organisms have been removed therefrom; provided, however, the standard containers of a more or less permanent nature may be fumigated or otherwise treated in a manner which will insure their freedom from any kind of living insect or organism.

5. That the quarantine room and other rooms in which the insects or other organisms are studied shall at all times be kept under lock and only those employees who are authorized by the Director of the Agricultural Experiment Station, University of California, or by a designated representative shall have access to such room or rooms.

6. Shipments of beneficial insects and other organisms consigned to the United States Department of Agriculture or the State may be processed in The Regents quarantine facilities upon written approval of The Regents.

7. That an accurate record shall be maintained of all importations and at appropriate intervals, and in any event not less frequently than six months, a report of progress of work and/or conditions of imported material shall be sent to the other parties to this agreement.

8. That interstate shipments of living imported species or varieties of insects or other organisms shall be made only upon approval of the Service.

B. It is Mutually Understood and Agreed:

1. That all importations, by any party hereto, into California from points outside the continental United States of any beneficial insects or other organisms shall be approved and agreed to in writing, in advance, by all parties to this agreement.

2. That The Regents and the State shall be advised, in writing, prior to execution, of all importations undertaken solely by the ARS and the Service and dealing with the direct importation into California of beneficial insects or organisms intended primarily for ultimate liberation within the State.

3. That no importations of beneficial insects or other organisms shall involve the entry into California of (a) plants which are hosts of citrus canker; (b) fruits or vegetables which serve as hosts of the Mediterranean fruit fly or related fruit flies from countries where such pests are known or believed to occur; or (c) hosts of injurious pests not known to occur in or to be widely distributed within the United States from localities where such pests are known or believed to occur, with such exceptions as may be agreed upon in writing by the parties to this agreement.

4. That the Director of the Agricultural Experiment Station of the University of California shall be in charge of and have supervision over all material with research potential imported by the State or the Regents under this agreement until necessary investigations are completed to determine the results of such importations. If satisfactory results are obtained from any importation, the progeny from such importation, after due written notice to the parties to this agreement, may be distributed by the Director, or a designated representative to other institutions or individuals believed to be competent and equipped to rear and/or liberate such progeny.

5. That all materials to be imported under this agreement shall be entered only on permits issued by the Service and copies of all applications for permits and copies of all permits so issued shall be furnished to the State.

6. That those imported shipments of beneficial insects or other organisms under this agreement which the State requires to be inspected shall be received and examined at the port of first arrival by authorized representatives of the Service, and such inspections shall be confined to such examination of the containers as may, in the judgement of the inspector, be necessary to determine that they are sufficiently secure and in such condition as will assure safe arrival at the designated quarantine facility. These shipments will be forwarded to the designated quarantine facility as expeditiously as possible.

7. That initial liberations of phytophagous organisms imported under this agreement shall be made in California only after written approval of the parties to this agreement. Subsequent liberations of progeny from the importations made under a given permit shall not need additional approval by the parties to this agreement. Such liberations shall continue to be recorded and reported in accordance with paragraph A.7 of this agreement.

8. That this Memorandum of Agreement is to define in general terms the basis on which the parties concerned will cooperate, and does not constitute a financial obligation to serve as a basis for expenditures. Each party will handle and expend its own funds. Any and all expenditures from federal funds in the U. S. Department of Agriculture made in conformity with the plans outlined in this Memorandum of Agreement must be in accord with the Department's Rules and Regulations and in each instance, based on appropriate finance papers. Expenditures made by The Regents of the University of California and the California State Department of Food and Agriculture, will be in accord with their Rules and Regulations. Funds of a cooperating party shall not be expended by a federal employee even though the cooperating party has no representatives stationed in the locality. In such cases, a federal employee may handle the accounts but shall forward the vouchers to the authorized agent of the cooperating party for payment. Cooperating parties should not send checks payable to federal employees or send them checks payable to "Cash" or "Bearer" for payment of local expenses.

9. That the responsibilities assumed by the cooperating parties are contingent upon funds being available from which the expenditures legally may be met.

10. No member of or delegate to Congress, or resident commissioner, shall be admitted to any share or part of this agreement or to any benefit that may arise therefrom, unless it be made with a corporation for its general benefit.

11. This Memorandum of Agreement represents a revision and supersedes the present agreement, which was effective January 14, 1964.

12. That this agreement shall become effective upon date of final signature and shall continue indefinitely, but may be modified by mutual agreement among the parties in writing and may be discontinued at the request of any of the parties. Request for termination or of major change shall be submitted in writing to the other parties not less than sixty (60) days in advance of the effective date desired; provided, that such termination shall not become effective until arrangements reasonably satisfactory to the other parties have been made for the destruction or other disposition of any materials, organisms or specimens which have been imported into California under this agreement and which, at the time of such termination are being used in laboratory tests or experiments.

CALIFORNIA STATE DEPARTMENT OF FOOD AND AGRICULTURE
signed: C. B. Christensen
Director

THE REGENTS OF THE UNIVERSITY OF CALIFORNIA
signed: J. B. Kendrick
Vice President, Agricultural Sciences Director, Agricultural Experiment Station

UNITED STATES DEPARTMENT OF AGRICULTURE AGRICULTURAL RESEARCH SERVICE
signed: Gail F. Sedgwick
Acting Administrator

UNITED STATES DEPARTMENT OF AGRICULTURE ANIMAL AND PLANT HEALTH INSPECTION SERVICE
signed: E. E. Norris
Acting Administrator

NOV 25 1974
Date

APPENDIX II
DETAILED HISTORY OF INSECT PATHOLOGY RESEARCH IN THE AGRICULTURAL RESEARCH SERVICE, ARRANGED BY LOCATION

Edited by P. V. Vail

The United States Department of Agriculture (USDA) has been involved in insect pathology and microbial control research since the early 1900s. Some of the early projects such as those for Japanese beetle and diseases of the honey bee provided the stimulus for modern day research programs and the acceptance of insect pathology and microbial control as distinct disciplines. Many of the basic research findings of the Agricultural Research Service (ARS) in these disciplines have provided the information necessary to develop both microorganisms as control agents and control methods for insect diseases in pest and beneficial species and also have found use in other disciplines such as medicine. This document was prepared by research scientists from most of the past and current ARS laboratories conducting research in insect pathology and microbial control. It describes research on insects of importance to food and crops, man and animals, and forests. The collection of histories provides the reader with research accomplishments and pertinent literature. The collection of histories is current through 1992. They are arranged alphabetically by state and country in which the research was conducted; see main Table of Contents.

As in other parts of this book, the full scientific name and taxonomic hierarchy of all organisms discussed in the text of this Appendix are cited only in the Index, where they are cross-referenced with the common name, if used in the text.

Acknowledgment: The editor expresses his sincere gratitude to Ms. Elisabeth Nye Fouse and Ms. Darlene Hoffmann, USDA-ARS Horticultural Crops Research Laboratory, Fresno, CA, the former for assistance and perseverance in typing, editing and organizing this document, the latter for assistance with the literature search, and to Dr. Martha Gilliam, USDA-ARS Carl Hayden Bee Research Laboratory, Tucson, AZ, and Dr. Leslie C. Lewis, USDA-ARS Ankey, IA, for reviewing the manuscript.

WESTERN VEGETABLE AND SUGAR BEET INVESTIGATIONS LABORATORY, MESA, AZ.

By Patrick V. Vail

In 1969, P.V. Vail joined the staff of the Western Vegetable and Sugarbeet Investigations Laboratory in Mesa, AZ, as Investigations Leader and centered his studies on microbial control of lepidopterous pests of vegetables with entomogenous viruses. While at the Mesa laboratory, Vail explored the host range of the nuclear polyhedrosis virus (NPV) isolated from alfalfa looper (Ac*M*NPV) (Vail et al. 1973b). These early studies showed that the cotton leafperforator (Vail et al. 1971a), the pink bollworm (Vail et al. 1972b), and diamondback moth (Vail et al. 1972a) were also susceptible to this virus. Extensive histopathological studies were also conducted on a number of the alternate hosts of Ac*M*NPV (Vail and Jay 1973). Vail et al. (1973b) were the first to show extensive complete and rapid replication of a baculovirus in an insect cell line. Occluded virus was as infective as *in vivo*

produced virus. Later, Hink and Vail (1973) developed the first plaque assay for an entomopathogenic virus using the same cell line-virus system.

Methods of mass producing noctuid larvae, their parasitoids and viral pathogens were also investigated. Several different larval diets and virus production methods were developed that provided high yields and minimized labor (Vail et al. 1973a). Several large-scale field tests were conducted near Tucson, AZ, demonstrating the feasibility of using several baculoviruses and *Bacillus thuringiensis* for control of the cabbage looper on lettuce (Vail et al. 1972c). The influence on parasitoid and predator populations was also determined. Later Vail et al. (1980) conducted further tests on the use of several NPVs and spray adjuvants for the control of cabbage looper infesting lettuce in Arizona. Also the merits of reducing cabbage looper populations on cotton with a baculovirus before it moves into lettuce was demonstrated (Vail et al. 1976b). These tests provided the first information that indicated area-wide suppression of an agricultural pest with a baculovirus might be feasible. Insects could be controlled on one crop or alternate host to reduce infestation in another possibly higher value crop.

As NPV infections were often found associated with the parasitoid *Voria ruralis* parasitism in mass-rearing systems, studies were conducted to determine if the parasitoid was responsible for virus transmission. Conversely, parasitism rates by *V. ruralis* were often masked by parasitoid larvae dying within diseased hosts prior to completion of development. At times *V. ruralis* larvae were found only in diseased larvae. Because of the long pre-oviposition period most of the virus acquired by the parasitoid while in the host was voided prior to the time the parasitoid was capable of parasitization (Vail 1981). Polyhedra were found in the midgut of parasitoids emerging from NPV-infected larvae. Viable polyhedra could be found in the meconia and adult feces. However, the infectivity of adult homogenates was quite low indicating that any virus in the adults was voided soon after emergence. The infectivity could be demonstrated for only several days after emergence. Thus it was demonstrated that adult parasitoids could act as mechanical vectors for short periods of time. *Voria ruralis* adults could help distribute virus inoculum to other sites under natural conditions. The possibility of host feeding as a means of virus transmission/dissemination was not investigated. In 1971, Vail transferred to the Western Cotton Research Laboratory in Phoenix, AZ.

WESTERN COTTON RESEARCH LABORATORY, PHOENIX, AZ. By Marion R. Bell and Patrick V. Vail

P.V. Vail and M.R. Bell conducted insect pathology/microbial control research at the Western Cotton Research Laboratory in Phoenix from 1971 to 1985. In 1971, Vail transferred to the Laboratory as Research Leader for cotton insects investigations. Vail continued to conduct research on *in vitro* production of the alfalfa looper NPV (Ac*M*NPV) using modified media (Vail et al. 1976a). The impact of applications of Ac*M*NPV on cotton leafperforator was also demonstrated (Vail et al. 1977a). As a result of ARS Pilot Test funding Vail et al. (1977b) evaluated several techniques as components of an integrated system for control of pink bollworm in the Southwest. Using commercial type applications, Ac*M*NPV was found to have little effect on pink bollworm populations, although infected larvae were obtained from treated plots. Vail et al. (1979), in cooperation with the ARS Insect Pathology Pioneering Research Laboratory, Beltsville, MD, demonstrated the *in vitro* infectivity of Ac*M*NPV liberated from polyhedra with digestive juices. This finding led to a potential alternative method to the commonly used alkali liberation techniques. Vail et al. (1989) also determined quantitatively the residues of Ac*M*NPV after field applications to cotton. A high correlation between residues and infection levels of cotton leafperforator populations was demonstrated. In 1975, Vail took a leave of absence to take a position with the International Atomic Energy Agency in Vienna, Austria.

Bell transferred from the Boll Weevil Research Laboratory, Mississippi State, MS, in 1972. He developed a technique for determining the feeding preference of newly-hatched pink bollworm larvae and used the method to develop a formulation which increased the effectiveness of pathogens (*Bacillus thuringiensis* (*Bt*) and baculoviruses) in laboratory and field studies. This research established that newly-hatched pink bollworm larvae could exhibit a feeding preference, and that the feeding behavior could be modified on cotton by the presence of these cotton-based feeding materials. Results of the field study demonstrated that cotton-based adjuvants increased the effectiveness of baculovirus against *Heliothis* spp. (sens. lat.) but failed to significantly affect efficacy for pink bollworms. The study also suggested a new method of insect control: the application of materials which elicit feeding in or on less important plant parts and which reduce the pest population by altering feeding habits. The materials identified in this study were further modified by Bell for cooperative studies with H.M. Flint (USDA-ARS, Phoenix) and P.D. Lingren (USDA-ARS, Lane, OK) for possible use in pink bollworm pest management programs, and R.T. Staten (USDA-APHIS, Phoenix) for possible use in a boll weevil program (Bell and Kanavel 1975, 1977a). Bell and Kanavel (1976) conducted basic investigations into the host-pathogen relationship between the pink bollworm and its cytoplasmic polyhedrosis virus (CPV). These studies described the relationship between dose, growth, and mortality, and viral effects were described which were previously unknown. This knowledge helped in his participation as a cooperative member in a team of ARS/APHIS personnel working to control this pathogen in a pink bollworm mass rearing facility. The clean-up procedures resulted in a 5-fold production increase (Bell and Kanavel 1976, 1977b; Stewart et al. 1976; Bell 1977).

Through a sequence of laboratory, greenhouse, and field research studies, Bell developed a practical feeding adjuvant (COAX™) that increased the effectiveness of pathogens as well as other insecticides in pest control programs. He conducted the research necessary to demonstrate its commercial possibilities and aided Proctor and Gamble, Inc., to develop a commercial product. This product reached annual sales of $15 million. The development of new chemical insecticides (i.e., pyrethroids) for cotton insect control decreased the quantity of product marketed. However, the insect management technique and product developed remain as a viable and efficacious alternative for *Heliothis* (sens. lat.) control in cotton, and continue to be used in limited areas of the U.S. and foreign countries. COAX™ has also been studied by many domestic and foreign scientists and shown to be effective in a variety of insect control programs (e.g., control of *Spodoptera* and *Helicoverpa armigera* in Israel) (Bell and Kanavel 1978; Bell and Romine 1980).

With the technical assistance of C.L. Romine, Bell conducted field studies to determine the potential of two microbial insecticides for control of cotton leafperforator. Results showed that a bacterium and virus mixture was effective in preventing damage. Since these pathogens had already proven useful in the control of *Heliothis* (sens. lat.) in cotton, their usefulness in the control of the cotton leafperforator provided further evidence for their use in pest management programs (Bell and Romine 1982).

Bell conducted laboratory experiments to study the effects of mixtures of the bacterium *Bacillus thuringiensis* and nuclear polyhedrosis viruses on several lepidopterous pests. The results of these tests aided in the understanding and evaluation of these pathogens when used under field conditions. Several important sublethal dosage effects were discovered during this research which could be very important to integrated pest management programs utilizing microbials. For example, a method of using prophylactic treatments of low, sublethal applications of *B. thuringiensis* is being used successfully by some growers (Bell and Romine 1986).

BEE RESEARCH LABORATORY, TUCSON, AZ. By Martha Gilliam

Martha Gilliam was awarded an ARS Cooperative Agreement Grant while at the University of Arizona to conduct research on immune mechanisms of the honey bee (Gilliam 1973). Part of this work involved *Bacillus larvae*, the causative organism of American foulbrood disease (AFB). The results showed that agglutinating substances are produced and disseminated rapidly within the body of the adult worker honey bee in response to an injection of a vaccine prepared from *B. larvae* (Gilliam and Jeter 1970).

In 1969, Gilliam received a Civil Service appointment as a Microbiologist at the ARS Bee Research Laboratory of the Carl Hayden Bee Research Center at Tucson. Her primary assignment was to define the normal microflora (bacteria, yeasts, and molds) of honey bees, their food (pollen and nectar), and environment and then to determine microbial contributions to honey bee nutrition, biochemistry, and physiology.

Gilliam began long-term cooperative research efforts with several scientists. Stephen Taber III, a Research Entomologist who preferred the title Apiculturist, retired from the Carl Hayden Bee Research Center in 1979. He and Gilliam continued to work together after his retirement. Dorothy Prest, a mycologist at Keuka College, New York, began working with Gilliam in 1971. After her retirement in 1984, she moved to Tucson and has been a Collaborator at the Carl Hayden Bee Research Center since then. L.J. Wickerham, the noted yeast taxonomist, retired from the ARS Northern Regional Research Laboratory in Peoria, IL, and was a collaborator at the Carl Hayden Bee Research Center from 1974–1985. Gilliam also has worked for many years with Robert Argauer, Research Chemist, ARS, Beltsville.

Results from the normal flora project obtained over 18 years were summarized by Gilliam (1989). It was shown that healthy honey bee eggs, prepupae, and pupae are free internally of microbes. Larvae can be inoculated with microbes from ingestion of contaminated food, but these are usually eliminated through defecation at the end of the feeding period. Emerging adult worker bees generally have no intestinal microflora until they are inoculated by trophallaxis and pollen consumption. Nectar contains few or no microbes.

Microflora of honey bees are dominated by Gram-variable pleomorphic bacteria, *Bacillus* spp., Enterobacteriaceae, Penicillia, and Aspergilli. Yeasts in bee intestines appear to be indicators of stress and are represented most frequently by *Torulopsis* spp. Ingestion of antibiotics used to control bee diseases, certain pesticides, and caging of both colonies or bees alters the intestinal microflora. Digestive enzymes in honey bees originate from the bees themselves, from pollen, and from micoorganisms.

Microbiological examination of various organs of mated and virgin queen honey bees revealed that yeasts rarely occur in queen bees, and molds occur less frequently in the guts of queen bees than in those of worker bees. Bacteria belonging to the genus *Bacillus* are present, although Gram-negative rods and Gram-variable pleomorphic bacteria were more numerous. The antimicrobial properties of royal jelly that is seemingly the diet of the queen bee throughout her entire life may prevent many microorganisms from becoming established in the gut. In contrast, pollen that is consumed by worker bees and food obtained from other bees in the colony are the primary sources of inocula for the gut microflora of this caste.

Pollen is the chief dietary source of proteins, amino acids, lipids, vitamins, and minerals for honey bees. Foraging bees collect pollen that is then packed into the comb cells of the brood comb. This store of pollen, which has undergone chemical changes, is called bee bread.

Studies on the microbiology of floral and corbicular pollen and of bee bread stored in comb cells of the hive demonstrated that pollen from a flower changes both biochemically and microbiologically as soon as a bee collects it due to the addition of secretions and microbes which produce and conserve a nutritive product for consumption. Molds, yeasts, and *Bacillus* spp. are the predominant microbes in pollen and bee bread. It appears that bees perform a type of "microbial farming" by inoculating pollen with specific microorganisms as they collect it and make it into a suitable mass to carry back to the colony. For example, *Torulopsis magnoliae*, a yeast, was added to pollen by the bees as were several *Bacillus* spp. and the molds *Rhizopus nigricans* (= *R. stolonifer)*, *Aureobasidium pullulans*, *Penicillium corylophilum*, and *P. crustosum*. *Bacillus* spp. are exploited industrially for their production of numerous antibiotics, fatty acids which are also antimicrobial, and enzymes. Unlike Gram-negative bacteria, they secrete their chemical products extracellularly in large quantities. The conversion of pollen to bee bread has been postulated to be a microbial process similar to that which occurs in the fermentation of green food materials stored in silos. Thus, *Bacillus* spp., yeasts, and molds may stabilize stored pollen just as they do silage on its removal from the silo.

The stored food of other social and solitary bees that were examined contain *Bacillus* spp., exclusively or predominantly, or no microbes. Also, there are similarities in the species of *Bacillus* associated with food of different origins in the nests of diverse bee species from various geographical areas (Gilliam et al. 1990a). Thus, a special association between *Bacillus* spp. and some bees may have evolved by which female bees inoculate food sources with these bacteria whose chemical products are responsible for the pre-digestion, metabolic conversion, fermentation, and preservation of food.

Gilliam and Argauer developed and used a sensitive reproducible fluorometric method for analyzing Terramycin (TM; oxytetracycline hydrochloride) in bees, medicated diets, and honey (Argauer and Gilliam 1974; Gilliam and Argauer 1975, 1981; Gilliam et al. 1979). TM is the antibiotic that is used to control the bacterial diseases AFB and European foulbrood (EFB). Previously, TM had been analyzed by laborious microbiological methods which often did not yield quantitative data and were hampered by the presence of naturally occurring antibacterial substances in bees and their products. The stability of TM in various diet formulations fed to bees for disease control, the times and temperatures at which the diets can be stored, and degradation of TM in the hive were determined. Because honey for human consumption must not contain residues, TM was also analyzed in honey after feeding various medicated diets to bees. Results showed that TM is extremely stable in antibiotic extender patties, pollen patties, and sugar dusts, but degrades rapidly in sugar solutions. TM does not present residue problems if sufficient time (4–6 weeks) is allowed between the last treatment and extraction of surplus honey regardless of the method used to treat the bees. No residues were found in honey from colonies fed antibiotic extender patties.

Gilliam and Taber (1973) and Prest et al. (1974) defined diseases and anomalies of honey bees in continuous bee production and in bees receiving artificial diets and massive amounts of pollen. This was one of the first published reports of chalkbrood disease, caused by the heterothallic fungus *Ascosphaera apis*, occurring in honey bees in the U.S. These studies also demonstrated that feeding massive amounts of pollen to rear all castes of honey bees throughout the year or feeding artificial diets to bees predisposes larvae and pupae to infections with fungi and adult bees to the disease caused by the protozoan *Nosema apis*. Taber and Lee (1973) reported that bee colonies in Arizona had peak infections of *N. apis* in the winter, but the disease virtually disappeared by late summer.

Gilliam and Dunham (1978) isolated *Bacillus pulvifaciens* from dead larvae of honey bees from Arizona and Iowa. This organism is associated with powdery scale, a rare disease. They found that "scales" (dried remains of dead larvae) that have different appearances and colors can contain the organism.

As chalkbrood continued to spread throughout North America and to cause serious problems in some locations, Gilliam devoted more effort to research on the disease. Larvae with chalkbrood become mummified. There had been speculation that *A. apis* was not a primary pathogen but was a saprophyte growing on larvae dead from other causes. Gilliam et al. (1978) found that eggs and pupae did not support the growth of *A. apis*, but larvae of all ages and pre-pupae were susceptible. Infection occurred both through ingestion of *A. apis* and by the growth of the fungus through the cuticle. The fungus grew on larvae dead from other causes, but as a saprophyte, *A. apis* did not produce "mummies". Variation in susceptibility of bee colonies was noted as an important factor in expression of the disease.

Gilliam (1986) then demonstrated the wide range of susceptibility of individual bee colonies to the same dose of inoculum, elucidated various stresses which can trigger expression of the disease, and defined the substrates in the colony which can serve as sources of reinfection when the proper stress conditions exist.

In other work, mating tests of separated strains of *A. apis* from chalkbrood mummies from various parts of the world demonstrated that all contained *A. apis* and that the pathogen in the U.S. does not differ from the one found elsewhere as had been suggested (Christensen and Gilliam 1983).

Gilliam et al. (1983a) showed that genetically-controlled hygienic behavior of worker honey bees aids in control of chalkbrood by increased uncapping and removal of diseased and dead larvae (mummies) and by increased removal or decreased survival of the pathogen in bees and hive products. Beekeepers can use simple techniques devised to test the hygienic behavior of their bees (Gilliam et al. 1983b). Queens whose progeny exhibits poor hygienic behavior should be replaced. This work demonstrated that bees could be bred for resistance to chalkbrood disease and is important since no effective chemical control agent has been found.

More recent work described improved, easier methods for testing hygienic behavior of bees (Gilliam et al. 1988; Taber and Gilliam 1988, 1989), showed that bee bread and guts of nurse bees were the major sources of the chalkbrood in susceptible colonies (Gilliam et al. 1988), and examined the role of normal microflora of bees and hive substrates in resistance of bee colonies to the disease (Gilliam et al. 1988). No antimycotic chemicals were produced by bees, brood, or hive substrates *per se*. However, microorganisms isolated from these sources were found to inhibit the growth of the pathogen. Most of these organisms were molds isolated from bee bread which were apparently introduced by the bees, as the pollen fed to the bees was remarkably free of microbes other than the pathogen. These results indicated that inhibitory molds, or their antimycotic products, which are part of the normal microflora of bee colonies, could be a control for the disease and that molds isolated from bee bread may play a role in resistance to the disease.

The honey bee chalkbrood pathogen was isolated from diseased larvae of a carpenter bee, *Xylocopa californica arizonensis*, in Arizona and from the Asian honey bee, *Apis cerana*, from Korea. *Ascosphaera apis* strains from both bee species mated with *A. apis* strains from western U.S. honey bees and are thus interfertile and identical (Gilliam 1990).

Because of recent interest in microbial control of ants, Gilliam et al. (1990b) reported on fungi isolated from a diseased queen rough harvester ant. Of the four molds isolated, either *Alternaria alternata* (as *tenuis*) or *Aspergillus flavus* var. *columnaris* appeared to be responsible for the mycosis. All of the fungi isolated were provided to other researchers for testing on fire ants.

Gilliam and Taber (1991) surveyed feral honey bee colonies for diseases, pests, and normal microflora and found only a few spores of *N. apis* and larvae of the greater wax moth. Honey bees from these colonies in central Arizona contained the same kinds of intestinal microorganisms as bees

from managed colonies in southern Arizona. There were similarities in the kinds of microorganisms in bees and wax moth frass from feral colonies. They concluded that diseases were rare in these feral colonies, 28 of which had been observed for over five years.

HORTICULTURAL CROPS RESEARCH LABORATORY, FRESNO, CA. By Patrick V. Vail, James E. Lindegren, and Darlene F. Hoffman

Insect pathology research at the Stored Product Insects Research Laboratory (now a part of the Horticultural Crops Research Laboratory), Fresno, CA, began in 1966 with the hiring of W.R. Kellen, a graduate of the University of California, Berkeley. Much of Kellen's earlier work (University of California, Berkeley and California State Department of Public Health, Bureau of Vector Control, Fresno) involved studying the effects of pathogens on mosquitoes. Some of his cooperative work with ARS personnel included host-parasite interrelationships with *Thelohania* from mosquitoes (Kellen et al. 1965, 1966). As an ARS scientist he conducted many studies on the ultrastructure, taxonomy, basic pathology and modes of transmission of protozoans that infected such insects as navel orangeworm, Indianmeal moth, and a number of coleopteran pests (Kellen and Lindegren 1968, 1971). Descriptions of these life stages have been valuable aids for identifying pathogens which are potential contaminants in established cultures. They also provide some indication of the potential of these organisms as microbial control agents.

The symptomatologies of some of these protozoans were quite unique and Kellen's studies provided methods of simple and accurate diagnoses for these infections. For example, a protozoan isolated from the navel orangeworm caused melanized encapsulations which were clearly visible beneath the integument (Kellen et al. 1977a). These melanized spots were useful in diagnosis of advanced cases of infection caused by this pathogen.

Kellen was the first to conduct studies on the use of *Bacillus thuringiensis* for the field control of the navel orangeworm in almonds (Kellen et al. 1977b). His results showed that proper timing of applications plus adequate volume and coverage were prerequisites for control of this insect. Results also pointed out the need for understanding adult and larval behavior in order to time applications for most effective control. The levels of control obtained indicated that the bacterial insecticide might be useful in an integrated pest management program. However, *B. thuringiensis*, up to the present time, has not been used commercially for the control of the navel orangeworm. With the increasing environmental and consumer concerns, the use of this pathogen may become more advantageous.

Kellen directed a study on the symbiotic relationships of a *Wolbachia* that occurs naturally in the reproductive organs of the almond moth, a cosmopolitan pest of stored products (Kellen et al. 1981). The microorganism occurs in both males and females, but is transovarially inherited only through the cytoplasm of the egg. Although male moths do not transmit the symbiont, the presence of *Wolbachia* in the male causes the sperm to be "conditioned" so that such sperm is only accepted by an oocyte that contains a similar strain of *Wolbachia*. Therefore populations of moths that harbor different strains of symbionts are not interfertile. Kellen conducted intensive ultrastructural studies of the symbiont and also showed the relationships between symbiotic and aposymbiotic strains of the moth. This was the first time that this relationship was described from a lepidopteran. Kellen et al. (1972) also conducted a pioneering study on *Rickettsiella* from navel orangeworm.

Kellen also conducted studies to elucidate the ultrastructure, pathogenicity and host specificity of two previously unknown small RNA viruses from larvae of the navel orangeworm, a serious pest of tree nuts in California. This investigation led to the discovery of the first known occurrence of a calicivirus in an invertebrate host (Kellen and Hoffmann 1981; Hillman et al. 1982). The ultrastructure of this virus was described by Hoffmann and Kellen (1982). Hillman et al. (1982) demonstrated two forms of the virus probably caused by partial degradation in the host's excreta and

compared their respective pathogenicities (Hoffmann and Hillman 1984). A picornavirus was also isolated and its pathogenic influence was described in the blood cells which are the primary tissue infected. These studies helped to focus attention on the small viruses of insects especially those species for which non-occluded viruses are unknown. Kellen conducted further studies on the small calicivirus, particularly on dose-mortality and the retarded growth responses of larvae (Kellen and Hoffmann 1982). No previous comparable studies with small non-occluded viruses had been conducted up to this time. Kellen found that stunted larvae usually succumbed to infection after an extended period in a moribund state during which they cease feeding, thus the term chronic stunt virus for this organism (Kellen and Hoffmann 1982). His research data indicated strongly that the virus was a suitable candidate as a biological control agent particularly from the standpoint of population management as opposed to a direct control procedure.

The thermal stability of the calicivirus declined rapidly at temperatures of 55 °C for 45 minutes or less. Also lower temperatures inactivated the virus but at a much slower rate. Of interest was the fact that larvae reared at 34 °C, even though infected, showed a strong resistance to disease progression. Kellen proposed that high temperature rendered the insect unsuitable for infection because the enzyme systems required for the replication of the virus *in vitro* were inhibited by the temperatures (Kellen and Hoffmann 1983a). He also concluded that these studies pointed to the importance of understanding the microclimatic conditions that exist in the host-ecological niche.

Kellen further studied the RNA viruses as related to the reduced longevity and fecundity of infected insects (Kellen and Hoffmann 1983b). His data showed that healthy moths lived about 15 times longer than their infected counterparts. Infected female moths laid 5- to 10-fold fewer eggs than their healthy counterparts. Moreover, healthy females mated with diseased males laid significantly fewer fertile eggs. These results showed the virus has subtle effects that could have significant impacts on host populations. Further studies may demonstrate inoculative releases of this virus are worthy of consideration as a pest management tool.

In concert with the above studies, Kellen initiated investigations to elucidate the role of male Indianmeal moths (IMM) in the autodissemination of viral pathogens. By using females as an attractant, Kellen lured male IMMs to a dust formulation of IMM granulosis virus which then contaminated the males. Contaminated males in turn mechanically spread the virus to the body surfaces of the female moth, especially in the genital areas during the act of copulation (Kellen and Hoffmann 1987). Spread of a disease agent through mating is an efficient way of infecting individuals in a population. Kellen retired in 1986.

In 1966, J.E. Lindegren began research at the Fresno location as an assistant entomologist. In his earlier studies, Lindegren, working with Kellen, discovered and helped to describe *Nosema plodiae*, a protozoan infectious to the IMM (Kellen and Lindegren 1968, 1971, 1973a, 1974b). Kellen's and Lindegren's early studies provided a point of reference for research on other undescribed microsporidans of stored product insect pests (Kellen and Lindegren 1969, 1970, 1972).

Later in his investigations of the protozoa, Lindegren isolated a rarely reported pathogen of nitidulid beetles, propagated it for the first time under laboratory conditions, and investigated its host range and life cycle. As a result of electron microscope studies, he observed unreported stages of this pathogen's life history in the navel orangeworm (Lindegren and Hoffmann 1976). In further studies he extended its host range to include 15 species of insects in six families in three orders, and three species of mites (Kellen and Lindegren 1973b, 1974a). This work stimulated further investigations into the biological control potential of this pathogen (Fukuda et al. 1976) and studies of its life cycle.

In the late 1970s, Lindegren began investigations on the control potential of entomopathogenic nematodes, primarily *Steinernema carpocapsae*. Early on, he found reasonably easy methods to

produce the nematode (Lindegren et al. 1979b; Hara et al. 1981) and tested it under field conditions (Lindegren et al. 1979a, 1981a and b; Poinar et al. 1981). With $10,000 funding each from both the University of California and USDA-CSRS Interregional Project 4 (IR-4; clearance of pest control materials for minor use) for evaluation of carpenterworm control in fig orchards, Lindegren and associates developed the first commercial use of an insect parasitic nematode in the U.S. This technology was transferred to biosis®, Inc. An Environmental Protection Agency (EPA) exemption from tolerance for entomopathogenic nematodes was obtained which stimulated commercialization of nematodes for insect pest control.

Lindegren's work on wood borers has been successfully used in the People's Republic of China, where it reportedly has saved highly valued shade trees. In addition, he demonstrated a broader host range of the nematode than was originally believed (Kaya and Lindegren 1983; Toba et al. 1983; Shapiro et al. 1985a; Lindegren 1990; Lindegren et al. 1992). One of his first field studies on the use of the nematode for control of the Colorado potato beetle was conducted in cooperative studies with the ARS Yakima Agricultural Research Laboratory (Toba et al. 1983). Initially dose-response curves were developed for this insect in the laboratory and again under field conditions. The studies showed that soil applications of entomopathogenic nematodes may be feasible as part of an integrated pest management program (Toba et al. 1983). These studies were later confirmed by industry and it is considered to be a safe and effective alternative for chemical insecticides used for Colorado potato beetle control.

Other early investigations included determining the efficacy of nematodes for navel orangeworm in almond orchards (Lindegren et al. 1978, 1981b). Nematode field persistence, dose response, optimal application timing and effectiveness when applied with commercial sprayers (both ground and air) were determined in cooperation with the University of California Cooperative Extension Service and the almond industry (Agudelo-Silva et al. 1987; Lindegren et al. 1987). At a later date this control methodology was turned over to industries interested in producing the nematode and to the U.C. Cooperative Extension Service for commercial evaluation. Ancillary studies showed honey bees were only slightly susceptible to *S. carpocapsae* (Kaya et al. 1982).

In cooperative tests in 1982 with the ARS Tropical Fruit and Vegetable Research Laboratory, Honolulu, HI, Lindegren conducted laboratory and field investigations which resulted in a nematode larvacidal soil drench for the reduction of Mediterranean fruit fly, oriental fruit fly, and melon fly populations (Lindegren and Vail 1986). Field evaluations of this entomophagous nematode as a soil treatment on Oahu and Maui in 1983, 1984 and 1985 indicated that the optimal concentration for control of "medfly" larvae when applied as a drench was approximately 500 nematodes per cm^2 (Lindegren 1990, Lindegren et al. 1990). Interest in this augmentative control method for fruit flies has been expressed by governmental agencies and industry (Lindegren 1992).

Lindegren, with other scientists at the Horticultural Crops Research Laboratory, developed a technique for measuring the respiration rates of *Steinernema feltiae* infective juveniles to obtain information for optimum storage conditions (Lindegren et al. 1986). As a result of these studies, Lindegren developed a method of reducing respiration and increasing storage life of entomopathogenic nematodes by osmotic desiccation (Popiel et al. 1987). He also found desiccated nematodes could be stored in a viable condition at sub-zero temperatures. This method provided a means of long-term mass storage and shipment of steinernematid and heterorhabditid infective juveniles.

Lindegren developed a simple, state of the art, *in vivo* rearing procedure for *S. carpocapsae* which produces only the infective juvenile stages. The method does not require the use of incubators, autoclaves or toxic disinfectants; provides an aerobic high relative humidity environment; screens against unwanted contaminants; and produces adequate nematodes for laboratory and small-scale

field tests (Lindegren et al. 1993). This method is currently being successfully used by private industry and other research facilities. In the late 1980s, Lindegren developed a process for storing entomopathogenic nematodes in a concentrated nematode-produced sponge-like mat or "nematode wool".

Lindegren also developed a selection method for increasing entomopathogenic nematode virulence, infectivity and production efficiency. As a result, the Kapow strain of *S. carpocapsae* produces 34% more infective juveniles six days earlier than the same unselected strain. The strain is also visibly more active, and at 50 nematodes per greater wax moth host larvae, exposures result in a three-hour earlier LT_{50} than non-selected strains. The Kapow selection is being produced commercially.

Lindegren is currently (1993) conducting cooperative studies (with the Western Cotton Research Laboratory, Phoenix, AZ) evaluating the control potential of pink bollworm with entomopathogenic nematodes (Lindegren et al. 1992). This approach looks promising and is stimulating the interest of industry.

D.K. Hunter joined the insect pathology research group at the Stored Product Insects Research Laboratory soon after his 1967 graduation from the University of California at Riverside. Hunter conducted research almost exclusively on entomopathogenic viruses of stored product pests infesting dried fruits and nuts. His investigations included cytological and ultrastructural studies, virus-host interactions and the development of the viruses as microbial control agents. In 1970, Hunter reported on a granulosis virus (GV) first isolated from the almond moth infesting stored peanuts from Georgia (Hunter and Dexel 1970). Electron microscope studies indicated a pathology similar to that reported for the Indianmeal moth GV (Hunter and Hoffmann 1970). Similar studies on pathogenicity were conducted by Hunter on the Indianmeal moth GV (Hunter 1970; Hunter et al. 1972; Hunter and Hoffmann 1973). Cross-infectivity tests showed that the Indianmeal moth GV failed to infect first instar larvae of tobacco, almond, and raisin moths, at concentrations much higher than the LD_{50} of Indianmeal moth. Hunter determined the influence of high temperature on respiration and mortality of Indianmeal moth exposed to other GVs (Hunter and Hartsell 1971). Larvae exposed to the virus had a lower respiration rate than healthy larvae. In a temperature mortality test, the highest mortality occurred at 32°C. Treated larvae at 37°C did not display granulosis symptoms, but they apparently harbored the virus. He noted that control larvae at 37°C were less developed, greenish and generally less healthy appearing than larvae reared at lower temperatures. These studies suggested that the infection was masked or thermally inhibited at high temperatures. Interestingly, larvae at 32°C were the first to die with granulosis. To evaluate the efficacy of direct applications of the Indianmeal moth GV to commodities prior to storage, virus suspended in water was sprayed on conveyor-borne almonds, peanuts, walnuts and raisins. These were then infested with Indianmeal moth eggs and held in simulated storage conditions. In every case, the virus treatment protected the commodity effectively (Hunter et al. 1973, 1975, 1977, 1979).

Because of the specificity of the virus, an investigation of its compatibility with malathion was conducted so that in combined applications beetles that are also storage pests would be controlled along with the Indianmeal moth which had become resistant to malathion. Results showed that the mixture of granulosis virus and malathion was more effective against the Indianmeal moth than either material alone. At the same time, the test beetles were significantly controlled (Hunter et al. 1975).

In 1978, P.V. Vail was transferred to the Horticultural Crops Research Laboratory to conduct investigations on the basic pathology and microbial control of pre- and postharvest pests. In a series of studies, he demonstrated that Ac*M*NPV was 10 times more infectious to tobacco budworm than to corn earworm, important pests of cotton and other crops (Vail et al. 1978). These studies pointed to the importance of knowing which species of the *Heliothis/Helicoverpa* complex was infesting a crop (Vail et al. 1978). Further studies with Ac*M*NPV and *Helicoverpa zea* and *Heliothis virescens*

showed that virus replication and inclusion body production were much lower in the corn earworm whether the inoculum was administered *per os* or by injection into the hemocoel (Vail et al. 1982). Non-occluded virus (NOV) production in six tissues of corn earworm was significantly reduced as compared to tobacco budworm (Vail and Vail 1987). The above studies provided a pathological basis for research conducted by Vail and Max Summers of Texas A&M University on the infectivity of Ac*M*NPV-like baculovirus isolates, variants and recombinants. These viruses were no more potent than the wild type Ac*M*NPV for corn earworm or tobacco budworm and it was concluded that the known viruses of the Ac*M*NPV type probably do not have the phenotypic variability needed for increased infectivity to corn earworm (Vail et al. 1982). Furthermore, passage of wild-type Ac*M*NPV through corn earworm did not increase its virulence, although three new variants were isolated. Therefore, other sources must be found, either natural, selected or engineered, of Ac*M*NPV-type baculoviruses having more activity towards corn earworm. In 1985, such a virus was isolated near Columbia, MO, from the celery looper, with a broad host range and high activity towards both *H. zea* and *H. virescens*. The virus was patented by ARS. Field tests were initiated in 1990 to determine the potential of this virus as a microbial control agent (Vail et al. 1992).

Together with T.J. Morris of the Department of Plant Pathology, University of California, Berkeley, Vail conducted research on a calici-like virus (*Trichoplusia ni* RNA virus [TRV]) isolated as a contaminant of an Ac*M*NPV preparation (Morris et al. 1981; Vail et al. 1983a). Vail and Morris found several noncontaminated preparations and traced the lineage of contaminated preparations. Quality control procedures were developed that would preclude contamination (Vail et al. 1983b).

Vail and associates found that a granulosis virus of the IMM could be produced much more cheaply and could provide excellent and cost effective protection (up to 100%) of dried fruits and nuts from this insect through the normal life of these commodities in marketing channels. Damage could be reduced to the point where an infestation would be of no economic consequence (Cowan et al. 1986). Further studies showed the virus will provide control for the time these commodities will remain in the marketing channels. Further developments of the formulation and production have led to a 10-fold reduction in cost and made the virus economically competitive with both presently used fumigants and newly developed controlled-atmosphere methods of control (Vail et al. 1991). This research was important because it provided a control method to the dried fruit and nut industries in a "niche" (e.g., marketing channels) which did not previously exist.

Studies were conducted to further elucidate the role of digestive juices in the susceptibility of various insects to Ac*M*NPV (Elam et al. 1990). By extraction of the gut juices of species with low and high susceptibility and subjecting polyhedra to these fluids it was determined that the digestive fluids were not a barrier to infection. They also found that infectivity patterns were different when polyhedra were dissolved in sodium carbonate solutions or digestive fluids suggesting different modes of dissolution (Elam et al. 1990).

In the early 1980s, the laboratory was approached by R.E. Teakle of Australia concerning the export of the Ac*M*NPV for testing on Australian *Heliothis/Helicoverpa* species. However, the virus could not be exported because of the concern of Australian quarantine officials that the virus might infect *Cactoblastis cactorum*, an important biological control agent of pricklypear cactus. Therefore, *C. cactorum* was imported to the Fresno laboratory and, based on bioassays, histological and restriction endonuclease studies of the virus versus *C. cactorum*, it was concluded that the insect was moderately susceptible (Vail et al. 1984). These results showed that caution should be used when introducing a new pathogen into an area where biological control organisms of related target hosts may exist.

An Insect Affecting Man and Animals Laboratory was located in Fresno from 1968 to 1977. Investigations of this laboratory were primarily involved with the blood-sucking Diptera. T.B. Clark

was hired in 1973. His research emphasis was on finding and identifying pathogens of these insects. He was one of the first investigators to conduct research on the impact of *Beauveria bassiana* on a number of mosquito species (Clark et al. 1968). Clark and O'Grady (1975) described a non-occluded virus from *Culicoides cavaticus*. Mortality rates ranged from 70 to 90% in field-collected larvae. Virus-like particles were observed in the epidermal cells, in and on the surface of muscle bundles, in gut cells and in the tracheal epithelium. Although similar in signs and symptoms to pathogens of *Culex tarsalis* and *C. salinarius*, attempts to cross transmit the pathogen to these and several other species were unsuccessful.

Clark also conducted investigations on a Tetrahymenine ciliate isolated from *Aedes sierrensis* in Fresno County, California (Clark and Brandl 1976). Melanized black spots on the cuticle were found associated with sites of invasion or attempted invasion by this organism. Successful invasion of the ciliate into the host occurred within 20 hours after exposure. Interestingly, cysts on the integument were lost during the molt and cast off with the exuviae during molting. As of 1976, the taxonomic status of this ciliate remained in question. Clark transferred to Lake Charles, LA, in 1974 and eventually became a staff member at the ARS Insect Pathology Laboratory in Beltsville, MD, where he conducted research on honey bees.

BOYDEN ENTOMOLOGICAL LABORATORY, RIVERSIDE, CA. By Patrick V. Vail and David K. Reed

An insect pathology/microbial control program was begun in the early 1960s at the USDA-ARS Boyden Entomological Laboratory on campus at the University of California at Riverside. At that time two research entomologists began research on the classical cabbage looper, singly-embedded nuclear polyhedrosis virus which is known by the present nomenclature as Tn*S*NPV. The first ARS experiments with this virus were conducted by J.C. Elmore in the late 1950s while still at Whittier, CA. In 1961 he published a paper on the control of the cabbage looper with this NPV (Elmore 1961). His promising results led to further tests by him and A.F. Howland. Instead of spraying the virus on plants as in the previous studies, Elmore and Howland investigated the possibility of artificially contaminating moths and thus disseminating the NPV to their progeny (Elmore and Howland 1964). They found that a maximum of 51% of the progeny from moths sprayed with a virus suspension were diseased. However, in the same set of tests they found the application of the virus by spray onto the foliage was more effective than dissemination by the moths. This work conducted in the early 1960s was a precursor of a pathology program that was in existence at the Boyden Laboratory until 1969.

In 1962, P.V. Vail assumed an appointment at the Boyden Laboratory and one year later began conducting research on various entomopathogenic viruses infectious to vegetable insects. These studies were both basic and applied in nature with the eventual goal of being able to understand and utilize these pathogens as control agents for vegetable insects. In the early days of semi-artificial diet laboratory assays of entomogenous viruses, formalin was a commonly used component in the diets to preclude or prevent microbial contamination and growth. However, formalin also was known to be an antiviral agent and Vail showed that formaldehyde, even at very low concentrations in the diet, caused inactivation and reduction of apparent activity in bioassays (Vail et al. 1968).

In attempts to find out more about the epizootiology and transmission of nuclear polyhedrosis viruses as they were used in the studies conducted by Elmore and Howland (1964), Vail conducted intensive basic research on the influence of the cabbage looper *S*NPV on the postlarval stages of the cabbage looper with attention to transmission of the virus to progeny. He found that, for the most part, adults emerging from pupae that were infected as larvae transmitted very little virus to their progeny either on or in the egg (Vail and Hall 1969b and c; Vail and Gough 1970a). However, pupae and adults could be infected by inoculation into the hemocoel. Vail investigated transmission by moths emerging from inoculated pupae and by moths that had been inoculated as adults and found that the

levels of transmission also were quite low. All of the transmission that did occur was on the surface of the egg or by contamination by the meconium or feces from the adult moths. No significant transmission of the viruses occurred in the egg even though the reproductive tissues of both sexes were found to be infected. Interestingly, pigmentation of many moths emerging from inoculated pupae was reduced significantly. Intensive histological studies were conducted (Vail and Hall 1969a).

In 1967, Vail isolated a cytoplasmic polyhedrosis virus from the cabbage looper which was found to have manifold effects on larval development, pupal and adult size, and adult deformities. He studied this virus intensively to measure the effects on reproduction as related to the size of emerging infected adults. Because of reduced size due to infection, reproduction of adults was significantly reduced. Although transmission of this virus also occurred on the egg, transmission of the virus within the egg was not demonstrated (Vail et al. 1967, 1970; Vail and Gough 1970a and b).

While at the Boyden Laboratory, Vail also conducted numerous field tests with entomogenous viruses (Vail et al. 1971c). These tests showed that both the nuclear and cytoplasmic polyhedrosis viruses could reduce cabbage looper populations when applied alone or in combination. The degree of control compared favorably with that obtained with chemical insecticides.

In 1967, Vail isolated a multiply-embedded nuclear polyhedrosis virus from a single larva of the alfalfa looper and proceeded to conduct in-depth studies on this virus (Ac*M*NPV) in which virions were occluded multiply in the polyhedral matrix. At first it was found that both the classical Tn*S*NPV and Ac*M*NPV were reciprocally infective to both the alfalfa looper and the cabbage looper (Vail et al. 1971b). Later studies showed that Ac*M*NPV had a much broader host range than any previously described insect virus. Because of this, host-range studies were conducted on other species of Lepidoptera including the beet armyworm and *Heliothis/Helicoverpa* spp. (Vail et al. 1971a, b and c; Vail and Jay 1973).

Vail conducted intensive basic studies on Ac*M*NPV including the histopathology and relative infectivity and also conducted tests with this virus in the field. Because of its broad host range, this virus changed the classical views concerning the specificity of nuclear polyhedrosis viruses. This virus has been studied by many investigators using *in vitro* and *in vivo* techniques. It was the first NPV found to replicate extensively and completely in an insect cell line (Vail et al. 1973b). Infectivity of polyhedra following one passage was normal. The host range of this virus is now known to include many species in numerous families of insects including many economically important species to agriculture and forestry worldwide.

In 1969, the pathology program at the Boyden Laboratory was terminated upon the move of Vail to the Western Vegetable and Sugarbeet Investigations Laboratory, Mesa, AZ. Later, after moving to Phoenix, AZ, Vail completed further studies on Ac*M*NPV for control of cotton and vegetable insects (see above). Now this virus is also prominently used in the field of medicine and biology for the production of biologically active compounds such as vaccines, proteins needed for immunology and complex therapeutic compounds.

Although reports of mite viruses are not common in the literature, one such virus was intensively researched by scientists at the Boyden Laboratory. This non-occluded virus attacks the citrus red mite exclusively (Shaw et al. 1967; Beavers and Reed 1972), and has potential for use in mite management programs. Extensive basic and applied research was conducted on this virus of the citrus red mite over a period of about 14 years by a number of scientists, principally D.K. Reed. The etiological agent was first characterized by Smith et al. (1959) as a spherical particle, 35 nm in diameter, but later identified by Reed and Hall (1972) and Reed and Desjardins (1982), as rod-shaped, 58 × 194 nm, and enclosed in envelopes, 111 × 266 nm. Such rods form in the nuclei of

midgut epithelial cells and generally acquire an envelope, composed of single or multiple layers, as they pass through the nuclear membrane. The spherical particles reported by Smith et al. (1959) are present in healthy, as well as in diseased mites (Reed and Desjardins 1978), being composed of three sizes, 18 nm in crystalline array, and 30 and 37 nm particles. The virus is apparently transmitted from mite to mite by contact with viral particles within feces and debris on the plant surface deposited by infected mites (Reed et al. 1975). The "suction cup" feeding mechanism of these mites (Jeppson et al. 1975), along with the abundance of virus rods within the hindgut cells being continually sloughed into the gut lumen to be defecated, indicates a highly infectious fecal pellet. Envelopment of the virions in a matrix of cellular material may explain why natural infective material on contaminated surfaces lasts so much longer than aqueous sprays (Reed et al. 1975). Gilmore and Munger (1963) reported eight days while Tashiro et al. (1970) reported 28 days residual activity from contaminated surfaces of lemons. Aqueous sprays generally survive only 2–4 hours (Gilmore and Munger 1963), probably inactivated by ultraviolet radiation. Tashiro et al. (1970) reported viruses in intact mites retained viability >28 days in the laboratory and postulated that such intact dead bodies could adhere to plant surfaces as reservoirs. Shaw et al. (1972) found complete viability of virus in infected mite bodies after 6.5 years in storage at −5°C. Acaricide use in glasshouses had no effect on initiation of epizootics (Shaw and Pierce 1972). Shaw et al. (1969) obtained good control of mites in glasshouses where temperatures were moderate. Laboratory studies indicated that virus particles within mite bodies were unaffected by normal orchard temperatures (40.5°C), but activity was lost after 6 hours exposure at 46°C and 1 hour exposure at 60°C (Reed 1974).

The formation of birefringent crystals within diseased mites makes identification simple and rapid (Smith and Cressman 1962). Reed et al. (1972c) related these crystals to normal production of fecal pellets, showed that high humidity inhibited such production (Reed et al. 1974), and developed a portable apparatus to detect such crystals in the field (Reed et al. 1972a).

Collections of diseased mites for research in the field was facilitated by using vacuum-suction machines, saving 95–98% over the cost of laboratory rearing (Shaw et al. 1971), and increased infection of collected mites was expedited by holding them on green lemons (Reed et al. 1972b). Since aqueous applications are inadequate for control of mites in the field, Reed et al. (1973) tested spray additives and extenders and found that extracted body fluids from cabbage looper larvae and pupae extended activity for 144 hours in the laboratory, although field trials were inconclusive.

The citrus red mite virus occurs naturally in mite populations throughout the citrus-growing areas of California and Arizona and exerts considerable natural control of large populations of mites (Tashiro and Beavers 1966; Shaw et al. 1968b). Although there now exists no economical or practical method of applying the virus (Shaw et al., 1968a) at opportune times, many growers and crop advisors recommend delaying acaricide applications in high mite densities to allow epizootics to become established. Hopefully, more research will be done in the future on practical usage of a viable management tool that has been, for the most part, neglected.

MEDICAL AND VETERINARY ENTOMOLOGY RESEARCH LABORATORY, GAINESVILLE, FL. By Albert H. Undeen and Donald P. Jouvenaz

One of the major long term objectives of the Insects Affecting Man and Animals Research Laboratory (currently named the Medical and Veterinary Entomology Research Laboratory) at Gainesville, FL, was mosquito control. This was, in large part, a response to the needs of the military. During the mid-1960s D.L. Bailey reported on some microsporida of mosquitoes (Bailey et al. 1967a and b) but a directed effort towards microbial control of mosquitoes really began at Gainesville with the work of E.I. Hazard (1963–81). The main goal was then, and remains, to find pathogens of mosquitoes that would exert continuous suppression on mosquito populations, without frequent reapplication. Although Hazard studied a wide variety of pathogens, his most important

work was with the microsporida. Working with J. Weiser in Czechoslovakia, he made the landmark discovery that "*Thelohania*" in larval and "*Nosema*" in adult mosquitoes were portions of life cycle stages of one species (Hazard and Weiser 1968). His taxonomic work on this group is summarized in a USDA-ARS Technical Bulletin (Hazard and Oldacre 1975) that is still in use for the identification of this large group of microsporida. Hazard also published detailed descriptions of their peculiar meiosis (Hazard et al. 1979; Hazard and Brookbank 1984). In the early 1970s, he also studied microsporida such as *Nosema algerae*, at that time under consideration for control of malaria vectors. After his transfer to Lake Charles, LA (see below), he continued working on microsporidan life cycles, describing the development and fusion of gametes of *Amblyospora*. Finally, working with A.W. Sweeney of Australia, the discovery was made that a copepod intermediate host was an essential part of the life cycle (Sweeney et al. 1985). The description of a third kind of spore in the copepod and its infectivity for mosquito larvae finally completed the life cycle of one of the commonest forms of microsporida in mosquitoes and other biting flies.

R.E. Lowe (1966–72) examined the potential of *Conidiobolus (*as *Entomophthora*) *coronata* (Lowe et al. 1968; Lowe and Kennel 1972). With a series of graduate students, he examined the control potential of several mosquito viruses (Federici and Lowe 1972; Hall and Lowe 1971, 1972; Lowe et al. 1970; Matta and Lowe 1969, 1970). As a result of this research, the viruses, at least for the moment, have been removed from consideration for biological control of mosquitoes.

K.E. Savage (1966–77) started as a technician and earned his M.S. degree with a thesis on the bionomics of *N. algerae* in 1966. He contributed interesting findings on transmission of malaria (*Plasmodium gallinaceum*) by mosquitoes concurrently infected with *N. algerae* (Savage et al. 1971). D.W. Anthony (1969–1979) also completed his M.S. degree while employed at the Gainesville laboratory and went on to develop procedures for electron microscopy studies on mosquito pathogens. Later, Anthony led a group that developed production and application methods for the use of *N. algerae* against anopheline mosquitoes, culminating in a field trial in Panama (Anthony et al. 1978a and b).

S.W. White (Avery) has worked on *N. algerae* at the Gainesville location since 1975. Her contributions have been in all areas of pathology and biological control. A major contribution was the description of the early stages of *N. algerae* development in mosquito larvae by electron microscopy (Avery and Anthony 1983). Research on the biology and biological control potential of anopheline pathogens (Avery and Undeen 1987b, 1990) and methodologies for pathogen surveys (Avery and Undeen 1987a) have been her long-term responsibility. She also brought the laboratory into the computer age.

Anthony retired in 1979, to be replaced a year later by A.H. Undeen (1980–present). While continuing work begun in Newfoundland on the control of simuliid larvae in small streams with *Bacillus thuringiensis israelensis* (Bti) he initiated research on microsporidan spores, concentrating on how they accomplished their seemingly explosive germination. Findings were summarized in a paper on the biophysical-biochemical basis of the germination process (Undeen 1990). He has used this knowledge of spore germination in work with the grasshopper biological control agent, *Nosema locustae* (Undeen and Epsky 1990), and in an effort to improve the storage time of *Edhazardia aedis*, a promising pathogen for container-inhabiting mosquitoes.

L.A. Lacey (1981–86) and Undeen described the effects of formulation and treatment parameters on the efficacy of Bti against black flies under natural conditions (Lacey and Undeen 1984) and developed a simplified method for dosage calculation in small streams (Undeen et al. 1984). Lacey went on to develop methods of application, and test a variety of formulations of Bti and *B. sphaericus* in many mosquito and black fly larval habitats. These bacterial products were shown to be useful additions to the larvicide arsenal. In the laboratory, Lacey developed testing protocols, and

explored new formulation ideas. The safety of *Bacillus* pathogens to non-target organisms was also investigated (Undeen and Lacey 1982; Lacey and Mulla 1990) and particularly on *Toxorhynchites* mosquitoes (Lacey and Dame 1982; Lacey 1983; Lacey and Harper 1986). Especially sought after was a formulation or isolate that would persist in the larval site for prolonged periods. *Bacillus sphaericus* partially met these requirements (Lacey et al. 1987). He investigated the long-term effects of *B. sphaericus* on the physiology and behavior of surviving mosquitoes (Lacey et al. 1987). Lacey left Gainesville in 1986 for a position with the U.S. Agency for International Development (AID).

J.C. Lord (1987–90) succeeded Lacey in this line of work. He conducted intensive research on sustained release formulations of Bti and *B. sphaericus* and conducted a worldwide search for new and better isolates of the latter. His most important publications are in press (as of 1993).

In 1985, after the closure of the Lake Charles, LA, Gulf Coast Mosquito Research Laboratory, J.J. Becnel, Tok Fukuda, Roy McLaughlin, and O.R. Willis were reassigned to Gainesville. Becnel completed his Ph.D. research at the University of Florida with a dissertation detailing the life cycle and biology of the polymorphic microsporida, based on research begun at Lake Charles with Hazard. He described the life cycles of microsporida in mosquitoes including *Edhazardia aedis*, a microsporidan isolated from *Aedes aegypti* in Thailand (Becnel et al. 1989). He is now (1993) evaluating its potential for control of container-inhabiting mosquitos. Fukuda took over the electron microscope facility and, with O.R. Willis, conducts searches for new pathogens.

Over the years, graduate students have played an important role in the Gainesville research program. In the early 1970s, James Matta worked with viruses, as did Don Hall, now a professor at the University of Florida, and Brian Federici, presently a professor at the University of California, Riverside. Later, Steve Hembree, an Army entomologist, published numerous papers on viral pathogens of mosquitoes. John Kelley, John Knell, Frank Van Essen, and John Putnam all did their thesis work on microsporida of mosquitoes.

The imported fire ants, *Solenopsis richteri* and *S. invicta* were introduced into the U.S. from South America ca. 1920 and 1940, respectively. By 1991, these medical and agricultural pests infested over 10^8 hectares in 11 southeastern states and Puerto Rico (Lofgren 1986). Recently, isolated colonies were detected in Arizona and California. If they become established in the more humid or irrigated areas of the western U.S., their range will increase substantially. In addition, a polygynous form of *S. invicta* having denser populations is spreading within the population (Glancey et al. 1987). The ARS Imported Fire Ant project began in 1968. Its biological control component began in 1974. Conceptually, the primary goal was the permanent amelioration of the imported fire ant problem through the establishment of a complex of host-specific natural enemies. A secondary goal was the development of a microbial insecticide(s).

As a Postdoctoral Fellow (1970–71) B.A. Federici, and later D.P. Jouvenaz of the Medical and Veterinary Entomology Research Laboratory and his colleagues, examined *S. invicta* from Florida and demonstrated that they were essentially free of host-specific natural enemies. In their native South American range, they are beset by pathogens, parasites, social parasites, and symbiotic predators.

The first specific pathogen of fire ants was observed by W.F. Buren, a medical entomologist and myrmecologist, who retired from the U.S. Public Health Service in order to pursue fire ant systematics at the Medical and Veterinary Entomology Research Laboratory under a grant from ARS. In 1973, Buren noticed cyst-like bodies in the gasters of alcohol-preserved workers from Brazil which were identified by E.I. Hazard as membrane-bound masses of microsporidan spores. With Hazard's guidance, J.D. Knell, a University of Florida Postdoctoral Fellow under G.E. Allen,

described the pathogen from fresh material, naming it *Thelohania solenopsae* (Knell et al. 1977). This pathogen proved to be ubiquitous in fire ants in South America.

The discovery of a pathogen of fire ants stimulated interest in biological control research. In the summer of 1974, the first of a series of trips to Brazil was made to search for natural enemies of fire ants. The team members were Hazard, Jouvenaz, W.A. Banks, and D.P. Wojcik. M.A. Naves, a Brazilian doctoral student at the University of Florida, accompanied the team as guide and interpreter. On this and four subsequent trips, research was headquartered at the Universidade Federale de Mato Grosso, Caceres, under an agreement with the University of Florida, negotiated by G.E. Allen.

Because of his interest and background in microbiology, pathology research was assigned to Jouvenaz; the arthropod symbionts became the province of Wojcik. Reasoning that the imported fire ants had escaped their specific natural enemies, Jouvenaz studied *S. geminata*, a fire ant known to be of Caribbean origin introduced into Florida long ago, as a model. Survey procedures for disease were developed and employed in an intensive survey in six states which confirmed the absence of disease in imported fire ants (Jouvenaz et al. 1977). The only microorganism found to be symbiotic with imported fire ants was a yeast-like fungus which was apparently only a nutritional burden (Jouvenaz and Kimbrough 1992).

In contrast to the imported species, *S. geminata* hosts several species of parasitic protozoa (Jouvenaz 1984), a rare mermithid nematode (Mitchell and Jouvenaz 1985), and a virus (Jouvenaz, unpublished). The microsporidan *Burenella dimorpha* Jouvenaz and Hazard (1978) was studied intensively as a model for basic pathobiology and development of techniques and became the subject of Jouvenaz's doctoral dissertation (1982). A review of this and other pathogens of fire ants may be found in Jouvenaz (1986).

During the early pathogen surveys in Brazil, the first virus known from fire ants (the second known ant virus) (Avery et al. 1977) and an undescribed protozoan were collected by Banks and Jouvenaz. Additional data on ant populations and incidence of disease in them were collected (Jouvenaz et al. 1980; Banks et al. 1985). From material collected abroad, Jouvenaz and Ellis (1986) described *Vairimorpha invictae* and its effects on the host.

More recent searches in Brazil provided a nematode, *Tetradonema solenopsis* (Nickle and Jouvenaz 1987). This parasite is able to invade adult queens and has the potential for eliminating established colonies. Taxonomic work has indicated that it is probably host-specific and, therefore, environmentally safe. Attempts to propagate a parasitized colony at the Medical and Veterinary Entomology Research Laboratory and at Caceres failed, due to rapid death of parasitized ants when subjected to stress. Valuable information on the arthropod symbionts of fire ants, such as their use of chemical mimicry to integrate into ant colonies (Vander Meer et al. 1989), was also gained. The observation of two non-pathogenic neogregarines (one of which appears identical to *Mattesia geminata* [Jouvenaz and Anthony 1979]) was of academic interest only. Attempts to study fire ant epizootiology and population dynamics in Brazil were frustrated by the extreme and prolonged dry season. On one occasion, however, fire ants had virtually disappeared from an area in which there was a very high population density with a high incidence of disease a few months earlier (Jouvenaz 1990b).

Under a new agreement with the Biological Control of Weeds Laboratory, USDA-ARS, in Argentina, Wojcik and Jouvenaz visited Argentina in October, 1987, to survey for natural enemies of fire ants. J.A. Briano joined the fire ant project and was trained at the Medical and Veterinary Entomology Research Laboratory; he subsequently completed course requirements for a M.S. degree at the University of Florida in 1991. In April 1988, Briano and Jouvenaz located acres in Argentina suitable

for monitoring disease and ant population dynamics. Under the direction of R.S. Patterson, who succeeded C. Lofgren as Research Leader upon the latter's retirement, Briano began monitoring the impact of naturally occurring *Thelohania solenopsae* and *Vairimorpha invictae* on field populations of fire ants.

Also during this period, two trips were made by Wojcik to collect fire ants for taxonomic study, zoogeographical records, and pathogen screening. In 1987, Wojcik and A. de Campos collected extensively in Brazil and in 1990, Wojcik, Patterson, and Briano sampled from a wide area including parts of Argentina and Uruguay. More than 1,000 samples were collected providing needed information on the distribution of *Tetradonema solenopsis* and other parasites. This work revealed that many pathogens known from Brazil were also found in Argentina, although the nematode *T. solenopsis* appeared to be absent. A new but rare mermithid nematode of dubious biological control value was found; efforts to propagate it failed (Jouvenaz and Wojcik 1990). The obligate endoparasitic fungus, *Myrmecomyces annellisaes*, not seen in Brazil, was found in Argentina. Arthropod symbionts — possible intercolonial vectors of disease — were abundant.

Susceptibility of fire ants to a wide variety of general entomopathogens, pathogens of other Hymenoptera, and even other orders was tested. Jouvenaz eventually demonstrated that typical entomopathogenic bacteria are not ingested, but are removed from food by pharyngeal filtration (Jouvenaz 1990a, 1991). Tests with commercially-produced steinernematid nematodes (biosys®, Inc., Palo Alto, CA) demonstrated that previous encouraging reports of control were a result of unrecognized nest relocation (Jouvenaz et al. 1990). Jouvenaz retired in 1991. Briano continued research on various aspects of fire ant biology and biological control in South America under the direction of Patterson.

SUBTROPICAL INSECTS RESEARCH LABORATORY, ORLANDO, FL. By William J. Schroeder and Clayton W. McCoy

An insect pathology program was initiated at the Subtropical Insects Research Laboratory, Orlando, FL, in 1966 with the hiring of C.W. McCoy. He was to conduct investigations on the microbial control of the citrus rust mite infesting Florida citrus. McCoy substantiated infection of the mite by the fungus *Hirsutella thompsonii* in the field, and also by infection of laboratory-reared mites with laboratory-produced spore material. McCoy and Kanavel (1969) then conducted research to determine the optimal solid media for culture of *H. thompsonii*. On several of the more productive media, maximum production (rates not absolute values) of conidia was obtained 12 days after inoculation. Growth was demonstrated to be dependent upon a number of nutritional factors in the complex media. McCoy et al. (1971) also showed that citrus rust mite could be suppressed with applications of fragmented mycelium. Therefore a liquid medium for the large-scale production of *H. thompsonii* in submerged culture was developed (McCoy et al. 1972). Aeration was essential for growth and sporulation did not occur in submerged culture. Later, mycelia obtained from submerged culture were formulated for applications in the field (McCoy et al. 1975). A review of the development of this fungus as a miticide was provided by McCoy and Selhime (1973). Later the fungus was produced commercially and registered by Abbott Laboratories. The product (Mycar®) was sold commercially until 1983; at this time it is not used commercially.

Research on entomopathogenic nematodes began in 1980 when entomologists at the Laboratory conducted a survey of soil insect pathogens of the citrus root weevil complex (comprised of Fuller rose beetle, the "little leaf notcher" [*Artipus floridanus*], the citrus root weevils [*Pachnaeus opalus* and *P. litus*], and the "sugarcane rootstock borer weevil" [*Diaprepes abbreviatus*]) and isolated heterorhabditid and steinernematid nematodes (Beavers et al. 1983). Early research was conducted with biosys® and H.K. Kaya of the University of California, Davis. It was not until 1987 that publications (Schroeder 1987, 1990) were generated on the potential use of this biopesticide for

management of the citrus root weevil complex. In general, when weevil larvae were exposed to nematodes in the laboratory and in greenhouse tests the infection rate was 60%. By 1988, it was possible to produce enough nematodes to attempt a pilot program for weevil management. The Orlando laboratory received $30,000 per year for three years to provide for production and application of nematodes on a 10-acre block of citrus. A cone ground trap was used to evaluate adult emergence (Schroeder 1990). With this efficacy data, entomopathogenic nematodes were added to the 1991 Florida Spray Guide (Schroeder 1992). In 1991, 10,000 acres of citrus groves and nurseries were treated. The acreage increased to 20,000 in 1992 and 30,000 by 1993.

INSECT BIOLOGY AND POPULATION MANAGEMENT RESEARCH LABORATORY, TIFTON, GA. By John J. Hamm

The Southern Grain Insects Research Laboratory was established in Tifton, GA, in 1960. In 1984, the name of the laboratory was changed to the Insect Biology and Population Management Research Laboratory. The mission of the laboratory was to develop control methods for corn earworm and fall armyworm, the primary pests of grain in the Southeast. The position of Insect Pathologist was originally held by Paul Surany who set up the insect pathology laboratory at Tifton but soon left to go to the Forest Service.

J.J. Hamm joined the staff at the end of 1962 to work on insect pathology and microbial control. This was a time when much research was being done on establishment and maintenance of insect colonies for potential use in mass production and release of sterile insects or for production of parasitoids. Part of the mission of the insect pathologist was to help maintain disease-free insects for mass production and research.

Hamm (1968) compared a nuclear polyhedrosis virus (NPV) of fall armyworm to a granulosis virus (GV) of fall armyworm from South America, and determined that the NPV had more potential for biological control because of the faster kill. Young and Hamm (1966) combined corn earworm NPV and fall armyworm NPV to protect sweet corn from both insects. Hamm and Young (1971) demonstrated the importance of an early-tassel treatment with corn earworm and fall armyworm NPVs for protection of sweet corn. Hamm and Young (1974) demonstrated that corn earworm moths fed NPV could transmit the virus to their progeny by surface contamination of the eggs.

Hamm (1982a) determined that the *Helicoverpa armigera M*NPV from the U.S.S.R. infected corn earworm, tobacco budworm, beet armyworm, and fall armyworm, but was about 200 times less virulent for fall armyworm than for corn earworm. Hamm (1982b) also discovered that the granulosis virus of *H. armigera* from South Africa was not restricted to the *Heliothis/Helicoverpa* complex, but would infect fall armyworm, beet armyworm, and cabbage looper in addition to corn earworm. However, this virus was not recommended for microbial control because of its slow kill and ability to interfere with faster acting NPVs.

Early tests on application of entomopathogens in irrigation water were conducted by Hamm and Hare (1982) using a set sprinkler system. A fungus, *Nomuraea rileyi*, two species of microsporida, *Vairimorpha heterosporum* and *Vairimorpha* sp., and the fall armyworm NPV were applied to whorl stage corn for control of the fall armyworm. Elcar®, a commercial preparation of *"Heliothis S*NPV", was applied to silking corn for control of the corn earworm. All pathogens tested were infective when applied through the irrigation system. The fall armyworm NPV produced higher rates of larval mortality of fall armyworm and reduced the number of parasitoids emerging from collected larvae more than the *Vairimorpha* sp. and *V. hetersporum*, which generally did not kill fall armyworms until they were full grown larvae or pupae. In late-season tests, when there were continuous natural infestations of fall armyworm, two applications of NPV were sufficient to initiate epizootics. The viral epizootic extended to fall armyworm larvae collected from corn silks, even though no

applications had been made directly to the silks. Corn earworm larvae collected from Elcar-treated plots had significantly higher rates of mortality due to NPV than larvae from control plots and there was a significant reduction in damage to corn ears in the Elcar-treated plots. Hamm and Young (1985) applied fall armyworm NPV and Elcar to corn through a cable-tow irrigation system and through a center pivot irrigation system for control of fall armyworm and corn earworm. In the cable-tow experiment on seedling corn, the percent mortality due to NPV in fall armyworm collected after the first and second applications was quite low, but it increased considerably after the third application. There was very little difference in effectiveness of the oil and water formulations of the virus. Also, there was little difference in percent mortality of corn earworm larvae treated with Elcar or an oil formulation of the *"Heliothis S*NPV". The mean damage index was significantly higher in the control than in the treated plots with no significant difference between the Elcar treatment and the oil formulation of NPV. The center-pivot test with Elcar on silking stage corn showed rather low mortality (25.3%) due to NPV nine days after initial application but a substantial increase in larval mortality (36.7 to 63.3%) on days 11 and 16 as the virus spread through the corn earworm population.

Hamm et al. (1986b) demonstrated that corn hybrids can affect the effectiveness of NPV for control of corn earworm. Elcar produced a greater reduction in number of corn earworm larvae on a corn hybrid with a tight husk extension than on a hybrid with a loose husk.

Three different ascoviruses were found infecting field collected fall armyworm, corn earworm, and tobacco budworm larvae (Hamm et al. 1986a). These viruses were easily transmitted by injection or by parasitoids stinging infected and then noninfected larvae, but were only mildly infective *per os*. The virus interfered with development of parasitoid larvae in infected hosts without any sign of infecting the parasitoid (Hamm et al. 1985). Because ascovirus-infected larvae remain small for a long time, they are attractive to parasitoids for a prolonged period and can result in the loss of numerous parasitoid eggs. Therefore, ascoviruses should not be recommended for microbial control of noctuid pests.

Hamm et al. (1988) reported the first baculovirus pathogenic to a parasitoid, *Microplitis croceipes*. This virus is associated with reduced rates of parasitism, failure of wasps to emerge from cocoons, and early mortality of adults that do emerge. This demonstrates the importance of checking parasitoid colonies for pathogens when importing them and when producing them for release or for research.

NATIONAL CENTER FOR AGRICULTURAL UTILIZATION RESEARCH, PEORIA, IL. By Michael R. McGuire

In 1940, the U.S. Congress provided for the establishment of four Centers located around the country to initiate research related to utilization of farm products. Since its inception, the National Center for Agricultural Utilization Research (NCAUR, formerly the Northern Regional Research Laboratory), located in Peoria, IL, has had a rich history in studying fermentation of various fungi and bacteria, including insect-pathogenic bacteria. Most of the early work with insect pathogens dealt with *Bacillus popilliae*, the causal agent of milky disease in the Japanese beetle. Some research was also done on biochemical aspects of *Bacillus thuringiensis* production but, more recently, work with encapsulation of *B. thuringiensis* in cornstarch has been the primary focus of the insect pathology work at the Center.

Milky disease. Following Dutky's pioneering work on the description of *B. popilliae* (see section below on Insect Pathology Laboratory, Beltsville, MD), there was much interest in developing means to mass produce the bacterial spores under liquid fermentation conditions. Commercial methods used to produce *B. popilliae* involved the inoculation of spores into live grubs and then holding the grubs until death. The larvae were then dried and milled and the bacteria quantified and formulated.

Clearly, these methods were laborious, time consuming, costly, and not capable of producing enough spores to provide for wide-scale biological control of the beetle (Rhodes 1965). In 1961, scientists at the laboratory developed a research project whose goal was to develop a fermentation system for the production of *B. popilliae* spores. Though spores had been produced on solid media before, production was very low and unacceptable. Similarly, early work revealed that *B. popilliae* vegetative cells could be grown in high numbers easily in fermentation but spore production was not possible. Initial work was aimed at the physiology of the insect. Did biochemical changes take place during the infection process and were these changes related to sporulation? Furthermore could this knowledge be used in creating an artificial medium suitable for growth and sporulation (e.g., Shotwell et al. 1963)? An exhaustive series of studies on chemical changes occurring in the hemolymph of infected grubs revealed an overall reduction of lipids, proteins, and carbohydrates, a phenomenon observed for other insect-pathogen relationships. However, large populations of vegetative cells that sporulated were never observed in larvae, suggesting that non-nutritional factors were operating to regulate the sporulation process (Bennett and Shotwell 1973). In 1965, Rhodes et al. reported enhanced sporulation of *B. popilliae* on solid media. Although only 0.1–0.3% of the viable cells sporulated, this represented a considerable improvement over existing methods. Then in 1966, Haynes and Rhodes reported the first production of *B. popilliae* spores in liquid medium. Although only approximately 2 million spores/ml (vs. 10 billion spores/ml hemolymph *in vivo*) were obtained, interest was high and the future looked promising. While conditions suitable for production of very large amounts of asporogenic cells were improved, the right combination of media ingredients necessary for increased spore production was never developed. The research conducted over the 15 years of the project resulted in the publication of more than 70 papers. Much basic information was obtained concerning infection processes, growth and sporulation *in vivo*, and physiological changes experienced by infected insects. Ultimately, however, the problem was not solved, and, despite numerous attempts by other research programs, *B. popilliae in vitro* spore production remains an enigma to insect pathologists and microbiologists.

Bacillus thuringiensis. As a spin-off of the work with *B. popilliae*, research was also initiated on various aspects of *B. thuringiensis* (Bt) production and host range. Biochemical aspects of Bt fermentation, sporulation, and outgrowth (e.g., Nickerson et al. 1975) were studied and some interesting work was done on the susceptibility of Japanese beetle to Bt. Sharpe (1976) reported the first instance of a beetle susceptible to Bt, but follow-up research suggested that larvae may be susceptible only during certain periods of their life cycle and that susceptibility was closely correlated to mid-gut pH and presence of food in the alimentary tract (Sharpe and Detroy 1979).

Formulation of bacteria in cornstarch. More recently, research aimed at extending the residual activity of entomopathogens (most notably *B. thuringiensis*) after application has resulted in the use of cornstarch as an encapsulating medium. Previous research indicated that *B. thuringiensis* remained viable for only a few hours if exposed to direct sunlight. Dunkle and Shasha (1988) developed a granular formulation that upon addition of suitable additives such as sunscreens or UV protectants (Dunkle and Shasha 1989) or feeding stimulants (Bartelt et al. 1990) could extend and enhance the activity of *B. thuringiensis* under field conditions (McGuire et al. 1990). Although granular formulations are suitable for some applications, sprayable formulations probably are used more frequently. McGuire and Shasha (1990) reported the development of a tank-mix formulation that upon spraying onto foliage would form a film that entrapped active ingredients (namely *B. thuringiensis* and associated sunscreens or feeding stimulants). As before, the formulation is composed of starch, but sugar is also added to enhance dispersing in the tank and subsequent adherence of the film to the leaf surface. Research is continuing on the formulation of insect pathogens at NCAUR and has been expanded to include viruses and fungi.

CORN INSECTS RESEARCH UNIT, ANKENY, IA. By Leslie C. Lewis

Nosema pyrausta, originally described as *Perezia pyraustae* from the European corn borer (ECB) in France, was first collected in the U.S. (Iowa and Ohio) by USDA-ARS entomologists W.G. Bradley and K.D. Arbuthnot (Steinhaus 1952). Researchers in ARS defined the role of this microsporidan as an important population regulator of ECB. It reduces the fecundity of adults (Zimmack and Brindley 1957; Lewis et al. 1971; Sajap and Lewis 1988a) and kills larvae when applied to infested corn plants (Lewis and Lynch 1978; Lublinkhof et al. 1979; Lewis 1982). Also, *Nosema pyrausta* is compatible with many other pest insect population suppressants: parasitoids — *Macrocentrus grandii* (Cossentine and Lewis 1987), *Lydella thompsoni* (Cossentine and Lewis 1988), *Trichogramma nubilale* (Sajap and Lewis 1988b); predators — common green lacewing (Sajap and Lewis 1989); and host plant resistance (Lewis and Lynch 1976; Lynch and Lewis 1976). In these relationships, *N. pyrausta* occasionally slightly reduces emergence, longevity, and fecundity of the beneficial insects but they easily coexist in the same ecosystem.

Some of the early work to utilize *Beauveria bassiana* to control ECB was conducted by George York at the former European Corn Borer Laboratory. He produced *B. bassiana* on wheat bran and ground the substrate containing the *B. bassiana* making a crude formulation that was applied to corn. He obtained upwards of 90% reduction of ECB larvae in small experimental plots (York 1958). Little additional work was conducted with *B. bassiana* and ECB until the late 1980s. Work at the Corn Insects Research Unit defined an endophytic relationship between the corn plant and *B. bassiana*. *Beauveria bassiana* colonizes the plant, moves within the plant, and provides control of ECB (Bing 1990; Lewis and Bing 1991; Bing and Lewis 1991). The mechanism of entry into the plant and movement within the plant is not known.

Research on *Bacillus thuringiensis* (Bt) has been emphasized at the European Corn Borer Laboratory/Corn Insects Laboratory/Research Unit since the early 1960s. Many ARS entomologists researched ways of formulating Bt to increase efficacy. Raun (1963) and Raun and Jackson (1966) successfully controlled ECB larvae with granular formulations of Bt. Later, Lynch et al. (1977a and b, 1980) reduced performance variability of Bt by standardizing commercial products on an international unit basis, by varying the amount of Bt per unit volume of carrier and by using foam and more uniform formulations. This work was the impetus for commercialization of Bt for ECB management. Presently *B. thuringiensis* formulated products are used widely by hybrid seed producers and some commercial growers.

Research was ongoing on basic aspects of *B. thuringiensis* and ECB while the developmental and application research was being pursued. Sutter and Raun (1966, 1967) described the histopathology of *B. thuringiensis* in ECB. They were the first to show that crystals damage the midgut epithelial cells allowing the gut contents to enter the hemocoel and cause a septicemia and death. Mohd-Salleh and Lewis (1982) demonstrated that neonate ECB larvae could be killed by crystals alone; however, older larvae had to be exposed to spores and crystals to maximize mortality. Lewis was a member of the international research group assembled by Howard Dulmage to investigate the spectrum of activity of *B. thuringiensis* (Dulmage 1981). This complete work is in its final stages of preparation and will eventually be published with Dulmage, Burges, and Lewis as editors.

The ECB is one of the very few economically important insect pests from which no virus has been isolated. Nuclear polyhedrosis viruses from alfalfa looper (Lewis et al. 1977) and *Rachiplusia ou* (Lewis and Johnson 1982) are, however, virulent against this insect. Field efficacy has been demonstrated but, with the commercialization of *B. thuringiensis*, there has been little effort to develop a virus formulation for ECB management.

U.S. GRAIN MARKETING RESEARCH LABORATORY, MANHATTAN, KS. By William H. McGaughey

Insect pathology research was initiated at the U.S. Grain Marketing Research Laboratory (USGMRL) in Manhattan, KS, in 1972 by W.H. McGaughey. This work was expanded in 1973 when L.A. Bulla, Jr., transferred to Manhattan. D.E. Johnson transferred to Manhattan in 1981, following the resignation of Bulla.

McGaughey's studies initially focused on evaluation of the feasibility of controlling moth infestations in stored grain using either the Indianmeal moth granulosis virus or *Bacillus thuringiensis* (Bt) (McGaughey 1975b, 1976, 1978b, 1980, 1982; Nwanze et al. 1975). Both agents were found to be compatible with other stored grain treatments and were stable enough in the stored grain environment to provide long-term moth control (McGaughey 1975a, 1983; Kinsinger and McGaughey 1976). A surface-layer treatment method was developed that concentrated the dosage at the surface layer of the grain where the moth infestations occur (McGaughey 1978b, 1980; McGaughey and Dicke 1980). This approach greatly reduced the amount of material required for treating bulk grain and made the approach much more attractive economically. From the mid-1970s onward, McGaughey's research concentrated on Bt, which was a much more promising candidate for EPA registration. Extensive data were obtained on host spectrum and susceptibility, histopathological effects, environmental stability, compatibility with other treatments, fate of residues in milled grain products, and efficacy in different commodities (McGaughey et al. 1975, 1980; Kinsinger and McGaughey 1976, 1979a and b; McGaughey 1978a and c, 1982; McGaughey and Kinsinger 1978; Johnson and McGaughey 1984). Studies were also done on the susceptibility of stored-grain moths to various strains of Bt (Kinsinger and McGaughey 1978; Kinsinger et al. 1980). This work culminated in the registration of Bt for moth control in stored grain in 1979. This was the first registration of a microbial product for use on stored grain. (See McGaughey 1986b for a review of research on use of *B. thuringiensis* as a grain protectant.)

Subsequently, McGaughey undertook large-scale field studies to evaluate various formulations and methods for applying Bt to bulk stored grain and to acquire data on the performance of the treatment under field conditions (McGaughey 1985b, 1986a). It was during the course of these studies that McGaughey discovered the potential for insect resistance to Bt δ-endotoxins (McGaughey 1985a; McGaughey and Beeman 1988). Subsequent studies involved efforts to characterize and elucidate the biochemical mechanisms of insect resistance to Bt and provided the first documentation of the role of midgut receptor binding in the mechanism of resistance (McGaughey and Johnson 1987; Han et al. 1988; Johnson et al. 1990, 1991; Van Rie et al. 1990; Aronson et al. 1991). (See McGaughey 1990 for a review of research on resistance.)

The research on insect resistance has had far reaching effects on the course of research on Bt. It has provided a fruitful avenue for significantly expanding the understanding of the modes of action and specificity of Bt toxins. It has also raised questions regarding the long-term usefulness of Bt genes in producing insect-resistant transgenic plants. As a result, there has been a large increase in research on insect resistance to Bt in government, academia, and industry. This effort has led to the discovery of laboratory and field resistance in several important pest insects, including Colorado potato beetle, tobacco budworm, and diamondback moth, and has focused the attention of regulatory agencies and industry on the need to develop strategies for preventing resistance in order to preserve the usefulness of this valuable biological insecticide.

Bulla's research on Bt strains when he was with ARS at the Northern Regional Research Laboratory (NRRL), Peoria, and at the USGMRL during the 1970s and early 1980s addressed a broad range of topics including nutritional requirements, metabolism, cytology of growth, sporulation and germination, and the biochemistry, molecular biology, and function of parasporal inclusion bodies

(Bulla et al. 1980). One of the first chemically defined synthetic media that allowed growth, sporulation, and parasporal crystal formation was developed by Nickerson and Bulla (1974). Various aspects of the intermediary metabolism of amino acids, polypeptides, carbohydrates, and lipids were described by Bulla's group (Bulla et al. 1970a and b, 1971a and b; St. Julian and Bulla 1971; Bulla and St. Julian 1972a and b; Nickerson et al. 1974). An ultrastructural analysis determined that the life cycle of Bt is characterized by three distinct major processes: vegetative cell division, spore development, and crystal formation (St. Julian et al. 1971; Afrikian et al. 1973; Bechtel and Bulla 1976, 1982). More recent studies have focused on the isolation, activation and physical, chemical, and insecticidal properties of the parasporal inclusion body or δ-endotoxin (Sharpe et al. 1975; Bulla et al. 1976, 1977, 1979, 1981; Schesser et al. 1977; Schesser and Bulla 1978, 1979; Tyrell et al. 1979, 1981a and b; Andrews et al. 1980). The mobilities of fatty acids in the plasma membrane during growth and sporulation were assessed *in vivo* using nuclear magnetic resonance (Bechtel et al. 1985). The subcellular origin and physiological function of the parasporal crystal and spore coat proteins, as well as the gene for the lepidopteran protoxin were also studied (Stahly et al. 1978; Aronson et al. 1982; Held et al. 1982). Rocket immunoelectrophoretic and enzyme-linked immunoadsorbant assays were developed for detecting and quantifying parasporal inclusion body proteins from subspecies *kurstaki* and/or *israelensis* (Andrews et al. 1980; Wie et al. 1982).

Johnson conducted research on Bt at the NRRL at Peoria beginning in 1972 and at the USGMRL after 1981. This research included many biochemical studies involving the bacterium and its crystal proteins, more recent studies concerning insect resistance to Bt, and a series of studies on the use of insect cell culture as a model system for investigating Bt insect toxicity. Certain insect cell lines respond to crystal protein from Bt, resulting in cell lysis. The response is specific and parallels insect larval mortality patterns from various subspecies of Bt. Several studies established the developmental patterns of insect culture response to Bt crystal protein (Johnson et al. 1980; Johnson 1981, 1987a; Johnson and Davidson 1984), and included development of a variant cell line that was resistant to crystal protein from Bt subspecies *kurstaki* (Johnson 1984). The system was used to measure the toxicity of wheat purothionins by Johnson and collaborators in 1984 (Jones et al. 1985). Several review articles summarized the work to date (Johnson 1987b, 1989). Some research still continues with insect cells involving their responses to specific cloned Bt toxin gene proteins.

GULF COAST MOSQUITO RESEARCH LABORATORY, LAKE CHARLES, LA. By Tokou Fukuda

In 1964, the ARS Entomology Research Division established a mosquito research laboratory in Lake Charles, LA, as a satellite laboratory to the Insects Affecting Man and Animals Research Laboratory of Gainesville, FL (now the Medical and Veterinary Entomology Research Laboratory). The purpose of the Lake Charles laboratory was to study the biology and ecology of the mosquitoes of the Gulf Coast area, especially Louisiana, in an effort to provide more effective means of mosquito control. Lake Charles was chosen because the Police Jury (County Commissioners) of Calcasieu Parish, LA, agreed to provide facilities with no charge. The original laboratory was located on the McNeese State College campus in a building shared with the mosquito research unit of the Louisiana Mosquito Control Association. D.B. Woodard was the first to arrive in the spring of 1964. H.C. Chapman arrived in October to recruit locally R.V. Cloud, F.E. Glenn, Jr., M.J. Gore, J.C. Hicks, and O.R. Willis to complete the original staff. A landmark year for the Lake Charles laboratory was 1967, when the laboratory became independent and assumed the name, Gulf Coast Mosquito Research Laboratory (GCMRL) with Chapman as the Investigations Leader. In 1970, the laboratory moved from McNeese State College campus to Chennault Air Force Base, where it remained until it was closed.

The earliest research of Chapman and Woodard dealt with the biology of Louisiana mosquitoes, specifically the blood feeding and oviposition habits of local mosquitoes (Chapman and Woodard

1965). During this time the availability of large numbers of mosquitoes provided Chapman with the opportunity to begin parasite and pathogen investigations. He was introduced to this subject when assigned from 1961 to 1964 to the University of California Mosquito Research Laboratory in Fresno, California, where much of the pioneering work on mosquito parasites and pathogens was carried out by W.R. Kellen and T.B. Clark, and J.E. Lindegren. Beginning in 1965, a large number of papers were published on fungal infections by *Coelomomyces* in Louisiana mosquitoes (Chapman and Woodard 1966), additional hosts of mosquito iridescent viruses (Chapman et al. 1966), a microsporidan in a Louisiana mosquito (Chapman and Kellen 1967), and nematode parasites in Louisiana Culicidae and Chaoboridae (Chapman et al. 1967); other papers on parasites and pathogens were published by Chapman and the staff of the GCMRL. Along with the ability to detect pathogens, Chapman possessed the unique ability to colonize mosquitoes; through his efforts colonies of 17 species were maintained at the GCMRL (Chapman and Barr 1969; Chapman 1970). In addition to conducting his administrative duties as Location and Research Leader, Chapman authored over 40 publications during this period. After his retirement in 1981, Chapman was appointed as a non-paid USDA-ARS Consultant/Collaborator to the GCMRL.

The first of several international projects that would involve GCMRL began in 1967. Chapman was asked by the United Nation's World Health Organization (WHO) to survey mosquito problems on Nauru Island in the South Pacific. During his survey he found several parasites and pathogens (Chapman 1967a), and reported on the mosquitoes found on the island and recommendations for their control (Chapman 1967b).

Woodard conducted research on various aspects of mosquito biology, parasites and pathogens. Some of Woodard's research on biology of mosquitoes include blood volumes ingested (Woodard and Chapman 1965) and egg hatchability of floodwater mosquitoes (Woodard et al. 1968; Woodard and Chapman 1970). His research began in 1968 with laboratory studies of the mosquito iridescent virus (Woodard and Chapman 1968) and extended to nematode studies where he demonstrated development of resistance of mosquitoes to nematodes (Woodard and Fukuda 1977). He also established a mermithid nematode in a field population of anopheline mosquitoes (Woodard 1978). Woodard left the GCMRL in 1976 to take a position as an entomologist with the ARS Screwworm Research Laboratory in Tuxtla Gutierrez, Mexico.

J.J. Petersen joined the staff of the GCMRL in 1966 after completing his Ph.D. at the University of Utah. Although he was recruited to study mosquito biology, his most important contribution was to the development of mermithid nematodes for mosquito control. Assisted by O.R. Willis, he compiled a list of potential hosts for mermithids (Petersen et al. 1969). He also developed mass rearing methods for the mermithid nematode *Romanomermis culicivorax* (as *Reesimermis nielseni*) (Petersen and Willis 1972a). The ability to mass rear the nematode made possible preliminary field tests in California and Louisiana (Petersen and Willis 1972b; Petersen et al. 1972). WHO also sponsored a field release of the nematode against the southern house mosquito (as *Culex pipiens fatigans)* in Bangkok, Thailand (Chapman et al. 1972). A large field test of a 40-hectare lake in El Salvador involving numerous applications of the nematode over seven weeks resulted in near eradication of the anopheline malarial vector (Petersen et al. 1978a and b; Willis et al. 1980). Petersen completed an extensive study of oviposition responses of Louisiana mosquitoes (Petersen 1969; Petersen and Chapman 1970; Petersen and Willis 1970, 1971). He continued to work with mermithid nematodes and had over 50 publications by 1978, when he transferred to the Livestock Insects Research Laboratory in Lincoln, NE.

T.B. Clark and Tokuo Fukuda were added to the staff of the GCMRL in 1967 and continued the parasite and pathogen work that Clark had started in California at the University of California Mosquito Research Laboratory at Fresno. During his short time at the GCMRL, Clark's contributions were his entomopathogenic virus research with Louisiana mosquitoes (Clark and Chapman 1969;

Clark and Fukuda 1971a) and the description of a new microsporidan in a Louisiana mosquito (Clark and Fukuda 1971b). Clark returned to California in 1970 to accept a faculty position at Fresno State University. He rejoined the USDA when the Western Insects Affecting Man and Animals Research Laboratory was relocated to Fresno. Clark's untimely death occurred in 1984 while on a field trip to Mexico for the Insect Pathology Laboratory of the Plant Protection Institute in Beltsville, MD (see section below).

After the departure of Clark, Fukuda continued viral transmission and pathogenicity studies on mosquitoes (Fukuda 1971; Fukuda and Chapman 1973; Fukuda and Clark 1975). He and Woodard collaborated on hybridization studies of saltmarsh and floodwater mosquitoes (Fukuda and Woodard 1974a and b). Fukuda's research on parasites and pathogens included a report of a new protozoan parasite in mosquitoes (Fukuda et al. 1976).

R.E. McLaughlin transferred to the GCMRL from the Boll Weevil Research Laboratory in Starkville, MS. McLaughlin began his work testing the effectiveness of *Bacillus thuringiensis* serotype H-14 (subspecies *israelensis)* (Bti) against the southern house mosquito (McLaughlin and Fukuda 1982), then turned his attention to rice field mosquitoes (McLaughlin et al. 1982; McLaughlin and Billodeaux 1983; McLaughlin and Vidrine 1984a). McLaughlin also developed a new method for dispensing liquid formulations of Bti into rice fields (McLaughlin 1983; McLaughlin and Vidrine 1984b), and contributed to the development of a standard bioassay to determine Bti potency (McLaughlin et al. 1984).

J.J. Becnel began his career with the USDA at the GCMRL in October 1980 after obtaining a M.S. degree at McNeese State University. Becnel's thesis research on the relative potency of combinations of chemical larvicides with Bti was done at the GCMRL. In 1982, Becnel was given the task of overseeing the operation of the newly installed electron microscope. After transfer of personnel of GCMRL to the Insect Affecting Man and Animals Research Laboratory in Gainesville, FL, he obtained a Ph.D. in entomology from the University of Florida in 1989.

E.I. Hazard transferred to the GCMRL in 1981 after 18 years of distinguished research at the Insects Affecting Man and Animals Research Laboratory in Gainesville, FL. Hazard continued his microsporidan work with the assistance of Fukuda and Becnel and completed a life cycle study of *Culicosporella lunata* in *Culex restuans* (Hazard et al. 1984) and also described gametogenesis and plasmogamy in microsporida (Hazard et al. 1985). He was instrumental in investigations leading to the discovery that a copepod intermediate host was required to complete the life cycle of *Amblyospora*, a microsporidan parasite of mosquitoes (Sweeney et al. 1985). Hazard became Location Leader of the GCMRL after Chapman's retirement in 1981. He initiated an effort to relocate the GCMRL to Louisiana State University in Baton Rouge, LA. Negotiations with LSU officials and the ARS Mid-South Area Office for the use of facilities were underway when Hazard's sudden death in March 1985 brought an end to the relocation plan.

Fukuda was named Acting Location Leader until a permanent Location Leader was installed. However, a decision was soon made to consolidate the GCMRL efforts with that of the pathology unit of the Gainesville laboratory and transfer the GCMRL personnel to Gainesville. The GCMRL was closed in October 1985 with the transfer of McLaughlin, Willis, Becnel, and Fukuda to Gainesville, FL (see above).

Because of the research and progress in the area of biological control of mosquitoes, in 1972 the GCMRL was named a WHO Collaborating Laboratory for Pathogens and Parasites of Mosquitoes (one of three in the world). In 1977, both Chapman and Petersen were appointed by WHO to the Scientific Working Group on Biological Control of Vectors (SWG/BCV) which periodically met in Geneva, Switzerland. These appointments involved numerous short-term consultantships to

developing countries. Because of the stature of GCMRL, Chapman was appointed for seven years (three as chairman) to the Steering Committee of the WHO/SWG/BCV.

The GCMRL, although relatively small, produced nearly 200 publications on mosquito biology and biological control in its 21-year existence and became known worldwide for its pioneering work in mosquito biological control. The success of the GCMRL was in no small part due to the field personnel, Cloud, Glenn, and Willis, who daily provided the material for examination or experimentation. The personnel proved not only to be outstanding scientists but contributed their services to mosquito control organizations. Chapman served as a member of the board of directors, vice-president and president of both the American Mosquito Control Association and the Louisiana Mosquito Control Association; Fukuda served as a member of the board of directors, vice-president and president of the Louisiana Mosquito Control Association; and Woodard served on the board of directors of the Louisiana Mosquito Control Association.

NORTHEAST PLANT, SOIL AND WATER LABORATORY, ORONO, ME. By Richard A. Humber

See Ithaca, New York.

BEE RESEARCH LABORATORY, BELTSVILLE, MD. By Hachiro Shimanuki and David A. Knox

Insect pathology in the USDA officially began in 1907 when the Bureau of Entomology employed G.F. White as a bee pathologist. The first Division of Bee Culture Laboratory was located in Somerset, MD, now a section of Chevy Chase, which borders on Washington, DC. The Laboratory was re-located a number of times in the Washington area until 1939 when it was moved to Beltsville, MD, where it is currently located. Although the laboratory was primarily known for its bee disease work, a number of its scientists who made their reputations in other specialties also made contributions to bee pathology. These include such names as E.F. Phillips, J.I. Hambleton, and W.J. Nolan.

G.F White was a pioneer, not only in bee pathology but also in insect pathology. He was the first in a long line of bee pathologists beginning a tradition of excellence in bee pathology which continues today at the Bee Research Laboratory in Beltsville. White differentiated American and European foulbrood diseases (White 1906); however, it was E.F. Phillips, in the introduction to White's (1906) publication on bacteria in the apiary, who named the diseases. White published monographs on American foulbrood (1907, 1920a), European foulbrood (1920b), Nosema disease (1919), and sacbrood (1917). After two years in the military, White returned to the Bureau of Entomology as a specialist on insect diseases. Later he was transferred to Moorestown, NJ, where he began a study on the diseases of the Japanese beetle in 1933. In less than two years, he was a member of a team that identified the "milky disease" as a means to control this important pest insect. White worked in Moorestown until his death in 1937.

A.P. Sturtevant was employed by the Bureau of Entomology, Bee Research Division, Somerset, MD, in 1916 to conduct studies on the etiology of bee diseases and the pathology of Nosema disease of honey bees. He was transferred to the Intermountain Bee Culture Field Laboratory, Laramie, WY, in 1926. Sturtevant was known primarily for his research on bee diseases, in particular the etiology of American foulbrood (Sturtevant 1924), a method to determine the presence of *Bacillus larvae* spores in honey (Sturtevant 1932, 1936), and many other papers on the diagnosis of bee diseases (Burnside et al. 1949).

C.E. Burnside began his career with honey bees in 1924 with the USDA Bureau of Entomology. He spent the summers of 1924–26 at the University of Michigan studying relative virulence of various

species of fungi and bacteria in relation to brood and adult bee diseases. Burnside was transferred in 1939 to the Divisional Headquarters of the Bureau of Entomology and Plant Quarantine, Bee Culture Unit in Beltsville, where he was responsible for the diagnosis of brood and adult bee diseases for the USDA. In 1942, due to World War II and the need to realign personnel, he was transferred to Laramie, WY. Burnside was noted for his research on fungi associated with honey bees (Burnside 1930), control of American foulbrood (Burnside 1931), bacteria associated with European foulbrood (Burnside 1934), and on septicemia (Burnside 1928), purple brood (Burnside 1935), chronic bee paralysis (Burnside 1945), and Nosema disease (Burnside and Revell 1948). Burnside died in 1949.

E.C. Holst was employed by the Beekeeping and Insect Pathology section of the Bureau of Entomology and Plant Quarantine of USDA in 1938. He was stationed in Laramie, WY, until 1942 when he was transferred to the Bee Culture Laboratory at the U.S. Agricultural Research Center in Beltsville. Holst was noted for the development of the "milk test" used by some to make a differential diagnosis of American and European foulbrood diseases (Holst 1946). In addition, Holst discovered the antibiotic, larvacin, produced by *Bacillus larvae*, the etiologic agent of American foulbrood disease (Holst 1948). Holst retired in 1951 and died in 1954.

A.S. Michael started his career at Beltsville in 1948 in the Bee Culture Laboratory. He became Laboratory Leader in 1958 and was Investigations Leader for bee diseases from 1962 to 1965. From 1965 to 1972, he served as the Assistant Branch Chief of the Apiculture Research Branch of ARS' Entomology Research Division. When ARS was reorganized in 1972, he became the first Laboratory Chief of the Bioenvironmental Bee Laboratory at Beltsville. Michael was recognized worldwide as an expert on bee diseases and he began the early logistical measures in preparation for the expected, eventual establishment of parasitic mites in the U.S. (Michael 1961, 1963). He was the first to recognize the potential use of ethylene oxide for the control of bee diseases (Michael 1964). Michael retired in 1975.

Hachiro Shimanuki started his career with the ARS Bee Disease Investigations Laboratory, Laramie, WY, in 1963. Three years later, he was transferred to the Bee Culture Laboratory in Beltsville. Shimanuki served in various capacities in Beltsville and is currently the Research Leader of the Bee Research Laboratory. Shimanuki's contributions have been divided between administration and research. He has served as the principal liaison between ARS and APHIS, Food and Drug Administration (FDA) and the EPA. His research is primarily on the etiology and control of bee diseases and bee nutrition. Recently he has been associated with the control of parasitic mites and the Africanized honey bee. Among his accomplishments are the use of high velocity electron beams to control bee diseases (Shimanuki et al. 1984), conduction of the first comprehensive survey for tracheal mites (Shimanuki et al. 1983) and coauthorship of a handbook on methods of diagnosing bee diseases (Shimanuki and Knox 1991).

Thor Lehnert was associated with the Bee Culture Laboratory in Beltsville from 1959–81, except for the period 1968–70 when he was stationed in Baton Rouge, LA. He was in charge of bee disease diagnosis until April 1976 when D.A. Knox took over that service. In 1981, Lehnert transferred to the USDA National Agricultural Library. His research was primarily on the control of Nosema and European foulbrood diseases (Shimanuki et al. 1969; Lehnert and Shimanuki 1973).

G.E. Cantwell spent most of his career with the ARS Insect Pathology Laboratory in Beltsville (see below) and was assigned to the Bioenvironmental Bee Laboratory from 1977 to 1980 only. Cantwell conducted research on the use of temperature extremes (Cantwell and Lehnert 1968), ethylene oxide (Cantwell et al. 1975), and carbon dioxide (Cantwell and Smith 1970) for the control of Nosema disease and the greater wax moth.

J.D. Vandenberg joined the Bioenvironmental Bee Laboratory in 1983 and was transferred to Logan, UT, in 1987. While in Beltsville, Vandenberg conducted research on laboratory rearing of honey bees (Vandenberg and Shimanuki 1987), the control of greater wax moth (Vandenberg and Shimanuki 1990a), safety of biorational pesticides for honey bees, and the half-moon syndrome of honey bees (Vandenberg and Shimanuki 1990b).

D.A. Knox began his career in the Bee Culture Laboratory in 1961 while enrolled as an undergraduate student. His research included safety testing of candidate biological control agents (Knox 1970). He did some of the first research on combining ethylene oxide fumigation and feeding oxytetracycline hydrochloride to reduce the recurrence of foulbrood diseases in honey bee colonies (Knox et al. 1976). Currently, Knox is in charge of the bee disease diagnostic service and is a coauthor of a handbook on bee disease diagnostic techniques (Shimanuki and Knox 1991).

T.B. Clark joined the Bioenvironmental Bee Laboratory in 1975 and transferred to the Insect Pathology Laboratory in 1981. He died in 1984 while on a collecting trip in Mexico. Clark made some significant contributions in bee pathology during the short time he worked on bees. He showed that the so-called rickettsial disease of honey bee was in reality a filamentous virus (Clark 1978). In addition, he identified a disease of honey bees caused by a spiroplasma which he later showed was found in the nectar of some plants frequented by the honey bees (Clark 1977).

E.W. Herbert, Jr., began his career with the USDA in 1966, as a part-time technician, and, except for three years with the military, he worked on honey bee nutrition (Herbert 1991) and its effect on European foulbrood disease (Herbert and Shimanuki 1982). When parasitic mites were discovered in the U.S., Herbert developed treatments against *Acarapis woodi* (Herbert et al. 1987) and *Varroa jacobsoni* (Herbert et al. 1988a). Herbert died in 1988 at the age of 45.

W.A. Bruce was transferred to the Beneficial Insects Laboratory (later Bee Research Laboratory) in 1987. His primary assignment was to develop laboratory rearing methods for honey bee parasitic mites. In addition, Bruce has worked on the control of parasitic mites (Herbert et al. 1988b) and the role of parasitic mites in the transmission of bee pathogens (Bruce et al. 1991).

N.W. Calderone joined the Bee Research Laboratory in 1992. His primary responsibility was to conduct research on the biology and control of parasitic mites. Calderone has concentrated on two approaches to mite control, a genetic solution and a chemical solution using botanical compounds that are environmentally safe. In addition to his work on mite control, Calderone is developing procedures to sample for mite diseases (Calderone and Shimanuki 1992) and will study the host-seeking behavior of parasitic mites.

Mercedes Delfinado-Baker was associated with the bee laboratory from the late 1960s to the late 1980s as a research associate, acarologist. She performed all the authoritative identification of mite samples received by the laboratory from all over the world. In fact, it was she who made the official identification of the honey bee mite, *Acarapis woodi*, in Mexico and later the identification of *A. woodi* (Delfinado-Baker 1984) and *Varroa jacobsoni* in the U.S., and was the first to report the occurrence of the mite *Melittiphis alvearius* in this country (Delfinado-Baker 1988).

INSECT PATHOLOGY LABORATORY/INSECT BIOCONTROL LABORATORY, BELTSVILLE, MD. By Jean R. Adams

The USDA became involved in research on microbial diseases for the control of insect pests many years ago with the research of S.R. Dutky at Moorestown, NJ. The Japanese beetle was discovered in Riverton, NJ, and soon became an economic pest in part because of the absence of natural enemies. In a search for diseased grubs, Dutky discovered a microorganism, later named *Bacillus popilliae*

Dutky, that successfully controlled the grubs of this pest (Dutky 1940, 1941a, b and c, 1963; White and Dutky 1940). He proceeded to develop procedures for mass production of the microorganism (Dutky 1942a) in grubs by injection with a microinjector which he developed (Dutky and Fest 1942), since it was not infectious *per os*, and he demonstrated that the organism produced was indeed *B. popilliae* (Dutky 1947). Then he developed a formulation of spore dust and worked out application procedures for its effective use (Dutky 1942b). Large areas of turf were treated, e.g., the mall grounds in Washington, DC, airport grounds, golf courses, and many communities elected to treat all areas containing turf. *Bacillus popilliae* has proved to be a very effective method to control the Japanese beetle and is still marketed today (see also Dutky 1992). Dutky and the Insect Pathology Unit at Moorestown was moved to Beltsville, MD, in 1954, with the formation of the Insect Pathology Pioneering Research Laboratory.

A.M. Heimpel came to the Insect Pathology Pioneering Research Laboratory in 1961 as Principal Insect Pathologist and later as Laboratory Chief. He was deeply committed to the field of insect pathology and was an inspiration to all who knew him. As leader of the laboratory, he always had time to listen, to guide and to encourage each person through difficult times in their research. He was intensely interested in the mode of action of insect pathogens, perhaps as a result of earlier studies with Tom Angus and other colleagues at the Insect Pathology Research Institute at Sault Ste Marie, Ontario, Canada. As R.M. Faust pursued studies to unravel the events in the insect gut following ingestion of *Bacillus thuringiensis* (Bt), Heimpel also advised and encouraged Russell Travers, Toshihiko Iizuka, and others on further studies on the genetic mechanisms controlling δ-endotoxin production. The knowledge obtained was crucial to genetic engineering studies that would come after his untimely death in 1979. He was also very interested in searching for new insect pathogens, mass rearing insects free of disease, and histological/cytological studies and cooperated with J.R. Adams in these areas of research. J.V. Thompson, previously with the Japanese beetle project, was reassigned to the disease diagnosis service under Heimpel's direction for several years before his retirement. He studied a new nuclear polyhedrosis virus of the almond moth (Thompson and Redlinger 1968) and a pathogenic strain of *Bacillus cereus* isolated from the cigarette beetle (Thompson and Fletcher 1972). Heimpel was awarded the USDA Superior Service Award in 1966 and the National Aeronautics and Space Administration (NASA) Group Award in 1970 for participation in studies in which lunar material returned from the first manned landing was examined for the presence of replicating agents which might be harmful to life on earth.

Heimpel was involved in safety testing of insect pathogens and developed testing protocols that were prerequisites for the registration of microbial agents. He also prepared two large documents for submission to the U.S. Environmental Protection Agency, one on the exemption from the requirement of a tolerance for use of Ac*M*NPV on lettuce and cabbage in cooperation with P.V. Vail, another ARS insect pathologist. Another was also prepared for the exemption from the requirement of a tolerance for use of milky spore disease bacterium, *B. popilliae*, on pastures. For further details of Heimpel's innumerable contributions to the Insect Pathology Laboratory (IPL), to the Society of Invertebrate Pathology of which he was a founding member, Secretary-Treasurer, Trustee and later Vice President, and his participation in national and international meetings and symposia the reader is referred to Faust's account of Heimpel's accomplishments (Faust 1984).

G.E. Cantwell came to the USDA in 1959 initially working with Dutky. After Heimpel became the leader of the laboratory, Cantwell's primary efforts were in developing strains of Bt for controlling the gypsy moth (Cantwell et al. 1961), greater wax moth (Cantwell and Shieh 1981), sciarid larvae (Cantwell and Cantelo 1982a), Colorado potato beetle (Cantwell and Cantelo 1984), and the Mexican bean beetle (Cantwell and Cantelo 1982b). He developed and produced a kit for the collection and shipment of pathogens for use by the World Health Organization (Cantwell and Laird 1966) and organized the "Registry of Tumors in Lower Animals" in conjunction with the National Institutes of Health and housed at the Smithsonian Institution of Washington, DC (Cantwell et al. 1968). He

developed several techniques for controlling diseases and pests of the honey bee, including *Nosema apis* (Cantwell and Lehnert 1968; Cantwell and Smith 1970; Cantwell et al. 1972; Lehnert and Cantwell 1978). Cantwell retired in 1985.

R.M. Faust came to the IPL in 1961 as an agricultural research technician while completing his B.S., M.S., and Ph.D. degrees in entomology, microbiology, and biochemistry. Over the years, his research dealt with such subjects as the chemical basis of the cell-cementing substances of insect tissues (Faust et al. 1967; Faust and Dougherty 1969), *in vitro* chemical reaction of δ-endotoxin of Bt (Faust 1968), the standardization of the δ-endotoxin produced by several varieties of Bt (Faust et al. 1971a and b), and the spectrographic elemental analysis of Bt and fall armyworm nuclear polyhedrosis virus (Sf*M*NPV) (Faust et al. 1973).

Faust then studied the mode of action of the δ-endotoxin of Bt (Faust et al. 1974a and b) and the effects of Bt variety *kurstaki* δ-endotoxin on isolated lepidopteran mitochondria (Travers et al. 1976). The extrachromosomal DNA in several varieties of Bt was examined as well as the occurrence of resistance to neomycin and kanamycin in *B. popilliae* and certain serotypes of Bt (Faust et al. 1979; Faust and Travers 1981). Extrachromosomal DNA was isolated and purified from serotypes of Bt pathogenic to Lepidoptera and Diptera larvae (Iizuka et al. 1981a) and comparative profiles of plasmid DNA were obtained from single and multiple crystalliferous strains of Bt subspecies *kurstaki* (Iizuka et al. 1981b) and Bt subspecies *darmstadiensis* (Iizuka et al. 1983). The comparative morphology and size distribution of the parasporal crystals from various strains of Bt were also reported (Faust et al. 1982).

Between 1982 and 1984, Faust's research emphasis was aimed at the characterization and comparative analysis of plasmid DNA and parasporal crystal structure from a diverse array of entomopathogenic bacilli related to cooperative efforts on gene manipulation and transfer (Abe et al. 1982, 1983, 1984; Wie et al. 1984). Faust also prepared chapters on the insecticidal protein genes of Bt (Faust and Adams 1989a), the plasmid biology of Bt (Faust et al. 1989), and the present and future strategies for improvement of Bt through gene manipulation (Faust and Adams 1989b). In 1988, he became a member of the ARS National Program Staff and is presently (1993) serving in that position covering basic insect biology and crop protection with special emphasis on pesticide resistance, insect neurohormones, and genetic sexing.

P.A.W. Martin joined IPL in 1981. The most successful aspect of her research has been the discovery of new Bt strains. She developed a method to isolate Bt spores from the environment, specifically from soil (Martin et al. 1985; Travers and Martin 1990). The method, named acetate selection, has become a standard procedure for Bt isolation (Travers et al. 1987). Samples were collected from all over the world (Martin and Travers 1989), and, because of the large number of samples received, it became necessary to develop novel techniques to process and characterize the isolates (Travers et al. 1987). From this research, Martin has received a patent on three Bt strains effective against Lepidoptera. She also demonstrated that Bt occurs everywhere and not necessarily in association with insects.

J.R. Adams came to IPL in 1962. One of her first projects was to study ten samples of cabbage looper NPVs collected from five different geographical areas in the U.S. Morphological differences were noted between the virus samples. Some polyhedra contained single virions (*S*NPV) embedded in the polyhedron matrix while others contained bundles of virions (*M*NPV) embedded in the polyhedron matrix (Heimpel and Adams 1966). Adams also described several viruses for the first time including: NPV from the zebra caterpillar (Adams et al. 1968); NPV from almond moth (Adams and Wilcox 1968); CPV from pink bollworm (Ignoffo and Adams 1966); an iridescent virus and an ascovirus from the bollworm/corn earworm (Adams et al. 1979a; Stadelbacher et al. 1978); rhabdovirus-like particles in the house cricket (Adams et al. 1980); and two virus-like particles in the Mexican bean

beetle (Adams et al. 1979b). Histopathological investigations were performed on each of the above host species noting the susceptible tissues, etc.; these were summarized in the Atlas of Invertebrate Viruses (Adams and Bonami 1991).

Cytological investigations also revealed that baculoviruses have two forms of virions. The virions occluded in polyhedra (PDV = polyhedra derived virions) are produced in susceptible cell nuclei and are involved in the process of invasion as PDVs are released from the polyhedra or VOs (viral occlusions) due to the alkalinity of the midgut. In the lumen of the midgut, the PDVs attach to microvilli and are taken into the nuclei of the midgut columnar cells where an initial cycle of replication usually occurs in the most virulent NPVs. The newly produced virions then bud through the basal plasma membrane where a part of the envelope which is acquired is modified with glycoprotein spikes or peplomers. These virions, called ECVs (extracellular virus), are involved in the systemic infection as ECVs attach to plasma membranes of cells of susceptible tissues and are taken in by a process of viropexis. The unenveloped nucleocapsids gain entry to nuclei where a cycle of viral replication occurs producing PDVs which are occluded in VOs or polyhedra (Adams et al. 1977; Adams and McClintock 1991).

A technique was developed for determining the osmolality of the hemolymph of insects; osmolality was measured for ten insect pest species (Adams and Wilcox 1973). This information aided the development of fixatives for insect tissues which would give optimal preservation, as well as the modification of insect cell culture studies for optimal cell growth and/or polyhedra production for each insect species. A technique for detecting defective or cracked VOs was developed by comparing scanning electron microscope (SEM) with dark field STEM (scanning transmission electron microscope) images of the samples (Adams 1985). By observation of thin sections of VOs, a quantitative technique was developed in which differences in numbers of virions/VO and numbers of virions/virus bundle were correlated with differences noted in mortality data (Tompkins et al. 1988a, 1991). Several SEM techniques were adapted and compared in order to obtain the maximum resolution of VO samples (Adams and Wilcox 1982).

A rickettsia-like organism has been identified in colonized cat fleas from one source but not other sources checked. Histopathological examinations revealed the microorganisms in the midgut, tracheal matrix, muscle, hypodermis, ovaries, and epithelial sheath of the testes (Adams et al. 1990).

S.J. Louloudes, a biochemist, transferred from the Insect Physiology Laboratory to the IPL in 1964. In early studies, he demonstrated that insect cells could not synthesize sterols and that fetal bovine serum added to the insect cell culture media was the source of sterols for the cells (Vaughn et al. 1971). His research focused on sterols and fatty acids of insect tissues and insect cell cultures, working with J.L. Vaughn and R.H. Goodwin in the development of insect cell culture media until his untimely death in 1984 (Goodwin et al. 1970, 1973; Vaughn et al. 1971; Samish et al. 1985).

In 1965, J.L. Vaughn joined the Insect Pathology Laboratory and began studies into the culture of insect cells and their use in the study of viruses with associates M.S.M. Stanley and R.H. Goodwin. At this time, the first cell lines from invertebrates had just been reported by Tom Grace (Grace 1962) in Australia. Early studies at Beltsville concentrated on developing an understanding of the tissues that would provide growing cells (Stanley and Vaughn 1968) and the development of suitable media and methods for establishing primary cultures (Goodwin 1975). Numerous cell lines were established from important insect pests in the U.S., e.g., corn earworm, gypsy moth (Goodwin et al. 1978), and fall armyworm (Vaughn et al. 1977). The cell line IPLB-SF-21AE has been the most important of these early cell lines as it was the parent line of several clones that have been used widely for the culture of genetically-engineered baculoviruses. The early cell lines from gypsy moth developed by Goodwin were the foundation of the important studies by E.M. Dougherty and D.E. Lynn that followed. Several new media formulations were developed during this time by Goodwin, one of

which, IPL-41, later modified by Weiss et al. (1981), is sold commercially. It was during this time that the use of cell cultures for the study of insect viruses became accepted. Among the contributions from this Laboratory, in addition to the cell lines, were methods for assaying insect viruses by end point dilution (Vaughn and Stanley 1970) and characterization of extracellular virus.

E.M. Dougherty came to the IPL in 1966 as a student and later worked as a technician as he pursued advanced degrees at the University of Maryland. The research for his M.S. degree involved identification and characterization of the ECV phenotype (Dougherty et al. 1975). His Ph.D. research continued investigations on the ECV relationship to cell attachment parameters and the effects of various inhibitors on macromolecular synthesis on both ECV and PDV phenotypes (Dougherty et al. 1981). Attempts to establish *in vitro* replication of granulosis viruses were unsuccessful; however, a unique cell line, TnR^2, was initiated. The long eclipse stage of granulosis virus *in vivo* was described as was the effect of granulosis virus infectivity on hormonal titers in the insect (Dougherty et al. 1989).

Over the last decade *Lymantria dispar* NPV (Ld*M*NPV) has been the focus of Dougherty's studies as he has collaborated with Martin Shapiro, D.E. Lynn, Tom McClintock (as a graduate student and then as a Post Doctoral Fellow), Post Doctoral Fellows David Guzo and Harold Rathburn, and support scientists Kim Guthrie and Martin Stranathan. The Ld*M*NPV virus-host interactions have been described and compared to the prototype *Autographa californica M*NPV (Ac*M*NPV). Ld*M*NPV replication has been described (McClintock et al. 1986a and b) and the genome mapped (McClintock and Dougherty 1988). Semi-permissive replication has been obtained with Ac*M*NPV in IPLB-Ld-652Y cell cultures while several other gypsy moth cell lines were nonpermissive (McClintock et al. 1986a). Both the IPLB-Ld-652Y cell line and the IPL-LdFB cell line, also semi-permissive for Ac*M*NPV replication, have been investigated at the transcriptional level (Guzo et al. 1992). Viral transcription appears normal by all criteria tested; however a translational block occurs in both systems. Guzo has recently discovered a macromolecular protein synthesis inhibition factor (MSIF) which effects cell translation and may be the Ac*M*NPV 64-kDa glycoprotein or some component or complex of this protein (Guzo et al. 1991a and b, 1992). Rathburn investigated the making of a baculovirus expression vector from this system. The systems developed by Lynn, Shapiro, and Dougherty have been or are currently being licensed by American Cyanamid as the first *in vitro* commercial baculovirus production system.

G.J. Tompkins came to IPL while a student and completed his B.S. and M.S. degrees, served in the U.S. Army in Vietnam, returned and then completed his Ph.D. His area of research included immunology, isolation, purification, and testing of new baculovirus isolates. He demonstrated conclusively that the *M*NPVs could replicate in more than one species, e.g., *Trichoplusia ni M*NPV replicated in corn earworm, but the *Helicoverpa zea S*NPV (Hz*S*NPV) would not replicate in cabbage looper (Tompkins et al. 1969). He demonstrated and reported for the first time that microencapsulation of baculoviruses with sunscreens significantly improved the efficacy of viruses used for control of cabbage loopers and imported cabbageworms on collards (Tompkins et al. 1988b). Tompkins also showed that the virulence of baculoviruses that have multiple host ranges can be altered when serially passaged in alternate susceptible hosts and permissive cell lines (Tompkins et al. 1988a) and reported for the first time that the virulence and internal morphology of *M*NPVs are altered when serially passaged in alternate susceptible hosts (Tompkins et al. 1981). He also reported for the first time that the addition of liposomal material to the cell culture medium used in culturing baculoviruses maintained the virulence of the *M*NPVs after being serially passaged in the cell lines. This demonstrated that some cell culture media may be deficient in required nutrients to maintain virulence in progeny virus harvested from the cell culture medium (Tompkins et al. 1991).

R.H. Goodwin joined IPL in 1968. He initiated cooperative studies with Adams and Louloudes leading to repeatable baculovirus replications in a noctuid moth pupal tissue cell line isolated from

the fall armyworm by Vaughn (Goodwin et al. 1970, 1973). He extended his cell culture virus replication studies to include the investigation of cell lines from other noctuid species of economic importance in various tissue culture media he developed (Goodwin et al. 1976). He initiated investigations within ARS on gypsy moth *in vitro* production systems by developing a number of pupal tissue-derived cell lines which had differing responses to various (homologous and heterologous) baculoviruses (Goodwin et al. 1978). This work was accomplished with special financial support from the U.S. Forest Service.

In cooperation with Adams, Goodwin compared the baculovirus virion morphologies of a number of the known baculoviruses with their host range, in order to determine if they could be separated by electron microscopy, e.g., wide-host-range baculoviruses (those having high mode and mean nucleocapsid numbers in the virion) with the narrower host range baculoviruses (lower mode and mean nucleocapsid numbers in the virion). This work resulted in the now accepted unicapsid and multicapsid baculovirus groupings (within Genus A) and the biological host range connection between these groupings and the more greatly differing single and multiple embedded groups (including the unicapsid-multiple embedded polyhedrosis of Genus A, the unicapsid-singly embedded granuloses of Genus B, and the non-embedded baculoviruses of Genus C).

Goodwin developed the first serum-free insect cell culture media that supported the continuous cultivation of insect cell lines and, with lipidic supplementations, the first serum-free insect cell culture media that supported serial continuous replication cycles of a baculovirus in an insect cell line from the gypsy moth. These investigations made clear the dependence of virus replication on the nutrition and metabolism of the host cell by defining several critical nutrients that control virus replication and assembly events (Goodwin and Adams 1980).

Goodwin's tissue culture media have been produced commercially, and his tissue culture research with other insect pathologists at Beltsville was honored with a merit-cash award for the team research on baculovirus cell culture replication studies. Industry and other researchers are now using cell lines developed by Vaughn together with cell culture media developed by Goodwin as models for the industrial production and study of baculoviruses in tissue cultures for several biotechnological and agricultural applications.

D.E. Lynn joined the IPL in January 1981 to fill the position vacated by Goodwin when he transferred to the ARS Rangeland Insect Laboratory in Bozeman, MT. Lynn came to Beltsville from a postdoctoral position at the Insect Attractants, Behavior and Basic Biology Laboratory in Gainesville, FL, after graduate work at Ohio State University. His research on insect cell cultures continued the type of research that Goodwin had performed at the IPL. Initial success at Beltsville was seen with the development of cell lines from *Diabrotica undecimpunctata* (Lynn and Stoppleworth 1984). This was only the second time cells had been successfully cultured from Coleoptera. Cell lines from other insects followed, most notable were cell lines from gypsy moth fat body which have led to a probable commercial system for production of the gypsy moth nuclear polyhedrosis virus (Ld*M*NPV) (Lynn et al. 1988, 1989).

Lynn has enjoyed productive collaboration with other members of the IPL as well as many scientists in other laboratories at Beltsville and elsewhere. Collaboration with scientists at Gainesville, H. Oberlander and S.M. Ferkovich, resulted in the discovery of a new developmental hormone (Lynn et al. 1985) which has effects in cell culture but whose effects in the insect are still unknown. Studies with the spiroplasma group in IPL (K.J. Hackett, R.F. Whitcomb, and T.B. Clark) resulted in the first growth of two previously uncultivable spiroplasma species, the Colorado potato beetle spiroplasma (Hackett and Lynn 1985) and the *Drosophila* sex-ratio spiroplasma (Hackett et al. 1986). Research with scientists in the Beltsville Insect Physiology Laboratory (currently the Insect Neurobiology and Hormone Laboratory), M.F. Feldlaufer and W.R. Lusby, led to the first report on the production of

the insect molting hormone 20-hydroxyecdysone by insect cell lines (Lynn et al. 1987). A collaboration with A.C.F. Hung (Beneficial Insect Laboratory, currently the Bee Research Laboratory) led to the development of cell lines from small parasitic wasps in the genus *Trichogramma* (Lynn and Hung 1986, 1991). One of these has recently been shown by Lynn to undergo morphological transformation into muscle-like cells in response to treatment with insect molting hormone (Lynn and Hung 1991). This is the first continuous insect cell line to have such a developmental capacity. Lynn's primary research has been studies with NPVs in cell cultures. His efforts with Dougherty and Shapiro have led to a system for producing the gypsy moth NPV in cell cultures.

Martin Shapiro transferred to the IPL in the fall of 1985 from the Gypsy Moth Methods Development Laboratory (USDA-APHIS) at Otis ANGB, MA (see below), and has continued his research studies on baculoviruses. The objective of his research has been to obtain information on factors affecting the performance of insect viruses so that viruses can be more effective in controlling insect pest populations. The factors being studied are: 1) virulence, 2) environmental persistence, i.e., radiation stability, and 3) host susceptibility. The main emphasis has been centered on the gypsy moth and its nuclear polyhedrosis virus (Ld*M*NPV).

Research on increasing viral potency has progressed through several stages. First, he identified the most virulent NPV isolates from North America and Asia (Shapiro et al. 1984). Second, he demonstrated that heterogeneity among samples within geographical isolates is a common phenomenon and developed a means to identify the most active samples (Shapiro and Robertson 1991). Third, he selected for a more virulent biotype from a heterogeneous NPV population using *in vivo* methodology. While *in vivo* selection reduced the heterogeneity, *in vitro* plaquing was required to obtain a genetically homogeneous biotype (Shapiro et al. 1992b). The selection process and the improved virus biotype(s) were licensed to American Cyanamid and a U.S. Patent was issued for this technology on July 21, 1992. The improved virus became part of a successful *in vitro* production system, which was licensed to American Cyanamid.

Shapiro continued and intensified research started at the APHIS Otis Methods Development Center at Otis ANGB, MA, on ultraviolet (UV) screens or protectants, as environmental stability is affected adversely by solar UV radiation. This research has been systematic and multifaceted and has included: 1) sunscreens for human usage (Shapiro et al. 1983); 2) insect tissues and metabolites (Shapiro 1984); 3) B Vitamins (Shapiro 1985); 4) dyes (Shapiro 1989; Shapiro and Robertson 1990); and 5) optical brighteners (Nickle and Shapiro 1992; Shapiro 1992). Research on UV inactivation and UV protectants has demonstrated the usefulness of several chemical structures as radiation protectants, indicated useful chemical structures, shed light on mechanisms of UV inactivation, and stimulated other scientists.

Recently Shapiro demonstrated that certain optical brighteners (i.e., selected stilbenes) acted as effective UV protectants and activity enhancers for the gypsy moth NPV (Shapiro and Robertson 1992). For the past two years, collaborators have demonstrated significant enhancement under field conditions, and this research has become part of an ARS-funded pilot program under R.E. Webb, ARS Insect Biocontrol Laboratory, Beltsville, MD). Subsequent research by Shapiro and J.J. Hamm (ARS, Tifton, GA) demonstrated that enhancement could occur with several viruses against the fall armyworm (Hamm and Shapiro 1992). This research was so attractive to American Cyanamid that a Cooperative Research and Development Agreement was obtained to investigate the mode of action of these brighteners. The use of brighteners was awarded a U.S. Patent on June 23, 1992 (Shapiro et al. 1992a) and was licensed to both Sandoz Inc. and to American Cyanamid.

In 1972, at an interdisciplinary conference at the Ciba Foundation in London, the field of spiroplasmology was launched with the description, by a Beltsville group of which R.F. Whitcomb

was a member, of a new group of helical mollicutes (Davis et al. 1972). The newly discovered organisms tracked the symptoms of the destructive stunt disease of corn, and were presumed to represent the etiological agent. The corn stunt agent was the first recognized representative of the spiroplasmas. Shortly after this discovery, as part of a major ARS reorganization, Whitcomb became a member of the IPL. Although the corn stunt spiroplasma played a pivotal role in the discovery of spiroplasmas and in the establishment of the genus *Spiroplasma*, it resisted attempts at cultivation. At the 1974 Bordeaux Mycoplasma Congress, Whitcomb, collaboratively with D.L. Williamson, announced that they had succeeded in cultivating the agent. Publication of this work (Williamson and Whitcomb 1975) laid the groundwork for laborious steps that culminated, 12 years later, in the establishment of a binomial name for the corn stunt spiroplasma (Whitcomb et al. 1986).

In part through the work of Whitcomb (Secretary of the Subcommittee on Taxonomy of Mollicutes of the International Committee on Systematic Bacteriology) and colleagues, the division Tenericutes was created as a prokaryotic taxon equivalent in rank with the Gram-positive and Gram-negative bacteria, and standards were developed for descriptions of new species (Whitcomb 1979). Within this division, the single class Mollicutes included, among others, the families Spiroplasmataceae and Acholeplasmataceae. There are now more than 40 species or putative spiroplasma species. The status of this grouping has changed continually as new spiroplasmas have been discovered (Whitcomb et al. 1983; Tully et al. 1986).

These discoveries were pursued actively by an international collaborative team including scientists from Beltsville, National Institutes of Health (NIH), State University of New York (SUNY) Stony Brook, and Institut National de la Recherche Agronomique (INRA), Bordeaux, France. Spurred by these emerging discoveries, this group soon reported spiroplasmas from citrus, *Drosophila* (Williamson and Whitcomb 1974) and ticks (Tully et al. 1976, 1981; Stiller et al. 1981). In insects, mollicutes multiplied readily, and in some they were clearly pathogenic (Whitcomb et al. 1973; Whitcomb and Williamson 1975, 1979). The citrus and corn spiroplasmas proved to be related (Tully et al. 1973). After the transfer of T.B. Clark to the IPL, this field of research exploded, with Clark's discovery of a spiroplasma causing mortality in honey bees (Clark 1977). This was followed in rapid succession by Clark's discovery of spiroplasmas in a multitude of insects, including other bees, wasps, beetles, flies, and butterflies (Clark 1982). It was this work, and subsequent collaborative works of Clark, Whitcomb and Hackett (Clark and Whitcomb 1984; Hackett and Clark 1989), that established *Spiroplasma*, discovered a mere decade before at Beltsville, as perhaps the most abundant and diverse microbial genus on earth. The genus contains organisms that invade horse flies, mosquitoes, beetles, and many other pest insects. Some of the spiroplasmas proved to be microbiologically unique. One of these was the group VII MQ-1 strain, which produces an eukaryotic-like methylase and stimulates production of tumor necrosis factor, proven to have biomedical applications. Unfortunately, Clark died in 1984 on a field trip to Mexico.

An entirely new approach to cultivation of fastidious mollicutes was inaugurated with Hackett and Lynn's (1985) use of insect cells to co-culture the Colorado potato beetle spiroplasma. This was followed (Hackett et al. 1986) through previously established collaborative ties, by cultivation of the sex-ratio spiroplasma, a transovarially transmitted male lethal organism. Work in the cultivation of these metabolically restricted and fastidious microbes led to insights into pathology and medical applications. Following cultivation of the corn stunt spiroplasms in M1D medium, J.G. Tully of the U.S. National Institutes of Health (NIH) and Whitcomb, pursuing leads developed in the IPL (Jones et al. 1977), cultured, in Whitcomb's SP-4 medium, the suckling mouse cataract spiroplasma, an organism originally thought to be a virus, later a spirochete, but finally revealed to be a spiroplasma. Koch's postulates (proof of pathogenicity; Stanier et al. 1957) were fulfilled for this spiroplasma (Tully et al. 1977). The M1D and SP-4 formulations have subsequently become standard media for cultivation of spiroplasmas and medically important mycoplasmas. For example, SP-4 medium is the medium of choice for isolation of the atypical pneumonia agent in man, and of a human genitourinary

mycoplasma. SP-4 is also the only medium that supports the growth of mycoplasmas believed to potentiate infection of the HIV virus in AIDS patients. The use of a complex medium to cultivate the suckling mouse cataract agent, an organism that attacks the brain of neonate mice, was followed (Hackett et al. 1987) by development of a completely defined medium for this very fastidious mollicute, and demonstration of the critical component sphingomyelin in the medium. Because of the high concentration of sphingomyelin in the brain, the linkage with brain pathology is explicable. This case has been used to illustrate the importance of nutritional studies as a window to the mechanisms of pathology.

Important accomplishments were also made in the understanding of spiroplasma ecology (Hackett and Clark 1989). These included: 1) demonstration of the dependence of spiroplasmas on internal, environmentally protected, microhabitats within terrestrial arthropods, including ticks and holometabolous insect orders; 2) establishment of spiroplasmas in all types of insect symbioses, including phoresy, commensalism, parasitism, and mutualism; 3) proof that spiroplasmas invade insect guts, blood, and tissues, including the brain; 4) fulfillment of Koch's postulates for many plant and animal spiroplasmas (Stanier et al. 1957); 5) demonstration of the role of flowers and leaf surfaces in the dissemination of most spiroplasmas; and 6) revelation of the major association of spiroplasmas with a number of pest insects.

Spiroplasmas were not the only mollicutes isolated from insects or plant surface habitats. Many species of nonhelical wall-less organisms also were isolated. Some of these organisms (Whitcomb et al. 1982; Williamson et al. 1990) proved to represent a new taxon of arthropod-associated mollicutes, which, paradoxically, also includes the first mollicute discovered, *Mycoplasma mycoides*, the agent of bovine contagious pleuropneumonia. The Beltsville group was closely involved in preparation of a comprehensive book about plant and insect mollicutes, Volume V of "The Mycoplasmas" (Whitcomb and Tully 1989), which was dedicated to Clark.

Throughout these years, the mollicute team also worked on mycoplasma-like organisms (MLOs) causing plant disease, and on the vectors that transmit these agents. For the MLOs that are pathogenic to their vectors (Whitcomb and Williamson 1979), this research was a synthesis of insect and plant pathology.

GYPSY MOTH METHODS DEVELOPMENT LABORATORY, OTIS ANGB, MA. By Martin Shapiro

ARS maintained a research unit at the APHIS Methods Development Center at Otis ANGB, MA, for several years. Initially, the primary research at Otis dealt with the development of mass rearing technology for the gypsy moth. As a team member, Martin Shapiro worked on artificial diets. As the insect pathologist, he worked on development of more efficient egg-disinfection procedures, and improved sanitation in rearing. Rearing costs were reduced 5-fold to $12–20 per 1,000 harvested pupae (Bell et al. 1978, 1981). These improvements led to the establishment of mass rearing programs for both *in vivo* virus (ARS) and sterile male (APHIS) production. These rearing techniques represented the "state-of-the-art" and have been utilized by other laboratories. In 1977, each member of the ARS research team was awarded a Certificate of Appreciation "For outstanding adaptability and proficiency as a team member in conducting research to develop technology to rear sufficient numbers of gypsy moth larvae to produce the gypsy moth virus on a commercial scale".

More simplified and efficient procedures for *in vivo* production of gypsy moth NPV were developed, culminating in a large-scale pilot plant production in 1979 (Shapiro et al. 1978, 1980, 1981; Shapiro 1981, 1982; Shapiro and Bell 1981, 1982a). More than 15 million insects were infected over a 100-day period, and more than 50,000 acre equivalents of NPV were produced. New and immediately applicable information was obtained regarding factors influencing both the yield and quality of the

virus product (Shapiro and Bell 1981; Podgwaite et al. 1983). Costs were reduced from $20–30 per acre to $150–200 per acre equivalent or less than one-tenth of previous costs. The development of a practical host-larval rearing and virus production system overcame a major barrier to the use of the gypsy moth NPV in operational pest management systems. The virus production technology was subsequently transferred to USDA-APHIS and to a private company.

Differences in the virulence of naturally occurring geographical isolates of the gypsy moth NPV from North America, Europe, and Asia were demonstrated. The most active isolates generally originated from North America; the least active isolate originated from Asia (Japan) (Shapiro et al. 1984). In a cooperative study, it was demonstrated that the greatest DNA homology between the North American standard (Hamden, CT) and other isolates occurred among North American isolates, intermediate homology occurred with European isolates, and no homology occurred with the Asian isolate (Shapiro and Dougherty 1985). *In vivo* selection of a North American isolate (Abington, MA) was initiated and was based upon the inherent heterogeneity of the wild-type virus population, utilizing time of larval death and LC_{50} as selectable traits. This research led to a patent (Shapiro et al. 1992a) and licensing to American Cyanamid of the selected NPV strain. Much emphasis was placed upon effective ultraviolet (UV) protectants, as environmental stability is affected adversely by solar radiation, especially in the UV portion of the spectrum. This research approach was multifaceted and has involved: 1) sunscreens for human usage (Shapiro et al. 1983); 2) insect tissues and metabolites (Shapiro 1984); and 3) B vitamins (Shapiro 1985). In addition, a UV-tolerant NPV biotype was obtained after selection (Shapiro and Bell 1984). Initial research was based upon the presumption that absorption in the UV-B portion of the solar spectrum was essential for good UV protection and excellent materials such as benzylidene sulfonic acid and uric acid were found. Subsequently, it was demonstrated that absorption in the UV-A portion of the spectrum was also very important and the effectiveness of such B vitamins as folic acid and riboflavin was shown (Shapiro 1985). In the case of folic acid, field efficacy was demonstrated by the U.S. Forest Service.

Research on the gypsy moth NPV also included the use of such chemicals as boric acid to increase host susceptibility (Shapiro and Bell 1982b), the effect of host stage upon quality and quantity of NPV production (Shapiro et al. 1986), and the use of alternate hosts to produce baculoviruses (Shapiro et al. 1982). Research was also initiated on the entomogenous nematode, *Steinernema carpocapsae* (as *Neoaplectana* or *S. feltiae*) against gypsy moth (Poinar et al. 1981; Shapiro et al. 1985a, 1985b).

BIOLOGICAL CONTROL OF INSECTS RESEARCH LABORATORY, COLUMBIA, MO. By Arthur H. McIntosh

In 1956, it was proposed that a research laboratory be established to conduct basic and applied research on the biological control (by parasitoids, predators, and pathogens) of insect pests. A decision was made in 1957, with the concurrence of the University of Missouri at Columbia (UMC), to locate the research laboratory in Columbia, MO. Factors which were important in selecting a site were both practical and historic: UMC had a long standing commitment to agricultural research; a well recognized Department of Entomology attracted high caliber scientific personnel; and modern, extensive library facilities were available. Construction began in 1965 and was completed in 1968. The new laboratory was called the Biological Control of Insects Research Laboratory (BCIRL). The mission of BCIRL was and is to discover, define, and verify biological control concepts and principles for the use of parasites, predators, and pathogens against destructive agricultural insect pests.

F.R. Lawson, who was in charge of the ARS Tobacco Research Laboratory in Oxford, NC, was the first director of the newly established ARS laboratory. C.M. Ignoffo directed the laboratory from

1971 to 1989. A.H. McIntosh assumed the directorship in 1989 and continues in that capacity at present (1993).

The year 1964 marked the arrival of Benjamin Puttler, a Research Entomologist, who was one of the first staff members of the BCIRL. The contribution to the insect pathology efforts by Puttler was his ability to discover and/or recognize diseases in field populations of pest insects and cooperate in studies of those that showed promise. He was the first to recognize the presence of the alfalfa weevil fungus, *Zoophthora phytonomi*, in the Mid-Great Plains and its potential as a factor in reducing alfalfa weevil populations (Puttler et al. 1978, 1980). His field observations of *Nomuraea rileyi* showed that the fungus has different levels of virulence in several of its hosts in the legume system (Puttler et al. 1976, 1978; Puttler and Long 1980). He also discovered potential agents for microbial control of the yellowstriped armyworm.

Studies involving dissemination of nuclear polyhedrosis virus (NPV) occlusion bodies (OB) in the environment, importation of exotic pathogens for the control of insect pests, and incorporation of feeding adjuvants with viral and bacterial insecticides were conducted by D.L. Hostetter, a Research Entomologist at BCIRL who joined the staff in 1966. Hostetter demonstrated that *Trichoplusia ni* NPV OB were disseminated through bird feces and that entomophagous insects such as sarcophagid flies which fed on diseased larvae also served as disseminators of virus (Hostetter and Biever 1970). The recovered virus was virulent for the target pest. Such studies were important in understanding the epizootics of virus diseases in the environment. Hostetter was also successful in demonstrating control of the imported cabbageworm with a granulosis virus imported from Canada (Hostetter et al. 1973). He demonstrated the effectiveness of *Bacillus thuringiensis* (Bt) against bagworm which resulted in expanding the label of this microbial pesticide for this insect. It was shown that the insecticidal activity of commercial preparations of Bt and a viral insecticide of corn earworm could be extended by the addition of adjuvants to formulations (Hostetter et al. 1975, 1982). Hostetter also showed that the use of a fungicide (Kocide 101WP) at recommended application rates had no deleterious effect on the entomopathogenic fungus of alfalfa weevil or the occurrence of epizootics in an endemic area. These findings are important to management techniques and decisions for the control of insect pests.

In more recent studies, two new multiple enveloped nuclear polyhedrosis viruses (*M*NPV) have been researched. An *M*NPV isolated from the yellowstriped armyworm in Missouri was shown to be host specific (Hostetter et al. 1990). An *M*NPV isolated from the celery looper (*Anagrapha* [=*Syngrapha*] *falcifera*) in Missouri was shown to infect more than 31 species of Lepidoptera (Hostetter and Puttler 1991). The *M*NPV from celery looper is equally effective against larvae of corn earworm and tobacco budworm as contrasted to the *Autographa californica M*NPV (Ac*M*NPV) which has a low virulence for corn earworm. The celery looper baculovirus (Af*M*NPV) was the first baculovirus ever patented (and it is a potential biological insecticide for commercial production and licensing because of its wide host range and effectiveness against the *Heliothis*/*Helicoverpa* complex and other lepidopteran larvae. This example of technology transfer between ARS and private industry has resulted in efforts to commercialize this virus by Sandoz Inc. and biosys®.

In 1968, K.D. Biever initiated studies to characterize the development of the nuclear polyhedrosis virus of the cabbage looper under programmed temperature regimes (Biever and Hostetter 1971, 1985). These data provided a reliable method of predicting and characterizing natural epizootics and determining expected larval mortality patterns when virus is used to control field populations of cabbage looper.

Biever, in cooperation with Hostetter, developed a biological pest control program for lepidopterous pests of wine and juice grapes (Biever and Hostetter 1975, 1989). This program eliminated the use of chemical insecticides by successfully substituting the judicious use of Bt, which is non-toxic to

humans and leaves no harmful residue. This program offers great potential for wide acceptance and implementation given present trends in pest control.

Biever carried out studies during 1974–1976 that established that imported cabbageworm stressed by temperature manipulation and/or inadequate diet moisture would exhibit overt infection and succumb to a subacute granulosis virus (Biever and Wilkinson 1978). Results of these studies highlighted the importance of environmental stressors in the recovery or infection processes for larvae exposed to virus.

A pest management system for control of the diamondback moth, the cabbage looper, and the imported cabbageworm in commercial cabbage production was developed by Biever (Biever and Hostetter 1978; Davis et al. 1985). A workable system was provided for growers which eliminated or minimized the use of chemical insecticides and reduced production costs through use of a microbial insecticide and a population monitoring system. Several commercial growers currently use this system for cabbage production.

In 1979 and 1980, Biever implemented laboratory and field cage studies that demonstrated that a predator, the spined soldier bug, could mechanically transmit an entomopathogenic virus to cabbage looper larvae via leaf surfaces and initiate epizootics that provided high levels of population suppression (Biever et al. 1982). These findings have opened a new area of research effort and opportunity involving the use of predators and parasites to vector specific insect pathogens in crop systems. Subsequently, Biever conducted studies that established the importance of placement of insect virus on the plants in relation to the specific feeding behavior of the target insect. He demonstrated that selective placement of the virus significantly increased its effectiveness and provided residual control.

Upon arrival at BCIRL in 1971, C.M. Ignoffo continued his research in the field of insect pathology and microbial control. Ignoffo was instrumental in the precedent development and registration of the world's first viral pesticide and in the formulation of protocols for registering candidate microbial pesticides (Ignoffo 1973a and b, 1979). The concept and initial research establishing the feasibility of virus production, safety to non-target organisms and field effectiveness was initiated by Ignoffo at USDA-ARS at Brownsville, TX (see below) and completed while he was with International Minerals and Chemical Corporation (IMC) at Wasco, CA. His research on the interrelationships between this registered virus (*"Heliothis S*NPV"), its *Heliothis*/*Helicoverpa* complex hosts, and the environment continues to the present date. Ignoffo's more recent research has focused on explaining the mechanism(s) of sunlight inactivation of microbial insecticides with specific reference to the *"Heliothis S*NPV", an entomopathogenic fungus (*Nomuraea rileyi*) and the bacterium, Bt. He was one of a few early investigators who advocated the importance of sunlight-UV inactivation of field-applied microbial insecticides and is the co-inventor of a patent describing a natural polyflavonoid (while at IMC at Libertyville, IL) that was used in commercial formulations as an UV-protectant for both chemical and microbial pesticides. He has utilized a number of UV protectants to successfully stabilize microbial insecticides in the field and has made important contributions to the understanding of the mechanism(s) of inactivation of microbial pathogens by sunlight (Ignoffo and Batzer 1971; Ignoffo et al. 1974, 1977c, 1989b, 1991; Ignoffo and Garcia 1978b).

Ignoffo, as the leader of an interdisciplinary research at BCIRL, evaluated the status and role of biological control agents such as parasites, predators, and pathogens in a soybean-model-ecosystem. Information from such studies provided knowledge on pest/natural enemy interactions as well as provided a model system for recommendations to soybean growers in Missouri and the Midwest. Furthermore, the basic and applied knowledge garnered from these studies was useful in the control and suppression of insect pests and the reduced use of chemical insecticides, increasing the return on investment to soybean growers (Ignoffo et al. 1976c; Ignoffo 1980).

Ignoffo also conducted basic and applied studies on the entomopathogenic fungus *N. rileyi* and demonstrated that it was a promising and safe microbial agent. An Experimental Use Permit (EUP), approved by U.S.-EPA for the use of *N. rileyi* as a mycoinsecticide, was granted to Abbott Laboratories. The EUP permitted industrial production of *N. rileyi* and its distribution to independent researchers conducting field tests in the southern U.S. Further studies were conducted by industry, university, and federal scientists to test the efficacy of *N. rileyi* as a mycoinsecticide. Results indicated *N. rileyi* can be effectively used as a prophylactic microbial control agent but has limited use unless directed at early instar larvae. Other studies involving *N. rileyi* included: strain identification, propagation, virulence of geographical isolates, storage stability, chemical sensitivity, environmental fate and dispersal, safety, formulation and timing of field application (Ignoffo et al. 1975a and b, 1976a, b, c and d, 1977a, b and c, 1978, 1979, 1982a and c, 1983, 1985, 1989a; Puttler et al. 1976; Garcia and Ignoffo 1977, 1978, 1979; Ignoffo and Garcia 1978a and b, 1985, 1987, 1991; Ignoffo 1981; Ignoffo and Boucias 1992).

Ignoffo conducted a series of studies on the possible role of fungal enzymes in the infection process (El-Sayed et al. 1991, 1992a and b; Gupta et al. 1991, 1992; Ignoffo and Garcia 1991). Most investigators used enzymes (proteases, lipases, chitinases) expressed by fungal mycelia to study the host-penetration-infection process. Ignoffo advocated concentrating on conidia (from *N. rileyi*) because they are primarily and intimately involved in penetration of the integument that eventually leads to the host's death (Ignoffo 1981).

Working in collaboration with M.H. Greenstone, an Arthropod Ecologist hired at BCIRL in 1982, Ignoffo also documented the host-range of a congener of *N. rileyi*, *N. atypicola*, which prior to that time had been known only from a few spiders (Greenstone et al. 1987).

Some of the earliest studies with a newly isolated mosquito bacterium (*Bacillus thuringiensis israelensis*) also were conducted at the BCIRL in collaboration with industrial and other USDA scientists (Ignoffo et al. 1980, 1981a and b, 1982b).

The arrival of A.H. McIntosh, a Research Microbiologist, in 1979 at BCIRL provided the much needed disciplines of insect cell culture and virology not previously available at the Laboratory. *In vitro* systems provide a means of conducting experiments at the cellular level that would be difficult or impossible to accomplish *in vivo*. Effort was concentrated on the worldwide important agronomic insect pest complex of *Heliothis/Helicoverpa* and its homologous single nuclear polyhedrosis virus (Hz*S*NPV).

McIntosh established the first insect cell lines from several major insect pests: tobacco budworm (McIntosh et al. 1981), *Helicoverpa armigera* (McIntosh et al. 1983), diamondback moth (Quhou et al. 1983), yellowstriped armyworm, corn earworm, imported cabbageworm, and *Heliothis subflexa*. These lines are routinely used in research projects at the BCIRL and have been requested both nationally and internationally by scientists for use in molecular biology, virology, genetics, biochemistry and physiology. McIntosh was the first to successfully apply the isoelectric focusing (IEF) technique for the identification of insect cell lines (McIntosh and Ignoffo 1983, 1989). Cell lines showed distinct patterns of their own, but could be closely correlated with their host or origin.

McIntosh demonstrated the feasibility of producing occlusion bodies of Hz*S*NPV in corn earworm and tobacco budworm cell lines and clones thereof (McIntosh and Ignoffo 1981; Lenz et al. 1991). Some clones produced significantly greater numbers of occlusion bodies (OB) and extracellular virus (ECV) than parental lines. The advantages of the *in vitro* system for virus production are that it provides a cleaner system, free from adventitious agents, one that is easily monitored, and could provide more continuity and flexibility during commercial production. The disadvantage of *in vitro* production lies in its greater cost. However, this problem is being solved with the development of

serum-free media in which the expensive component, fetal bovine serum (FBS), has been excluded. Hz*S*NPV has been produced in corn earworm lines grown in serum-free media with greater production of both OB and ECV than observed in cells grown in medium containing serum (McIntosh et al. 1991). Since insect cells can be produced in large-scale suspension cultures, the major impediment for commercial production of Hz*S*NPV *in vitro* is the low market demand. In a study of viral infectivity, it was discovered that virions released from OB by alkali treatment could be made more infectious for cell cultures by treatment with a proteolytic enzyme, proteinase K (McIntosh and Ignoffo 1988).

McIntosh et al. (1984), in one of the few complete studies of this kind, showed that *in vitro* specificity paralleled *in vivo* specificity and that *M*NPV tended to have a broader host range than *S*NPV. He demonstrated that Af*M*NPV has a wide host range *in vitro* and produced the highest ECV titer in the *H. subflexa* cell line (McIntosh 1991). *In vitro* systems can serve as a rapid means for establishing the host range of viral isolates from nature.

In 1980, with the arrival of T.A. Coudron, a Research Chemist, research was initiated that resulted in the discovery of biochemical pathways leading to basic information on virulence and infectivity of entomopathogenic fungi. Coudron discovered a complex enzyme profile used by entomopathogenic fungi for the degradation of chitin. The information provided significant detail about characterization of the enzymes involved in the infectivity of these organisms (Coudron et al. 1984). A two-enzyme system was shown to be secreted by entomopathogenic fungi for the degradation of insect chitin which was comprised of multiple forms of the enzymes in the system. Coudron also demonstrated a correlation of the chitinolytic activity with virulence where a pronounced increase in chitinolytic activity appeared in entomopathogenic strains prior to and at the time of infection (El-Sayed et al. 1989). A new semi-liquid medium and techniques for rearing entomopathogenic fungi were also developed that were ideal for the extraction of proteolytic enzymes produced by most Hyphomycetes (Coudron et al. 1985).

In 1985, W.C. Rice, a Research Microbiologist, initiated studies to map and characterize the genome of Hz*S*NPV and to identify site(s) and genes controlling desirable traits so as to develop techniques for manipulating these genes for enhanced effectiveness of the virus. Rice sequenced the Xho I F DNA fragment (6,964 base pairs) of the Hz*S*NPV. He found a 738 base pair open reading frame (orf) coding for the polyhedrin gene that was translated into a 246 amino acid polypeptide. DNA sequence analysis of the Xho I F fragment revealed the presence of 44 orf's. Ten orf's whose molecular weights were 10,000 daltons or greater were translated into polypeptides and used to search the National Biomedical Research Foundation (NBRF) protein data base. Other than polyhedrin, only orf-4067 was homologous to a family of proteins, whose members belong to the kinase gene family. The presence of a putative kinase gene in the sequence of the baculovirus DNA has led to the use of the kinase assay as a direct biochemical marker.

Serial passage studies of isolate Vhl in tissue culture cells performed by Rice resulted in the generation of an assortment of restriction endonuclease variants which fit into a number of discrete classes. Viral genomic changes were detected which were consistent with DNA insertions and/or deletions (McIntosh et al. 1987). Representatives of each class were bioassayed in corn earworm larvae and extrapolated LC_{50} values revealed an 800-fold difference in larval infectivity, indicating that possibly genes involved in virulence were disrupted (Rice et al. 1989).

RANGELAND INSECT CONTROL RESEARCH, BOZEMAN, MT. By Douglas A. Streett

In 1961, the Grain and Forage Insects Branch, Entomology Research Division, ARS, under the direction of R.G. Dahms, established a biological control of grasshoppers research project. J.E.

Henry was hired by Frank Cowan to initiate this project at the Rangeland Insect Laboratory at Bozeman, MT.

Historically, attempts to control grasshoppers and locusts with fungi and bacteria produced some encouraging results, but most attempts had little or no effect on grasshopper population densities. Several gregarines, an undescribed neogregarine, an amoeba (*Malameba locustae*) and a microsporidan (*Nosema locustae*) had been reported in grasshoppers. While not highly virulent, *M. locustae* was sufficiently detrimental to laboratory colonies of grasshoppers that it was necessary to develop therapeutic measures for disease control (Henry 1968; Henry and Oma 1975).

Field surveys of grasshoppers were conducted to determine the prevalence of known grasshopper pathogens and to isolate previously unknown pathogens. Two new species of microsporida were found and described — *Nosema acridophagus* (Henry 1967, 1969a) and *N. cuneatum* (Henry 1971b); and the first entomopoxvirus in Orthoptera was isolated from the migratory grasshopper (Henry and Jutila 1966; Henry et al. 1969). A crystalline array virus was also isolated from field-collected twostriped grasshopper. It represented the first isolation of an RNA virus infectious to grasshoppers and it appears to be one of the smallest viruses isolated from any living system (Jutila et al. 1970; Henry 1973; Henry and Oma 1973). Two new entomopoxviruses were also isolated from grasshoppers, and a cooperative study was initiated with W.H.R. Langridge of the Boyce Thompson Institute at Cornell University to do structural protein and DNA studies (Langridge and Henry 1981; Langridge et al. 1983).

Financial and physical limitations made it necessary to select one organism for investigation as a potential grasshopper microbial control agent. *Nosema locustae* was selected on the basis of virulence, host range, potential for mass production and prolonged storage, suitable viability in the habitat of the host, low cost application techniques, and potential for registration as a microbial insecticide. Like most microsporida in their respective hosts, *N. locustae* was not highly virulent. If applied when the predominant stages were third instars, *N. locustae* caused about 50% density reduction of various species within four weeks postapplication and 30–50% infection among survivors (Henry 1971a; Henry et al. 1973; Henry and Oma 1974a). In addition, infections result in significant reductions in fecundity among the survivors. The host range of *N. locustae* includes 58 species of grasshoppers, a species of cricket, and a pigmy grasshopper (Henry 1969b). Most species of grasshoppers and some species of crickets appear to be susceptible. *Nosema locustae* can be mass-produced with relative ease (Henry 1978); however, some difficulty has been experienced in storage of spores (Henry and Oma 1974b).

Studies of natural epizootics indicated that *N. locustae* should reduce both the extent and frequency of grasshopper outbreaks on rangelands, providing applications were made early in the season against economic densities and before serious damage occurred (Henry 1972). Henry (1978) reported on application techniques for *N. locustae* and potential for registration as a microbial insecticide.

In 1975, a large-scale pilot test on 37,312 hectares of rangeland was initiated. *Nosema locustae* was applied by aircraft at two rates and compared with a standard rangeland insecticide treatment of malathion, and with no treatment. The high dosage caused significant reductions in grasshopper densities during the season of treatment. A panzootic among grasshoppers caused by the fungus *Entomophaga grylli* occurred early in the second season and apparently reduced the prevalence of *N. locustae*. Nevertheless, the high rate caused significant reductions, and the low rate appeared to cause slight but not significant reductions in grasshopper densities during the two subsequent seasons. Parasitism of grasshoppers by entomophagous flies and nematodes decreased sharply in malathion-treated plots, but tended to increase in *N. locustae*-treated and untreated plots (Henry and Onsager 1982).

Nosema locustae became the first protozoan to be registered as a microbial insecticide in the U.S. in 1978. Another study was conducted to increase efficiency of production of spores of *N. locustae*. The differential grasshopper is a hardy species for laboratory rearing with a higher survival potential that results in greater spore production (Henry 1985). Oma and Hewitt (1984) reported that the females of this grasshopper infected with *N. locustae* consumed less food than uninfected females, but there was no significant difference in food consumption by infected and uninfected males.

Cooperative projects were initiated with scientists from Argentina; Carlos Lange and Georgina Luna came to Bozeman for training in insect pathology. Experimental infections were conducted with *N. locustae*, *N. acridophagus*, and *N. cuneatum* in 12 species of Argentine acridids in order to determine their susceptibility. All 12 species were susceptible to *N. locustae* (Luna et al. 1981). Lange returned to Bozeman in 1985 for further studies. A new species of microsporida, *Perezia dichroplusae*, was described from the Argentine grasshopper *Dichroplus elongatus* (Lange 1987).

D.A. Streett came to the Rangeland Insect Laboratory in 1980 as a post-doctoral scientist. The incidence of infection and transmission of an undescribed microsporidan in field populations of two species of grasshoppers were studied (Streett and Henry 1984). Because the original description of *N. cuneatum* was done with light microscopy, an ultrastructural investigation was undertaken and reported by Streett and Henry (1987).

During 1981–1983, studies funded by U.S.-AID were conducted on the susceptibility of West African grasshoppers to *N. locustae*. Application of spores on wheat bran to field plots in Cape Verde and Mauritania resulted in infection of most species of Acrididae. Based on the taxonomic diversity of these species, it was likely that most, if not all, West African grasshoppers were susceptible to infection by *N. locustae* (Henry et al. 1985a). Pathogenic microorganisms isolated from West African grasshoppers included entomopoxviruses, protozoa, fungi, and a rickettsia (Henry et al. 1985b, 1986). The DNA from six orthopteran entomopoxviruses were characterized. Restriction enzyme patterns for each of the viruses was found to be unique (Streett et al. 1986). Cross-infectivity studies of these six viruses to various species of grasshoppers showed that some isolates appeared to infect grasshoppers of different taxa, whereas some isolates seemed to be restricted to particular taxonomic groups of grasshoppers (Oma and Henry 1986).

The Grasshopper Integrated Pest Management (GHIPM) Project was organized in 1987 in response to record-setting grasshopper infestations that blanketed millions of acres of U.S. rangeland in the mid-1980s. Initiated as a pilot study, the project was designed to develop and integrate grasshopper control strategies into a total system for use by managers of public and private rangelands. The GHIPM Project was a co-operative effort managed by the APHIS in association with other USDA agencies and the U.S. Department of Interior, Environmental Protection Agency, state universities, and rancher associations. The mission of the Pathology Group at the Rangeland Insect Laboratory was to further develop known pathogens as control agents and look for possible unknown pathogens which could be developed as control agents. A viral DNA probe was developed to detect early entomopoxvirus infections in grasshoppers (Streett and McGuire 1988).

In November, 1987, Henry retired and Streett was hired to head up the pathology group. Henry is still active in on-going grasshopper control projects in Africa and the development of *Vairimorpha* sp. as a control agent for the Mormon cricket.

JAPANESE BEETLE LABORATORY, MOORESTOWN, NJ. By Michael G. Klein

See Wooster, OH. See also Beltsville, MD, for early history.

PLANT PROTECTION RESEARCH UNIT, ITHACA, NY. By Richard A. Humber

A program and laboratory for study of fungal entomopathogens for use in biological control was established and built at Orono, ME, in 1972 and moved to the Cornell University campus in 1978. Personnel were initially housed in the Boyce Thompson Institute and, in 1989, moved to the U.S. Plant, Soil, and Nutrition Laboratory. Before moving to Ithaca, the program was focused on an international cooperative effort involving the Rothamsted Experimental Station and the Pasteur Institute to develop techniques to mass produce and germinate resting spores of entomophthoralean fungi (now known as *Conidiobolus thromboides* and *C. obscurus*) for use against aphids (Soper et al. 1975).

A research collection of entomopathogenic fungal cultures started by Richard S. Soper and taken over in 1976 by Richard A. Humber evolved into one of the largest collections of microbial germplasm in ARS, and the world's foremost collection of entomopathogenic fungi. As of 1991, the ARS Collection of Entomopathogenic Fungal Cultures (ARSEF) comprised more than 3,200 isolates from more than 250 fungal species that are distributed on request. The catalog of the ARSEF culture collection (Humber 1992) is widely distributed. Staff at ARSEF provide identification of fungal pathogens without charge, and are internationally recognized for research on the biology and systematics of these fungi (e.g., Humber 1981, 1989; Roberts and Humber 1984), providing critical support worldwide for basic and applied programs involving fungal entomopathogens.

From 1980 to 1991, a program was established on the biology, epizootiology, and practical use of entomophthoralean fungi in the *Entomophaga grylli* species complex infectious to grasshoppers and locusts. The program led to the successful field establishment of an Australian isolate against grasshoppers in North Dakota under the auspices of a large-scale IPM demonstration project on grasshopper control (GHIPM). This project yielded the unexpected discovery that sun-basking by diseased grasshoppers may raise their body temperatures enough to cure infections by microbial pathogens (Carruthers et al. 1988b).

Early studies on grasshopper fungi led to the realization that many fungi in the Entomophthorales (and also many ascomycete and deuteromycete pathogens of invertebrates) routinely stop sporulating when desiccated but again produce infective spores when rehydrated. A process for drying mycelial mats of *Zoophthora radicans* (for use initially against spruce budworm) was developed and patented (McCabe and Soper 1985). Dried mycelia can be milled, stored, and rehydrated upon application to produce fresh infective spores in the field. Now, dried mycelia techniques are used successfully with diverse fungal entomopathogens. It is the predominant methodology worldwide for the practical application of fungi to control invertebrate pests.

Classical biological control introductions involving fungal entomopathogens are relatively rare, but the ARS Plant Protection Research Unit (PPRU) played a key role, in cooperation with the Commonwealth Scientific and Industrial Research Organisation (CSIRO), in successfully introducing a pathogen of spotted alfalfa aphid (SAA) (Milner and Soper 1980; Milner et al. 1982). The PPRU screened strains of *Zoophthora radicans* from the ARSEF culture collection for activity against SAA and guided the introduction of an Israeli strain of the pathogen into northeastern Australia. At the time, SAA was causing severe damage to Australian alfalfa and was the focus of a major pest control program within CSIRO.

In 1910–11, a Japanese pathogen of gypsy moth was introduced to six sites around Boston (Speare and Colley 1912) with no apparent successful establishment. This entomophthoralean fungus, which was later described as *Entomophaga maimaiga* (Soper et al. 1988), was nearly forgotten until Soper collected it in Japan in 1984 and began new studies of its potential to control gypsy moth (e.g., Shimazu and Soper 1986). A fungus causing widely publicized mortality of gypsy moth larvae across

the northeastern U.S. during 1989 and 1990 proved to be *E. maimaiga*. Because the fungus causing the panzootic was biochemically indistinguishable from Japanese strains of *E. maimaiga*, and because no modern introductions of *E. maimaiga* were made in the affected regions, it was inferred that the massive mortality of gypsy moth must have been caused by the fungus introduced 80 years earlier by Speare and Colley (Hajek et al. 1990). This case provides a rare and outstanding instance where it may be possible to follow the long-term survival and dispersal of an introduced insect pathogen.

Beauveria bassiana, the most common fungal entomopathogen, is distributed worldwide. The pathogen has been used widely to control Colorado potato beetle (CPB) in the former Soviet Union as well as various lepidopteran pests of both corn and forests in the People's Republic of China. However, it has not been commercialized or used widely in the U.S. or Europe. The PPRU coordinated the first substantive pilot field testing of *B. bassiana* in the U.S. against CPB in several potato-growing states (Hajek et al. 1987; Anderson et al. 1988).

During the 1980s, it became increasingly clear that many pathogens of insects had shown a poor track record for practical use in biological control programs because of insufficient understanding of how these disease agents operate under field conditions. An appreciation of the value of epizootiological studies (Onstad and Carruthers 1990) and modelling of host-pathogen interactions became a high priority in many invertebrate pathology laboratories. Leading work in these subjects was undertaken by the PPRU on *B. bassiana* against CPB and entomophthoralean pathogens against grasshoppers. These studies yielded a modular computer program called "Simulation Environment for Research Biologists (SERB)" (Larkin et al. 1988) that facilitated the rapid construction of useful simulation models by persons having no specialized background. A simulation modelling approach has been instrumental in evaluating and guiding epizootiological studies on grasshopper pathogenic fungi (Carruthers et al. 1988a).

HORTICULTURAL INSECTS RESEARCH LABORATORY, WOOSTER, OH. By Michael G. Klein

Following the transfer of the Insect Pathology Unit from Moorestown, NJ, to Beltsville, MD, in 1954, research on pathogens of the Japanese beetle ceased for many years. W.E. Fleming (1968) reviewed the many published and unpublished reports on efforts to control the Japanese beetle with protozoa, fungi, nematodes, bacteria, and rickettsia from 1920 (shortly after the discovery of the Japanese beetle near Moorestown, NJ) until 1964. This excellent summary has made a wealth of information available to insect pathology students and researchers.

Most of the information during the past 40 years on pathogens of the Japanese beetle has centered on the use of *Bacillus popilliae*, the causal agent of milky disease. Ladd and McCabe (1966) followed up the earlier milky disease colonization program by surveying the state of New Jersey. They found the milky disease organism active at colonization sites, and movement of the bacteria into uninoculated areas. Schwartz and Townshend (1968) reported that *B. popilliae* caused an increase in hemocytes in diseased larvae early in the infection process, but no alteration in the coagulation of the hemolymph. Further work by P.H. Schwartz (Schwartz and Sharpe 1970) demonstrated that spores of *B. popilliae* produced *in vitro* lacked infectivity when fed to Japanese beetle larvae. Problems in obtaining *in vitro* sporulation, and lack of infectivity of the spores that were produced, led to the cessation of efforts by USDA in this area.

The Japanese Beetle Laboratory was moved from Moorestown, NJ, to Wooster, OH, in September 1971. M.G. Klein et al. (1976) prepared a bibliography of the milky disease bacteria. Nearly one third of the 250 citations dealt with bacterial physiology as a result of the efforts to produce *B. popilliae* on artificial media. Since that time, over 80 additional papers on milky disease bacteria

have been published. Fleming and Ladd (1979) updated information for the homeowner and other turf grass managers on the use of milky disease for suppression of Japanese beetle populations.

During the past ten years, Klein (1981, 1982, 1986, 1988, 1989, 1992; Klein and Jackson 1992) has focused attention on the prospects of using milky disease bacteria against scarab larvae throughout the world, and examined the problems that prevent more successful use of the bacteria. Recently the misidentification and lack of infectivity in bacteria produced on artificial media was demonstrated (Stahly and Klein 1992). The use of other bacteria (Klein and Jackson 1992) and other microorganisms against scarab and non-scarab pests of turf have also been explored (Klein 1982, 1988, 1989; Kaya et al. 1992, 1993; Cranshaw and Klein 1994). Klein (1990, 1993) also examined the past use of entomopathogenic nematodes against soil-inhabiting pests, identified the obstacles to greater acceptance of these organisms in the suppression of pest populations, and demonstrated that they could be used as inoculative agents (Klein and Georgis 1992).

The mission of the Japanese Beetle Laboratory has been expanded to cover other horticultural pest insects, and to develop new application technologies. Insect pathology will remain an important component.

U.S. VEGETABLE LABORATORY, CHARLESTON, SC. By Kent D. Elsey and James M. Schalk

In 1967, F.P. Cuthbert, Research Entomologist at the U.S. Vegetable Laboratory, Charleston, SC, discovered a mermithid nematode parasitizing *Diabrotica* spp. in the Charleston area (Cuthbert 1968). This nematode was described by Poinar (1968) and named *Filipjevimermis leipsandra.* Subsequent research on this nematode at Charleston involved mass rearing (Creighton and Fassuliotis 1982), temperature relations (Elsey 1989, 1991), seasonal fluctuations in the field, and infectivity in the laboratory (Creighton and Fassuliotis 1980). Attempts to augment natural populations in corn plantings against *Diabrotica* larvae were hindered by problems associated with soil moisture and temperature interactions.

Several entomopathogenic fungi attack sweetpotato weevil, including *Beauveria bassiana*, *Isaria* sp., and *Metarhizium anisopliae*. Both *B. bassiana* and *M. anisopliae* were shown to have some potential for management of the weevil (Chalfant et al. 1990). Entomopathogenic nematodes that attack the weevil include *Steinernema* sp. and *Heterohabditis heliothidis*. Unidentified heterorhabditid species and other rhabditid nematodes have been isolated from sweetpotato weevil in southern Florida. A heterorhabditid nematode, 'HP88' strain, was more effective than a steinernematid nematode and chemical insecticide in suppressing weevil populations and protecting roots from damage (Chalfant et al. 1990).

In another study, interaction between larvae of the banded cucumber beetle, a resistant sweetpotato cultivar, a susceptible sweetpotato clone and an arthropod nematode, *H. heliothidis* (South Carolina strain) were evaluated. No significant interactions between the nematode and cultivar type were observed, and adult emergence was drastically reduced when second instars were exposed to the nematode in both cultivars. When second instars were exposed to the nematode, the duration of the adult eclosion period was reduced because of the lower number of insects emerging. The nematode had no effect on emergence or duration of eclosion period of third instars. Higher levels of parasitism in younger larvae can be attributed to their longer development time which increases their exposure to the parasite. The mobility of third instars may be greater than younger larvae allowing them to evade the parasite. They may also be less susceptible to the parasite. The duration of the eclosion period was negatively correlated with adult weight (Schalk and Creighton 1989).

Efficacy of *Steinernema carpocapsae* (All Strain) against banded cucumber beetle larvae was investigated (Schalk unpublished). Late first instar and early second instar larvae were confined in

crispers in the laboratory and exposed to the nematode at the rate of 1/1.2 g of soil (blasting sand). Emergence of adults in the untreated controls were 80% while 0.5% emergence was observed in the parasite treatment. Mean adult weight was 14.6 mg for the controls and 8.2 mg for the parasite treatment.

NORTHERN GRAIN INSECTS RESEARCH LABORATORY, BROOKINGS, SD. By Jan J. Jackson

G.R. Sutter initiated the insect pathology/biological control program at the Northern Grain Insects Research Laboratory (NGIRL), Brookings, SD, in 1965. During the late 1960s, several cutworm species and the armyworm were serious pests of small grains and corn in the Northern Plains. Calkins and Sutter (1972) developed techniques to assist surveys of parasitism and diseases in field populations. To support pathological studies, rearing methods were developed for the army cutworm (Sutter and Miller 1972) and the pale western cutworm (Sutter et al. 1972). Rearing methods were also developed for the parasitoids *Glyptapanteles militaris* using the armyworm (Calkins and Sutter 1976) and *Copidosoma bakeri* using the army cutworm. The histopathology of rickettsia-like organisms in four species of carabid beetles (Sutter and Kirk 1968) and a poxvirus (Sutter 1972), a non-occluded virus (Sutter 1973), and a granulosis virus (Jackson and Sutter 1985) in the army cutworm were subsequently reported. McCarthy et al. (1975) further characterized the poxvirus of the army cutworm.

Entomological research at the NGIRL shifted to an emphasis on corn rootworms in the early 1970s. Southern corn rootworm larvae and adults of the western and northern corn rootworms were found to be insensitive to treatments with *Bacillus thuringiensis* and *B. popilliae* (Sutter 1969). Field surveys for parasites and diseases of corn rootworm adults in South Dakota yielded no parasites and few pathogens. Collections of adults from other Corn Belt states also yielded few parasites or pathogens but the incidence of natural enemies increased with collections from states along the southern boundary of the rootworm population distribution. Gregarine protozoans were frequently found in field collected adults but the incidence was low most years. Gregarine infections in laboratory colonies were often extensive and when combined with nutritional stress, high adult mortality was observed. Gregarine morphology, development, pathogenicity, and cultural methods to reduce gregarine infections in laboratory colonies of rootworms were described (Brooks and Jackson 1990). In 1983, studies on insect-parasitic nematodes for larval corn rootworm control were initiated. *Filipjevimermis leipsandra* and several steinernematids were found to be pathogenic for rootworm larvae and pupae. Jackson and Brooks (1989) described the pathogenicity and immune response of four strains of *Steinernema carpocapsae*. The susceptibility of larval stages and development in rootworm larvae and pupae was described (Jackson 1985). Laboratory and field evaluations have been encouraging but improved efficacy is needed.

COTTON INSECTS RESEARCH LABORATORY, BROWNSVILLE, TX. By Carlo M. Ignoffo, Howard R. Bullock, Leslie C. Lewis, and Clayton C. Beegle

In 1959, investigations in insect pathogens/microbial control began in the Rio Grande Valley at Brownsville, TX, with the employment of C.M. Ignoffo. Ignoffo focused his basic and applied research on the use of entomopathogens to control cabbage looper on truck crops, and *Heliothis/Helicoverpa* spp. and other lepidopterans infesting cotton. Ignoffo conducted early research on the effects of *Bacillus thuringiensis* (Bt) on pink bollworm larvae which included the effects of temperature and humidity on mortality (Ignoffo 1962a and b). Later field cage tests were conducted with Bt for the control of the pink bollworm (Ignoffo and Graham 1967). Earlier attempts by investigators to continuously rear the cabbage looper generally were unsuccessful because of contaminants many thought to be inherent occult viruses. This was proven false when methods were developed to mass rear the cabbage looper using aseptic techniques and a newly developed semi-

synthetic diet (Ignoffo 1963a). In further studies, Ignoffo determined the sensitivity of Bt to various antimicrobial substances commonly used in insect semi-artificial diets that might influence its activity (Ignoffo 1963b). These studies demonstrated the undesirable effects of some of these materials on Bt and the consequent influence on apparent activity in bioassays. Their potential to control Bt contaminants in mass rearing was also demonstrated. Later, Ignoffo and Dutky (1963) demonstrated the antimicrobial effects of sodium hypochlorite on the viability and infectivity of Bt and *Beauveria* spores and the nuclear polyhedrosis virus (NPV) of the cabbage looper. Ignoffo (1964a) also studied the effects of temperature and water on the viability and virulence of Bt spores. The above studies were important to the later development of mass rearing, production and standardization systems for the *Heliothis/Helicoverpa* and cabbage looper NPV.

Ignoffo's efficacy studies with microbial control agents were conducted using Bt for the control of the cotton leafworm, a pest of cotton in the southern U.S. (Ignoffo et al. 1964). These studies led to more intensive studies on the development of baculoviruses and other entomopathogens as insect control agents.

The previous studies by Ignoffo (1963a) on mass rearing the cabbage looper served as a basis for developing mass production methods for the singly embedded NPV infectious to this species. The studies on antimicrobial agents previously conducted also were incorporated into the production schemes in order to reduce extraneous microbial contaminants. Ignoffo (1964c) published the first mass production method for a baculovirus utilizing the newly developed semi-artificial diet. This was the first publication on insect virus production in which live host plants were not used for the host insect used for production. Ignoffo (1964b) described bioassay procedures also utilizing the new semi-artificial diets which provided methods for determining virulence of the produced virus as a basis for standardization of production lots. The methods for cabbage looper and corn earworm rearing and virus production were later consolidated into a methodology publication (Ignoffo 1966d).

Ignoffo's earlier work led to an intensive study in 1961 of a nuclear polyhedrosis virus infectious to the *Heliothis/Helicoverpa* complex as a microbial control agent (Ignoffo 1973a). This bollworm/budworm complex was selected because of the worldwide distribution of species which are severely destructive to many economic plants (e.g., cotton, corn, tobacco, tomatoes, vegetable crops, seed crops). The virus used in these studies and eventual commercialization was first isolated from diseased *Heliothis/Helicoverpa* larvae attacking cotton in the Rio Grande Valley of Texas (Ignoffo 1965a). Annual costs to control *Heliothis/Helicoverpa* were extremely high. Before commercialization of the virus, its effectiveness against field populations on several crops, amenability to continuous large-scale production under laboratory conditions, nucleic acid composition, and its effects on man, other animals and plants were determined (Estes and Ignoffo 1965; Ignoffo 1965a, b, and c; Ignoffo and Heimpel 1965; Ignoffo et al. 1965). These studies indicated further development was warranted.

Steps toward the eventual commercialization began conceptually in 1961 and continued through early 1965 at the Brownsville laboratory (Ignoffo 1965a, b, and c; Ignoffo et al. 1965). From 1962 until 1964, basic research on insect host mass production, virus production, activity and standardization was conducted which set parameters for pilot plant and full production phases. Field tests on corn, cotton, and grain sorghum were conducted with the virus resulting from the above studies (Ignoffo 1965d; Ignoffo et al. 1965). Safety tests (Ignoffo and Heimpel 1965) were also initiated in anticipation of submitting a registration package to the U.S. Food and Drug Administration (FDA).

The rearing techniques developed in this program made it possible to produce large numbers of *Helicoverpa zea* larvae, and resultant virus production throughout the year. The virus was produced continually from May through August 1963, providing large amounts of standardized material for

field testing as described above. Approximately 250,000 larvae were produced during this period or enough to treat 2,000–8,000 acres of cotton. The methods and procedures developed during this time were then adopted to pilot production and production phases.

Other studies conducted in support of this project included the effects of temperature on *H. zea* larvae exposed to sublethal doses of the virus (Ignoffo 1966b). Because it was possible that the virus might be used in tank mixes with chemical insecticides and adjuvants, the influence of these materials on the virus was determined (Ignoffo and Montoya 1966) as well as the possible use of dust formulations of virus (Montoya and Ignoffo 1966). Ignoffo and Garcia (1966) also determined the influence of pH on the activity of inclusion bodies which could be of major concern in certain parts of the United States having highly alkaline water. Ignoffo (1966a and c) determined the influence of larval age on susceptibility of both the bollworm and tobacco budworm. In 1965, Ignoffo was employed by Bioform Corporation, later acquired by International Minerals Corporation, to develop the *Heliothis/Helicoverpa* virus into a commercial product. The *"Heliothis S*NPV" was registered in 1970. FDA granted a temporary exemption from the requirement of a tolerance. It was the first baculovirus registered and mass produced for commercial use. Commercial products based on this exemption were initially made available by International Minerals Corporation, Libertyville, IL, and Nutrilite Products Inc., Buena Vista, CA. In the late 1970s and early 1980s, Sandoz Inc., San Diego, CA, produced and marketed the virus under the trade name of "Elcar"™. Although still registered, the virus is not now produced commercially or sold for control of the bollworm/budworm complex in the U.S. More cost competitive chemical pesticides (i.e., pyrethroids) introduced during the late 1970s and early 1980s eliminated the market.

H.R. Bullock became a member of the insect pathology investigations at Brownsville, Texas in 1965 after having a post doctoral appointment at the ARS Insect Pathology Laboratory in Beltsville, MD. Bullock and Dulmage (1969) conducted tests with Bt for control of the pink bollworm, which had recently also become a serious pest of cotton in Arizona and California. Their laboratory tests indicated larvae were highly susceptible and they therefore conducted field cage studies to determine if the microbial had potential for pink bollworm control. They found that rosetted blooms and mines were reduced, and number of bolls was higher, and concluded that Bt should be investigated under field conditions for pink bollworm control. Bullock (1967) also conducted research on the persistence of the *"Heliothis S*NPV" on cotton foliage and found that most activity was lost after one day. He proposed losses may be due to ultraviolet (UV) light and/or mechanical loss. Bullock et al. (1970a) conducted further studies on inactivation of *"Heliothis S*NPV" by determining the influence of monochromatic UV on activity. Wavelengths of 257 nm and 307.5 nm inactivated the virus. Visible and infrared may also have had an effect. Bullock also evaluated encapsulated *"Heliothis S*NPV" polyhedra obtained from the National Cash Register Company (Dayton, OH). Such encapsulated polyhedra had increased persistence under field conditions. These studies further helped in the understanding of factors which may affect virus persistence under field conditions, one of the major impediments to the development of viruses as microbial control agents.

Bullock et al. (1969) found that high concentrations of formaldehyde would reduce cytoplasmic polyhedrosis virus (CPV) contamination of pink bollworm eggs but the effect also was dependent upon the level of contamination present. They concluded that surface contamination of eggs was an important means of virus transmission. They also noted the eggs were not dechorionated and thus timing of the treatment was not critical. In further investigations, Bullock et al. (1970b) noted the adverse effects of CPV infection on pink bollworm such as delayed development, larval mortality, reduced longevity, and fecundity of diseased moths. However, egg hatch and mating were not affected. Bullock (1972) determined the therapeutic value of heat treatments for a cytoplasmic polyhedrosis virus infectious to tobacco budworm larvae. He also noted teratological effects incurred with increasing temperatures. These two treatments provided several methods of managing CPV in insect colonies.

H.T. Dulmage became a staff member in the mid-1960s and conducted research on *Bacillus thuringiensis* (Bt). In the early development of Bt, the spore was thought to be the sole source of insecticidal activity leading to emphasis on spore production in commercial fermentations. This led to the acceptance of spore count as a method of standardization. However, Dulmage and Rhodes (1971), and others, demonstrated that there was no reliable relationship between spore-count and potency. When it was determined that the δ-endotoxin was the primary insecticidal component, conferences were convened to develop a protocol to standardize Bt products on an international unit (IU) basis (Dulmage 1973a and b). A preparation of Bt subspecies *thuringiensis* (designated E-61) was adopted as the international standard and was assigned a potency of 1000 IU/mg (Dulmage et al. 1971; Dulmage 1973a). Meanwhile, industry had adopted a more potent strain of Bt from subspecies *kurstaki*. Thus, the U.S. Environmental Protection Agency requested that a standard be produced and adopted of the same serotype as that being commercially produced (subspecies *kurstaki*). In 1972, HD-1-S-1971 was adopted as the Primary U.S. Reference Standard with an assigned potency of 18,000 IU/mg (Dulmage 1973a and b). Today, all preparations of Bt produced in the U.S. for use against lepidopterous larvae are standardized against HD-1-S-1971 or its successor HD-1-S-1980. Standard HD-1-S-1980 has a potency of 16,000 IU/mg. Some companies also use an international HD-1 standard which was initially standardized against HD-1-S-1971. Dulmage also contributed to the protocol used to standardize Bt subspecies *israelensis* (McLaughlin et al. 1984).

Dulmage (1970a) isolated a Bt subspecies *kurstaki* (first identified as subspecies *alesti*; see de Barjac and Lamille 1970) from diseased pink bollworm larvae. This isolate, designated HD-1 (HD = Howard Dulmage) by Dulmage, proved to be from 20 to 200 times more potent than the isolates used in existing commercial products (Dulmage et al. 1978). In 1970, Abbott Laboratories entered the market with Dipel®, the first commercial preparation based on HD-1. Dulmage accumulated isolates of Bt world wide to study diversity within and between isolates. To accomplish this task, he formed the International Cooperative Program on the Spectrum of Activity of Bt (BtICP).

BtICP was designed to find more potent isolates of Bt to use in the control of insect pests. This program was also developed to learn more about the insecticidal, serological, and bacteriological characteristics of the toxins produced by different Bt isolates.

Dulmage contributed substantially to developing insect-diet-based assays to standardize Bt products (Dulmage et al. 1971, 1976; Burgerjon and Dulmage 1977; Beegle et al. 1982). His assay was the first to propose the use of a standardized insect and a standardized procedure to determine IUs of products. Many of the present day assays are modifications of the technique.

Dulmage was a member of a team that determined that isolates within subspecies of Bt could be distinguished by crystal serology (Krywienczyk et al. 1978, 1981). He also contributed significantly to early work with fermentation media to produce spore/crystal powders with maximum yields of activity (Dulmage 1970b, 1971; Dulmage et al. 1970; Salama et al. 1983). He was also a member of many research teams that investigated insecticide activity of many isolates of Bt and *B. sphaericus* against many insects (Davidson et al. 1984; Dulmage and Aizawa 1982; Trottier et al. 1988); identified previously unknown isolates (Dulmage and de Barjac 1973; Rodriguez-Padilla et al. 1990); identified factors affecting insecticidal activity (Lacey et al. 1978); and conducted initial research on the genetics and protein chemistry of *B. thuringiensis* (Gonzalez et al. 1981; Yamamoto et al. 1983).

C.C. Beegle joined the laboratory in 1976 through a Cooperative Agreement with Texas A&M University in order to expand the Bt research program; he became an ARS scientist in 1977. The first standardized assay developed to determine potency of Bt products specified the incorporation of aureomycin with larval diet to eliminate vegetative stages of Bt. Research by Beegle et al. (1981b), however, showed that LC_{50} values of Bt, when neonatal larvae of three insect species were used in bioassays, were not significantly different when antibiotic was omitted from the insect diet.

Conversely, when the antibiotic chlortetracycline hydrochloride was incorporated into the bioassay diet of 4-day-old larvae, the LC_{50} values were increased from 2 to 67 times. Beegle et al. (1986) developed the assay defining the use of subspecies *kurstaki* (HD-1-S-1980) as the reference standard used in the U.S. Also, it was found that the use of a standard will not in all cases correct for differences in assay techniques (Beegle 1990); thus, a new assay was jointly developed by ARS and U. S. commercial firms to determine potencies of lepidopterous-active preparations (Beegle et al. 1991). Even though sophisticated, highly repeatable, standardized bioassays have been developed, researchers cannot duplicate the impact of the environment in laboratory settings, i.e., field performance dosages cannot always be extrapolated from laboratory data (Beegle et al. 1982).

Beegle was actively involved in research on production of exotoxins by certain isolates (Mohd-Salleh et al. 1980), use of new methods such as crystal serology to determine that some mosquito-active isolates of Bt have mixed crystals (Krywienzcyk et al. 1981), identification of isolates with superior potencies (Beegle 1983; Beegle and Yamamoto 1983), and use of fermentation to increase potencies of Bt isolates (Beegle et al. 1991). He also determined the half-life of insecticidal activity on cotton leaves was between 15 and 2 days (Beegle et al. 1981a).

KNIPLING-BUSHLAND U.S. LIVESTOCK INSECTS RESEARCH LABORATORY, KERRVILLE, TX. By Richard E. Gingrich and Kevin B. Temeyer

Research with arthropod pathogens at the Livestock Insects Laboratory (now the Knipling-Bushland U.S. Livestock Insects Research Laboratory), Kerrville, TX, began in 1964 with investigations by R.E. Gingrich on the use of *Bacillus thuringiensis* for control of horn, stable, and house flies. The objective was to develop microbial feed additives that would pass through the bovine intestine and control larvae that normally develop in contact with the feces. After demonstrating that currently available commercial Bt products were active when fed to cattle it was learned that the β-exotoxin was the toxic agent (Gingrich 1965; Gingrich and Eschle 1966, 1971; Gingrich and Haufler 1978). Applications by incorporation in slow release boluses deposited in the rumen and by incorporation in daily rations of range cubes were successful for controlling larvae in feces and, in case of the latter application, for reducing adult horn fly populations on range cattle (Gingrich 1984). The safety of β-exotoxin applied in this manner was demonstrated when cows produced normal offspring after sustained ingestion of β-exotoxin during pregnancy. In further studies, it was determined that the soluble exotoxins produced by Bt are heterogeneous in chemical character, spectrum of susceptible host insects, and mammalian toxicity. The potential of Bt for control of biting lice was also demonstrated (Hoffmann and Gingrich 1968; Gingrich et al. 1974).

Gingrich participated in the International Cooperative Program (BtICP), initiated by another ARS scientist, H.T. Dulmage, to study the spectrum of activity of Bt (Dulmage et al. 1981). Using horn fly larvae, and the "goat louse", *Bovicola* sp., he demonstrated the persistence of exotoxins in the experimental samples distributed to cooperators for bioassay and presented further evidence of the heterogeneity among them.

This research continued through 1982 when K.B. Temeyer was hired to continue Bt research begun by Gingrich, and to assess the potential development, using recombinant DNA technology, of Bt as a microbial agent against biting flies. In addition to the cooperative screening work with Dulmage, work with β-exotoxin was being conducted in Kerrville. Previous work had clearly demonstrated the toxic effect of β-exotoxin to fly larvae. In order to assess the toxicity of components other than β-exotoxin, it was necessary to develop an assay capable of determining how much β-exotoxin was present in a particular preparation of Bt. This was accomplished through use of high performance liquid chromatography (HPLC) (Oehler et al. 1982). Further research demonstrated that β-exotoxin from *B. thuringiensis* subspecies *morrisoni* was differentially toxic to male and female mice, with

males being more sensitive than females (Haufler and Kunz 1985). β-exotoxin was also shown to exhibit toxic and teratological effects to larvae of the oriental rat flea (Maciejewska et al. 1988).

Careful analysis of the literature, together with thorough review of the horn fly larvae bioassay results obtained with various strains of Bt appeared to suggest that the crystal protein of *B. thuringiensis* subspecies *israelensis* (Bti) might be larvicidal to horn flies, but that the Dulmage preparations were not stable under prolonged storage. Bioassay of freshly grown Bti preparations confirmed that subspecies *israelensis* was larvicidal to horn flies. Biochemical separation of endospores, crystal protein, and low-density particulate matter coupled with bioassay revealed that the larvicidal activity resided in the crystal protein (δ-endotoxin) and low-density particulate fractions. The toxicological properties of the two fractions were distinct, suggesting the presence of at least two different Bti toxins possessing larvicidal activity to horn flies. Both toxins appeared at sporulation, and were not produced in the presence of streptomycin, an inhibitor of protein synthesis, suggesting that Bti produced two sporulation-specific proteins which were larvicidal to horn flies (Temeyer 1984). This was the first report of Bt crystal protein toxicity to muscid flies and the first report of the presence of a second Dipteran-active toxic protein produced by Bti. The possibility that one of the Bti toxins might be related to β-exotoxin was considered. *Bacillus thuringiensis* subspecies *israelensis* was not known to produce β-exotoxin, an ATP analog exhibting strong larvicidal activity to flies and produced by a number of Bt strains during vegetative growth (see Sebesta et al. 1981). Further analysis, together with HPLC confirmed that neither Bti preparations contained β-exotoxin (Temeyer 1990b). These results suggested that there were at least three distinct toxins which might form the basis for development of a Bti-derived control methodology for biting flies through the use of recombinant DNA technology. Interestingly, preparations of *B. sphaericus* known to exhibit high toxicity to mosquito larvae failed to demonstrate toxicity to horn fly larvae by bioassay (Temeyer unpublished). It is not known whether *B. sphaericus* toxins are ineffective to horn fly larvae, or whether they are inactivated by components of the bovine fecal medium.

Identification of specific toxic proteins was difficult due to problems in obtaining biochemical separation of the multiple crystal proteins present in subspecies *israelensis* (Chilcott et al. 1983; Pfannenstiel et al. 1984; Thomas and Ellar 1984). It seemed that a more convenient approach might be to clone the individual crystal protein components separately into a non-toxic genetic background such as *B. subtilis*, and screen recombinants expressing the various Bti crystal proteins separately and in combinations to assess individual toxicity of proteins, and the potential synergistic interactions which might occur. Construction of organisms containing recombinant DNA from another species required approval by a Recombinant Advisory Committee (RAC) or an institutional biosafety committee (IBC) in accordance with the "NIH Guidelines", whereas construction of homologous recombinants of Bt did not require advance approval. But there was no well characterized cloning system available for Bt. There was considerable confusion within the agency and elsewhere at the time as to what body had the authority and regulatory jurisdiction to conduct biosafety reviews. This situation resulted in considerable delay in commencement of the planned experiments. The ARS Southern Plains Area had no IBC and only one laboratory then conducting recombinant DNA research. Approval to construct recombinant microorganisms containing Bti toxin genes was granted by the ARS Beltsville Area IBC in 1986. However, by that time, the key personnel at Kerrville were heavily engaged in research to develop a recombinant vaccine for cattle grubs (*Hypoderma* spp.).

There were a number of problems encountered in attempts to develop a homologous cloning system for *B. thuringiensis*. These included instability of recombinant DNA in *Bacillus* spp., the lack of homologous cloning vectors, and the lack of reliable methods for generating protoplasts for transformation (Chang and Cohen 1979), and then regenerating cell walls for the transcipient protoplasts. In addition, bioassays were extremely cumbersome, as well as problematic due to variability in bovine fecal matter resulting in occasional high mortality in control groups. This condition presented a strong disincentive to laborious preparation of small amounts of test material

knowing that subsequent bioassays could use all of the available material without providing any useable data. Therefore, it was important to determine if simple modifications of the horn fly larval medium or bioassay procedure could increase reliability of bioassays.

As a first approach to development of a semi-defined horn fly larval medium to replace the bovine fecal medium used in bioassay, a series of supplementation experiments were performed to determine the permissible osmotic parameters and to test the effects of supplementation with simple nutritional additives. Initially, sucrose was chosen as a test supplement for determination of permissible osmotic parameters, as it was thought unlikely to be toxic or even be taken up by the larvae. Thus, it probably would function as an inert solute in the bioassay system. Surprisingly, all concentrations of sucrose tested resulted in death of the larvae, as did many other carbohydrates. It was noted, however, that the larvae frequently migrated out of the fecal medium prior to death, and that, in some cases, gas evolution was apparent in the larval (fecal) medium, suggesting fermentation was taking place. Addition of streptomycin and monitoring of fecal medium pH versus time following carbohydrate supplementation confirmed that fermentation and consequent wide swings in the supplemented fecal medium pH appeared to be responsible for larval death (Temeyer 1990a) rather than direct toxicity of sugars as had been previously suggested for similar systems (Galun and Fraenkel 1957). It was also found that lipids appeared to be nutritionally limiting factors in horn fly larval nutrition, and supplementation with cholesterol, inositol, corn oil, or egg yolk resulted in production of heavier larvae and pupae, and increased survival to adulthood (Temeyer unpublished). Routine supplementation of bovine fecal medium with cholesterol, inositol, egg yolk, corn oil, or a combination of these, did not interfere with bioassays of preparations containing one or both of the two Bti toxins (Temeyer unpublished). It is interesting to note other strains of Bt have also been shown to possess similar toxicity to horn fly larvae as has subspecies *israelensis* (Temeyer unpublished). One of these, strain CAT-44 of *B. thuringiensis* "var. *fluffiensis*", obtained its name in a somewhat novel manner. P.A.W. Martin (Beltsville) had been attempting to determine the ecological niche occupied by Bt, and isolated strains of Bt from nearly everywhere she had looked. One day a visiting friend remarked, "Your lab smells like my cat's feet!". Just for fun, Martin made a paw imprint on a petri plate containing Bt-selective agar, and a number of colonies developed, including a strain with previously unknown characteristics. When she was talking with a reporter for a news article and related the story of how the strain was isolated, the reporter asked for the strain name. Martin replied that according to usual procedures strains are named after the source of discovery (place or person), she supposed that this strain should be named *"fluffiensis"* since the name of the cat was "Fluffy". The name stuck, though it has not been published in scientific literature.

Cloning experiments generally produce transcipient populations consisting of several thousand to several million potential recombinants. Screening such a large number of potential recombinants by bioassay was clearly not feasible. Alternatively, development of monoclonal antibodies was believed to offer a method for screening recombinant bacteria for production of Bti presumptive toxins which could then be subject to bioassay after selection of high expression recombinant clones. Therefore, a series of hybridomas secreting monoclonal antibodies specific for various component crystal proteins of Bt were constructed (Temeyer et al. 1986; Temeyer unpublished). U.S. Patent No. 4,945,057 (Temeyer et al. 1990) was granted covering development and use of hybridomas and their monoclonal antibodies.

Production of Bt protoplasts was determined to be unreliable by routine methods, and early experiments indicated that Bt cultures varied in sensitivity to lysozyme, with lysozyme-sensitive cultures developing resistance to lysozyme with the growth phase. Alternative methods using a commercially available N-acetylmuramidase or simple autolytic digestion improved the removal of Bt cell walls for production of protoplasts or cell-free lysates (Temeyer 1987). Unfortunately, the

difficulty in regenerating the cell walls after complete removal has not yet been overcome, making protoplast transformation an, as yet, unreliable method for genetic exchange in *B. thuringiensis*.

Instability of recombinant DNA in *Bacillus* species has been a frequently encountered problem. It is generally believed that the instability is a result of a combination of properties of the available cloning vectors and uncharacterized recombination pathways in *Bacillus* spp. Progress has been made in molecular characterization of potential mechanisms of recombination for different cloning vectors in *Bacillus* spp. (Temeyer and Chapman 1987; Hopkins et al. 1990; Temeyer et al. 1991). In addition, new cloning vectors are being developed which appear to exhibit improved stability in *Bacillus* spp.

Additional experiments conducted with Tom Benoit (ARS, College Station, TX) verified that there was no cross-resistance to Bti in bioassays using fly strains with known resistance to pyrethroid or organophosphate pesticides (Temeyer and Benoit unpublished). As of November 1991, several of the Bti crystal protein genes have been cloned in *Escherichia coli* at the Kerrville laboratory. Reporter gene constructs are being developed to evaluate expression of unknown genes in alternate genetic backgrounds, as well as new cloning vehicles for Gram-positive bacteria with specific improvements in plasmid structure.

HONEY BEE RESEARCH, WESLACO, TX. By William T. Wilson

In 1985, W.T. Wilson of the Honey Bee Disease Investigations Laboratory, Laramie, WY, moved to the ARS Subtropical Agricultural Research Laboratory at Weslaco, TX, to continue studies on the honey bee.

A rare internal protozoan (*Malpighamoeba mellificae*) was discovered in honey bee colonies in the southcentral U.S. that were experiencing adult bee mortality and severe population loss (Wilson and Collins 1992). With the arrival of the Africanized honey bee in south Texas in the autumn of 1990, a portion of the Weslaco bee research program was directed towards the diseases and parasites of this more defensive bee. Current studies are directed towards determining whether bees of African ancestry (Africanized) are more resistant to *Acarapis woodi*, *Varroa jacobsoni* and *Nosema apis* than bees of European ancestry. In 1988, A.M. Collins was appointed Research Leader of the Honey Bee Research Unit at Weslaco. In 1992, construction started on a new building to house the research staff and facilities.

BEE BIOLOGY AND SYSTEMATICS LABORATORY, LOGAN, UT. By John D. Vandenberg

The Bee Culture Laboratory at Logan, UT, was established in 1947 under the direction of F. Todd. In 1973 the unit was named the Bee Biology and Systematics Laboratory.

Insect pathology research at the laboratory concentrated on chalkbrood in the alfalfa leafcutting bee, but related studies of fungus infections of other bees have also been reported. Much of the work on leafcutting bee chalkbrood has been done cooperatively in the last 15 years. Specific Cooperative Research Agreements for this research, funded by ARS, were established with W.P. Stephen (Oregon State University), N.N. Youssef (Utah State University), D.F. Mayer (Washington State University), and L.P. Kish (until 1988) and C.R. Baird (University of Idaho). Additional cooperation and support has been provided throughout this period by the Northwest Alfalfa Seed Growers Association.

Significant research accomplishments are many, and include the first record of chalkbrood in North America (Baker and Torchio 1968). Studies of fungi associated with the alkali bee and other bees (Batra and Bohart 1969; Batra et al. 1973) and studies of chalkbrood in the "blue orchard bee", *Osmia lignaria propinqua* (Youssef et al. 1985; Rust and Torchio 1991) are the only studies of

pathogens of these bees. Other accomplishments of laboratory scientists and specific cooperators constitute the history of research on chalkbrood in the alfalfa leafcutting bee.

The alfalfa leafcutting bee is a commercially important pollinator of alfalfa in western North America. Bee populations are maintained near alfalfa fields in nest shelters filled with wooden, styrofoam or paper nest materials with drilled holes. Female bees construct a linear series of leaf-lined cells within the tunnels. Each cell is filled with pollen and nectar before an egg is laid. The bees overwinter as mature larvae (prepupae) and emerge as adults in early summer. Chalkbrood was first reported from commercial alfalfa leafcutting bee populations in 1974. Since then it has spread throughout most areas of bee cultivation. Larval mortality due to this disease can exceed 50% in some populations.

Fichter et al. (1981) developed a laboratory rearing system for alfalfa leafcutting bee larvae which facilitated a series of studies on chalkbrood etiology and pathogenesis. Initially, a viral etiology followed by secondary fungus invasion was suggested for this mortality. However, Vandenberg and Stephen (1982) clearly showed *Ascosphaera aggregata* to be the causative agent of chalkbrood in the alfalfa leafcutting bee. Vandenberg et al. (1980) and Stephen et al. (1981) demonstrated pertinent aspects of chalkbrood epizootiology. As healthy adults first emerge from their nests, they are sometimes forced to chew through or around a sibling chalkbrood cadaver. In so doing, these adults can become covered with spores. Spores on adult females contaminate the pollen provisions of their offspring and thus spread the disease to the next generation. Bee population management techniques designed to minimize exposure of newly-emerging adults to chalkbrood cadavers result in lower disease prevalence.

Vandenberg and Stephen (1983a, 1984) and McManus and Youssef (1984) demonstrated the pathogenesis, reproduction and sporulation of chalkbrood. Spores must be ingested by larvae and then germinate in the gut. The pH within the midgut is near neutral, but the redox potential is quite low. Extensive multiplication occurs within the hemocoel before death. Certain color changes characterize chalkbrood within a few days after death. A pink or tan patch develops initially, usually visible in the abdomen. Within a day after death the cadaver is uniformly brown or gray. Fungi in cadavers destined not to sporulate remain tan colored as they dehydrate. The mycelia in the process of sporulation within cadavers usually turn light gray or white prior to development followed by pigmentation of black spore cysts beneath the host cuticle. Sporulation is usually complete within 1–2 weeks after death.

Other *Ascosphaera* species are capable of infecting the alfalfa leafcutting bee. Vandenberg and Stephen (1983b) showed that although the alfalfa leafcutting bee is susceptible to infection by *A. apis* and *A. proliperda*, the pathology is distinctly different. Youssef et al. (1984) detailed infection of the alfalfa leafcutting bee by *A. proliperda*.

Stephen and Fichter (1990a and b) successfully selected for leafcutting bee resistance to chalkbrood. After appropriate backcrosses, they concluded that resistance was probably polygenic in their selected lines. Consequently, resistance would likely be quickly swamped by feral or managed bees if resistant bees were introduced for pollination purposes. Resistance can be maintained, however, in isolated populations subject to continued selection pressure.

In a series of studies, Maghrabi and Kish (1985a and b, 1986, 1987a and b) used morphology, cytology, and isozyme electrophoresis to examine the complex relationships among species of Ascosphaerales. Their study of 52 *A. aggregata* isolates from throughout the western U.S. (Maghrabi and Kish 1987b) revealed considerable uniformity in morphology and electrophoretic patterns. These authors raised legitimate questions concerning the specific and generic status of these fungi (Maghrabi and Kish 1987a; Kish et al. 1988). Because *A. aggregata* sporulates in some cadavers and

not in others, it is presumed to be heterothallic, but necessary definitive studies (starting with single spore isolates) have not been conducted. (*Ascosphaera apis*, the causative agent of chalkbrood in the honey bee, is known to be heterothallic). However, McManus and Youssef (1991) recently reported a method for *in vitro* sporulation of this fastidious fungus. Consequently, studies of basic fungus biology and genetics may now be possible.

Most recently, Vandenberg (1992a) developed a quantitative laboratory bioassay system. Larvae are most susceptible when inoculated at 1–3 days of age, and less susceptible at 5 days of age. LD_{50}s were between 100 and 200 spores per larva, and probit regression slopes were near 10. Both average time to death and the weight of sporulated cadavers were inversely correlated with dose. However, the proportion of cadavers sporulating was highest at intermediate doses and lower at both high and low doses. Adults that survived inoculation as larvae exhibited no sublethal effects as judged by size and sex ratio.

A large number of bees used for commercial alfalfa pollination in the United States are purchased from Canada because chalkbrood is not common there. Vandenberg (1992b) tested the hypothesis that these bees are more susceptible to chalkbrood because of their previous lack of exposure to the disease, but he found no difference in susceptibility between U.S. and Canadian bees. Beekeepers can therefore use bees from either source without incurring increased risk of chalkbrood in their bee populations. Further studies of the roles of bee nutrition and abiotic factors in chalkbrood susceptibility are underway.

Kish (1980) developed a technique for germination of high percentages of *A. aggregata* spores *in vitro*. This method was an essential tool for later studies of sporicides and chalkbrood control methods. After extensive screening of potential sporicides, Stephen et al. (1982) identified a few halogen compounds (including sodium hypochlorite) as having the best potential for incorporation into bee management schemes. Kish (1983) demonstrated the efficacy of high temperature treatments in killing spores, and Kish and Panlasigui (1985) determined the efficacy of a series of preservatives as potential sporicides.

Separation of the overwintering bees within their cocoons from nest materials followed by nest material decontamination are essential steps in prophylactic disease management. Both cocoons and nest materials may be effectively treated by dipping in hypochlorite solutions (Mayer et al. 1988). Alternatively, nest materials may be treated with high temperatures (Kish 1983).

Youssef and McManus (1985) and Youssef and Brindley (1989) tested the efficacy of three fungicides — captan, botran, and carbendazim — by incorporating each fungicide with fungus spores in the provisions of laboratory-reared larvae. Their findings were similar for all three fungicides: low doses resulted in reduced chalkbrood incidence, and higher doses caused larval mortality. Fichter and Stephen (1987) tested nine fungicides at a series of doses, also using laboratory-reared bee larvae. Both benomyl and carbendazim effectively controlled chalkbrood and did not harm developing larvae. In contrast to field studies by Parker (1984, 1985, 1987, 1988; see below), captan did not significantly reduce chalkbrood and caused mortality or extended developmental times for bee larvae.

In a series of field studies using thrice-weekly dust applications in nest shelters, Parker (1984, 1985, 1987, 1988) demonstrated the efficacy of captan for chalkbrood control. Other fungicides tested — benomyl, botran, and carbendazim — were not effective. In contrast to the laboratory findings of Fichter and Stephen (1987) and Youssef and McManus (1985), Parker noted no effect of captan on larval survival. Both Fichter and Stephen (1987) and Parker (1984, 1985, 1987) noted an increased frequency of non-sporulating forms of chalkbrood with increasing fungicide dose. This phenomenon could help control the spread of chalkbrood to the next generation of bees. Mayer et al. (1990)

applied six fungicides in fields of leaf sources used by bees for nest construction. None was consistently effective, compared to controls, in reducing chalkbrood; however, captan was not included in their test. Clearly, additional studies are needed before any of these fungicides can be recommended or approved for field use.

In summary, research on chalkbrood in the alfalfa leafcutting bee conducted by scientists and cooperators of the ARS Bee Biology and Systematics Laboratory has provided a solid foundation for bee management and disease control. Research continues on several fronts, including studies of bee genetics, chalkbrood susceptibility, fungus molecular biology, and prophylactic and chemical control.

YAKIMA AGRICULTURAL RESEARCH LABORATORY, YAKIMA, WA. By K. Duane Biever

From 1953 to 1988, several entomologists at the Yakima Agricultural Research Laboratory have evaluated microbials as part of their ongoing research programs on fruit and vegetable insect pests.

During the 1960s, J.F. Howell evaluated the nematode *Steinernema carpocapsae* against the codling moth. Applications of the nematode were directed at the overwintering populations and were ineffective. In the late 1970s, Howell (1979) developed a new method for storing and collecting the nematode. This was a spin-off of a program evaluating the nematode against the bertha armyworm and the "spotted cutworm", *Xestia* (as *Amathes*) *c-nigrum*. Foliar treatments were not effective for the bertha armyworm and provided 40–50% mortality of the cutworm. In 1980 and 1981, H.H. Toba evaluated two species of nematodes (*S. carpocapsae* [as *feltiae*] and *S. glaseri*) for activity against the sugarbeet wireworm (SBWW) and the Colorado potato beetle (CPB) (Toba et al. 1983). They demonstrated that inundative soil applications of *S. carpocapsae* in field cages reduced larval populations of CPB and SBWW, 71 and 29%, respectively.

Howell evaluated the codling moth granulosis virus (SAN 4061, Sandoz Inc., San Diego, CA) in apple orchards in 1981 and 1982. The virus caused larval mortalities of 72 to 82% for the first generation and 32 to 74% for the second generation.

Researchers at the Yakima Laboratory participated in a 3-year pilot test evaluating the efficacy of foliar applications of *Beauveria bassiana* for control of the CPB (Hajek et al. 1987). R.L. Chauvin supervised the project in 1983 and K.D. Biever, reassigned from the ARS Laboratory in Columbia, MO, in early 1984, assumed leadership of the project through its completion in 1985. Foliar treatments reduced first generation CPB populations by 65%, suggesting that *B. bassiana* could be an important component of an IPM system. In 1987, as part of a program on developing an insect management system for potatoes, Biever evaluated several rates of a strain of *Bacillus thuringiensis* specific to the CPB (M-ONE™, Mycogen Corporation) under an Experimental Use Permit. Two applications, at rates from 1 to 4 quarts per acre (22,500 IU/mg), against the first generation reduced larval populations from 17 to 55%.

STORED PRODUCTS LABORATORY, MADISON, WI. By Wendell E. Burkholder

Insect pathology/microbial control research began at the Stored Products Laboratory at Madison, WI, in the late 1950s. During that time, research with several dermestid species of the genus *Trogoderma* was impeded by epizootics of the neogregarine protozoan *Mattesia trogodermae*. The pathogen caused severe epizootics in the laboratory and was suspected of suppressing field populations of *Trogoderma* species in grain bins and in food processing and storage facilities. In the process of developing insect cultures free of the pathogen, it was observed that the diseased insects fluoresced a bright yellow-green under 366 mμ ultraviolet light (Burkholder and Dicke 1964). The UV technique is a convenient tool assisting in both insect rearing and research to monitor for the presence of *Mattesia* spores.

Subsequent studies were conducted of the pathogenicity and development of *M. trogodermae* and infection rates as influenced by transmission, dosage, and host species (Schwalbe et al. 1973a and b, 1974). The infection rates varied among the six species of *Trogoderma* that were studied. In 1974, the use of pheromones to lure insects to a pathogen inoculation device was proposed (Burkholder and Boush 1974). In theory, the spore-laden insects would eventually return to their natural habitats and infect others of the same species. The theory was successfully tested in experiments in which *T. glabrum* males were lured by the synthetic female sex pheromone to inoculation devices containing the protozoan spores. The males subsequently transmitted the spores to females and to the later generations (Shapas et al. 1977; Burkholder and Shapas 1978; Burkholder 1981).

HONEY BEE DISEASE INVESTIGATIONS LABORATORY, LARAMIE, WY. By William T. Wilson

The first USDA field laboratory in apicultural research was established in Laramie, WY, in 1926 under the name Intermountain States Bee Culture Field Laboratory in cooperation with the University of Wyoming (Anonymous 1926). The first director was A.P. Sturtevant, a bacteriologist and bee disease specialist. The microbial control laboratory and staff offices were located on campus while the "honey house" (field laboratory and workshops) was situated on the university's agronomy farm. The primary reason for establishing the facility in Laramie (elevation of 7200 feet) was the total separation from commercial beekeeping. Since there were no suitable controls for the infectious diseases of honey bees (e.g., American and European foulbrood), except burning of the entire colony, it was necessary to study the diseases in an isolated area (Hitchcock 1966). The name of the laboratory was later changed to Honey Bee Disease Investigations Laboratory. Sturtevant retired in 1958 (Anonymous 1959) and J.D. Hitchcock became director of the laboratory.

Many of the early field studies on genetic stocks of honey bees with heritable resistance to American foulbrood disease caused by *Bacillus larvae* were made by Sturtevant and his associates at Laramie, where the resistance of honey bee larvae to the bacterium was first proven to be related to larval age (Woodrow 1941a; Hitchcock 1958) and the ability of adult bees to reduce the spore content of ingested honey through selective filtration in the honey bee stomach (Sturtevant and Revell 1953). The Laramie staff was involved in the development of the Island Hybrid which was the first semi-resistant stock of bees that became commercially available to beekeepers (Sturtevant 1949). Basic studies on *B. larvae* spores for tolerance to heat (Burnside 1938) and other factors were accomplished (Sturtevant 1930). A milk test for the diagnosis of American foulbrood based on proteolytic enzymes was developed at Laramie (Holst 1946). A unique study in bee pathology showed the behavior of worker bees towards brood infected with American foulbrood (Woodrow 1941b). The first description of a rare gregarine parasite of honey bees was another significant contribution (Hitchcock 1948). Hitchcock studied the yearly occurrence of *Nosema apis*, *Malpighamoeba mellificae* and species of *Acarapis* mites (excluding *Acarapis woodi*) in honey bees shipped to Laramie from the Gulf States and in colonies wintering in Wyoming (Hitchcock, personal communication 1992). Most of this work was accomplished in the 1930s through the 1950s.

Starting in the 1960s with the employment of H. Shimanuki and J.O. Moffett, basic microbiological and applied field studies were expanded. Staff contributions concerned the relative resistance to certain antibiotics of different strains of bacteria that cause bee diseases (Lehnert and Shimanuki 1981), descriptions of hemocytes in bee hemolymph and other studies of bee blood (Gilliam and Shimanuki 1967, 1970, 1971), discovery of a new antibiotic (tylosin lactate) for control of American foulbrood (Hitchcock et al. 1970), techniques for gas sterilization of wax combs, studies towards the possible control of various bee viruses, factors affecting the spread and control of protozoan diseases (nosema and amoeba) (Moffett et al. 1969), and pathogenicity of various bacteria and fungi to the alkali bee (Shimanuki, unpublished data). Both Shimanuki and Moffett transferred to other ARS laboratories in the late 1960s.

W.T. Wilson joined the laboratory in 1968 and expanded the program on the etiology and control of American foulbrood. Through a courtesy appointment to the Graduate Faculty at the University of Wyoming, Wilson expanded the graduate student program at the ARS facility. Soon after his arrival, he developed a new technique for administering antibiotics to honey bee colonies that enhanced the efficacy of Terramycin for foulbrood control (Wilson et al. 1970, 1971; Wilson and Elliott 1971). This technology transferred rapidly to industry and over a period of more than 20 years antibiotic extender patties have saved the beekeeping industry millions of dollars through less foulbrood and improved colony health. Currently the patties show some value in the control of *A. woodi*.

Basic bee pathology studies centered on bacterial mechanisms and pathways in American foulbrood (Wilson and Bitner 1970; Bitner et al. 1972) and to a lesser extent bee viruses (Nunamaker et al. 1985). *Penicillium waksmanii* growth was studied as a biological control for American foulbrood (Tutt and Wilson 1975; Wilson et al. 1978). Hitchcock and Christensen (1972) discovered chalkbrood caused by *Ascosphaera apis* in honey bees in the central United States and the fungal disease was studied extensively at Laramie (Mehr et al. 1976; Menapace and Wilson 1976; Menapace and Hale 1984; Rose et al. 1984; Stoner and Wilson 1985). A bee disease and parasite survey of Mexico was accomplished in 1980 by Laramie scientists (Wilson and Nunamaker 1983; Wilson et al. 1984). In 1972, Wilson was appointed Research Leader.

In February 1985, Wilson established a research program on mite control, and in May, he was directed by the ARS Administrator to close the Laramie Bee Laboratory and to move to Weslaco, TX (see above).

EUROPEAN PARASITE LABORATORY\EUROPEAN BIOLOGICAL CONTROL LABORATORY, SÈVRES, BÉHOUST, AND MONTPELLIER, FRANCE. By Tadeusz J. Poprawski and Lawrence A. Lacey

The European Parasite Laboratory (EPL) was established in France in 1919, and for many years USDA and cooperating scientists were stationed there to conduct exploration and other research on parasites and predators of arthropod pests that had become established in the U.S. (see Sections A1a of Chapters I–III and B1a of Chapter IV). In 1981, an insect pathology project was initiated for the first time at an ARS overseas laboratory, at EPL, then located at Sèvres, a suburb of Paris, France. The purpose of the project was to find and evaluate species and strains of exotic entomopathogens present in Europe that would have potential for use against insect pests in the United States. The research was conducted under cooperative agreements between ARS and other agencies, since there was no permanent position for an insect pathologist.

G.C. Soares, Jr., was the first scientist in charge of the pathology program. He was stationed at the Biological Control Research Laboratory of the French National Institute for Agronomic Research (INRA) at La Minière, near Versailles, from October 1, 1981, to November 30, 1982, working under a Cooperative Agreement between ARS–EPL and INRA. During his tour, Soares worked on EPL program pests, including *Otiorhynchus* and *Sitona* weevils (Soares et al. 1983; Aeschlimann et al. 1985), and sent a number of shipments of insect viruses and fungal pathogens to ARS locations at Beltsville, MD, and Ithaca, NY, respectively, for further evaluation. Soares prepared a 67-page report of the project, which is unpublished but on file at the ARS Biological Control Documentation Center (BCDC), Beltsville, MD, and the European Biological Control Laboratory (EBCL), Montpellier, France.

In 1983, T.J. Poprawski began conducting pathology research in Europe under a USDA–INRA Cooperative Agreement, which terminated March 30, 1984. He continued to study entomopathogens of EPL's program pests, including *Otiorhynchus* and *Sitona* weevils, gypsy moth, onion maggot, *Heliothis/Helicoverpa* species, and filth flies (Poprawski et al. 1985a, b, and c), and sent numerous

shipments of fungal pathogens to the ARS location at Ithaca. He also prepared a second report of the project; this 74-page unpublished report is also available at Beltsville and Montpellier. In April 1984, Poprawski left to spend a one-year training session on the Entomophthorales at the ARS Insect Pathology Research Unit at Ithaca, NY, under the direction of Richard S. Soper.

I. Majchrowicz, on leave from the Polish Academy of Agriculture's Department of Entomology at Szczecin, Poland, filled the vacant pathology position from April 1 to September 30, 1984, under another joint research agreement (with INRA), and prepared the third, 60-page, report of the project. R. Le Brun, on a sabbatical from the University of Rhode Island, worked at EPL from September 1, 1984, until August 23, 1985. His main duty was to help establish the Insect Pathology Unit Laboratory at EPL's new location in Béhoust, a small village about 40 km west of Paris. N.K. Maniania was employed as a pathology technician from February to October 1984 under the ARS–INRA agreement. When this agreement was terminated in October 1984, Majchrowicz returned to Poland and Maniania joined EPL's staff as temporary pathology technician.

After training in the U.S., Poprawski returned on April 1, 1985, to the EPL at Béhoust, under a Specific Cooperative Agreement with Boyce Thompson Institute for Plant Research, Ithaca, until August 1, 1987, and as an ARS Research Entomologist thereafter. His first duty was to finalize establishment of the Insect Pathology Unit laboratory, which became functional by mid-May 1986. Poprawski resumed explorations for and research on pathogens of a number of insect pests, including the onion maggot, filth flies, *Empoasca vitis*, *Sitona* and *Otiorhynchus* weevils, southern green stink bug, and range grasshoppers. Research included, but was not limited to, bioassays of fungal pathogens and their toxic metabolites, interactions of parasites and fungal pathogens in arthropod control, safety of fungal pathogens to beneficial insects, genetic variability of fungal isolates, and impact of chemical pesticides on fungal pathogens (Riba et al. 1986; Poprawski et al. 1988; Goettel et al. 1990; Majchrowicz et al. 1990).

From mid-April 1988 until September 22, 1990 (when Poprawski was transferred to the ARS Plant Protection Research Unit at Ithaca, NY), EPL pathology research was redirected primarily to the Russian wheat aphid and other cereal aphids. Poprawski (with F. Gruber and other EPL entomologists) conducted exploration for and collection of natural enemies of the aphids in Turkey, Bulgaria, Yugoslavia, Greece, and the Moldavian, Kirghiz, Uzbek, Kazakh, and Ukrainian republics of the former Union of Soviet Socialists Republic. Explorations in the former U.S.S.R. were conducted under the auspices of a newly established joint U.S.A.–U.S.S.R. program on biological control of pests. Numerous shipments of aphid fungal pathogens were sent to the ARS laboratory at Ithaca. (Parasites and predators were also shipped to several ARS, APHIS, and university locations in the U.S.) Reports of the explorations were prepared and are on file at Beltsville and Montpellier. Additionally, research projects concentrated on the interaction of parasites and fungal pathogens of Russian wheat aphid. Poprawski determined, through bioassays, the relative pathogenicity of naturally occurring aphid pathogens to Russian wheat aphid and its parasites. Studies were also conducted to determine the influence of the introduction of various parasite and pathogen combinations on Russian wheat aphid populations. Entomophthoralean fungi, primarily *Zoophthora radicans* and *Pandora neoaphidis*, along with other species collected, were utilized in these studies, and bioassayed against *Aphelinus* and *Aphidius* parasite species. These studies were useful to evaluate potential introductions of pathogens and parasites into the U.S., as well as forming a basis for future research both at EPL/EBCL and in U.S. laboratories (Kiriac et al. 1990; Gruber et al. 1991; Kovalev et al. 1991; Poprawski et al. 1992a, b, and c).

The insect pathology program became an integral, ARS-funded part of the ARS overseas program at the time of the consolidation of the two ARS European laboratories (Béhoust and Rome) at Montpellier, France, in September 1991 (see Chapter IV), and with the assignment in October 1991

of L.A. Lacey to the newly established EBCL; Poprawski served as advisor for the program from his departure until Lacey's arrival.

Establishing and outfitting the pathology laboratory and foreign exploration for natural enemies of the sweetpotato whitefly (SPWF) and Russian wheat aphid (RWA) and other cereal aphids has been the principal activity of EBCL's Pathology unit since Lacey's arrival. Collections of pathogens and other natural enemies have been made over a broad geographic range (Spain, Greece, France, Russia, Egypt, Pakistan, India and Nepal) and under diverse climatic and environmental conditions. Several isolates of *Paecilomyces fumosoroseus* and other fungi from SPWF from the Indian subcontinent and several Hyphomycetes and Entomophthorales have been isolated from RWA and other cereal aphids in France, Spain, Russia, and the Indian subcontinent. Isolations of pathogens also were made from orchard and urban pests including codling moth, gypsy moth, and thrips.

In addition to collecting and shipping activities, research was started on the effects of a variety of environmental parameters that enhance or limit the activity of fungal pathogens of Homoptera. Numerous fungal isolates have been sent to the ARS Collection of Entomopathogenic Fungal Cultures (ARSEF) at Ithaca, NY.

Cooperative relations in most of the host countries where collections have been made during 1991-1992 have resulted in additional collection and shipment of natural enemies to EBCL and the U.S. It is envisioned that cooperative efforts will continue in southern India, Pakistan, Crete, and Spain, along the lines of applied studies and student exchange.

In the Montpellier area cooperative relations have been established with scientists of INRA, Centre International de Recherche Appliqué et de Développement (CIRAD), and Ecole Nationale Supérieure Agronomique de Montpellier. The EBCL Pathology Unit is developing a cooperative program with Jacques Fargues and other INRA colleagues recently assigned to Montpellier from the INRA Laboratory in La Minière.

JAPANESE BEETLE CONTROL PROGRAM, AZORES, PORTUGAL. By Lawrence A. Lacey

The Japanese beetle control program on the island of Terceira (Azores, Portugal) was implemented under the direction of USDA-ARS International Activities (now Office of International Research Programs). Michael G. Klein (USDA-ARS, Wooster, Ohio) has been advising the Azorean Department of Agriculture and the University of the Azores on the use of biological control agents for control of the beetle since 1984. From January 1990 until October 1991, Lawrence A. Lacey was assigned to the island to implement a biological control program based on insect pathogens and parasitic insects (Lacey et al. 1994; Mendes et al., 1994). Transfer of proven technology was a key goal of the project. Research in a number of areas still is required in order to determine the best suited natural enemies for effective control. To this end, efficacy and other studies have been conducted on a number of pathogens (bacteria, fungi, protozoa) and parasites (nematodes, arthropods) (Lacey et al. 1993). The most efficacious control agents against larvae are the nematode, *Steinernema glaseri* and the fungus, *Metarhizium anisopliae*. The construction of a laboratory and pathogen production facility was completed prior to Lacey's departure. The facility enhances continuation and expansion of the project's control activities on a sustained basis. Lacey and Klein continue to be involved in the Azores project through field work and advisory activities. Increased exploration for pathogens and parasites of the beetle in Japan and China and their utilization in the island's control program will be the main ARS activity over the next few years.

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APPENDIX III
DETAILED HISTORY OF BIOLOGICAL CONTROL IN THE FOREST SERVICE
Edited by M. E. Dix

I. PREFACE. By Mary Ellen Dix

The Overview (Chapter V) and Appendix III summarize Forest Service research and control efforts with biological agents from 1953 to 1993; some earlier studies are also discussed. The overview briefly describes trends and directions of biological control activities. Appendix III is an in-depth review of research and control efforts on specific insects and groups. However, the appendix is not all inclusive. It includes efforts on major pests, long-term studies on natural control agents, studies that had unique outcomes, and applications of biological control agents. Small studies that identified natural enemies of minor pests and determined their impact, or those that involved implementation of a biological control technique were not included unless they were part of a larger effort on a forest pest. Some taxonomic revisionary studies (e.g., Schmid 1969b; Torgersen 1974), and other notes on the identity and biology of natural enemies (e.g., Wickman 1964; Harman and Kulman 1967; Schmid 1970b; McKnight and Tagestad 1972; Mitchell and Maksymov 1977; Pasek and Kearby 1984; Galford 1985; and Thompson and Solomon 1986) also were excluded from this appendix.

Appendix III is generally arranged by damage category and pest. Exceptions are the sections on mites and nematodes, and on *Bacillus thuringiensis*, where long-term progress crosses pest species boundaries. As in other parts of this book, complete scientific names of all organisms mentioned in the text are given in the Taxonomic Index for the entire publication.

II. BIOLOGICAL CONTROL OF ARTHROPODS

A. Bark Beetles (Coleoptera: Scolytidae)

1. Black turpentine beetle, *Dendroctonus terebrans* (Olivier). By Mary Ellen Dix

The black turpentine beetle (BTB) is a native pest of slash pine and longleaf pine in the southern U.S. Many Forest Service (FS) scientists evaluated native endoparasitic nematodes, clerid beetle predators, and extraregional mites (Moser and Dell 1980; Moser 1981; Kinn 1984a and b; Moser and Bogenschutz 1984; Moser et al. 1978) for suppression of BTB. Although these natural enemies may have considerable impact on BTB populations, they often are ineffective during epidemics. Miller et al. (1987) identified an exotic coleopteran predator, *Rhizophagus grandis*, as a potential control agent. This beetle is a predator of the European spruce beetle in England, Europe, eastern Siberia, and Turkey (Bevan and King 1983). In 1985, Gregoire et al. (1986) demonstrated that *R. grandis* was attracted to frass produced by its European host and to frass produced by three species of native North American bark beetles, BTB, southern pine beetle (SPB), and spruce beetle. Moser selected *R. grandis* for importation and release against the BTB because both BTB and *D. micans* have long life cycles and gregarious larvae. If successful, *R. grandis* could also prey on SPB (Moser 1989).

In 1986 and 1987, Gregoire shipped 300 pairs of *R. grandis* from Belgium to the USDA Forest Service Forestry Center at Pineville, near Alexandria, LA, to test methods for rearing the predator on BTB and SPB and obtaining sterilized eggs. The semi-artificial rearing method selected involved raising *R. grandis* in plexiglass sandwiches inoculated with about 20 BTB larvae (Moser 1989). The resulting predator eggs were surface sterilized in White's solution (Barras 1972) to reduce the chance of introduction of microorganisms from Europe. During 1987, this method was used to mass produce *R. grandis* in the laboratory and the first 20 pairs of the beetle were released in April 1988 (Moser 1989). The establishment and potential long-term impact of *R. grandis* on the BTB populations is not known.

2. Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins. By Mary Ellen Dix

During the 1950s, the Douglas-fir beetle seriously threatened stands of Douglas-fir, the leading commercial tree species in the U.S. In 1956, Forest Service's Intermountain Forest and Range Experiment Station initiated a long-term study on the ecology and biology of the beetle and on its natural enemies (Furniss 1967). Massey (1956) identified nematode parasites of the beetle (see also section on Mites and Nematodes). Between 1958 and 1962, Furniss examined nematode parasitism rates and found that they varied little by sex but varied with localities, standing and felled trees, and maturity of beetles (Furniss 1967). During this same period, Ryan evaluated the biology, habits, and embryology of the braconid parasite *Coeloides brunneri* in western Oregon and identified possible means to manipulate *C. brunneri* populations for controlling the Douglas-fir beetle (Ryan and Rudinsky 1962; Ryan 1963). In 1959, adult beetles were found to be parasitized by the pteromalid *Karpinskiella paratomicobia*. However, Furniss (1968) found that parasitism may actually increase the survival rate of the beetle's offspring. Oregon State University published a technical bulletin that described and identified the immature stages of Douglas-fir beetle parasites and predators (Kline and Rudinsky 1964), part of the results of a cooperative university-Forest Service study.

3. Spruce beetle, *Dendroctonus rufipennis* (Kirby). By Mary Ellen Dix

Since 1898, periodic epidemics of the spruce beetle (*Dendroctonus rufipennis,* formerly known as the Engelmann spruce beetle, *D. engelmanni*) occurred in the Rocky Mountains and the Pacific Northwest. Initial studies on biological control of the spruce beetle targeted identification of natural enemies and assessment of their impacts.

In 1941, the Division of Forest Insect Investigations of the Bureau of Entomology and Plant Quarantine (BEPQ) and the Colorado Agricultural and Mechanical College initiated a study to obtain data on the beetle's life history and habits and to develop practical control methods for massive outbreaks. Massey and Wygant (1954) summarized the results of this study and identified important natural enemies and their impacts. They reported that woodpeckers could locate and destroy up to 75% of the brood, while hymenopteran, dipteran, and coleopteran natural enemies could locate and destroy up to 50% of the brood.

A 1947 BEPQ study identified prey of woodpeckers and sapsuckers by analyzing the stomach contents of 135 birds in Colorado. Sixty-five percent of the arthropods in the birds' stomachs were spruce beetles, 13% were other scolytids, 12% were formicids, and 6% were cerambycids (Massey and Wygant 1954, 1973).

After another severe outbreak of spruce beetle in Colorado during the 1960s, the Rocky Mountain Forest and Range Experiment Station funded several studies with Colorado State University to learn more about the natural enemies of the spruce beetle. Seven species of parasites were successfully reared and a taxonomic key to larvae was developed (Jensen 1967). During observations of woodpecker behavior in infested stands, it was found that abundance of three-toed, hairy, and downy

woodpeckers was closely related to beetle abundance. Pairs of woodpeckers often confined their activities to small areas of infested stands (Baldwin 1968a and b; Koplin and Baldwin 1970). Subsequent studies assessed the effects of stand densities on woodpecker predation (Shook and Baldwin 1970; Koplin 1972).

The current outbreak of spruce beetles in Alaska and northwestern Canada began in the mid-1980s. Although parasites have been identified, research has concentrated on the use of silvicultural and other management techniques.

4. Mountain pine beetle, *Dendroctonus ponderosae* Hopkins. By Richard F. Schmitz

Except for one attempt to introduce an exotic predator, biological control efforts directed against the mountain pine beetle (MPB) on lodgepole pine concentrated on identifying and assessing the relative abundance and effectiveness of native predators and parasites. Recent studies evaluated predator responses to pheromones and kairomones produced during beetle colonization of the host tree.

Current understanding of the biology, abundance, and impact of entomophages on MPB in lodgepole pine was gleaned from earlier studies by BEPQ entomologists at the Forest Insect Laboratory at Coeur d'Alene, ID, on MPB bionomics and ecology, and on the enhancement of native natural enemy species. These studies, combined with results of later studies in lodgepole pine, western white pine, and ponderosa pine, provided the understanding needed to ensure that potential introductions of exotic beneficial species did not adversely impact native beneficial species. Basic biologies of the biological control agents found in the three host trees are similar. A key to the common parasites and predators of the MPB in these host species was prepared by Rasmussen (1976).

Insect parasites and predators. Bedard (1939, 1940, 1942) and DeLeon (1929, 1930, 1931, 1934a and b, 1935a and b) conducted most of the early studies on the biology, distribution in the host tree, and relative effectiveness of insect parasites and predators in western white pine and lodgepole pine. DeLeon (1931) described the developmental stages, aspects of the biology, and effectiveness of parasites, predators, and other associated insects of the beetle on western white pine. In 1934, he published an annotated list of the parasites, predators, and other fauna associated with the beetle in western white and lodgepole pines (DeLeon 1934b) (Table 1). Almost 50 years later Chatelain and Schenk (1983) conducted a similar study to determine relative abundance and within-tree distribution of insects inhabiting MPB-infested lodgepole pine in central Idaho and northeastern Oregon. Results of this study were similar to those described by DeLeon (1934b) and Amman and Cole (1983). DeLeon and subsequent investigators considered the following Hymenoptera to be most important parasites of MPB: *Coeloides dendroctoni*, *Dinotiscus* (as *Cecidostiba*) *dendroctoni*, *D. acutus*, *D.* sp., and *Roptrocerus xylophagorum* (as *Pachycerus eccoptogastri*).

Parasitism of MPB by *C. dendroctoni* averaged about 16% (DeLeon 1931). DeLeon (1931, 1935a) considered this braconid to be the most important parasite of MPB brood because most larvae were parasitized when they were about to pupate and had a high probability of reaching the adult stage. Investigations of the life stages, biology, and effectiveness of *Coeloides* spp. were more complete than similar studies on the remaining parasites (DeLeon 1934a, 1935a).

DeLeon (1931) ranked the dipterous predators as the second most important natural control, followed by certain coleopterous species. The dolichopodid, *Medetera aldrichii*, fed on almost any species of larva, including its own, and was considered the most important dipteran predator (DeLeon 1935a). However, cannibalism by *M. aldrichii* larvae adversely affected predator abundance. *Medetera aldrichii* larvae either partially consumed MPB larvae before abandoning them to search for more prey, or consumed most of the larvae. Predators that only partially consume a prey have been shown to destroy more prey than those that entirely consume each prey (Amman and Cole 1983). Nagel and

Fitzgerald (1975) found that when prey are scarce, *M. aldrichii* larvae consume most of each prey before seeking another, suggesting this behavior may be density-dependent. Overall, *M. aldrichii* was considered to be less effective than *C. dendroctoni* because many of the immature beetle larvae destroyed by *M. aldrichii* in the fall would probably have died from other causes before maturing.

Despite the abundance of predaceous adult and larval clerid beetles (DeLeon 1934b; Reid 1957), DeLeon (1934b) discounted their impact on MPB brood survival. More recent laboratory studies have established their potential effect on MPB survival. Schmid (1970a) found that each *Enoclerus sphegeus* adult killed one MPB adult per day, and Amman (1970) found *E. sphegeus* larvae consumed an average of 16 large or 38 small MPB larvae while completing development. Larvae of another clerid, *Thanasimus undatulus*, consumed an average of 18 large or 35 small MPB larvae to complete development (Amman 1972). The effectiveness of adult clerids in preying upon adult MPB as they colonized trees has not been measured.

In laboratory rearings, parasites and predators destroyed between 2.5 and 6.5% of the MPB eggs contained in log sections cut from field-infested trees during four summers (Amman and Cole 1983). Nematodes, parasites of both mature and immature MPB, destroyed the most eggs (1.13 to 4.06%) (Massey 1966a, b and c). This loss was fairly evenly distributed thoughout the galleries. The nematode *Mikoletzkya pinicola* was identified by Massey as the only nematode present in cultures established from these laboratory rearings and was observed preying on MPB eggs (Amman and Cole 1983). Unidentified fungi caused the second greatest loss of eggs (0.76 to 1.80%), with the greatest loss usually occurring in the first few inches of the gallery (Hunt et al. 1984). Unidentified mites accounted for predation of only two eggs (0.06%) during one season. Most mites appear to be saprophytic (fungus feeders), or, if predaceous, fed on other organisms under the bark (Rust 1933, 1935). Predatory mites were not found during examination of MPB populations in Colorado and South Dakota (Boss and Thatcher 1970).

Although not included in these studies, *M. aldrichii* may destroy 40 to 50% of MPB eggs (DeLeon 1935a). Schmid (1971) reported *M. aldrichii* larvae preyed on eggs in the first few inches of the egg gallery and consumed from 12 to 25 eggs each during 15 days of laboratory rearing.

Abundance of MPB in relation to bole infestation patterns. During the 1930s, Bedard evaluated factors regulating the abundance of MPB within the tree. He found that the abundance of beetle brood and associated insects along the bole of infested western white pine trees varied with tree species and among trees. Distribution of MPBs among trees seemed related to bark thickness with thicker-barked trees having more brood, and infested length within a tree varied with bark thickness, tree diameter and height. MPBs were most abundant in the thicker bark located in the basal portion of the tree (Bedard 1937).

Distribution of predators was similar to that of MPB; predators were more numerous where beetle brood densities were the highest. The parasite *C. dendroctoni* also was most abundant where larval densities of MPB larvae were the highest and the bark was thin enough for oviposition. Parasites that use ventilation or entry holes for oviposition were most abundant in the thicker-barked portion of the tree.

MPB survival was measured in endemic, epidemic, and postepidemic infestations (Amman 1984). Significantly more MPB ($P < 0.01$) survived in endemic (3.7%) infestations than in epidemic (1.4%) and postepidemic (0.5%) infestations. Natural enemies accounted for 8, 33, and 4% of total MPB losses in endemic, epidemic, and postepidemic infestations, respectively. The greatest predation of MPB at epidemic levels was attributed to larvae of the dolichopodid fly *M. aldrichii* (13%) and woodpeckers (15%). Interestingly, although mortality caused by most predators and parasites was

density-dependent, clerid predation was not. Clerids consumed a greater percentage of MPB larvae at endemic infestation levels, but accounted for only 0.9% of the brood mortality.

Cole (1981) and Amman and Cole (1983) compared measures of component probabilities for MPB brood mortality in infested lodgepole pine forests in the Intermountain Region that were ascribed to 11 specific mortality factors including five natural enemies. Probabilities of death were computed for each factor during pre-epidemic, epidemic, and post-epidemic stages. These data revealed that lethal winter temperatures and drying of the phloem in the early summer, and not natural enemies, were the two major causes of MPB brood mortality. *Medetera aldrichii* apparently was the most important natural enemy because predation increased with MPB brood density during pre-epidemic and epidemic stages of infestation, and with increasing MPB brood densities associated with increasing tree diameters. These findings suggest that predation by *M. aldrichii* larvae is a significant factor in reducing MPB brood survival in large-diameter trees during the post-epidemic period. In contrast, larval predation by the clerids *Thanasimus undatulus* and *Enoclerus sphegeus* was negligible. Impact of predation by adult clerids on adult MPB while initiating attacks on a tree was not measured. Probability of parasitism by *C. dendroctoni* increased with brood density in 9-inch (23-cm) diameter trees, and decreased with brood density in 12-inch (30-cm) diameter trees (Cole 1981; Amman and Cole 1983).

Overall predation by woodpeckers was low. The greatest woodpecker predation occurred during the pre-epidemic stage in the 12-inch (30-cm) or smaller diameter trees when the entire woodpecker population searched the few infested trees. However, as the beetle population became epidemic, the woodpecker population did not increase proportionally to the beetle population and consumed proportionally less of the beetle population. In the post-epidemic stage, woodpeckers did not consume proportionally as many beetles as they did during the pre-epidemic stage. Low woodpecker predation levels in 15-inch (38-cm) trees was probably due to increased difficulty in removing larvae from the thicker bark (Cole 1981, Cole and Amman 1985).

Bedard (1938) found that MPB brood mortality from natural enemies was constant on all four sides of the tree, although MPBs were most abundant on the north and east sides of western white pine in 1935 and on north and west sides in 1936.

Natural enemy effectiveness. Bedard (1939) evaluated the overall impact of natural enemies on MPB populations. He found that parasites destroyed an average of 54% of the brood in windfelled trees, and 65% of the brood in standing trees. MPB populations were reduced when 21 or more individual natural enemies were present per ft^2 (930 cm^2) of bark surface. He recommended against chemical treatment of windfalls when 30% of the brood were parasitized or when there were parasites in the base of standing trees (Bedard 1933b).

Effectiveness of *Coeloides dendroctoni* was limited by parasite behavior, life cycle, and reproductive potential, hyperparasitism, and bark thickness (DeLeon 1935b). The parasites usually were found in *Ips*-infested pines and were not present in sufficient numbers during the first few years of a MPB infestation to destroy many of the larvae. Their abundance increased slowly. Most *C. dendroctoni* remained in the tree almost a year after the host beetles were killed and then stayed within the original "epicenter" of infestation instead of moving into the outlying groups of MPB infested trees. Many *C. dendroctoni* were hyperparasitized by *Eurytoma* sp. and *Gelis* sp.

Accessibility of the beetle brood influenced abundance of beneficial species. Bedard (1939) found that beneficial insects were not equally distributed among trees comprising an infestation. Parasites, which oviposit through the bark, were most abundant in thin-barked trees, while predators were most abundant in thick-barked trees (Bedard 1939; Dahlsten and Stephen 1974). Thick-barked sugar pine had few parasitized beetles and large numbers of predaceous beetle larvae (Struble 1942).

The effect of predators on flying beetles is difficult to measure. The robber fly *Laphria gilva* killed about 1% of flying MPB in ponderosa pine stands of the Black Hills (Schmid 1969a) and were captured in large numbers in passive traps in MPB-infested lodgepole pine stands (R.F. Schmitz; data on file at Forestry Sciences Laboratory, Ogden, UT, January 1981).

Parasites were found to be most abundant in trees where the MPB brood was in stages suitable for oviposition (Bedard 1939). Parasites were most abundant in western white pine in August because the larvae were suitable hosts at that time when most parasites were ready to oviposit. In contrast, MPB adults in lodgepole pine do not mature until late May or June and their larvae were too immature to be parasitized in August. In addition, western white pine growing on moist sites were shown to have more natural enemies than those growing on dry sites, leading Bedard (1939) to recommend that these "reservoir" white pine trees growing on moist sites be left untreated during chemical control programs.

Augmentation using semiochemicals. The responses of beneficial insects to synthetic semiochemicals used to manipulate MPB populations were measured by Borden (1974, 1977) and Lindgren and Borden (1989). Chatelain and Schenk (1983) evaluated the use of synthetic attractants to augment abundance of these beneficials in lodgepole pine stands in central Idaho and northeastern Oregon. The clerid predator *Thanasimus undatulus* responded to sticky traps baited with either frontalin or *exo*-brevicomin (Chatelain and Schenk 1984). Abundance of *T. undatulus* adults was increased on pines baited with frontalin before (May to mid-July) or during (mid-July to September) the MPB flight period. Baiting the trees before the bark beetle flight period was the most effective augmentation method because baiting was concurrent with peak *T. undatulus* flight activity but before the onset of peak MPB flight. This technique assured that this predator was attracted to the study trees before competing sources of attraction were created by MPB infestation of nearby non-study trees. Baiting brood trees in this manner increased the incidence of *T. undatulus* larvae threefold and mortality of emerging MPB adults by 7.1%, but did not significantly reduce MPB brood survival or consequent tree mortality. Thus, frontalin could be used to increase substantially the predator population and to enhance other control tactics within a pest management program (Chatelain and Schenk 1984). Such attempts would likely be more feasible at low or endemic levels of MPB.

Avian predators. The impact of birds on MPB populations during the flight period can be substantial (Rust 1929, 1930). The stomachs of 15 of 18 birds caught in lodgepole pine forests contained from one to 289 MPB. MPB represented up to 20% of the food volume. In 1929, nighthawks consumed the most MPB, an average of 76 MPB/bird (n=10), but their impact was minimal because of their limited occurrence. Three-toed and hairy woodpeckers averaged only two MPB/bird (n=5), but had a greater impact because they were more abundant. However, in 1930, quantities of beetles taken by nighthawks and woodpeckers were reversed because the MPB infestation moved to another area. Nighthawks averaged only five beetles (n=14), because they stayed within their established breeding grounds. Woodpeckers averaged 33 beetles/bird (n=8), because they moved with the MPB outbreak.

Birds can have a substantial impact on flying MPB populations. Stallcup (1963) censused birds and analized their stomach contents in a ponderosa pine stand in Colorado. He estimated that birds consumed 8.5% of adult MPB during their flight period and identified additional species of bird predators (Table 1). Woodpeckers consumed numerous MPB and caused the desiccation of many more by exposing the larvae when opening the bark. Prey size is an important factor affecting predation by woodpeckers, which avoid trees containing small larvae and concentrate on trees containing large larvae (Koplin and Baldwin 1970). At high elevations in northwest Wyoming, woodpeckers preyed mostly on parent beetles because of the small size of larvae (Amman 1973). During epidemics, woodpeckers are believed to have an insignificant effect on MPB populations

(Berryman 1976). However, during endemic periods, they may play an important role in keeping populations in check.

Nematode parasites. Massey (1957), Steiner (1932), and Thorne (1935) described nematode parasites of MPB and made observations on their biologies and habits (see also Mites and Nematodes section). Reid (1958) studied the influence of the nematode *Sphaerulariopsis hastata* and found a one-third reduction in number of eggs produced by infested beetles.

Introduction of an exotic predator. In July 1982, an attempt was made to introduce an exotic predator as a biological control agent against MPB in lodgepole pine in the Intermountain Region. R.F. Schmitz, a research entomologist assigned to the MPB research work unit located at Ogden, UT, obtained a dipterous predator of larvae, *Palloptera modesta* (as *parallela*), from the ARS Beneficial Insects Research Laboratory in Newark, DE, originally received from the USSR. He released the predator in an active MPB infestation that was building to outbreak levels on the north slope of the Uinta Mountains in the Burnt Fork Drainage of the Wasatch National Forest, UT. The adults were received just prior to the onset of peak MPB flight and attack and were released in mid-July on caged lodgepole pine that had been attacked in May by the pine engraver and a few MPB. One 6-inch by 12-inch (15.2-cm by 30.4-cm) bark sample was removed from the caged area on each tree after release of the predators. Examination of these samples revealed abundant bark beetle brood but no predaceous *Palloptera* larvae. Final evaluation was scheduled for the spring of 1983. Unfortunately, record-breaking warm temperatures and heavy rains combined to produce extremely heavy spring runoff that destroyed bridges and roads, preventing access to the release area. This prevented bark samples from being removed prior to anticipated predator emergence from the trees included in the release. There have been no further attempts to establish this predator. (R.F. Schmitz, unpublished data; Coulson 1992.)

Conclusions. Most measurements of the incidence, distribution, and relative effectiveness of beneficial agents were made at epidemic levels of MPB, when beetle populations were the least manageable. The population dynamics of these beneficial agents need to be evaluated at low or endemic levels of MPB. Also, efforts to assess the effects of synthetic bark beetle semiochemicals on the ecology and diversity of beneficial species need to be expanded, especially for semiochemicals used to suppress beetle populations. Because many beneficial insect species can prey upon or parasitize several bark beetle species, use of attractants to concentrate bark beetle populations for suppression purposes is likely to disrupt the natural distribution of the associated beneficial species. There is a need to develop methods for measuring the impact of such treatments on the distribution and effectiveness of beneficial agents.

5. Smaller European elm bark beetle, *Scolytus multistriatus* (Marsham). By Mary Ellen Dix

The smaller European elm bark beetle (SEEBB) is the primary vector of Dutch elm disease in American elm. The beetle was first discovered in the U.S. near Boston, MA, in 1909 and since then has spread from coast to coast (Chapman 1910). Both importation and release of foreign parasites and augmentation of native parasites have been studied as control measures.

During 1964 and 1965, three species of braconid parasites were sent from France to the Forest Service's Central States Experiment Station Laboratory in Delaware, OH (USDA Forest Service 1965). In the fall of 1964, a laboratory culture of the braconid *Dendrosoter protuberans* was established there on SEEBB. In the following months, the parasite was successfully mass-produced on these beetles. During the summer of 1965, B.H. Kennedy released and successfully recovered *D. protuberans* (USDA Forest Service 1966; Kennedy 1970). Subsequent studies determined that *D. protuberans* overwintered and competed favorably with three native parasite species (Kennedy 1970). Interspecific competition among the parasites for hosts was later found to impact adversely

parasite abundance. If larvae of the native parasite *Entedon leucogramma* have matured enough on a host before *D. protuberans* oviposited on the same host, the immature *E. leucogramma* larvae will survive (Kennedy 1981).

By 1967, a technique was developed for rearing *E. leucogramma* and also *D. protuberans* from SEEBB raised on artificial media (Galford 1967; Kennedy and Galford 1972). This technique could be used to mass-rear other SEEBB parasites. In addition, it was found that the SEEBB parasites *E. leucogramma*, *Spathius benefactor*, and *Cheiropachus colon* were attracted to Multilure™, a commercial pheromone used to attract and trap SEEBB. Because large numbers of parasites could be caught on sticky traps baited with this attractant, Kennedy recommended delaying SEEBB trapping programs until just before overwintering beetles emerged. This strategy would protect parasites that emerge before the SEEBB adults in the spring. The pheromone also could be used to attract parasites to infested trees (Kennedy 1979).

6. Southern pine beetle, *Dendroctonus frontalis* Zimmermann. By Mary Ellen Dix

The southern pine beetle (SPB) is the most destructive native bark beetle in the southern U.S. SPB larvae, tree pathogens carried by the beetles, or a combination of larvae and pathogens girdle infested trees. Tree mortality can be spectacular. Trees die within a few months of infestation, and entire stands can be decimated within a season (Thatcher 1981). Removal of all infested trees, and harvesting of uninfested trees before they reach maturity are recommended control procedures. Natural enemies are another possible control method. Biological control research and application efforts can be divided into three eras: a pre-Expanded Southern Pine Beetle Research and Applications Program (ESPBRAP) era, an ESPBRAP era, and a post-ESPBRAP era.

Pre-Expanded SPB Pine Beetle Research and Applications Program. Before 1974 (pre-ESPBRAP), natural enemies studies by Forest Service scientists and their university and State Forest Service cooperators were focused on identifying SPB parasites, predators, and associates (Thatcher 1960; Dixon and Osgood 1961; Thatcher and Pickard 1964; Overgaard 1968; Moore 1970a and b, 1971, 1972; Moser and Roton 1971; Moser et al. 1971a and b). Moore (1970a and b, 1973a and b) also evaluated pathogenicity of bacterial and fungal isolates from SPB in North Carolina. Dix compared relative abundance, attack height, daily activity patterns, and other aspects of the behavior and biology for certain hymenopterous parasites of SPB and the predator *Thanasimus dubius* during a severe outbreak in the early 1970s (Dix and Franklin 1974, 1977, 1978, 1981, 1983). Research on related *Ips* species and other *Dendroctonus* species was limited to identifying natural enemies and aspects of their biologies (Bedard 1965; Furniss 1968; Jouvenaz and Wilkinson 1970). Information available in 1974 on the identity and biologies of bark beetle natural enemies lacked the depth needed to develop realistic population models for detecting and predicting forest population trends and control strategies for SPB and associated *Ips* bark beetles. Additional expanded studies were needed on the impacts, biologies, and interactions of bark beetle natural enemies.

Expanded SPB Research and Applications Program. Responding to public concern over damage caused by a severe SPB outbreak in the early 1970s and the lack of a comprehensive management strategy to address it, Congress established the 6-year ESPBRAP in 1974. Congress subsequently appropriated over $2 million per year to the Forest Service and USDA's Cooperative State Research Service (CSRS) (Shea 1985). The ESPBRAP's mission was to develop coordinated, short-term programs to implement available technology for reducing losses and to develop new short- and long-term forest pest management systems that would effectively suppress or prevent infestations. This program focused on understanding the population dynamics of the SPB; obtaining information needed to develop integrated models for predicting impacts, population levels, and forest susceptibility; and developing suppression techniques with pheromones and insecticides. One broad ESPBRAP goal was to complete studies on natural enemies that could be used as potential control

agents. This goal was later narrowed to developing sampling techniques and obtaining information on specific biological agents critical to understanding SPB population dynamics or predicting population trends (Thatcher 1981).

ESPBRAP also funded related studies by scientists in the U.S. Forest Service, in universities, and in state forest services to accomplish these goals. The results were summarized by Berisford (1981) and were shared among investigators and other experts at formal and informal meetings. The funded studies can be broadly divided into the following categories: identification and sampling, population dynamics, and host preference.

Initial efforts identified additional natural enemies and developed tools for their identification, and assessment of their impact and distribution. Moser (1975) identified 32 species of mites that were predaceous on SPB. Larval and adult keys for rapid identification of natural enemies were developed (Kinn 1976; Finger and Goyer 1978; Goyer et al. 1980). Stephen and Taha (1976) developed a protocol for sampling natural enemies. Other investigators determined seasonal, geographic, and within-tree distributions and biologies of selected arthropod natural enemies in different states (Berisford 1976; Smith 1978; Dixon and Payne 1979a and b; Goyer and Finger 1980); Smith and Goyer 1980; Nebeker and Purser 1980). The impacts, roles, and prey preferences of four species of avian predators of the SPB in Texas were studied (Kroll and Fleet 1979; Kroll et al. 1980). Sikorowski et al. (1979) evaluated SPB mortality from different pathogens and seasonal prevalence of SPB pathogens in Mississippi and Alabama.

In 1980, an exclusion cage for assessing SPB mortality from natural enemies was developed. This technique was used to determine the linear relationship between number of SPB eggs per 100 cm of gallery and number destroyed per predator (Linit and Stephen 1983). Miller (1984a and b) also used an exclusion-interference technique to determine *Ips* spp. mortality during brood development and during different generations.

Other researchers developed techniques for identifying previous hosts of natural enemies and assessing the impact of alternative hosts on natural enemy abundance especially when preferred hosts were scarce. Miller and others used immunodiffusion and immunoelectrophoresis techniques to produce antisera specific for SPB, black turpentine beetle, and *Ips* spp. (Miller 1979; Miller et al. 1979). Kudon and Berisford (1980, 1981) compared free fatty acids in parasites and their bark beetle hosts, and studied host preferences. They found that most bark beetle parasites exhibit a strong preference for the host species from which they originated and will disperse to search for those hosts rather than parasitize a different species. These observations were confirmed in subsequent field trials (Kudon and Berisford 1985).

Post-Expanded SPB Research and Applications Program. Research and application efforts on the SPB and its natural enemies for the most part stopped when funding by the ESPBRAP ceased. However, a few Forest Service scientists in the Southern Forest Experiment Station continued their efforts. Miller et al. (1987) published an overview that discussed the potential for biological control of *Dendroctonus* spp., including the SPB. This publication targeted semiochemicals and insect natural enemies of related bark beetles for additional research. Dixon and Payne (1980) identified several SPB natural enemies that were attracted to SPB semiochemicals. McGregor and Miller (1989) reported the attraction of *Thanasimus undatulus*, a predator of Douglas-fir beetle, to pheromones of SPB and MPB. Miller et al. (1989) studied responses of insect associates of allied bark beetle species to aggregation pheromones.

In 1991, a 30-year record of SPB activity in east Texas was analyzed and it was determined that the structure of SPB populations was due to delayed response to density-dependent factors that could involve natural enemies and was not due to density-independent factors such as climate (Turchin et

al. 1991). Also in 1991, scientists at the Forestry Sciences Laboratory in Stoneville, MS, began a long-term field study to assess the role of predators on SPB population dynamics. They developed cages for excluding predators and determined impacts of decreased predator abundance on SPB abundance (Taylor 1991). Study results will improve models describing the population dynamics of the SPB and help develop long-term strategies to manage the pest.

At the same time, John Reeves, a Forest Service entomologist at Pineville, LA, began studies on effects of native natural enemies on SPB populations and their pattern of variation during the outbreak cycle of the pest. Reeves is measuring the impact of natural enemies on within-tree rate of increase in SPB by comparing the increase rates for SPB exposed to natural enemies with those of unexposed caged SPB. He then will relate the pattern of variation in natural enemy impact to the phase of the SPB outbreak cycle. Reeves also assessed the impacts of adults of the clerid beetle *Thanasimus dubius* on SPB found on and under the tree bark during mass attack, and of *T. dubius* larvae on SPB immatures within the phloem. Although results of this study have not been published, Reeves found that *T. dubius* had a much longer than expected development time. This finding could have significant implications on SPB management because existing protocol calls for the removal of trees that have been vacated by SPB, but which still contain immature *T. dubius* (J. Reeves, personal communication).

7. Mites and nematodes as natural enemies of bark beetles. By Donald N. Kinn

An epidemic of the spruce beetle that began in 1940 and lasted into the mid-1950s ultimately destroyed eight billion board-feet of lumber in Colorado, Idaho, and Montana (Massey 1956). Research on the biology and control of this pest by personnel of the Rocky Mountain Forest and Range Experiment Station began in 1944. Initially, artificial control tactics were employed, but these proved to be too expensive. Consequently, studies were initiated in 1950 to determine the feasibility of combating this insect using natural control agents. Observations revealed that the galleries of this pest were heavily infested with nematodes. C.L. Massey, the only nematologist with the Rocky Mountain Forest and Range Experiment Station, was assigned to the Forest Insect Laboratory at Albuquerque, NM, which is maintained in cooperation with the University of New Mexico (Massey 1974).

Although nematodes had been found associated with the mountain pine beetle and several European bark beetles, little was known of the numbers, species, or effect that nematodes have on their host. Therefore, the objective of the study was to survey and identify nematode parasites and associates of the spruce beetle. Ultimately, four endoparasitic species were found associated with this pest. *Sphaerulariopsis dendroctoni* was found in the body cavity of adult beetles with infestation rates ranging as high as 35%. This species is a true parasite and does not kill its host, but it does reduce oviposition of infested females by 62%. *Contortylenchus reversus* and *Ektaphelenchus obtusus* also were found in the body cavity, in immature instars as well as adults. *Parasitorhabditis obtusa* infests the alimentary canal of all instars of the spruce beetle. *Contortylenchus reversus*, like *S. dendroctoni*, greatly reduces egg production by infected females. The effect of *E. obtusus* on its host is not known and Massey (1956) suggested that *P. obtusa* has little effect on its host. Thirteen other nematode associates of the spruce beetle were collected from the galleries.

In 1957, studies were initiated on nematode parasites and associates of *Ips confusus*. This beetle was responsible for killing major portions of pinyon pine on 800,000 acres in New Mexico and Arizona (Massey 1960a). Three species of endoparasitic nematodes were recovered from the larvae, pupae, and adults of *I. confusus*. One of these internal parasites, *Contortylenchus elongatus*, reduces the egg-laying potential of infected beetles by 50%, but parasitism by this nematode does not result in the death of the host. The parasite's life cycle closely parallels that of its host (Massey 1962a). Mating occurs in the host gallery and the female parasitizes beetle larvae and pupae. Eggs are deposited in

the body cavity of the host only after the insect becomes an adult. The earlier in its development that an immature beetle is infected, the more pronounced is the reduction in fecundity. The other two species of nematodes found internally in *I. confusus*, *Parasitaphelenchus gallagheri* and *Parasitorhabditis obtusa* have little effect on the insect (Massey 1960a). Four additional nematode species, including one new species, were recovered from beetle galleries.

Surveys of nematodes and associates of bark beetles were expanded to include more and more bark beetle species. Studies on the nematode parasites and associates of the fir engraver in New Mexico revealed two species of internal nematodes (Massey 1964a, 1964b). These species, *Sulphuretylenchus elongatus* and *Neoparasitylenchus* (as *Sulphuretylenchus*) *scrutillus*, are unusual in that they first sterilize and then kill their host. Massey (1964a and b) credits these parasites with the decline and termination of an infestation at Ruidoso, NM. He speculated that biological evaluations predicting the decline of infestations may be based on the short galleries produced by infested beetles. In addition to the two parasitic species, 11 other species of nematode associates were found with this insect. All were described as new by Massey (1964a and b).

Furniss (1967) examined populations of the Douglas-fir beetle from Idaho and Utah for nematode associates. About 97% of the insects examined were infested with at least one species of nematode. Parasitism did not vary significantly between male and female beetles. Furniss speculated that some nematode associates of the Douglas-fir beetle may serve as prey for predaceous mites during those periods when immature instars of the beetle are not available.

A recent ecological study of nematode parasites of *Ips* beetles from California and Idaho revealed that infection rates by *Contortylenchus* spp. and *Parasitorhabditis* spp. increase in later emerging beetles (Choo et al. 1987).

In the southeastern U.S., Moore (1970a) sprayed the bark of southern pine beetle-infested shortleaf pines with *Steinernema carpocapsae* and a wetting agent and obtained a 44% reduction in brood adults. This tactic, if perfected, would probably be practical in high value or wilderness areas only. Kard (1991) found no mortality of southern pine beetle larvae that could be attributed to *Steinernema* that were sprayed onto the bark of infested loblolly pine bolts.

An outbreak of the roundheaded pine beetle in ponderosa pine on the Lincoln National Forest, NM, killed over 5000 trees between 1961 and 1965. A survey of nematodes associated with this insect revealed 25 species, of which nine were new to science, and two internal parasites, *Sulphuretylenchus stipatus* and *Parasitaphelenchus dendroctoni* (Massey 1966a). Like other nematode parasites of bark beetles, the life cycles of these are closely synchronized with that of their host.

The above studies by Massey and others established that the effect of endoparasitic nematodes on their bark beetle hosts generally involve: 1) reduced fertility, 2) delayed emergence, 3) altered behavior, 4) reduced flight ability, or 5) possible decreased adult longevity.

Surveys of nematodes associated with bark beetles throughout the U.S. revealed numerous new species (Massey 1957, 1958, 1960b, 1962b, 1963, 1964a and b, 1966b, 1967, 1969, 1971). Massey (1962b) suggested that some nematodes of the family Diplogasteridae found under the elytra of bark beetles may be predaceous on beetle eggs. However, no experimental evidence of predation exists. A rhabditid species observed on dead eggs of the mountain pine beetle was actually feeding on spores of a fungus, *Beauveria* sp., which was responsible for the death of the eggs (D.N. Kinn, unpublished data).

By the time Massey retired from the Forest Service in 1972, he had discovered and described more than 55 new species of nematodes associated in one way or another with bark beetles. In his final publication (Massey 1974), he described 50 additional new species and illustrated 32 parasites and 112 nematode associates of bark beetles.

Massey (1966c) speculated that: 1) the lethal potential of a parasitic nematode might be increased on a novel host species of the same or closely related genus, 2) it may some day be possible to mass rear nematodes for introduction into bark beetle infestations, 3) the planned introduction of infested beetles into a beetle population may result in an increase in the percentage of sterilized beetles, 4) if the life cycle of parasitic nematodes could be altered in such a way that they attain maturity in immature beetles, their effect would be more pronounced, 5) external symptoms exhibited by nematode-infected beetles may be used to predict pest population trends, and 6) nematodes are excellent candidates for integrated control strategies because many kinds of insecticides have no effect on them when applied as water emulsions against host beetles.

In 1952, forest entomologists employed with the BEPQ were transferred to the U.S. Forest Service Division of Forest Insect Research (FIR). At the request of the Texas Forest Pest Action Committee, the Southern Forest Experiment Station assigned one entomologist, R.E. Lee III, to southern pine beetle (SPB) research, locating him first in Liberty and then in Nacogdoches, TX. In 1955, Lee was replaced by R.C. Thatcher. In the same year, the Southern Forest Experiment Station formed a team of three entomologists responsible for aerial detection, evaluation and control activities associated with SPB and other major bark beetle pests.

In 1959, Thatcher prepared a project analysis titled "The Southern Pine Bark Beetles" in which he reviewed the literature and outlined general research needs for the five bark beetle species that attack southern pines. This document was revised and published as a Southern Forest Experiment Station Occasional Paper (Thatcher 1960). One of the recognized needs cited in this paper was research into chemical, biological and silvicultural means of dealing with bark beetles. It was also noted that lack of basic information was a handicap to applied research. This analysis, and the formation of a State and Private Forest Pest Management Division in Region 8, led to the formation of a Forest Insect Research Unit at Pineville, near Alexandria, LA, with W.H. Bennett as Project Leader. The original mandate charged to this unit was to investigate the biology and control of the SPB, black turpentine beetle (BTB), and other bark beetles. Early research undertaken by the unit was to improve chemical formulations and techniques for bark beetle control. With the transfer of J.C. Moser into the unit in late 1962, research on the natural enemies of these bark beetles began. Moser, the first of eventually six research scientists, and Bennett initiated studies on insect and acarine associates of the SPB and other bark beetles during the first year of the unit's existence. Research on mite associates involved two cooperative research grants, one with H.B. Boudreaux, Louisiana State University, Baton Rouge, and the other with E.A. Cross, then at Northwestern State College, Natchitoches, LA. Contact was made with numerous mite taxonomists throughout the world to aid in species identifications and descriptions. Entomologists within the Forest Service and several entomologists outside the U.S. were contacted with the aim of finding acarine enemies of other bark beetles that might be more effective than native mites in maintaining the SPB at endemic levels. By 1964, more than 700 mite specimens had been collected from various bark beetles and distributed to ten taxonomists for identification. This initial survey revealed 26 new species of mites distributed among 12 families. Partial life histories of four possible natural control agents were determined. These species, new to science at that time, were *Macrocheles boudreauxi*, *Schizosthetus lyriformis* (= *Eugamasus lyriformis*), *Trichouropoda australis*, and *Siteroptes bennetti* (= *Pygmephorus bennetti*). None of these species were observed to feed on any instar of the SPB. *Macrocheles boudreauxi* fed on other mites, *S. lyriformis* fed on other mites and nematodes, and both *T. australis* and *S. bennetti* appeared to feed on fungi. Upon completion of these and other studies, an addendum to Thatcher's project

analysis listing known insect and mite associates of bark beetles of southern pines and the possible roles of these associates was prepared by Moser and L.S. Pickard in 1964.

With urging from the Texas Forest Service, the Director of the Southern Forest Experiment Station decided the unit should take an entirely different approach to bark beetle research. Therefore, beginning in late 1962 additional funds were provided to increase its staff to six scientists working as a team to develop silvicultural and biological control of the SPB in relation to its environment and describe the causes of epidemics. At that time, felling and spraying infested trees with chemicals was the only method used to control infestations. The goal of the newly formed unit was to develop silvicultural and biological measures that prevent rather than control outbreaks. Most, but not all, the research undertaken by members of the unit was conducted on the Kisatchie National Forest, LA, and the pine species most often studied were loblolly and shortleaf pine.

Surveys of mites associated with bark beetle-attacked trees revealed many species previously unknown to science (Woodring 1963, 1966; Hunter and Moser 1968; Smiley and Moser, 1968, 1970; Woodring and Moser 1970) some of which are only passively associated with bark beetles. Observations on the biology of some of these species were published (Woodring 1969) and keys prepared for selected groups of mites (McGraw and Farrier 1969; Kinn 1976). Throughout the duration of these studies, new mite species and heteromorphic forms of known species continued to be discovered (Cross and Moser 1971; Smiley and Moser 1974, 1975, 1984a and b, 1985; Hunter et al. 1989). Many of these species are inhabitants of pine bark but others are parasitic on bark beetles (Moser 1979; Moser and Vercammen-Grandjean 1979; Cross et al. 1981). Sampling methods were improved (Kinn 1979), phoretic preferences in site of attachment to their hosts and attachment times observed (Roton 1978), and seasonal and spatial fluctuations in populations of mite associates noted (Kinn 1982; Stephen and Kinn 1980).

In 1966, Bennett wrote the unit's first problem analysis. The approach to solving the SPB problem was divided into three areas: insect biology and physiology, site and host-physiological relationships, and bark beetle associates. The latter included a continuation of research on mite associates and proposed research on nematode associates. By this time about 100 species of mites had been found associated with trees infested by one or more of the five bark beetles of southern pines (Moser and Roton 1971). Most of these species seemed to feed on other mites or bluestain fungi. However, several natural enemies of bark beetles, other than SPB, were found. Eight species were suspected to feed on SPB (Moser 1975).

The first formal Research Work Unit (RWU) Description was prepared by Bennett in 1971. The study areas proposed were divided into three phases: the mensurational phase, the ecological phase, and the management phase. The ultimate goal of the research was to coordinate silvicultural and biological techniques with other promising control measures. Research on natural control agents, primarily mites, continued to be supported by base funding of the unit. Revisions of the RWU Description approved in 1978 and 1982 continued to include studies on mites and nematodes as natural control agents of the SPB.

In 1974, the USDA Combined Forest Pest Research and Development Program (CFRP) was established and the six year Expanded SPB Research and Applications Program (ESPBRAP) funded. Although natural and biological control studies were given a low priority, a few such studies were funded. Studies on the natural control of SPB by mites and nematodes by Moser were funded by ESPBRAP for two years. This enabled the unit to add another full time employee to work on biological control. D.N. Kinn joined the unit in 1975 and was assigned the task of verifying the feeding habits and life histories of those mites that appeared to be natural control agents. His duties were later expanded to include the impact of endoparasitic nematodes on SPB populations. Several other studies outside the Forest Service were also funded by ESPBRAP. These included those by P.P.

Sikorowski (Mississippi State University) and G.E. Allen (University of Florida) who investigated the impact of pathogens on SPB, and by V.G. Perry and R.C. Wilkinson (University of Florida) who investigated the impact of endoparasitic nematodes on SPB.

The life cycles of three of the most common mesostigmatid mites associated with SPB were determined (Kinn and Witcosky 1977; Kinn 1983, 1984a). All active instars of these species fed on nematodes, including the free-living instars of endoparasitic nematodes. The relationship of these mites with their bark beetle hosts appears to be one of phoresis and mutualism (Kinn 1980). Bark beetles provide the means by which the flightless mites are transported to new beetle infestations, and the beetles may benefit from reduced nematode parasitism due to the feeding activity of the mites. However, the presence of phoretic mites appears to adversely affect beetle flight (Kinn and Witcosky 1978).

Numerous disease agents were found in SPB populations (Knell and Allen 1978; Pabst and Sikorowski 1980) causing an average mortality of 22% over a 2-year study period (Sikorowski et al. 1979). A microsporidan was found to be prevalent in endemic SPB populations but scarce in epidemic populations (Bridges 1987). The incidence of endoparasitic nematodes (*Contortylenchus* spp.) was found to be as high as 24% in some populations (Joye and Perry 1976) and one species, *C. brevicomi*, reduced beetle fecundity (MacGuidwin et al. 1980). In addition, there was evidence that endoparasitic nematodes may alter the flight capabilities or host finding behavior of infected SPB (Atkinson and Wilkinson 1979; Kinn and Stephen 1981). The flight behavior of female engraver beetles also appears to be altered by endoparasitic nematodes (Kinn 1984b). By 1981, a total of 16 papers reporting research on microorganisms, nematodes, and mites, funded in total or part by ESPBRAP, were published.

In the 1978 RWU Description, it was recognized that the SPB is intimately associated with a large number of other organisms and that an understanding of the life processes of the pest and its associates was essential if models that forecast population trends were to be developed along with control strategies to augment beetle population suppression by natural enemies.

The concept of "new associations" (Pimentel 1963) was applied to mites preying on bark beetles. *Pyemotes giganticus*, an egg parasite of the "Douglas-fir pole beetle" (*Pseudohylesinus nebulosus*), was imported from the western U.S. and studied as a possible extraregional parasite of the SPB (Moser 1981). Although this mite readily attacks beetle eggs in the laboratory, it parasitizes less than 1 percent of bark beetle eggs in the field. Therefore, this species was never released in the south for SPB control. Life histories of several other pyemotid mites were also determined. *Pyemotes parviscolyti* attacks all immature instars of *Pityophthorus annectens* (as *P. bisulcatus*) in the field, but never comes in contact with economically important bark beetles (Moser et al. 1971a). A European species, *Pyemotes dryas*, was found to feed on SPB under laboratory conditions, but would not become phoretic on any North American bark beetle and is thus a non-viable candidate for biological control of North American bark beetles (Moser et al. 1978).

An ecological paper (Wilson 1980) based on data gathered by Forest Service personnel theorized that mite species closely associated with their host would be less efficient control agents than those not dependent upon the host for transport. With the realization that the most common mite associates of the SPB may be beneficial rather than detrimental to beetle populations, research was undertaken to clarify the relationships existing among the various mite and nematode species present in the subcortical habitat and the role of various microorganisms in the ecology of bark beetles.

Tarsonemid mites were found to vector the bluestain fungus, *Ceratocystiopsis ranaculosus* (Bridges and Moser 1983, 1986; Moser 1985; Moser and Bridges 1986), which can be detrimental to SPB development. Methods were developed to rear bark beetles free of mites (Moser and Bridges 1983;

Kinn and Roton 1988). Because the unit was known for its expertise on mites, numerous mite species collected from forest pests throughout the world were first sent to the Pineville, LA, laboratory and then forwarded to various taxonomic experts. Among these mites was *Pyemotes barbara*, a potential natural control agent of cone and seed insects (Moser et al. 1987).

In a new RWU Description in 1987, research on mites, nematodes and microorganisms was phased out of the unit's mission and in 1989 Moser retired. Research on mites and nematodes conducted at the Pineville, LA, laboratory had led to the realization that not only do some of these organisms prey on or parasitize bark beetles but others have potential as indices for predicting pest population trends.

Not all research on biological control of the SPB was conducted at the Pineville laboratory, and not all biological control research was aimed at controlling this pest. At the Southern Forest Experiment Station at Gulfport, MS, Kard (1991) studied the possibility of controlling SPB larvae using steinernematid nematodes. Although laboratory tests were very successful, field trials were disappointing. Earlier field studies conducted out of the Southeastern Forest Experiment Station revealed that successful survival of *Steinernema carpocapsae* was dependent upon moist environments or a relative humidity above 90% (Moore 1970a, 1973a). Steinernematid nematodes have also been reported as potential control agents of other forest pests (Schmiege 1963; Moore 1973a).

Before the creation of a Forest Insect Work Unit in Louisiana, mites had been noted as associates of bark beetles and were suspected of being natural enemies of these pests. DeLeon (1930) in an unpublished report noted that nematodes and mites were often associated with the mountain pine beetle (MPB), and in other unpublished reports Bedard (1932, 1933a) noted that two unidentified mite species fed on the eggs of the Douglas-fir beetle under laboratory conditions. Rust (1933) reported up to 85% of pine engraver (as *Ips oregonis*) eggs destroyed by mites. In the Pacific Southwest, Lindquist and Bedard (1961) reported on the biology and taxonomy of *Tarsonemoides* (as *Iponemus*) species parasitizing eggs of *Ips* engraver beetles. Beal (1965) credited nematodes with terminating a fir engraver outbreak in New Mexico and mites, along with insect parasitoids, as playing major roles in stopping a SPB outbreak in Texas. Boss and Thatcher (1970) studied mites associated with *Dendroctonus* and *Ips* species in the Rocky Mountain region. Although no mites were found to attack *Dendroctonus* species, a *Dendrolaelaps* sp. preyed upon eggs of numerous *Ips* species, and mites of the genus *Iponemus* selectively parasitized eggs of *Ips* beetles.

B. Shoot and Trunk Borers and Sheathminers. By Mary Ellen Dix and Shivanand Hiremath

1. Shoot borers and sheathminers (Lepidoptera: Tortricidae and Yponomeutidae)

In 1915, entomologists of the Bureau of Entomology's Division of Forest Insects' Gypsy Moth Laboratory in Melrose Highlands, MA, initiated a long-term study to identify lepidopterous insect pests and their parasites in the northeastern U.S. This study focused on rearing field-collected lepidopteran larvae and documenting their distribution and food preferences. The entomologists also identified all emerging parasites and documented aspects of their life cycles. R.C. Brown (Entomologist-in-Charge of the Bureau's Division of Forest Insect Investigations, New Haven, CT) encouraged the entomologists to collect extensively and rear microlepidopteran tree pests, such as shoot borers (*Rhyacionia* spp., *Retinia* spp., and *Petrova* spp.) and sheathminers (*Taniva* spp., and *Zelleria* spp.). These early studies provided information on the identity and distribution of the tree pests and their parasites. Such data often were the earliest available information on the species and have been an invaluable resource for later forest entomologists. When the USDA reorganized in the early 1950s, these records were transferred to the Northeastern Forest Experiment Station of the Forest Service. J.V. Schaffner, Jr., summarized the results of the microlepidoptera study in 1959. (Results of the similar study of macrolepidoptera and their parasites was published by the Bureau of

Entomology in 1934 [Schaffner and Griswold 1934]. Other research on biologies and releases of parasites of forest insects by USDA entomologists prior to 1953 is discussed in Chapters I and II above.)

During the 1960s and 1970s, Forest Service entomologists continued to identify natural enemies of shoot borers and other microlepidoptera, and to describe their biologies (e.g.: Yates 1960, in Georgia; Miller et al. 1961, in Minnesota; Stevens 1966, 1971, in California; Torgersen and Coppel 1969, in Wisconsin; Koerber and Struble 1971, in California; Yates and Beal 1971, in Georgia; Brewer and Stevens 1973, in Colorado; McKnight 1973, in Colorado; Jennings 1975, in New Mexico; and Yates et al. 1981, in Georgia). Shoot and tip borers of the genus *Rhyacionia* received considerable attention at all Forest Experiment Stations in the U.S. (Yates 1967a and b). However, except for the European pine shoot moth and the Nantucket pine tip moth, most studies were short-term and focused on pests of local or regional importance. A more detailed discussion of these studies follows. By 1967, entomologists had identified over 100 species of parasites of *Rhyacionia*. Yates (1967b) reviewed published papers on the genus *Rhyacionia* and developed a key to both native and introduced *Rhyacionia* parasites. This key also contained notes on parasite biologies and introductions, and listed relevant publications.

European pine shoot moth, *Rhyacionia buoliana* (Denis & Schiffermüller). This moth is an introduced insect that damages the buds and shoots of pines. The moth was discovered on Long Island, NY, in 1913 and by 1915 had spread to Ohio (Miller and Neiswander 1955). By 1958, the borer was found in red pine plantations from eastern Canada and northeastern U.S. south to Virginia, and as far west as Wisconsin and Michigan (Torgersen and Coppel 1965). In the late 1960s, the shoot moth was discovered in pine plantations, in Christmas trees and in planted trees in residential areas around Puget Sound in Washington (Ryan and Medley 1970).

Parasites of this shoot moth have been introduced into the U.S. and Canada to control outbreaks of the pest since 1928 (Dowden 1962; McGugan and Coppel 1962a). Over 700,000 individuals representing more than 16 species were introduced between 1928 and 1958 (Dowden 1962; Miller 1967). In Michigan and Ohio alone, about 16,000 parasites were released between 1959 and 1962 (Miller 1967). However, these releases were considered to be failures because of poor parasite survival and lack of long-term moth control (Arthur and Juillet 1961; Turnbull and Chant 1961; Miller 1967). Arthur and Juillet (1961) speculated that unfavorable release conditions reduced parasite survival and chance of establishment.

During the 1950s and 1960s, Forest Service and university entomologists initiated a series of studies to learn more about parasite complexes in Ohio, Wisconsin, Michigan, and Washington. These scientists investigated parasite bionomics, impacts, and biologies (Miller and Neiswander 1955; Miller 1959; Torgersen and Coppel 1965). They discovered that in spite of the massive earlier introductions, parasite populations were lower in North America than in Europe. The European braconid parasite *Orgilus obscurator* was, however, discovered to be established at several sites in Michigan after an earlier release in Ontario (Miller 1970).

During the 1960s and 1970s, studies were initiated under Public Law 480 (PL-480) with cooperators in Yugoslavia, Poland, India and other countries to identify potential parasites for importation and release in the U.S. The PL-480 scientists inventoried parasites, assessed their impacts, developed rearing techniques, identified alternative hosts, and obtained other needed information to accelerate parasite releases and enhance their establishment in the U.S. (Koehler and Kolk 1969; Vasic 1972; Rao and Chacko 1972; Forest Service Annual Reports).

In 1969, 5,365 female *Itoplectis quadricingulata* were released on a 40-acre site in western Washington to suppress populations of *R. buoliana* (Ryan and Medley 1970). The Forestry Sciences

Laboratory in Corvallis, OR, mass-reared this ichneumonid parasite prior to release. The parasite infested about 30% of the shoot moth larvae and about 50% of the stocked cohorts of the greater wax moth larvae at the site. Ryan and Medley (1970) concluded that the host-tree shoots and buds surrounding the shoot moth larvae probably protected them and hampered parasitism. However, they felt that host preferences and searching behavior of the parasite needed to be more fully understood before the parasite could be recommended for control of the European pine shoot moth.

Nantucket and western pine tip moths, *Rhyacionia frustrana* (Comstock) and *R. bushnelli* Busck, and southwestern pine tip moth, *R. neomexicana* (Dyar). In the late 1800s, the Nantucket pine tip moth (NPTM) was discovered in New England. This tortricid is now distributed from southern New England to Florida and west to eastern Nebraska and Texas. The larvae mine the buds and new growth of young trees in pine and Christmas tree plantings, thereby stunting growth and killing the trees. The western pine tip moth (WPTM) damages native and planted ponderosa, red, jack and Scotch pines in Montana, the Dakotas, Nebraska, Arizona and New Mexico (Powell and Miller 1978). Daniel T. Jennings (1975), an entomologist with the Rocky Mountain Forest and Range Experiment Station in Albuquerque, NM, identified parasites and predators of the southwestern pine tip moth, and assessed the impact of spiders and other predators on its abundance.

Numerous researchers have identified natural enemies of NPTM and WPTM (Cushman 1927a and b; Yates 1960, 1966, 1967a and b; Eikenbary and Fox 1968; Nash and Fox 1969; Dick and Thompson 1971; McKnight 1973; J.E. Pasek unpublished data). Yates (1967a) developed an X-ray technique for detecting parasites in concealed tip moth larvae. He also identified diagnostic characteristics for the interpretation of radiographs of shoot tips containing *Rhyacionia* spp. and their parasites and predators. This technique permitted the selective rearing of tip moths and their parasites without the destruction of their microenvironment.

The most famous release of NPTM parasites occurred in Nebraska. Between 1902 and 1909, the WPTM immigrated into young ponderosa pine plantations in the Nebraska National Forest. By the early 1920s, pines in this man-made forest were severely damaged by WPTM. In 1924, Cushman and other Bureau of Entomology (BE) entomologists identified parasites of NPTM that might be useful for control of WPTM in Nebraska (Cushman 1927a and b). The next year, pine tips infested with parasitized NPTM from Virginia were sent to Nebraska where L.G. Baumhofer, an entomologist assigned by the BE to control the outbreak, reared and released the parasites. In 1926, the process was repeated with tips collected in both Virginia and Massachusetts (Graham and Baumhofer 1927). Nine species of parasites were released in 1925; 11 species were released in 1926 (Dowden 1962). In 1927, Graham and Baumhofer identified the parasites of WPTM in the Nebraska National Forest and described their biologies. One parasite, the ichneumonid *Campoplex frustranae* became established and controlled the WPTM within five years. Survival of the other parasite species was poor (Dowden 1962). During the 1930s, southwestern pine tip moth abundance increased rapidly in the forest and it became the primary pest there. *Campoplex frustranae* did not parasitize this species.

Melvin E. McKnight of the Rocky Mountain Forest and Range Experiment Station (RM) location at Bottineau, ND, reared WPTM and NPTM from infested shoots collected throughout the Great Plains. He reared *C. frustranae* from samples collected in the Nebraska National Forest, De Smet, SD, and in western North Dakota (McKnight 1973; Unpublished data, RM, Lincoln, NE). During the mid-1980s, Judy Pasek (RM, Lincoln, NE) reared and identified tip moth parasites, while evaluating the impact and seasonal activity of WPTM and NPTM in eastern Nebraska (J.E. Pasek, unpublished data). In the early 1990s, Carol Bell (Forest Pest Management, Region 1, Missoula, MT) identified natural enemies of *Rhyacionia* spp. as part of her M.S. research to evaluate abundance, distribution, and impact of shoot borers in the western Dakotas and eastern Montana (C. Bell, unpublished data).

Nash and Fox (1969) applied the nematode DD-136 (*Neoaplectana carpocapsae*) to NPTM-infested pines. The nematode killed more first generation larvae than second or third generation larvae. Subsequent use of the nematode was not recommended because survival of the nematode was poor (Nash and Fox 1969).

Other shoot borers and sheathminers. In the western U.S., a series of short-term regional studies was initiated on the biologies and impacts of natural enemies of several species of shoot borers and sheathminers. R.E. Stevens (1966, 1971), of the Pacific Southwest Forest Experiment Station (PSW), identified natural enemies of the "ponderosa pine tip moth", *Rhyacionia zozana*, in California. Later, Niwa (1988), of the Pacific Northwest Forest Experiment Station (PNW), re-examined *R. zozana* populations in California and Oregon, and identified their natural controls and assessed their impacts on moth abundance. Stevens later transferred to the Rocky Mountain Forest and Range Experiment Station (RM) in Fort Collins, CO, where he studied the biologies and identified the parasites of the pine needle sheathminer and "pinyon pitch nodule moth", *Petrova arizonensis* (Stevens 1971; Brewer and Stevens 1973).

Larvae of the "metallic pitch nodule moth", *Retinia metallica,* mine the growing tips of ponderosa and other pines in the Great Plains; such mining stunts and deforms the trees (Dix et al. 1987). In 1986, Mary E. Dix, of the RM station at Lincoln, NE, began a study to identify and assess the impact of natural enemies on abundance of *R. metallica* in pine windbreaks. The identities, impacts, and biologies of parasites were determined through rearing trials and field observations. Dix also identified potential predators on branches and documented their seasonal abundance. She found that spiders were the most abundant predator on the trees and that their abundance was influenced by the surrounding vegetation (Dix 1991b; unpublished data). In cooperation with entomologists and wildlife biologists from the University of Nebraska, Dix currently (1993) is assessing the impact of vegetative diversity and agroecosystem management practices on predator abundance in tree-crop and tree-turf ecosystems. Results of this research will be used to develop techniques for increasing survival of natural enemies of tree pests. By manipulating ecosystem diversity and by modifying agriculture and turf management practices, natural enemy effectiveness may be enhanced.

Predators. Spiders are among the most abundant arthropod predators found on trees. Population densities of arboreal spiders are estimated to exceed 645,000 spiders/hectare (Jennings and Collins 1987). However, despite their ubiquitous occurrence and predatory habits, few studies have addressed the importance of spiders in forest ecosystems. Unless spiders are actually observed feeding on their prey, or "stock" their prey in webs, it is difficult to determine their diets, prey preferences, and impacts on target forest pests. Consequently, information on the roles spiders play in maintaining and regulating forest pests of pine is very limited. During the 1970s, Jennings (RM, Albuquerque, NM) collected, identified, and described habitat preferences of spiders found on pines and other trees in New Mexico, Colorado, Texas, Nebraska, South Dakota, and Wisconsin (Jennings 1972, 1981; Jennings and Toliver 1976; Cutler et al. 1977; Cokendolpher et al. 1979; Jennings et al. 1989). He found that crab and lynx spiders were common on pines and in pine-juniper ecosystems (Jennings 1974, 1981; Jennings and Toliver 1976; Cutler et al. 1977). Crab spiders were observed feeding on the pine butterfly (Jennings and Toliver 1976), on scarab beetles (Jennings 1974) and on southwestern pine tip moth (Jennings 1975; Lawson et al. 1983).

Most studies have concerned the identification of all spider species associated with a defined ecosystem or on tree species (Jennings 1972, 1974; Jennings and Dimond 1988; Cokendolpher et al. 1979; Jennings et al. 1989, 1990a and b; C.L. Griswold, unpublished data). Related observations have been made on spider biologies, feeding behaviors, and prey (Jennings and Toliver 1976; Cutler et al. 1977; McDaniel and Jennings 1983; Hayes and Lockley 1990). Spiders in spruce and fir were identified by Hilburn and Jennings (1988) and Jennings et al. (1990a), but little else is known about natural enemies of shoot borers in spruce-fir forests. In Nebraska, Dix (unpublished data) collected

information on the identity, distribution and impact of spiders on *Retinia metallica* population dynamics. She also has documented the distribution of spiders in tree-crop and tree-turf landscapes.

Many species of spiders are usually highly mobile, nocturnal, and secretive in their behavior; consequently, it is extremely difficult to assess their effectiveness in regulating prey populations. Three general approaches to evaluation of spider effectiveness have been developed: 1) direct observations and assessment of hunting spiders with and without prey; 2) direct observations of web-spinners and their catches, including "stocked" prey in webs; and 3) indirect assessment of predation on target insects by immunological assays. Hayes and Lockley (1990) observed the nocturnal feeding behavior of wolf spiders in cotton fields on Coleoptera and Diptera. They found that prey selection and temporal activities showed a distinct separation by species and developmental stage.

2. Trunk borers

Boring insects tunnel through the wood, killing or severely weakening, and degrading lumber of infested trees. They tend to have few natural enemies because they are protected within their host tree for most of their life cycles and are difficult to detect. Available information on natural enemies is obtained through direct observation of their feeding or searching behavior or by rearing the borer larvae. During the 1970s and 1980s, James D. Solomon, of the Southern Forest Experiment Station (SO), Stoneville, MS, identified parasites, predators, and pathogens of the carpenterworm, clearwing moths, and other hardwood borers in Mississippi. Solomon and Toole (1968) also observed carpenterworm pupae trapped in galleries by fungal mycelia. McKnight and Tagestad (1972) (RM, Bottineau, ND)) and Dix (unpublished) (RM, Lincoln, NE) identified parasites reared from the carpenterworm and lilac borer, respectively, in the Great Plains, and observed bird predation on adult carpenterworms (unpublished data, RM, Lincoln, NE).

Woodpeckers can destroy large numbers of overwintering trunk borer larvae. Woodpecker predation on several species of hardwood borers was reported in Ohio and Mississippi (Solomon 1969; Hay 1972; Galford 1985) and on longhorned beetles in California firs (Wickman 1965).

3. Root borers

Phyllophaga spp. larvae (June beetles or white grubs), are widely distributed in the U.S. and other parts of the world. While generally considered an agricultural pest of field crops and turf, the grubs injure the roots of nursery seedlings, newly transplanted saplings, trees and ornamentals by chewing off or girdling the roots (Wilson 1977). White grubs can become a major pests on economically important pine and fir seedlings (Stone and Schwartz 1943; Shenfelt et al. 1954; Fowler and Wilson 1971, 1975; Sutton 1975; Fowler et al. 1982; Bruhn and Heyd 1986; Kard and Hain 1987a and b, 1988; Mitchell et al. 1992). Damaged seedlings have inadequate nutrient uptake and support, and are predisposed to various soilborne fungal pathogens, such as species of *Fusarium*, leading to the death of the seedlings. The consequence is a sparsely populated pine plantation that needs to be replanted at a great expense.

Traditionally, whenever threshold levels of white grub infestations were predicted, chemicals such as aldrin and chlordane were used to prepare the soil before planting the seedlings (Fowler and Wilson 1975, 1982; Kard and Hain 1988; Baxendale et al. 1992). While these methods were usually effective, they often resulted in cost overruns and were environmentally unsafe for humans and other animals. Although management practices can be used to reduce the mortality of the seedlings from white grub damage, plant vigor and overall plantation productivity is reduced.

In recent years, several different approaches were evaluated for control of white grubs (McLeod et al. 1986; Kard and Hain 1987b; Kard et al. 1988). Entomopathogenic nematodes were used as a part of

an IPM program to control white grubs (Kard et al. 1988; Forschler and Gardner 1991; Redmond and Georgis 1991). Similarly efforts with entomopathogenic fungi such as *Verticillium lecanii* (Gour and Dabi 1988), *Beauveria bassiana* and *Metarhizium anisopliae* (Poprawski and Yile 1990) had limited or no impact. Poprawski and Yile (1990) isolated a iridescent virus strain from grubs of *Phyllophaga anxia*. Although injection of this virus into white grubs caused mortality, it was ineffective under field conditions. All of the above approaches were ineffective in controlling the white grubs.

Scientists at Delaware, OH, are using genetically-engineered ectomycorrhizal fungi (EMF) to develop species-specific methods that can be easily integrated into other control methods. These transgenic EMF alter the microclimate around the conifer roots and produce nutrients and protectants that protect the young pines. Advantages of transgenic EMF over other methods of chemical and biological control methods include the ability to form a protective mantle around the roots and increased environmental safety through use of symbiosis specific promoters.

Strains of the fungi *Laccaria bicolor* and *Paxillus involutus* were isolated from red pine plantations and found to be very effective colonizers of several pine species (Richter and Bruhn 1989, 1990, 1993). A particle gun-mediated transformation system was developed for these strains and successfully used to insert genes into these fungi for Hygromycin resistance (selectable marker), beta glucuronidase (GUS, reporter gene; useful for tracking transgenic EMFs), and a gene encoding BtCryIIIA, an insecticidal crystal protein (ICP) from *Bacillus thuringiensis* (Bt). These inserted genes were stably integrated and functioning properly in transformed *L. bicolor* and *P. involutus*.

The presence and expression of GUS gene in the seedlings was tested by a modified microfuge tube procedure of Roberts et al. (1989). Mycorrhizal synthesis experiments showed that the transgenic EMFs retained their ability to form a mycorrhizal mantle around pine roots, expressed GUS, and thus provide protection against root pests like white grubs. However, the CryIIIA protein was not very effective on *Phyllophaga anxia*, but was effective on elm leaf beetle larvae. Bioassays with transformants already developed are using elm leaf beetle or other susceptible species to determine the efficacy of expression of Bt genes in EMF. The research unit in Delaware, OH, plans to use these techniques to introduce Bt genes from the Bt strain Buibui and other strains which are effective against scarabs. These techniques can be integrated with other traditional control methods for white grubs and also has the potential for biological control of bacterial/fungal pathogens of trees.

C. Hardwood Defoliators

1. Cottonwood leaf beetle (*Chrysomela scripta* Fabricius) and other chrysomelid beetles (Coleoptera). By Leah S. Bauer and Mary Ellen Dix

The cottonwood leaf beetle (CLB) is a native defoliator of *Populus* spp. throughout North America. The larvae and adults are most damaging to newly established plantings of cottonwoods and hybrid poplar. The beetles may complete up to seven generations per year in the southern U.S., where conventional pesticides are frequently used for their suppression.

In Mississippi, adults and larvae of the coccinellid *Coleomegilla maculata* feed on the eggs and larvae of CLB. In 1979, Neel and Solomon (Southern Forest Experiment Station [SO], Stoneville, MS) initiated a study designed to augument *C. maculata* abundance in young poplar plantations in Mississippi. In March of 1979 and 1980, they collected adult *C. maculata* at their aggregation sites and released them in young cottonwood plantations. The release was of limited success, because *C. maculata* were recovered from the trees for fewer than 14 days after their release (Neel and Solomon 1985; Solomon and Neel 1985).

During the 1980s and 1990s, isolates of *Bacillus thuringiensis* (Bt) were discovered that were toxic to some coleopterans. In 1988, Bauer (North Central Forest Experiment Station [NCFES], East Lansing, MI) initiated studies to identify Bt isolates with activity against the CLB (Bauer 1990; D. Bradley and M. Harkey [University of Washington, Seattle], K.D. Biever [ARS, Yakima, WA], L.S. Bauer, and M.-K. Kim [Chonbuk National University, Seoul, Republic of Korea], unpublished data), and the imported willow leaf beetle, an exotic pest of poplar and willow (Bauer 1992). Bauer conducted field trials with formulated Bt-based insecticides, determined the impact of Bt on leaf beetles, and described the ultrastructural damage caused by Bt CryIIIA toxin on the CLB midgut cells (Bauer and Pankratz 1992; Koller et al. 1992). Since 1989, a population of CLB has been selected with Bt CryIIIA toxin and high resistance (>1000 times) to the toxin has evolved. In 1992, studies were initiated to understand mechanisms of Bt resistance in both CLB and Colorado potato beetles. Resistant populations are also being evaluated for cross-resistance to other Bt toxins. The results of this research are critical to the development of resistance management strategies for transgenic plants that contain Bt toxin genes (Bauer, unpublished data). Research on resistance to Bt is being conducted in cooperation with C. Noah Koller, Robert M. Hollingworth, and Mark E. Whalon at the Pesticide Research Center, Michigan State University, East Lansing, with funding by the USDA Competitive Grants Program.

No indigenous pathogen was known from CLB despite extensive life table studies, until Bauer discovered a microsporidan from CLB collected near Ames, IA. This newly described microsporidan, *Nosema scripta* (Bauer and Pankratz 1993), may be an important natural control factor of CLB, although the geographical extent of this pathogen throughout the range of CLB is not known. *Nosema scripta* is transovarially transmitted, and infected beetles die in the egg or larval stages. Beetles that survive to the adult stage are smaller, lay fewer eggs, and die sooner than their uninfected counterparts. Bauer described the pathology and taxonomic status of *N. scripta* using light and electron microscopy, and studied cross-infectivity with two other chrysomelid species.

2. Elm spanworm, *Ennomos subsignaria* (Hübner) (Lepidoptera: Geometridae). By Mary Ellen Dix

The elm spanworm is a serious lepidopteran defoliator of many broadleaved tree species, particularly oaks, hickories, black walnut, and red maple (Drooz 1980; Drooz et al. 1976). Davis (1960) identified parasites of the elm spanworm in Georgia. A decade-long outbreak collapsed in 1964 primarily because of an egg parasite, initially identified as *Telenomus alsophilae* (Ciesla 1963, 1964; Drooz 1964), but which was later shown to be a new species, *Telenomus droozi* (Drooz et al. 1976; Muesebeck 1978). The apparent success of *T. droozi* in controlling the elm spanworm and the success of *T. alsophilae* against the fall cankerworm (see below) spurred an effort to culture both species of parasites on other hosts because elm spanworm were difficult to rear. A geometrid, *Eutrapela clemataria*, was selected for mass rearing *T. alsophilae* (Fedde et al. 1976, 1982). Attempts to rear *T. droozi* were not successful.

In 1973, a second species of egg parasite, *Ooencyrtus ennomophagus*, ended an elm spanworm outbreak in Connecticut. Drooz and Solomon (1980) reported that the parasite could be cultured on eggs of the poplar tentmaker, but parasite yield from tentmaker eggs decreased with time. Subsequent research by Arnold T. Drooz, an entomologist with the Southeastern Forest Experiment Station (SE) in Research Triangle Park, NC, and colleagues determined that the parasite could be reared on chilled *E. clemataria* eggs and that cold storage of the eggs did not decrease parasite yields (Drooz and Weems 1982; Drooz and Barham 1985).

In the early 1980s, research on elm spanworm and other defoliators by Drooz, G.F. and V.H. Fedde and other SE entomologists ceased because of program redirection. Drooz was transferred to Olustee, FL, and the Feddes resigned.

3. Fall cankerworm, *Alsophila pometaria* (Harris) (Lepidoptera: Geometridae). By Mary Ellen Dix

Outbreaks of the fall cankerworm, a hardwood defoliator in the Appalachian Mountain region of Virginia and North Carolina, were frequent between 1960 and 1973, but varied in duration and severity (Fedde et al. 1973). The cankerworm overwinters as eggs in masses attached to branches. Gerhard F. Fedde (SE, Research Triangle Park, NC) surveyed egg masses in Virginia and North Carolina for parasites. He found that *Telenomus alsophilae* was the most common of the three parasite species reared from the eggs (Fedde 1977; Fedde et al. 1973). This parasite was found initially in Connecticut in 1945 (Schread 1945) and later was collected in Virginia (Rauschenberger and Talerico 1967). Fedde also found that a very aggressive strain of *T. alsophilia* attacked cankerworm eggs in the mountains of Virginia in late winter (Fedde et al. 1973). He described characteristics of parasite emergence holes that can be used to differentiate among the three parasite species (Fedde 1979).

Telenomus alsophilae was a possible candidate for mass production and release because of its wide geographic distribution and high survival in fall cankerworm eggs. However, mass production required readily available host eggs that were easy to maintain. Fall cankerworm eggs are difficult to maintain in the laboratory, which made them poor candidates for rearing parasites. Fedde evaluated host preferences of *T. alsophilae* in the laboratory and found that the species could parasitize eggs of 12 different species of geometrids and two species of noctuids. He concluded that the broad host range of this parasite made it the best candidate for mass rearing and release against lepidopterous eggs (Fedde 1977).

Drooz, G.F. Fedde (SE, Research Triangle Park, NC) and Vicki H. Fedde (SE, Athens, GA) developed a technique for chilling host eggs so that they could be preserved in a state suitable for sustaining egg parasites (Fedde et al. 1979). They used this technique to maintain and mass-produce *T. alsophil*ae on a surrogate host, the geometrid *Eutrapela clemataria.* Then the parasite was mass-released to control two geometrid defoliators in Colombia, South America. However, a laboratory test of the parasite against one of the pests, *Glena bisulca* on *Cupressus lusitanica*, was unsuccessful (Drooz and Bustilla 1972). In 1976, *T. alsophilae* was successfully established on the other geometrid, *Oxydia trychiata*, a native Colombian defoliator of introduced conifers and several species of hardwoods. *Telenomus alsophilae* was the first insect parasite to control a forest pest from a genus different from that of its natural host (Drooz et al. 1977b).

4. Arthropod parasites and predators of the gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae). By Thomas M. ODell

Introduction. The gypsy moth was introduced into Massachusetts from France in 1868. When initial attempts at eradication were abandoned, interest increased in the importation of exotic species of natural enemies to suppress populations of the gypsy moth and slow the spread of the pest. In 1904, the State of Massachusetts and the USDA Bureau of Entomology appropriated funds to import natural enemies of gypsy moth. In 1934, the Bureau merged with the Bureau of Plant Quarantine to become the Bureau of Entomology and Plant Quarantine (BEPQ). Abolished in 1953, this Bureau's forest pest research functions were distributed to the Divisions of Forest Insect Research and Blister Rust Control of the Forest Service (Dunlap 1980). Philip B. Dowden and Paul A. Godwin, both with some gypsy moth research experience in the BEPQ, were assigned to the Northeastern Forest Experiment Station's (NEFES) Forest Insect and Disease Laboratory, New Haven, CT. While in the BEPQ, Dowden conducted some of the earliest significant investigations on the biologies of gypsy moth parasites (Dowden 1933, 1934a and b, 1935). Dowden continued to work on the biology of gypsy moth parasites (Dowden 1961) at the NEFES Laboratory at New Haven, and conducted one of

the first, if not the first, inundative releases of *Cotesia melanoscelus*[1] (as *Apanteles*). The releases were made in the southern Lake Champlain region of Vermont, and resulted in no significant difference in percent parasitism by *C. melanoscelus* between treatment and control (Dowden and Reardon 1967).

The foreign exploration and importation program for exotic parasites of gypsy moth, initiated by the Bureau of Entomology in 1904, has been one of the most massive efforts in biological control history. The Bureau's role in this effort is well documented by Reardon (1981a). This review will concentrate on the Forest Service's contributions to biological control of gypsy moth by arthropod parasites and predators between 1960 and 1990.

Foreign Projects - Public Law 480. In the late 1950s, following extensive aerial application of DDT to eradicate gypsy moth infestations, the use of this pesticide was abandoned because of increasing concern about the effects of chlorinated hydrocarbons in the environment. The need for safer methods for controlling gypsy moth stimulated support for development of biological control techniques. In the early 1960s, efforts resumed to search for new natural enemies. Between 1960 and 1975, the Forest Service, under Public Law 480, supported five overseas projects on the gypsy moth and its natural enemies, during which many natural enemies were imported into the U.S.:

- Project in Spain, 1960-65: *Project No. E25-FS-10* -- "The study of parasites, predators, and diseases of the gypsy moth and the possibility of their application in the biological control", conducted from May 11, 1960, to May 11, 1965. N. Romanyk, Servicio de Plagas Forestales, C. Marques de Mondejar 33, Madrid, Spain, was Principal Investigator.
- Projects in India, 1961-71*: Project No. A7-FS-8* -- "Survey for natural enemies of the gypsy moth", conducted from July 25, 1961, to July 24, 1966. V.P. Rao of the Indian Station, Commonwealth Institute of Biological Control, Bangalore-6, India, was the Principal Investigator. *Project No. A7-FS-51* -- "Evaluation of hymenopterous parasites of gypsy moth and the study of the behavior of promising species" replaced the previous Indian project and was conducted from March 1, 1967, to August 31, 1972. V.P. Rao and P.R. Dharmadhikari, Indian Station, Commonwealth Institute of Biological Control, were the Principal Investigators.
- Projects in Yugoslavia, 1967-77: *Project No. E30-FS-9* -- "A biological method of control of injurious insects *Lymantria dispar* L. and *Diprion pini* L." was conducted from February 1, 1967, to December 31, 1971. Dr. Konstantin Vasic, Institute of Forestry and Wood Industry of Serbia, Kneza Viseslava 3, Belgrade, Yugoslavia, was the Principal Investigator. *Project No. E30-FS-79* -- "The effectiveness of certain parasites and predators to control gypsy moth" was conducted from April 1, 1972, to March 31, 1975. Dr. K. Vasic of the Institute of Forestry and Wood Industry of Serbia, was the Principal Investigator. This investigation was continued under Project No. E30-FS-79-JB-47, "Investigation of the possibility to use a pure line of gypsy moth with shortened diapause and *Apanteles* spp. for biological control of gypsy moth", December 22, 1975, to November 30, 1977, again with K. Vasic as Principal Investigator.

Summaries of these projects were prepared by Reardon (1981b).

The "Accelerated" Research Program. In 1958, Robert W. Campbell (NEFES, New Haven, CT) initiated studies to investigate the population dynamics of gypsy moth. His life table analysis of

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[1]Editor's (JRC) Note: When the species *Apanteles melanoscelus* was placed in the genus *Cotesia* by Mason (W.R.M.) (1981), there was some confusion among biological control authors as to the proper gender ending for the specific epithet, and the species is given as *Cotesia melanoscela* in some subsequent publications. However, according to R.W. Carlson, ARS Systematic Entomology Laboratory, Beltsville, MD (personal communication), *Cotesia melanoscelus* is grammatically correct, as is also indicated in Mason's paper.

outbreak populations in Glenville, NY, 1958-64, and sparse populations in Eastford, CT, 1965-68, suggested that arthropod parasites and a carabid predator, *Calosoma sycophanta*, had a minor role in gypsy moth population dynamics (Campbell 1981). These studies resulted in several publications which discuss, in part, parasite interaction in gypsy moth populations and their influence on gypsy moth behavioral evolution (Campbell 1963a and b, 1981; Campbell and Sloan 1976).

In 1971, following a dramatic increase in gypsy moth defoliation through northeastern U.S., a 5-year accelerated research and development program was initiated. Along with "redirected" USDA research funds for university and state agencies, ARS and the Forest Service increased base funding and resources for gypsy moth research and development (McManus and McIntyre 1981).

In 1972, as part of the Forest Service's accelerated research program, the Intensive Plot System (IPS) was established (Campbell and Bean 1971). The IPS, developed to expand on Campbell's earlier population dynamics studies, was comprised of six study areas of 12 hectares (29.65 acres) each in three states: two each in Massachusetts, New York, and New Jersey. Reardon (1981c) summarized the results of IPS parasite investigations in 1972 and 1973:

> "The 1972 and 1973 average percentage of parasitism data (12 and 14 percent, respectively) as determined by four collection techniques indicates that parasites by themselves, as an individual mortality factor, did not remove a significant proportion of the host population, and did not function to limit the rate of increase of the gypsy moth in these areas. Nevertheless, parasites did remove a portion of the host population and in combination with other mortality factors would have an influence on the rate of increase of the host."

Specific parasite species relationships to site, gypsy moth, and disease have been documented by Reardon (1977) and Reardon and Podgwaite (1976). Unfortunately, investigation of the causes of gypsy moth mortality in the IPS was eliminated for economic reasons soon after it was initiated, thus limiting further development of information on the role of natural enemies in gypsy moth population dynamics. As Reardon (1981d) pointed out in suggesting areas for future parasite/gypsy moth research, there was still an "urgent need for the development and use of standardized techniques to sample host and parasite populations across many geographical areas," and a need for "intensive studies of those species established in North America as well as of exotic species" in order to "understand their specific ecological requirements and interactions with other species".

The Expanded Research Program. In 1975, the USDA responded to the need for additional methods to manage the increasing gypsy moth problem by planning and initiating the USDA Expanded Gypsy Moth Research and Application Program as part of the Combined Forest Pest Research and Development Program (Ketcham and Shea 1977). The Expanded Program complemented the accelerated effort and set specific objectives. The goals of the Program as set forth in Congressional hearings and the resultant appropriations bill included the statement that "The effectiveness of available and newly introduced parasites will be evaluated". The Expanded Program funded a number of extramural studies within the scope of this objective; however, only studies conducted directly or cooperatively by the Forest Service are summarized here.

Between 1975 and 1980, an intensive laboratory and field evaluation of the tachinid *Blepharipa pratensis* was made (Godwin and ODell 1981). The general goal of the research was to determine, using population-study techniques, whether there was an aspect of the life history or behavior of this fly that would lend itself to manipulation so that the species could be managed as a biological control agent. Specific objectives were: 1) to develop methods to count the fly in its various life stages; 2) to identify major mortality factors required for the development of life tables and for the development

of population models; 3) to develop methods of rearing the fly in the laboratory; and 4) to describe the fly's reproductive behavior.

Laboratory and field behavior investigations were carried out primarily at the USDA Forest Service's Forest Insect and Disease Laboratory Field Station, Branford, CT. Population studies were conducted in Eastford, CT, Washington Township, PA, and New Lisbon, NJ. The five-year investigation essentially accomplished its objectives: methods for sampling and assessing the viability of the various life stages were developed (ODell et al. 1974; Shields 1976; Godwin and ODell 1977, 1979, 1981); mortality-causing agents were identified and a determination made of their impact on fly survival (Godwin and ODell 1981, 1984; Godwin and Shields 1984); components of the reproductive behavior of the tachinids *B. pratensis* and *Parasetigena silvestris* were identified (ODell and Godwin 1979a, 1984; Godwin and ODell 1981); and a system for rearing *B. pratensis* in the laboratory was developed (ODell and Godwin 1979b; Godwin and ODell 1981). These results led to the formulation and implementation of an augmentative release of *B. pratensis* in 1978. Wild flies collected in Pennsylvania were held until egg laying was initiated. In June, 173 and 165 females were released in two 0.5-hectare study areas, respectively. Life stages of *B. pratensis* and gypsy moth were sampled. Based on host larval counts and parasite recovery in the two control sites, the host and parasite followed population trends expected in an areawide declining host population; however, in the release areas, instead of the expected 59% decline in *B. pratensis* observed in the control area, the *B. pratensis* population increased two-fold. This increase was attributed to the augmentative release (Godwin and ODell 1982).

During the expanded program, preliminary studies were conducted to determine the feasibility of using parasites in combination with pathogens in an integrated approach for managing gypsy moth populations (Raimo and Reardon 1981). In 1975, Richard C. Reardon, Forest Service, Forest Pest Management, Hamden, CT, evaluated the inundative release of three parasite species, *Glyptapanteles liparidis*, *C. melanoscelus*, and *Brachymeria intermedia*, individually and in combination with *Bacillus thuringiensis* (Bt), against gypsy moth in forests in Centre and Union Counties of Pennsylvania. Treatment with parasites alone had no effect on defoliation or population levels as compared with controls. Bt provided significant foliage protection with or without parasites, indicating that the parasite releases had no effect (Reardon et al. 1976; Raimo and Reardon 1981).

Raimo et al. (1977) conducted studies at NEFES, Hamden, CT, to show that *C. melanoscelus* could transmit the gypsy moth nuclear polyhedrosis virus (NPV) to gypsy moth larvae, and to develop methods of contaminating parasites that could augment efforts to initiate epizootics artificially in gypsy moth populations. These studies successfully demonstrated that *C. melanoscelus* is capable of transmitting lethal doses of NPV to gypsy moth larvae. In preliminary field investigations using parasites contaminated with virus, the combination of parasites and pathogens was shown to be a potentially feasible integrated pest management approach (Raimo and Reardon 1981).

With support from the Expanded Gypsy Moth Research and Application Program, exotic parasites were again sought for establishment in northeastern U.S. *Anastatus ?kashmirensis*, an eupelmid parasite collected from the "Indian gypsy moth", and the braconid *Aleiodes* (as *Rogas*) *lymantriae*, a solitary larval endoparasite of gypsy moth in Japan, were sent to the ARS Beneficial Insects Research Laboratory quarantine facility in Newark, DE, in 1975 and 1978, respectively. Preintroduction evaluations were conducted for both species by William E. Wallner at NEFES, Hamden, CT. The evaluation of *A. ?kashmirensis* led to a recommendation that the parasite not be released, based primarily on the apparent ineffective role of *A. ?kashmirensis* as a primary gypsy moth parasite, its propensity as a facultative hyperparasite, and the difficulty of morphologically distinguishing *A. ?kashmirensis* from *A. disparis*, an egg parasite introduced earlier and known to be widely established in northeastern U.S. (Wallner 1981).

Evaluation of *A. lymantriae* was conducted between 1978 and 1988. Laboratory experiments spanning 125 parasite generations included investigation of genetics, alternate hosts, host density factor effects on parasite sex ratio, and effect of Bt on parasitism rate (Wallner et al. 1982; Wallner and Grinberg 1984; Grinberg and Wallner 1991). Field releases of *A. lymantriae* were made in eight states: New Haven area, CT, 1981, 1982, 1984; Cecil County, MD, 1982; Addison County, VT, 1982; Provincetown, MA, 1983; Halley, PA, 1983; Loudoun County, VA, 1983; Gratiot County, MI, 1983; Vermont (Sandgate, Colchester, Pownell, Milton), 1984; Maryland (Eastern Shore), 1985; and Corvallis, OR, 1986. Within-year recoveries of *A. lymantriae* cocoons were made in the majority of sites, but evidence of establishment has not been found (W.E. Wallner, personal communciation).

Under a US/USSR Science and Technology Agreement, and arranged by the Working Group in Forestry, forest protection delegations representing the Forest Service, other USDA organizations, and cooperating state agencies, visited the Soviet Union to work with Soviet scientists in the field on integrated pest management of hardwood defoliating insects, including the gypsy moth. The first visit, in 1975, introduced the U.S. delegation to Soviet research on the gypsy moth and other hardwood defoliators, including research on population dynamics of gypsy moth (Simeone et al. 1975). The second visit, in 1978, focused attention on biological methods of control of the gypsy moth and other forest pests (McKnight et al. 1978). The third visit, in 1981, focused on integrated pest management and provided an opportunity to import to the U.S. parasites that might be of use in limiting the severity of gypsy moth populations in the U.S. (McKnight et al. 1981). The visits provided an excellent opportunity to obtain information on the role of parasites of gypsy moth in the USSR that could be used in development of studies in the U.S. (see Simeone et al. 1975; McKnight et al. 1978, 1981). In addition, two species of parasites, *C. melanoscelus* and *Compsilura concinnata*, were shipped to the U.S. for evaluation and comparison with *C. melanoscelus* and *C. concinnata* populations present in northeastern U.S. The strain of *C. concinnata* from the USSR was being evaluated by P.A. Godwin, NEFES, Forest Insect and Disease Laboratory, but was lost in 1982, apparently to reproductive failure. The USSR strain of *C. melanoscelus* was evaluated by Mark Ticehurst at the Biological Control Laboratory, Pennsylvania Department of Environmental Conservation, Middletown, PA, for field release in 1982.

In 1981, the USDA Office of International Cooperation and Development (OICD) sponsored the first U.S. forest protection team visit to the People's Republic of China (PRC). Led by Max W. McFadden, USDA Forest Service, the six-member team reviewed integrated pest management practices in the PRC and investigated opportunities for scientist and student exchange, and for the development of studies in integrated forest pest management research, including the exchange of biological materials (McFadden et al. 1982). As a result of this visit, a Scientific and Technological Cooperative Research Agreement on Natural Enemies of Gypsy Moth was developed. Under this agreement, six scientific team exchange visits were made between 1982 and 1988. Funding for the visits was borne, in part, by the OICD, the Forest Service, and the host institution in the PRC, the Chinese Academy of Forestry, under the Ministry of Forestry, Beijing.

The objective of the first trip (1982) was to survey for natural enemies of the gypsy moth and evaluate them for potential importation into the U.S. for biological control purposes (Schaefer et al. 1982). The three-member team, W.E. Wallner, NEFES, Hamden, CT, R.M. Weseloh, Connecticut Agricultural Experiment Station, New Haven, and P.W. Schaefer, ARS, Newark, DE, Team Leader, collected gypsy moth larvae in 11 different sites and confirmed the presence of 22 invertebrate parasite and 10 predator species. All of these natural enemies were considered for possible importation into the U.S., but official PRC policy prevented any living material from leaving the PRC at that time. Species diversity was greatest at Menjiagang, Heilongjiang Province, in northeast PRC, where gypsy moth population density was moderate. Population densities were low in the ten other collection sites (Schaefer et al. 1984).

In 1983, T.M. ODell, of Forest Service's Center for Biological Control of Northeastern Forest Insects and Diseases, Hamden, CT, and P.W. Schaefer, Team Leader, using the recommendations of the 1982 team, returned to Menjiagang, Heilongjiang Province, to collect and evaluate the natural enemies of gypsy moth in this particular area. The team estimated that gypsy moth population density was 1/20th of that in the previous year. The cause of population decline from the previous "moderate" density in 1982 could not be determined. Egg masses were not easily found, but many old *Glyptapanteles liparidis* cocoons were found suggesting that this gregarious braconid may have contributed to the decline. In 1983, the US/PRC scientific team collected only 594 gypsy moth larvae in approximately 400 person-hours of intensive search; 71% of these were collected in three larch plantations under the bark of *Larix* spp. trees. Approximately 49% of the collected larvae produced parasites. Parasites emerged from 291 of the collected larvae; tachinids (*Parasetigena* and *Blepharipa* spp.) accounted for 70% of these; *G. liparidis* accounted for 30%. The relatively low population density of gypsy moth suggests that these parasites have excellent host searching capabilities. This year the U.S. team was allowed to export live insects to the U.S. *Glyptapanteles liparidis* cocoons, tachinid spp. puparia, and gypsy moth egg masses were received by the ARS quarantine laboratory, Newark, DE, in July 1983. This was the first importation of gypsy moth parasites from the PRC. Unfortunately, no adults emerged from the tachinid puparia, and the *G. liparidis* colony was lost due to poor mating and the subsequent absence of females (Schaefer and ODell 1983).

In 1982, 1983, and 1986, delegations of Chinese scientists visited the U.S. to review biological control programs for forest insects and procedures for laboratory production of gypsy moth and its parasites. These trips resulted in the development of a proposal for a joint long-term study to determine the significance of the alternate host relationship of gypsy moth and "pine caterpillars" (*Dendrolimus* spp.) for maintaining parasite populations.

In 1987, Andrew M. Liebhold (University of Massachusetts) and Carol B. ODell and T.M. ODell (Team Leader) (Center for Biological Control of Northeastern Forest Insects and Diseases, Hamden, CT) visited the PRC to help establish permanent research plots and initiate the "alternate host" study noted above. In addition, the team's objectives included assisting Chinese scientists to develop techniques for rearing parasites of "pine caterpillars" on gypsy moth, and selecting promising parasites for introduction and establishment in the U.S.

The accomplishments of the 1987 US/PRC scientific exchange included: 1) a permanent plot was established in Yuan Ming Yuan Park, Beijing, for continuing research on natural enemies, particularly those which alternatively attack "pine caterpillars"; 2) two parasites, *G. liparidis* and *Casinaria nigripes*, were collected from "pine caterpillars" and successfully cultured on the gypsy moth; 3) *G. liparidis* was established on F_1 sterile gypsy moth larvae (via F_1-sterile egg masses brought into PRC by the U.S. team), imported to the U.S., and successfully colonized for evaluation at the Forest Service's Insect Rearing Facility, Hamden, CT; and 4) the tachinids *Exorista rossica* and *Exorista japonica* were identified as the major parasites of gypsy moth emerging from large larval collections made in the Beijing plot. This was the first record of *E. japonica* on gypsy moth in the PRC; this species has been recorded as a parasite of *Dendrolimus* spp. (ODell et al. 1987).

The US/PRC Scientific and Technological Cooperative Research Agreement on Gypsy Moth between 1982 and 1987 established an excellent scientific relationship and provided the biological basis for continuing cooperative investigations. Only five of the more than 20 parasite species recovered from gypsy moth collected in the PRC have been established in the U.S. from previous importation programs. One of the major reasons for this difference in parasite diversity is a lack of appropriate alternate hosts in the northeastern U.S. In the PRC, there are at least four and perhaps as many as 11 gypsy moth parasites that also attack "pine caterpillars" (ODell 1987). One of these, *G. liparidis* was recovered from gypsy moth at virtually all collection sites and at host densities ranging

from sparse to moderate. The PRC *G. liparidis* strain, imported into the U.S. in 1987, and now in culture at the Forest Service's Insect Rearing Facility, Hamden, CT, is one of several parasites found in the PRC being evaluated for release in areas outside the northeastern U.S., where it has failed to establish after several releases (see Hoy 1976).

Gypsy Moth Research and Development Program. In 1984, the Forest Service initiated a research program designed to develop the knowledge and technology that is necessary to maintain gypsy moth populations at economically and socially acceptable levels through integrated pest management techniques. Unlike some research programs before it, the Gypsy Moth Research and Development Program (GMRDP) for extramural research stressed maintenance of gypsy moth populations at low levels. Parasite research was included under two of the seven program objectives: "Develop the means to utilize parasites as regulators in low level gypsy moth populations", and "Evaluate the role of integrated pest management for gypsy moth". T.M. ODell, Center for Biological Control of Northeastern Forest Insects and Diseases, Hamden, CT, coordinated GMRDP parasite extramural research. The focus of the research was to obtain the information necessary to equate "percent parasitism" with generational mortality, i.e., evaluation of (real) parasite impact. The information developed includes the results of six years of field and laboratory experiments conducted by Joseph S. Elkinton, University of Massachusetts, and his graduate students. Information on competition between agents has been developed so that the capability of three parasite species (*Parasetigena silvestris, Cotesia melanoscelus*, and *Brachymeria intermedia*) to regulate gypsy moth populations was determined. In addition, information was developed for measuring the impact of parasites on generational mortality without specifically quantifying distribution and abundance of individual parasite species or guilds. The K factor analysis developed by Elkinton simplified all aspects of assessing the generational mortality due to parasites on host population dynamics, including host sampling in various stand types and host densities (Elkinton et al., 1989; Gould et al. 1989, 1990).

Cooperative gypsy moth parasite research at the University of Maryland focused on developing methods for measuring parasite contribution to mortality usually recorded as "unknown." Under the direction of Michael J. Raupp, a method for measuring unknown mortality due to stinging by *Cotesia melanoscelus* was developed (Thorpe et al. 1990). The technique used in this study should be useful for similar studies with other parasites.

Other gypsy moth parasite research conducted during the GMRDP included a survey of parasites in a mesic and adjacent intermediate and xeric forest habitat in Salisbury, VT (1984-85) directed by Bruce Parker, University of Vermont. The study was conducted when gypsy moth population density was <10 egg masses per acre. Results indicate that *Compsilura concinnata* was the dominant parasite in all three sites, for both years. Diversity and distribution during each year were determined (Skinner et al. 1993). Also, a laboratory study of the behavior of *Ooencyrtus kuvanae*, an egg parasite of gypsy moth, was conducted to discern the parasite's host selection response in different light regimes. The study showed that low levels of light significantly reduce host finding (ODell et al. 1989).

A major part of the GMRDP was the development of the Gypsy Moth Life System Model (GMLSM). The four main components of the GMLSM are: stand submodel, gypsy moth submodel, pathogen submodel, and predator/parasite submodel. The development of the predator/parasite submodel has resulted in the evaluation and summary of an extensive literature base. Six parasites (*Ooencyrtus kuvanae*, *Cotesia melanoscelus*, *Blepharipa pratensis*, *Brachymeria intermedia*, *Parasetigena silvestris*, and *Compsilura concinnata*) and one predator (*Calosoma* sp.) were simulated. Mortality caused by these natural enemies is affected by gypsy moth and natural enemy densities, and gypsy moth location. Development of this submodel is an on-going process. Further documentation and development of data on each species, and their compensatory interactions, are needed to ensure the submodel simulates the "real world" (Sheehan 1987).

The need to develop an integrated pest management (IPM) approach to the gypsy moth problem has been recognized as an important objective throughout the period of accelerated research and development (1975-present). The Maryland Gypsy Moth Integrated Pest Management Pilot Project (1983-87) was a cooperative effort of the Maryland Department of Agriculture and the USDA. Project funding and coordination was provided by the Forest Service, State and Private Forestry, Forest Pest Management (Reardon et al., 1987). Major emphasis was placed on evaluating the new technology developed from the GMRDP. This included the use of applied biological controls. Parasites were the only component of the natural enemy complex that was manipulated. Emphasis was placed on maximizing their diversity, abundance, and effectiveness through augmentation. This was accomplished by collecting and redistributing parasites from the generally infested areas that were not abundant in the project area (Reardon et al., 1987). In 1985, a Korean strain of *Cotesia melanoscelus* was released sequentially over a three week period at an average level of 12,000 females per hectare in three isolated mixed-hardwood woodlots infested with gypsy moth in Queen Annes County of Maryland's Eastern Shore. The objectives of the study were to determine the effect of inundative releases of laboratory-reared *C. melanoscelus* on the mortality of the gypsy moth and to determine apparent rates of parasitism occurring in different gypsy moth habitats. The laboratory colony used to produce the released *C. melanoscelus* originated from the Kyeonggi Province of South Korea and was obtained from the ARS Beneficial Insects Research Laboratory, Newark, DE, during 1983. Significantly higher rates of parasitism were achieved, but the inundative release of *C. melanoscelus* failed to reduce gypsy moth populations, as determined from egg mass counts (Kolodny-Hirsch et al. 1988).

Future Research. From 1992, forest insect research began an increased emphasis on understanding the ecological roles and effects of native and exotic insects, including established and exotic parasites of the gypsy moth. Two experimental techniques developed during the GMRDP will be increasingly important to research on gypsy moth biological control and its role in ecosystem management. In addition, in the fall of 1992, the USDA Forest Service Quarantine Laboratory, located in Ansonia, CT, was dedicated. This new research facility will have an important function in future gypsy moth biological control programs.

One technique used by Forest Service scientists and cooperators since 1985 artificially manipulates host densities to study density-dependent relationships of gypsy moth. Using field-collected and laboratory-reared gypsy moth egg masses, high densities of trap hosts were created in otherwise low density gypsy moth populations. The results indicate that spatially density-dependent mortality caused by parasites is important in the maintenance of low densities (Liebhold and Elkinton 1989; Gould et al. 1990; Wilmot et al. 1994). In 1992, a study was initiated to document long-term changes in gypsy moth parasite species composition in ecologically diverse habitats along the "leading edge" of gypsy moth infestation in Virginia. This cooperative study, under the direction of Fred P. Hain, North Carolina State University, uses sterile gypsy moth larvae, derived from laboratory-produced F_1-sterile egg masses (Mastro et al. 1989), to create small areas (1 hectare) of high host densities (Hasting et al. 1994).

In 1991, the Forest Service began investigating techniques for identifying biotypes of biological control agents. Utilizing isozyme techniques, the genetic structure of populations of *C. concinnata* is being studied (Sanchez 1992). Correlation of breeding population genetics of *C. concinnata* with collection site (habitat) will enhance understanding of exotic parasite introductions and increase our capability for investigating the bioecology of gypsy moth parasites.

The USDA Forest Service Quarantine Laboratory. The Forest Service Quarantine Laboratory at Ansonia, CT, is certified to confine and colonize entomophagous and phytophagous arthropods and entomopathogens for biological control research. The integrity of the 3100 square foot quarantine area is maintained by a double air lock entry/exit system equipped with light traps; three negative

pressure zones, each equipped with air conditioning, HEPA filtration and 100 mesh exhaust screening; double glazed, break-proof windows; a pass-through autoclave disposal system; and strict personnel protocols. An automatic generator maintains the negative pressure system during power failure and a professional security company monitors system failure, fire, and unauthorized entry. Environmental chambers provide space for rearing and studying large numbers of arthropods. All insect handling is performed inside HEPA-filtered biological safety cabinets to contain insects and protect worker health. Management of the facility is designed for cooperative research with state, federal, and international biological control projects.

5. Development of "Gypchek™", a gypsy moth pathogen. By John D. Podgwaite and James M. Slavicek

Development of the gypsy moth nuclear polyhedrosis virus (LdNPV) product, Gypchek™, can be traced to the early 1900s when Reiff (1911) speculated that the "wilt disease" of gypsy moth caterpillars could be utilized to control the pest. Results of some limited field trials supported the concept (Glaser and Chapman 1913). At the time, however, spraying with lead arsenate was the popular gypsy moth control tactic and that tactic persisted, at least for large scale gypsy moth control, until the emergence of DDT in the 1940s. After a decade of environmental saturation with DDT, it became clear that this chemical was not going to eradicate the pest from North America and that it posed a serious health hazard to man and beneficial wildlife. The search for environmentally compatible pesticides then began in earnest, and interest in LdNPV was renewed.

Forest Service research on LdNPV began in the early 1950s at the Northeastern Forest Experiment Station's Laboratory on the Yale University campus in New Haven, CT. In a major reorganization that saw responsibility for forest insect research shift from the USDA Bureau of Entomology and Plant Quarantine to the FS, P.B. Dowden became the leader of a primordial Insect Pathology and Microbial Control work unit that would eventually grow to be the driving force behind the development and registration of Gypchek™. Dowden and F.B. Lewis, an entomologist within the unit, conducted some probing experiments to assess the effectiveness of LdNPV treatments (suspensions of field-collected NPV-killed gypsy moth larvae) on individual gypsy moth infested oak seedlings. Results from those experiments were encouraging and prompted the testing of LdNPV in combination with *Bacillus thuringiensis* (Bt) (which at the time was in its infancy as a microbial control agent) in a series of field trials in New York State in 1961-63 (Lewis and Connola 1966). Those field trials were undertaken more for the hope of increasing Bt mortality than for assessing the efficacy of LdNPV. Results showed some LdNPV effectiveness but were compromised by what was later to be determined as antagonistic properties between Bt and LdNPV when the two agents were sprayed together.

In 1963, F.B. Lewis, who had assumed the work unit leadership upon Dowden's transfer to ARS, and W.D. Rollinson tested NPV alone on a one acre (0.4 hectare) plot of mixed oak in the White Memorial Forest, Litchfield, CT (Rollinson et al. 1965). The treatment reduced the gypsy moth egg mass population in the plot by 95 percent but, more importantly, the results were instrumental in securing a strong FS policy and funding commitment toward developing gypsy moth NPV as a microbial insecticide.

In 1965, two years after a fire had displaced the laboratory staff to temporary quarters in West Haven, CT, J.D. Podgwaite and H.M. Mazzone, both microbiologists, joined the work unit. Their studies focused on safety and production aspects of LdNPV and were in response to U.S. Environmental Protection Agency (EPA) directives that required candidate microbial pesticides to undergo a rigorous registration process, much the same as that required for chemical pesticides. At the time, the EPA directives were in the absence of firm guidelines and it was left to the scientists in the work unit to develop protocols and conduct tests with minimal input from EPA. From the results

of a variety of studies that followed (Lautenschlager and Podgwaite 1977, 1979; Lautenschlager et al. 1978, 1979; Mazzone et al. 1976; Podgwaite et al. 1979), it became clear that although LdNPV was safe for man and the environment, it was not one of the more virulent insect viruses, and, further, it retained its pesticidal activity for only a few days following application to foliage (Lewis 1981; Lewis and Yendol 1981).

In 1968, the work unit moved into permanent quarters in the Forest Insect and Disease Laboratory (now the Center for Biological Control of Northeastern Forest Insects and Diseases) in Hamden, CT, and work continued toward finding a more virulent LdNPV strain (than the original Connecticut strain), developing a cost-effective LdNPV-production system in collaboration with ARS scientists (Shapiro et al. 1981) and finally, developing a tank mix with sunlight protective properties. By 1972, progress warranted further field testing and, between 1973 and 1978, a variety of field experiments were conducted to evaluate several LdNPV formulations, dose rates, and spray systems against a range of gypsy moth populations (Yendol et al. 1977; Wollam et al. 1978; Lewis et al. 1979). From these evaluations emerged a direct aerial suppression tactic with LdNPV that under optimal conditions could be expected to provide 50-80% population reduction and enough foliage protection to prevent defoliation and subsequent physiological tree stress.

In 1978, more than half a century after Reiff's insightful suggestions, Gypchek™, a technical product consisting of LdNPV-killed gypsy moth larvae that were dehaired, lyophilized and ground into a fine powder, was registered (EPA registration No. 27586-2) as a microbial pesticide.

Unfortunately, the registration of Gypchek™ did not result in immediate widespread acceptance. The product was costly to produce and, compared to Bt products and other chemical pesticides, difficult to mix in a tank. Also, the product often clogged nozzle systems. Further, commercial producers were interested in developing products that would satisfy a broad market and were hesitant to commit substantive resources to a product that could be used against only one insect. So it was not surprising that in the early 1980s, with the growing acceptance of Bt as the microbial of choice for gypsy moth control and the emergence of the insect growth regulator (IGR) Dimilin™ in the market place, Gypchek™ was relegated to "specialty product" status.

Research did continue toward developing an easy-to-use formulation containing an effective sunscreen. However, by the mid 1980s progress was minimal, and it became clear that Gypchek™ was becoming more of a "scientific curiosity" than an effective gypsy moth control agent. Then a series of changes occurred that once again brought Gypchek™ to the forefront. First, the technical product itself was modified from a "whole cadaver" preparation to a freeze-dried powder prepared from an aqueous blend of larval cadavers. That resulted in a more homogeneous product that did not clog nozzle systems. Second, the recommended dose was increased five-fold. Finally, an improved tank mix, incorporating the lignosulfonate sunscreen Orzan LS™, was developed. Field tests of the "modified" Gypchek™ and tank mix were very successful with results comparable to those obtained with Dimilin™ and Bt (Podgwaite et al. 1987; Podgwaite and Reardon 1989; Webb et al. 1989). Coincidental with these Gypchek™ successes, environmentalists were raising serious concerns as to the safety of Bt and Dimilin™ products for non-target insects and beneficial wildlife. Once again interest in Gypchek™ has rekindled, and the FS is working closely with industry partners in the development of a commercially-produced Gypchek™ that will be available for gypsy moth management in the near future.

The Insect Pathology and Microbial Control Work Unit at Hamden, now headed by M.L. McManus, will continue to conduct Gypchek™ methods improvement research along several lines: the isolation, evaluation and field testing of naturally occurring LdNPV isolates that are more virulent than those found in the current product; the evaluation of genetically-modified LdNPV isolates having enhanced pesticidal properties; the development and field testing of "ready-to-use"

Gypchek™ formulations; and finally, the development and testing of a variety of Gypchek™ intervention tactics targeted to meet the needs of individual gypsy moth management programs.

Gypchek™ research and development at Hamden has been truly a broad-based team effort and this brief historical accounting has only highlighted major events and developmental phases. In addition to those individuals cited above, the within-unit technical support of R.B. Bruen, P.D. Dusha, H.B. Hubbard, R.A. Lautenschlager, K.S. Shields, and R.T. Zerillo has been particularly valuable as has the long-standing support of FS-Forest Pest Management staff, in particular that of R.C. Reardon. The cooperative efforts of Animal and Plant Health Inspection Service (APHIS) and ARS personnel in the development of an LdNPV production facility and the subsequent manufacture of a product by APHIS has been, and continues to be, vital as the FS transfers responsibility for Gypchek™ production to the private sector. Also, state and private organizations have played a major role in the effort; the Pesticide Research Laboratory at Pennsylvania State University, and the Boyce Thompson Institute for Plant Research at Cornell University are but two of many. Finally, all those that have lent support, but go unnamed here, are recognized for their contributions toward making LdNPV a safe and effective microbial pesticide.

Biotechnology also offers a new approach for the development of improved biological and biorational control agents for forest insect pests and diseases. A new Research Work Unit, "Applications of Biotechnology in Forest Pest Management", located at the Forestry Sciences Laboratory, Delaware, OH, was created in the Northeastern Forest Experiment Station in 1987 to apply biotechnology to the area of biological control, and is now headed by Project Leader J.M. Slavicek. Scientists in the unit are focusing on development of Gypchek™ and other improved viral strains for use in gypsy moth control efforts that are competitive with other controls in terms of cost and efficacy. Enhancement of viral potency and efficacy (killing speed) would increase effectiveness of the *Lymantria dispar M*NPV (LdMNPV).

High viral production costs can be addressed indirectly through generation of a viral strain with a potency greater than that of Gypchek™. Efforts to enhance viral potency have focused on the identification of naturally-occurring isolates that exhibit biological activities greater than the Gypchek™ product. Several viral genotypic variants that exhibit potencies three-fold greater than Gypchek™ have been isolated (Slavicek and Podgwaite 1991). These isolates are being assessed as possible replacement viruses for Gypchek™. Other approaches for enhancement of viral potency may be devised once the molecular basis for viral potency is understood. Earlier studies have focused on the molecular characterization of the Ld*M*NPV (Slavicek 1991a and b; Bischoff and Slavicek 1993). Current efforts are focused on the identification of potency determinants in two Ld*M*NPV genotypic variants that exhibit approximately 50-fold differences in potency.

To mitigate the low viral efficacy, a genetically-engineered Ld*M*NPV strain was generated that exhibits enhanced killing speed. To enhance viral killing speed the ecdysteroid UDP-glucosyl transferase gene was inactivated (Riegel and Slavicek 1993). This viral gene product prevents larval molting in virally infected insects. Insects infected with the engineered EGT-virus attempt to molt and in the process usually die. The overall effect is for infected insects to die earlier and, as a result, less foliage is consumed.

Production of Ld*M*NPV in cell culture bioreactor systems offers another approach to decreasing production costs (Slavicek 1992). Cell culture production systems offer the advantages of a cleaner product, ease of manipulation, and scale-up in comparison to production in gypsy moth larvae. However, an impediment to cell culture production is the high frequency of few polyhedra (FP) mutant formation during viral replication in cell culture. This viral mutant produces very few polyhedra, and those that are produced are essentially noninfectious (Slavicek et al. 1992). To solve this problem, scientists at Delaware have developed a Ld*M*NPV viral strain that exhibits enhanced

polyhedra production stability during propagation in cell culture (Slavicek 1991c). A patent has been obtained for this viral strain (Patent # 5,420,031), and a Notice of Allowance was received from the U.S. Patent and Trademark Office on a patent application that covers the use of the improved viral strain for gypsy moth control.

Further enhancement of viral potency and efficacy may be devised by manipulation of the processes of polyhedra formation and virion occlusion. Several Ld*M*NPV mutants exhibiting abnormalities in these processes have been identified. Characterization of these mutants at the molecular level will identify viral genes involved in the processes of polyhedra formation and virion occlusion. Manipulation of these genes may generate viral strains with enhanced potency and efficacy traits.

6. Spring cankerworm, *Palaecrita vernata* (Peck) (Lepidoptera: Geometridae). By Mary Ellen Dix

The spring cankerworm severely defoliates Siberian elm, a tree commonly planted in field windbreaks in the northern Great Plains. In 1968, two branches of the Forest Service (Northern Region and the Rocky Mountain Forest and Range Experiment Station), and the University of North Dakota, conducted a successful demonstration of spring cankerworm control in field windbreaks with Bt. Formulations, application times, and application methods were compared for effectiveness in controlling spring cankerworm (Hard et al. 1979). A reevaluation of the sites in 1979 found that defoliation was reduced for more than one year (Hard 1979).

Dix (Rocky Mountain Forest and Range Experiment Station, Lincoln, NE) observed a melyrid beetle, *Malachius ulkei*, feeding on spring cankerworm eggs. Late instar beetle larvae apparently migrate to Siberian elm windbreaks in early spring and feed on spring cankerworm eggs before crops germinate. She noted that *M. ulkei* disappears from the trees to move into crops about the time the cankerworm eggs hatch. Beetle larvae apparently search for food in the windbreaks when food is scarce in the surrounding crops (Dix 1991a). This was the first example of a benefical arthropod obtaining food and protection from tree windbreaks in a tree/crop ecosystem.

7. Willow sawflies (Hymenoptera: Tenthredinidae). By Karen M. Clancy and Mary Ellen Dix

The sawfly, *Pontania* sp. nr. *pacifica*, forms leaf galls on "arroyo willow" in northern Arizona (Clancy et al. 1986). In PhD dissertation research that was partially funded by the Forest Service, Karen M. Clancy (now with Rocky Mountain Forest and Range Experiment Station, Flagstaff, AZ) examined the importance of temporal variation in tri-trophic level interactions among the willow, this leaf-galling sawfly, and its natural enemies (inquilines and ectoparasites) from 1981 to 1984 (Clancy and Price 1986). The phenology of sawfly oviposition and larval development differed dramatically between two study sites at Flagstaff and Oak Creek, as did enemy-caused larval mortality. At Oak Creek, sawfly larval survival was high, mortality from natural enemies was low, and sawfly oviposition occurred early in the period of willow growth. In contrast, sawfly larval survival was low at Flagstaff, a high proportion of the larvae were killed by natural enemies, and oviposition occurred late in the period of willow growth. Offspring of sawflies that oviposited early at Flagstaff suffered higher rates of larval mortality from natural enemies than offspring of sawflies that oviposited later. Clancy and Price (1986) concluded that there may have been a phenological shift by the Flagstaff *Pontania* population to synchronize with "windows of time" that maximize survival and enemy-free space. Clancy and Price (1989) also determined that sawfly death from natural enemies was twice as much as from plant resistance and over six times greater than mortality from intraspecific competition.

8. Large aspen tortrix, *Choristoneura conflictana* (Walker) (Lepidoptera: Tortricidae). By Mary Ellen Dix

In 1966, 1978, and 1983 the large aspen tortrix defoliated large areas of trembling aspen in interior and south-central Alaska (Beckwith 1968; USDA Forest Service 1983). Residential trees had reduced growth or were killed after several years of severe defoliation. The tortrix also periodically severely defoliates aspen in the coastal forests of Oregon, Washington, and British Columbia (Holsten and Hard 1985).

Parasites and other natural controls are recognized as a factor in regulating tortrix populations. Typically, tortrix populations are high for several years before rapidly collapsing, apparently due to an increase in abundance of natural enemies. Torgersen and Beckwith (1974) identified 24 parasite species, described their biologies, and developed a key to the parasites.

In 1980, commercial insecticides were unavailable to homeowners for control of the moth. Holsten and Hard (State and Private Forestry, Anchorage, AK) tested formulations of *Bacillus thuringiensis* (Bt) in the laboratory to determine their effectiveness in controlling the moth (Holsten and Hard 1981). A 1981 field test to determine the efficacy of these liquid Bt formulations, was unsuccessful because the Bt was applied after the larvae had significantly defoliated the trees (Holsten and Hard 1981). Holsten and Hard applied the Bt to younger larvae in 1983 and successfully controlled the tortrix and minimized defoliation (Holsten and Hard 1985).

9. *Bacillus thuringiensis*. By Mary Ellen Dix, Leah S. Bauer and Al Valaitis

The bacterium *Bacillus thuringiensis* (Bt) is an attractive alternative to chemical pesticides because it is non-toxic to the environment, relatively harmless to non-target organisms including beneficial parasites and predators, and selectively pathogenic against specific leaf-feeding insects. Because of the specificity of Bt, it can be used in combination with natural enemies and other control techniques.

In the late 1950s, commercial preparations of the microbial insecticide *Bacillus thuringiensis thuringiensis* (Bt) became available for control of leaf-feeding Lepidoptera. Between 1960 and 1993, Forest Service and university scientists identified and screened Bt strains that could be used to control defoliators of hardwoods (gypsy moth [GM], cottonwood leaf beetle, and cankerworms) and conifers ("spruce budworms", Douglas-fir tussock moth, and hemlock defoliators). Studies also were conducted to understand the biology, mode of action and taxonomy, to improve potentcy of formulations and to develop and refine application techniques. Results of these cooperative efforts on GM have been summarized by R.C. Reardon, N.R. Dubois, and W. McLane in an unpublished Forest Service manuscript (Reardon et al. 1994). Although most research efforts on hardwood defoliators focused on GM as discussed here, results were applied to other defoliators and are discussed in those specific sections.

Early research activities, 1961-69. During the 1960s, Forest Service entomologists designed studies to determine if Bt could be used to control leaf-feeding Lepidoptera, to screen Bt strains, and to obtain fundamental information needed to improve Bt effectiveness. In 1961, F.B. Lewis and D.P. Connola (Northeastern Forest Experiment Station [NE], New Haven, CT) initiated a three-year study to explore the possibilities of using Bt to control GM. Although their results were inconclusive, they determined that Bt could be effective in controlling the moth. They also improved formulations and application techniques, and gained considerable information and experience (Lewis and Connola 1966).

Lewis et al. (1964) evaluated various strains of Bt and found that they differed in potency. No relationships were found among taxonomically related Bt varieties and source insects. Cosenza and

Lewis (1966) biochemically characterized and determined the pathogenicity of four wild-type spore-forming *Bacillus* spp. that were isolated from dead or diseased GM. Using uniform growth conditions, N.R. Dubois (NE, New Haven) found that the activity spectrum of taxonomically-related Bt strains ranged greatly, and strains of different serotypes could have equal potency (Dubois 1968; Dubois and Squires 1971). But, larvae of similar age and different geographic populations differed in their susceptibility to specific Bt preparations.

Although effectiveness of aerially-applied Bt was initially improved through strain selection, formulation modification, and improved foliage coverage, single aerial Bt applications were less effective than conventional insecticides. Lewis and Connola (1966) determined that multiple applications overcame the variation in larval developmental rates and susceptibility to Bt. They also showed that incorporation of compatible adjuvants improved the sticking quality of Bt on foliage. Dubois (1965) found that the addition of the sticker-antievaporant Pinolene #1674 to spore formulations extended spore viability and pesticide activity up to four times. Lewis and Connola (1966) observed that when a commercial preparation of Bt was diluted and then fed to GM larvae, feeding activity increased markedly, while feeding activity decreased when the GM were fed only washed crystal fractions.

During early experiments, control of GM by aerial spraying Bt was evaluated solely on the basis of reduction in number of egg masses. This method did not allow separation of treatment effects from natural mortality. Connola et al. (1966) developed a method for correlating egg-mass density reduction with ten-minute larval counts in the field, frass collections, and defoliation counts.

Accelerated research activities, 1970-79. Although fundamental studies during the 1960s provided information to develop Bt as an alternative pesticide, additional research was needed to develop and refine Bt application methods for practical and effective use. However, during the 1970s, most Forest Service research efforts on GM concentrated on nuclear polyhedrosis viruses (NPV) and efforts on Bt were minimal, except for participation in strain evaluation and comparison tests (Lewis and Etter 1978). This extensive screening program was maintained because bioassays were the only reliable method to evaluate pesticidal activity of Bt strains. Most research on formulations, application methods, and impacts of Bt on GM parasites was conducted by non-FS scientists. An exception was an evaluation by Dubois et al. (1971) of mist blower ground applications in New Jersey and Massachusetts.

In 1970, a new strain of Bt, HD-1, was isolated by ARS scientists and commercially produced that increased the pesticidal activity of Bt at least 15 times (Dulmage 1970). In 1972, Lewis et al. (1974) evaluated five formulations of Bt against GM in New York, New Jersey, and Pennsylvania. Although adequate coverage was obtained, rain reduced the effectiveness of these formulations. Subsequent tests by W.G. Yendol (Pennsylvania State University) and others determined that three different commercial preparations of a high potency Bt strain effectively reduced GM populations (Yendol et al. 1973). Foliage protection and larval mortality of these Bt preparations was not affected by application rate. Furthermore, foliage protection could last up to a month (Yendol et al. 1973). However, a subsequent study by Lewis et al. (1974) with aerially-applied Bt did not reduce GM populations to the desired levels, even though foliage protection was adequate. Rainy, cool weather was found to affect the results adversely.

New strains of Bt were continually isolated. Dubois (1978) screened 350 isolates representing 14 serotypes against GM larvae to determine the activity spectrum against GM. Dubois and Gunner (1974) found that numerous Bt strains from healthy GM larvae became pathogenic to their host after culture in chitinase-inducing media. Dubois (1977), in an extensive study on the pathogenicity of Bt to healthy GM, found that numerous chitinolytic microorganisms could be isolated from healthy

third-, fourth- and fifth-instar larvae. The acquisition of this microflora appeared to be associated with increased mobility of the maturing larvae.

Research activities, 1980-93. Although considerable progress was made during the 1970s on the development of new strains, improved formulations, and multiple application techniques providing significant foliage protection, Bt performance was erratic in both ground and aerial tests. Extended GM egg hatch and development times, and short residual activity of Bt adversely affected results and reduced their acceptance. Also, the high cost of the product and the double application discouraged general and large scale use even in environmentally-sensitive areas (Dubois 1986). More potent strains, improved formulations with longer residual activity, and more effective application techniques were needed before Bt would be widely used (Dubois and Lewis 1981).

By 1981, new strains and formulations were identified that exhibited potentially higher potency and longer residual activities than the standard HD-1 strain (Dulmage 1981). Dubois (1981) identified two laboratory strains (HD-243 and HD-263) of Bt with increased pathogenicity against GM. However, an aerial field test of these strains in Connecticut determined that they were less effective than the standard, commercially-available HD-1 strain, and that they, too, required two applications (Andreadis et al. 1982). Another strain (NRD-12), isolated in 1981 from spruce budworm, was found to have three to four times the toxicity of other strains against GM and other species of Lepidoptera. Field studies with this strain demonstrated less defoliation and longer effectiveness than the earlier test strains (Dubois 1985a and b; Dulmage et al. 1985; Dubois et al. 1988). Dubois (1986) also demonstrated that a synergism between Bt (HD-1) and a β-exotoxin increased susceptibility of GM larvae to Bt. However, strains and preparations that were most susceptible to GM were not necessarily the same ones that were toxic to spruce budworms (Dubois et al. 1989a). By 1990, Bt formulations had changed from oil-based to aqueous and contained adjutants (i.e., stickers) and ultraviolet screens that increased the persistence of Bt.

In 1980, application costs were high because multiple applications of Bt were required to control GM. A cooperative trial by scientists of the University of Connecticut and the FS found that a single high-dose application gave adquate coverage, significant reduction in larval density and excellent foliage protection, if it was properly timed. This high Bt dosage was compatible with most natural enemies; parasitism by *Cotesia melanoscelus* increased, that by the tachinids *Compsilura concinnata* and *Parastigena silvestris* was unaffected, and that by *Blepharipa pratensis* decreased (Andreadis et al. 1983). Wallner et al. (1983) and Webb et al. (1989) also found that high doses of Bt did not adversely impact parasitism by the braconid wasps *Aleiodes* (as *Rogas*) *lymantriae* and *C. melanoscelus*. However, Weseloh et al. (1983), Wallner et al. (1989) and Woods et al. (1988) reported that levels of NPV decreased in GM after application of Bt, probably because larvae infected with NPV died prematurely. A cooperative study by the FS, APHIS, and Pennsylvania State University scientists demonstrated that high dosages of the Bt product Thuricide 64 LV™ was effective in reducing defoliation and egg mass density when applied to 3rd- and 4th-instar GM larvae (Dubois et al. 1991). This expanded the time available for Bt application.

Coordination of research and application activities was improved by the establishment of a Bt technical committee in 1986 and a Forest Service National Steering Committee for Aerial Application of Pesticides Against Eastern Defoliators in 1988 also helped improve coordination of activities related to microbial pesticides. The establishment of the Northeast Forest Aerial Application Technology Group (NFAAT), an ad-hoc group of scientists and practitioners from the Forest Service, APHIS, ARS, Pennsylvania State University, and University of Connecticut, generated interest in the improvement of aerial application of Bt and other microbials. This group met several times a year to identify and prioritize research needs, and then jointly conducted laboratory and field studies designed to standardize methods and improve the performance of Bt (McManus 1990). Between 1989 and 1992, a series of studies was conducted to increase the efficacy

of Bt through improvement of ground and aerial application technologies. Dubois and McLane (1991) compared the effectiveness of hydraulic sprayers and mist blowers.

Cooperative studies by scientists at Pennsylvania State University and Forest Service (M.L. McManus, NE, Hamden, CT) developed a technique that quantified the volume of spray deposition throughout the canopy at a single-leaf resolution (Yendol et al. 1990). Bryant and Yendol (1991) used this technique to determine the single-leaf deposition characteristics of aerially-applied Bt. They found that the quantity of spray arriving at the top and between each tree in the hardwood forest was highly variable. However, the average spray penetration was adequate to provide a lethal dosage in the lower canopy. Related studies (Dubois et al. 1989b, 1990, 1993) determined the most effective drop size and dispersal method at different volume rates and formulations. The optimal dose or volume of Bt varied with the GM outbreak stage. However, dispersal through the canopy and deposit on the leaves was most effective at rates of 7.0 liters/ha^2.

In 1988, a multi-year cooperative study among the Pesticide Research Laboratory at Pennsylvania State University, the Forest Meteorology Research Project at the University of Connecticut, APHIS, and Forest Pest Management's Appalachian Integrated Pest Management (AIPM) Project was initiated to evaluate, refine and adapt existing microbial insecticide technology for use in minimizing the spread of GM from the leading edge of the outbreak; the goal of the study was also to quantify the effects of local microclimate processes in and near the canopy on deposition patterns of aerially-applied Bt (Miller et al. 1990). Both Gypchek™ and Bt reduced numbers of egg masses and had similar levels of defoliation. However, only the control plots displayed a second wave of natural NPV mortality. Although these results were promising, additional studies are needed to determine how intervening with low-density microbials impacts GM population dynamics and to determine climatic conditions for optimal delivery of spray material (Podgwaite et al. 1993).

High dosages of applied Bt, geographic variation in wild GM response to Bt, and the demonstrated resistance to Bt in some populations of other Lepidoptera species indicate the potential for development of genetic resistance of wild GM populations to Bt. Rossitor et al. (1990) studied resistance in three natural and one laboratory populations of GM by challenging 2nd-instar larvae with the HD-1 strain of Bt. Initial results of this study indicate that susceptibility variations are due to growth and development differences that are products of both the genotype and maternally-determined status of the egg.

As a result of the identification of more potent strains and the development of improved application technologies during the 1980s by cooperative efforts among researchers, the use of Bt in operational control programs had changed from 2-4% of the total area treated for GM control in 1980 to over 63% in 1990 (R.C. Reardon, unpublished data). The development of improved strains, delivery systems and insecticidal crystal protein technology will increase this percentage during the 1990s.

Cry proteins. Studies during the past two decades have shown that the insecticidal crystal proteins (ICPs; i.e., δ-endotoxins, the Cry family of proteins) from the gram-positive Bt bacterium can be effective biological control agents for suppression of destructive insects in forestry and agriculture. Bt δ-endotoxins are protoxins which are converted by midgut proteinases in the target insect to form activated toxins with an apparent size of 60-65 kDa. The activated toxins bind to specific receptors on the surface of the midgut epithelial cells of susceptible insects, and cause rapid inhibition of potassium ion (K^{+})-dependent amino acid transport (Sacchi et al. 1986), changes in the permeability of the midgut membranes (Harvey and Wolfersberger 1979), and eventual lysis of the midgut epithelial cells and death of the insect. Ongoing research by FS scientists at Hamden, CT, and Delaware, OH (NE), and university cooperators is identifying Cry proteins toxic to GM and other forest defoliators, and determining their mode of action.

Three insecticidal proteins produced by *B. thuringiensis* subsp. *kurstaki* HD-1 have been identified and designated as CryIA(a), CryIA(b) and CryIA(c). These three proteins differ in their primary structures, and these toxins exhibit significant variation in their insecticidal activity (Whiteley and Schnepf 1986; Dubois 1992). Although all three proteins are toxic to GM, only CryIA(a) shows any significant toxicity against silkworm larvae. Several factors, including synergism with microflora in the forest environment and solubilization of the ICPs and proteolytic activation of the protoxin, have been proposed to explain the differences in the insecticidal spectrum among the toxin proteins (Knowles and Ellar 1986; Haider et al. 1986; Dubois 1992; Dubois and Dean 1993). However, in many studies the main factor determining the specificity of a toxin in insects has been attributed to the presence or absence of a specific receptor in the midgut of susceptible and resistant insect larvae, respectively, and the degree of affinity of the receptor for the toxin protein (Hofmann et al. 1988; Van Rie et al. 1989, 1990a).

The receptor for the CryIA(c) insecticidal protein in tobacco hornworm and GM was recently purified, and identified as the midgut brush border membrane-bound aminopeptidase-N (AP-N) by FS scientists in Delaware, OH (NE) and their cooperators. The purified receptors offer a means for rapid screening of δ-endotoxins from new Bt isolates that exhibit high affinity binding and activity with specific insect pests. The correlation of the presence of high affinity receptors and insecticidal activity indicate that binding is a crucial step in conferring toxicity. However, in some cases, the binding of Cry insecticidal proteins to the midgut membrane could not be corroborated with *in vivo* toxicity results (Wolfersberger 1990; Van Rie et al. 1990a and b). These results suggest that post-binding events, such as the ability of the toxin to integrate into the midgut epithelial membrane, contribute to the *in vivo* differences among the structurally related δ-endotoxins in their insecticidal properties.

Studies of site-directed and homolog-scanning mutagenesis of the Bt δ-endotoxins have provided information concerning the functional domains and the location of specific regions of the δ-endotoxins involved in receptor binding, and the irreversible interaction of the toxin with the insect midgut membrane (Schnepf et al. 1990; Ge et al. 1991; Wu and Aronson 1992). Similarly, future research that characterizes the molecular sites on the insect Bt receptors involved in binding these toxins, and the role of the receptors in facilitating the insertion of the toxin into the membrane will be valuable in elucidating the mode of action of Bt δ-endotoxins and should facilitate the rational design and synthesis of new, improved insecticidal proteins by protein engineering methodologies. Protein engineering may also be utilized to modify an existing Cry protein with respect to solubility, proteolytic stability, and receptor specificity and affinity.

Because of the results of the many cooperative research efforts among federal and state scientists and applications personnel over the past 30 or more years, Bt has become the preferred method for control of GM and other forest defoliators. Future research will continue to advance the application technology and the understanding of Bt biology and its mode of action.

D. Conifer Defoliators

1. Blackheaded pine sawfly, *Neodiprion excitans* Rohwer (Hymenoptera: Diprionidae). By Mary Ellen Dix

The blackheaded pine sawfly defoliates pines throughout most of the southeastern U.S. and Central America, causing serious damage to pine sawtimber in the Gulf Coast region (Thatcher 1971). In 1966, W.H. Bennett (Pineville, LA [SO]) developed a problem analysis on natural control of sawflies affecting southern pine. Preliminary studies indicated that polyhedral viruses held potential for controlling these pests, but later inconclusive field studies, the lack of controlled temperature and

humidity units for rearing the insects to maturity and priority research on SPB in 1971 precluded more extensive studies on the blackheaded and other pine sawflies in Louisiana.

A.T. Drooz, a Forest Service defoliator expert, and R.C. Wilkinson (University of Florida) identified larval and pupal parasites of the sawfly and two other *Neodiprion* spp. in northern and western Florida and Belize, Central America, and assessed their impacts on pines (Drooz et al. 1977a; Wilkinson and Drooz 1979). Because the parasites and fungal pathogens of sawflies in Belize and Florida were similar or closely related species (Wilkinson and Drooz 1979), no natural enemies were targeted for importation or later evaluation as potential biological controls.

2. Parasites and predators of the Douglas-fir tussock moth, *Orgyia pseudotsugata* (McDunnough) (Lepidoptera: Lymantriidae). By Mary Ellen Dix

The Douglas-fir tussock moth (DFTM) severely defoliates Douglas-fir and other true firs periodically in the Pacific Northwest and Canada. Outbreaks generally last two to four years before populations collapse in response to a combination of parasites, predators, diseases, and starvation (Mason and Wickman 1988).

The importance of natural enemies in regulating DFTM populations has long been recognized. In the early 1930s, parasites were reared from DFTM eggs, larvae, and pupae (Balch 1932). During the 1960s, nuclear polyhedrosis virus (NPV) and *Bacillus thuringiensis* (Bt) were used to control DFTM in a series of pilot projects conducted by entomologists of the Northern Region of State and Private Forestry (R-1, in Missoula, MT) (Tunnock 1966). Scott Tunnock identified causes of DFTM mortality at project sites in Montana and Idaho. He found that diseases (mainly a naturally occurring NPV) as well as parasites and predators contributed to the collapse of outbreaks after two to four years (Tunnock 1973, 1975). Boyd E. Wickman, Richard R. Mason, and Clarence G. Thompson of the FS Pacific Northwest Experiment Station (PNW) and other forest entomologists also observed similar collapses of outbreaks in Washington and Oregon and identified causes of the collapses (Mason and Thompson 1971; Tunnock 1973; Wickman et al. 1973). These scientists used parasite abundance to monitor the progress of DFTM outbreaks. Tunnock surveyed egg masses and predicted future defoliation levels in advance of several Forest Service pest management projects by comparing egg mass abundance with amount of parasitism and predation of the egg masses (Tunnock 1974; Tunnock et al. 1974).

In 1974, research on DFTM parasites and predators and their impact on the population dynamics of DFTM accelerated after Congress approved the Expanded DFTM Research and Application Program. Robert D. Averill, Rocky Mountain Region, State and Private Forestry (R-2, Denver, CO), Scott Tunnock (R-1), Richard R. Mason (PNW), and Donald L. Dahlsten, University of California, Berkeley (UCB) studied DFTM outbreaks and non-outbreak populations in California, Oregon, and Washington. They reared and identified natural enemies of all DFTM life stages in Colorado, Montana, Idaho, Oregon, Washington, and California (Mason 1976, 1981a; Tunnock et al. 1976; Averill 1976; Dahlsten et al. 1977; Mason et al. 1983; Mason and Torgersen 1987). Torolf R. Torgersen (PNW) (1977) developed a key for identifying natural enemies of DFTM larvae. He described a new species of ichneumonid parasite, *Hyposoter masoni*, that was reared from first- and second-instar larvae collected at several sites (Torgersen 1985b). Torgersen and Mason (1979) also published a key to the parasites and predators of DFTM egg masses. Dahlsten et al. (1977) assessed the impact of NPV on natural enemy complexes in low to moderate DFTM populations.

Egg parasites were found to play an important role in keeping population levels low. Rates of parasitism were evaluated in Colorado, California, and the Northwest (Mason 1976; Averill 1976; Dahlsten et al. 1977; Mason et al. 1983; Mason and Torgersen 1987). It was found in these studies that *Telenomus californicus* could parasitize more than 50% of the eggs, especially when DFTM

levels were low (Mason et al. 1983; Mason and Torgersen 1987), and that abundance of the parasite increased with decreased egg mass densities (Dahlsten et al. 1977). For these reasons, *T. californicus* was a good candidate for augmentative releases. In 1979, Torgersen and Mason began a series of one- to five-year studies to learn more about the parasite, including its range, geographical abundance over time, and the relationship between proportion of egg masses attacked and mean parasitization rate (Torgersen and Mason 1985). Successful parasitization of DFTM eggs by *T. californicus* was found to be dependent on parasite reproduction. Ryan et al. (1981) evaluated the effects of mating, female age, photoperiod, host storage temperatures, and host availability on reproduction of the egg parasite in the laboratory, and found that reproduction was greater in newly stored eggs than older eggs. Sower and Torgersen (1979) determined that applying a DFTM pheromone to a site did not interfere with host selection by the egg parasites. Thus, the pheromone and egg parasite could be used simultaneously to control DFTM.

Although a number of natural controls had thus been identified, their role in the regulation of DFTM population at high and low levels was poorly understood. From 1976 to 1981, DFTM populations were periodically surveyed in California, Oregon, and Washington for natural enemies and the impacts of parasites and predators on DFTM abundance were assessed (Dahlsten et al. 1977; Mason et al. 1977, 1983; Torgersen et al. 1983; Mason and Torgersen 1987). Torgersen and Dahlsten (1979) found that arthropod and avian predators were major causes of larval mortality in non-outbreak populations of DFTM. They found that in most low-density populations, relatively few larvae were killed by parasites and disease compared to the number killed by predators. Stable DFTM populations apparently are rich in predaceous spiders, ants, birds, and other predators (Mason and Overton 1983; Mason et al. 1983; Mason and Torgersen 1987).

Torgersen and associates used a stocking technique to assess predation on overwintering egg masses, larvae, and pupae in Oregon, Idaho, and California (Mason and Torgersen 1983; Torgersen et al. 1983; Torgersen and Mason 1987). The most important predators of overwintering egg masses were birds (red-breasted nuthatch, dark-eyed junco, and Nashville warbler), and a tree-foraging ant (*Camponotus* sp.) (Torgersen and Mason 1987). Twenty-one species of birds were identified as predators or probable predators of DFTM larvae and pupae; nine species were observed feeding on larvae and pupae, and 12 species were observed foraging on tree branches from which larvae and pupae disappeared. The predominant larval and pupal predators were the red-breasted nuthatch, dark-eyed junco, and mountain chickadee (Torgersen et al. 1984b). The pentatomid *Podisus serieventris* was also an important larval predator. One *P. serieventris* was capable of destroying all stocked DFTM larvae in cages (Mason 1981b).

During 1972-81, Mason, Dahlsten and colleagues identified and determined the distribution of spiders on Douglas-fir. They found that spiders were the most abundant predator in the system and that arthropod predation on early instar DFTM larvae was a key factor in DFTM survival (Mason 1976, 1981b; Dahlsten et al. 1977; Mason and Overton 1983; Mason and Torgersen 1983; and Mason et al. 1983). Fichter and Stephen (1979, 1981) developed an ELISA (enzyme-linked immunosorbent assay) that permitted quantification of predation by polyphagous arthropods. Bioassays of spiders fed DFTM were positive for up to ten days after feeding. Similar assays of the pentatomid predator *Podisus maculiventris* were positive in half of the individuals for three days post feeding (Fichter and Stephen 1984). Scattered information on the identities and biologies of spiders was consolidated in a key to the most common arboreal spiders of Douglas-fir and true fir forests of the Pacific Northwest (Moldenke et al. 1987).

The studies discussed above provided limited information on the relative densities and importance of spiders in regulating DFTM populations. In 1981, Mason began a study to compare the relative densities and importance of spider families on firs in the interior Pacific Northwest, Southern Cascades, Northern Cascades, and Blue Mountains (Mason 1992). Mason and Paul (1988) found that

Metaphidippus aeneolus, one of the most common arboreal spiders in the fir forest, readily preyed on small larvae in the laboratory and the field, and hypothesized that *M. aeneolus* was an important predator of the small larvae. Mason also found that spiders frequently outnumbered all other arthropod predators in the trees, and that species of each specific spider family inhabited a specific part of the foliage. Furthermore, familial structure and abundance of arboreal spider communities are similar within fir forests. Mason concluded that this underlying organization of spider communities should make spider populations more predictable (Mason 1992).

3. Douglas-fir tussock moth pathogens. By Mauro E. Martignoni

Outbreaks of the DFTM have occurred in many regions, from British Columbia to Arizona and New Mexico, from the Rocky Mountain states to the Cascade and Siskiyou ranges of Washington, Oregon, and California. Since the first reported infestation at Chase, BC, in 1916, several major outbreaks have occurred in stands where conditions changed rapidly in favor of tussock moth survival. Stoszek and Mika (1979) discussed the history of these outbreaks and described the site and stand characteristics associated with DFTM infestations. These infestations last typically about three years and usually terminate abruptly. Infectious agents were long suspected as a cause of epizootics among outbreak level populations of DFTM. A nuclear polyhedrosis virus (NPV) was first diagnosed in DFTM larvae collected in June 1947 by R.L. Furniss near Troy, OR (Steinhaus 1951). Larvae collected in August 1947 by J.C. Evenden in Colville, WA, and Orofino, ID, were also diagnosed as being infected with NPV. Both Furniss and Evenden considered the disease to be an important factor in the natural control of DFTM (Steinhaus 1951). Hughes and Addison (1970) found that two distinct NPVs, a unicapsid morphotype and a multicapsid morphotype, infected larvae of DFTM. Martignoni et al. (1969a and b) reported the occurrence of a cytoplasmic polyhedrosis virus (CPV) in DFTM.

Research. In 1964, when DFTM outbreaks were in progress throughout the northwestern U.S., Clarence G. Thompson, head of the newly created insect pathology project ("Diseases of Western Forest Insects") of the Forest Service's Pacific Northwest Forest and Range Experiment Station (PNW), initiated a comprehensive program to develop a microbial control method using one of the NPVs of the DFTM (Thompson 1979). The insect pathology project was located in modern, well-equipped facilities at the Forestry Sciences Laboratory in Corvallis, OR.

Initial laboratory studies in 1964 led to a small-scale simulated NPV field trial in 1965 (Thompson and Maksymiuk 1979). The positive results of this trial persuaded the Forest Service (FS), in 1966, to start a first Research and Development Effort ("Forest Service Joint Effort") to develop a viral insecticide against the DFTM. A pilot test by another branch of the FS in Idaho, in 1965, used a very low dose of NPV (10^9 polyhedral inclusion bodies per acre) and gave inconclusive results (Tunnock 1966). Fortunately, this test did not have a negative impact on the decision to proceed with the development of a viral insecticide. The Forest Service Joint Effort included the following studies: virus characterization, acute toxicity-pathogenicity tests, pilot-plant scale virus propagation, production control procedures, formulation of spray mixtures, spray physics, and field tests. In 1973, all participants of the Joint Effort met to review the combined results and to prepare recommendations for future studies. In view of the promising results, the group decided to complete the toxicity-pathogenicity studies with the viral preparation and to apply to the Environmental Protection Agency (EPA) for an Experimental Use Permit (EUP) for the virus against the DFTM. The EUP was granted in 1974. Research on the virus was accelerated in 1974 through special one-year federal funding and greatly intensified in 1975 and following years under the new "USDA Expanded Douglas-fir Tussock Moth Research and Development Program". The appropriation bill for this program was included in the "Forest and Rangeland Renewable Resources Planning Act", signed into law by President Gerald Ford on August 17, 1974. Kenneth H. Wright, entomologist at the PNW station in Portland, OR, was appointed Program Manager of the large multidisciplinary research team. Research and application studies continued until 1978 along well defined activity

schedules, as outlined in Appendix 1 of the compendium on Douglas-fir tussock moth research and development (Brookes et al. 1978). This compendium was the culmination of many years of cooperative research by federal, state, and university scientists; it also served as a very effective avenue of transfer of knowledge on the DFTM to forest managers.

During the period 1974-76, sufficient funding was provided to the PNW insect pathology project at Corvallis to complete additional laboratory and field studies. Virus strain identification, virus potency standardization, mammalian and fish toxicity-pathogenicity tests, and large-scale forest treatments with experimental virus preparations provided the knowledge needed to optimize virus dosage, timing, and spray strategies. These studies were urgently needed also because the EPA had reaffirmed its 1972 stand on the ban of DDT, then the only insecticide capable of effectively controlling DFTM. On February 26, 1974, the EPA granted the FS its last emergency authorization for the use of DDT against the DFTM in Idaho, Oregon, and Washington. Russell E. Train, then Administrator of the EPA, approved use of DDT against DFTM only "... with the greatest personal reluctance". In granting that application, Train also urged the FS to intensify research efforts and to find more environmentally-acceptable alternatives for controlling the moth (Train 1976). The intensive research and application work by the insect pathology project at the Forestry Sciences Laboratory at Corvallis provided ample data for final registration of the technical grade virus preparation. Registration of the product, named "BioControl-1™," was approved on August 11, 1976 (EPA Registration No. 27586-1). Data on production, activity, and safety of the virus were summarized by Martignoni (1978) and results of the field efficacy tests were presented by Stelzer and Neisess (1978). As shown by these authors, the viral preparation proved to be safe and presented no undue risks to humans and the environment when sprayed in Douglas-fir forests. The field efficacy tests proved that DFTM populations could be controlled at an aerial application dose of 1.1 x 10^9 viral activity units per acre, or about 10^{11} polyhedral inclusion bodies (PIB) per acre. Larval population reductions from 90-97% were reported and no insect survival to the pupal stage was observed in several treated plots. Significantly, viral applications also gave excellent foliage protection.

At the height of research activities under the leadership of C.G. Thompson, the microbial control team at the Forestry Sciences Laboratory consisted of three entomologists, one microbiologist, one chemist, one electron microscopist, two entomology technicians, two microbiology technicians, one physical science technician, and one equipment specialist. In May 1977, Secretary of Agriculture Robert Berglund presented the team with a Science and Education Superior Service Award for outstanding effort in developing the use of the NPV product for control of the DFTM.

Virus Propagation. Viruses reproduce exclusively within living cells. Therefore, successful mass propagation of viruses is linked to successful mass production of susceptible host cells. Based on propagation technology, production cost, and capital investment, living DFTM larvae are currently (1993) the preferred substrate for production of the NPV used for control of this pest (Martignoni 1979, 1984).

The FS awarded contracts for virus propagation in DFTM larvae to a private laboratory in 1966, 1972, and 1974. The total output of these contracts was 9861 acre (3990 hectare) doses. Most of this material was urgently needed for the initial field trials and for toxicity-pathogenicity tests in mammals, birds, and fish. After 1974, it proved very difficult to find private laboratories willing to undertake production of virus at an acceptable cost. In 1979, a major production contract was terminated by the contractor because of difficulties and high costs associated with raising large numbers of larvae.

In November 1980, FS Region 6 established a Baculovirus Production Facility (a field unit of Forest Pest Management) at the Forestry Sciences Laboratory in Corvallis, OR. The facility was organized

into three work sections: insect diet production, insect production, and virus propagation. Further details of the work at the facility are provided by Bergstrom (1985). The first manager of the Baculovirus Production Facility, from 1980 to 1985, was Donald W. Scott. Since 1985, Anita S. Hutchins has been manager of the facility. Mauro E. Martignoni, of the Forestry Sciences Laboratory, was adviser to the facility until the end of 1985. Depending on required production levels, the number of laboratory technicians and aides at the facility varied from a low five to a maximum of 12. The output, measured in amount of virus required to treat one acre (2.471 hectares) of forest, varied from a low of 30,000 acre (74,130 hectare) doses per year to a maximum of 100,000 acre (247,100 hectares) doses per year. The total product now (1993) stockpiled under refrigeration is sufficient to treat approximately 400,000 hectares (988,400 acres) (Anita S. Hutchins, personal communication).

The Baculovirus Production Facility was closed in June 1993, except for a minimum of technical personnel and equipment dedicated to maintenance of DFTM strain GL-1, the inbred strain used for bioassay of virus production lots.

The virus propagated at the facility was exclusively strain MEM-75-STANDARD of the multicapsid NPV (*Baculovirus*, Op*M*NPV) of DFTM. Since 1978, the passage level of this virus strain was stabilized by adoption of a seed-lot system (M.E. Martignoni, unpublished data). A large primary virus lot ("seed lot") was prepared and preserved in numbered ampoules under refrigeration. Each ampoule serves as inoculum for propagation in a small batch of larvae (first passage). Virus harvested from these larvae ("secondary inoculum") is used for inoculating production larvae (second passage). Thus, no more than two passages separate the final product from the 1978 seed lot virus. There is still (1993) a substantial supply of the original seed lot for future use. Virus strain MEM-75-STANDARD is also preserved as ATCC VR-992 at the American Type Culture Collection, Rockville, MD.

Although the Baculovirus Production Facility was capable of producing and testing NPV, the material had to be processed in a way that guaranteed concentration of viral inclusion bodies and exclusion of unwanted larval debris. Packaging must assure long-term stability of the agent. Virus processing is achieved by wet slurrying of larval cadavers, centrifugation of the slurry, lyophilization of the clean sediments, screening, and vacuum packing; these operations must be done with methods and equipment that permit a high rate of recovery of active virus. When the Facility was established in 1980, those involved in planning were aware that private industry would have the equipment and knowledge needed to accomplish this work, whereas the FS had the best knowledge and personnel for rearing tussock moth larvae and propagating the virus. Thus the FS facility was not furnished with the costly equipment needed for this processing phase. That decision proved correct. The major processing contractor for BioControl-1™ was Espro, Inc., of Columbia, MD. The first of several contracts awarded to Espro by the FS was signed in June 1988 (Aldis E. Adamson, personal communication). About 90% of the virus produced by the facility had been processed by 1992, when the last contract expired and Espro was acquired (in a joint venture) by Crop Genetics International and DuPont.

The cost of production of BioControl-1™ is determined principally by the cost of rearing the DFTM. The rearing cost can account for up to two-thirds of the total production cost. The latest (January 1991) estimate of the cost of BioControl-1™ was just under $8 per acre-dose, processing and packaging included (A.S. Hutchins, personal communication). This cost is certainly acceptable in the context of long-term management of valuable Douglas-fir stands.

Concluding Remarks. Research accomplished during 15 years (1964-78) by the insect pathology team at the Forestry Sciences Laboratory in Corvallis, OR, demonstrated that a *Baculovirus* is an effective and host specific control agent for DFTM larvae. It is an environmentally safe agent and an

economically feasible alternative to chemical insecticides. BioControl-1™ is the first virus registered in the U.S. for use against a forest insect. The viral product and the forest application strategies developed by the FS team have been integrated into practical forest management systems. A substantial amount of virus is stockpiled by the FS for use against future DFTM outbreaks. The goals of the Expanded Douglas-fir Tussock Moth Research and Development Program and the mandates of the EPA concerning microbial control of outbreaks of this forest insect were fully met.

4. European pine sawfly, *Neodiprion sertifer* (Geoffroy) (Hymenoptera: Diprionidae). By Mary Ellen Dix

The European pine sawfly, an introduced species, was first recorded at Somerville, NJ, in 1925 (Schaffner 1939). It defoliates red and other pines from New England and southwestern Ontario, west to South Dakota and south to Missouri. In 1977, the ichneumonid parasite *Lophyroplectus oblongopunctatus* was successfully introduced to control this sawfly (Kraemer et al. 1979). In 1980, M.A. Mohamed and associates collected parasitized sawfly cocoons from Wisconsin field sites and overwintered them in the laboratory. The next spring they sprayed an aqueous suspension of a nuclear polyhedrosis virus from the European pine sawfly on the emerging *L. oblongopunctatus*. The infected parasites successfully transferred the virus to the sawfly larval colonies in the field (Mohamed et al. 1981).

5. Hemlock defoliators. By Mary Ellen Dix

Outbreaks of the hemlock sawfly, "blackheaded budworm", and the western hemlock looper severely defoliate western hemlock in Washington, Oregon, southeast Alaska and northwestern Canada. Heavy tree mortality followed severe sawfly and budworm defoliation during the early 1950s and 1960s (Downing 1957; Crosby 1965) and a severe looper outbreak in Alaska during the mid-1960s (Torgersen 1971).

Natural enemies can play an important role in regulating populations of both the sawfly and the looper. Torgersen (1968) identified parasites reared from hemlock sawfly cocoons, noted their abundance, and developed a key to the larval remains of seven parasites of the sawfly (Torgersen 1969). This key can be used to assess levels of sawfly parasitism and predict control needs. Torgersen also reared eight species of parasites from pupae of the hemlock looper and developed a key to the ichneumonid parasites (Torgersen 1971).

A 1963 field test of *Bacillus thuringiensis* (Bt) against the looper in southwest Washington was unsuccessful because lethal doses of Bt did not persist in the crowns (Carolin and Thompson 1967).

6. Introduced pine sawfly, *Diprion similis* (Hartig) (Hymenoptera: Diprionidae). By John H. Ghent

The introduced pine sawfly, a pest native to Europe and Siberia, was discovered in Connecticut in 1914 (Britton 1915). In 1977, the sawfly was collected for the first time in North Carolina, in the Linville Falls area of Avery County. A survey of the introduced pine sawfly population in North Carolina during the winter of 1978 revealed that less than one percent of the sawfly larvae were parasitized (Drooz et al. 1979). The sawfly population was expected to increase and cause extensive damage to the area's white pine because of the lack of natural controls and the pest's bivoltine life cycle.

In 1979, a research and applications program was initiated by Forest Pest Management and Forest Insect and Disease Research. J.H. Ghent (Forest Pest Management, Southeastern Region) and A.T. Drooz (Forest Insect and Disease Research, Southern Forest Experiment Station) were directed to develop and run a parasite rearing facility in the Linville Falls area (Drooz et al. 1985a).

They selected the torymid parasite *Monodontomerus dentipes* for rearing because it had reduced abundance of the introduced pine sawfly during an earlier outbreak in Wisconsin (Coppel et al. 1974; Drooz et al. 1985a). In 1979, introduced pine sawly cocoons were collected from populations near Amery, WI. Emergent parasites from this collection were used to initiate a mass-rearing program for *M. dentipes* (Fedde 1975). From July 1979 until the spring of 1981, a total of 14,000 parasites were released in North Carolina. Parasitism rose from 0.8% in 1979 to 44.9% by the winter of 1980. By the spring of 1981, introduced pine sawfly populations had effectively collapsed around the release area and the parasite rearing facility was closed (Drooz et al. 1985a). Over a decade later, *M. dentipes* still helps keep populations of the introduced pine sawfly below outbreak levels.

7. Jack pine budworm, *Choristoneura pinus* Freeman (Lepidoptera: Tortricidae). By Mary Ellen Dix

The jack pine budworm, a native species, severely defoliates jack pine in the Lake States. Outbreaks occur sporadically at six- to ten-year intervals and persist for two to four years (Benjamin 1956). Numerous university and Forest Service scientists have identified natural enemies and evaluated their impacts. In 1954, Benjamin and Drooz (1954) identified an egg parasite, six larval parasites, and ten pupal parasites in Michigan. They noted that two parasites, *Itoplectis conquisitor* and *Apanteles fumiferanae*, appeared to be important in reducing budworm populations.

In 1965, entomologists at the University of Michigan initiated a study on the population dynamics of the jack pine budworm that included assessment of the impact of predators and parasites on budworm populations. They reared 26 species of parasites and four species of hyperparasites from the budworm. Parasitism was highest in second instar larvae. *Apanteles* (sens. lat.) sp. and *Glypta fumiferanae* were the most abundant parasites of the second-instar larvae, and *I. conquisitor* was the most important pupal parasite (Allen et al. 1969). W.J. Mattson (North Central Forest Experiment Station) and cooperators found that 28 species of birds and mammals attacked budworms in Michigan. Bird predation helps regulate endemic budworm populations, but apparently was also an important mortality factor in large forests during budworm outbreaks. In small forests, bird predation was high because non-resident birds moved into the jack pine community and added to mortality caused by resident birds (Mattson et al. 1968). During the late 1960s, D.T. Jennings (North Central Forest Experiment Station) studied predators of the budworm in Minnesota and Wisconsin. He identified six species of ants in Wisconsin that actively preyed on late instar larvae of jack pine budworm after they were inadvertently dislodged from their feeding sites (Jennings 1971). The North Central Forest Experiment Station budworm project ceased because supporting funds were no longer available in the early 1970s, and Jennings transferred to New Mexico, in 1968.

8. Larch casebearer, *Coleophora laricella* (Hübner) (Lepidoptera: Coleophoridae). By Roger B. Ryan

The larch casebearer was discovered on tamarack in Massachusetts in the late 1800s, presumably having arrived from its native Europe as an inadvertent introduction on planting stock. From there, its population spread and intensified throughout much of the northeastern U.S. and southeastern Canada and dispersed westward.

Research on biological control of the larch casebearer in North America has passed through three rather distinct phases. Although serious defoliation of tamarack occurred in some areas for over 40 years, the first phase of biological control research did not begin until the 1930s, when European parasites were released. Studies of the biology of larch casebearer and its natural enemies in Europe (e.g., Thorpe 1933; Eidmann 1965; Jagsch 1973) furnished valuable information to guide that and subsequent biological control efforts in North America. Between 1931 and 1939, the governments of Canada and the U.S. collected host material in central Europe and released several species of

parasites (Dowden 1934a and b, 1962; Dowden and Berry 1938; Graham 1944, 1949, 1958; Webb 1953; McGugan and Coppel 1962b; Clausen 1978; see also Chapter II of this publication). Thorpe (1933) suggested that the ichneumonid *Diadegma laricinellum* (as *Angitia nana*) was the most promising biological control agent. P.B. Dowden, later of the Northeastern Forest Experiment Station and then working at the Bureau of Entomology Gypsy Moth Laboratory at Melrose Highlands, MA, initially reported (Dowden 1934a,) that only three species were "true internal parasites suitable for liberation". These were the species recommended by Thorpe, *D. laricinellum*, plus *Agathis pumila* (as *Bassus pumilus*) and *Chrysocharis laricinellae*. *Dicladocerus westwoodii*, an external parasite, was not initially released, probably because Dowden felt that "in general external feeders are polyphagous [and] sometimes develop on primary parasites" (Dowden 1941). Dowden initially released only the three internal parasite species named above, but in 1936, after investigating the biology of *D. westwoodii*, released it as well (Dowden 1962). Although Dowden also reported the release of two species of *"Horogenes"*, they were both later considered to be *Diadegma laricinellum* (Carlson 1979). The Canadians released the same four species and *Cirrospilus pictus*. Dowden, however, considered the hyperparasitic tendencies of *C. pictus* sufficient grounds to deny its release; he also reported that it was already in North America (Dowden 1941).

Collections of larch casebearer in Europe were made at two different times in the spring, an early collection to obtain overwintering *C. laricinellae*, and a later one when larvae were feeding, to obtain other parasite species. *Diadegma laricinellum* proved elusive to obtain from European collections. In Canada, a total of only 200 was released at three sites in four different years (McGugan and Coppel 1962b). In the U.S., the numbers released were higher, 3580 adults at seven sites over five years, but Dowden (1934a) reported that the adult parasites emerging from European collections died before susceptible host larvae (needleminers) were present in U.S. field release sites. Releases probably were too small and ill-timed to give the species a reasonable chance for establishment of *D. laricinellum*. On the other hand, the release dates reported for *D. westwoodii* (McGugan and Coppel 1962b) were probably too late for the adults to parasitize susceptible host larvae. Only two species, *A. pumila* and *C. laricinellae*, became established.

In spite of the failure of two of the parasite species to establish, results of the biological control effort during that first phase were gratifying. The buildup of *A. pumila* coincided with decreased larch casebearer populations (Graham 1949), a pattern that was repeated as the pest dispersed westward. *Chrysocharis laricinellae* was slower to increase and in many areas increased far less than *A. pumila*. There were suggestions that *C. laricinellae* might be a negative contributor to biological control because it parasitized hosts already containing *A. pumila* (Graham 1949). When most unparasitized hosts are in the pupal stage, *C. laricinellae* attacks a higher percentage of *Agathis*-parasitized than unparasitized larvae apparently because the prolonged development of the parasitized individuals makes them available for parasitization for a longer period; critical assessment of this interaction, however, was not addressed until later (Quednau 1970a).

This first phase of biological control extended through the 1950s as the host dispersed westward into the Lake States on tamarack; established parasites were released in the new areas from previously established populations (Webb 1953, 1957; Coppel and Shenefelt 1960; Webb and Denton 1967; Webb and Quednau 1971).

The second phase of biological control, confined to eastern North America, took place during the 1960s and 1970s when biological research on the host and its natural enemies intensified (Cody 1963; Sloan 1965; Sloan and Coppel 1965a, b, and c, 1968; Quednau, 1966, 1967a, b, and c, 1968, 1969, 1970a and b; Cody et al. 1967; Coppel and Sloan 1971; Rush 1972; Raske and Schooley 1979).

F.W. Quednau, stationed at the Canadian Department of Fisheries and Forestry's Forest Research Laboratory at Sainte-Foy, Quebec, conducted detailed investigations of the larch casebearer and its

parasites, including life-table work to assess the interaction between *A. pumila* and *C. laricinellae*, that highlighted this period (see above cited references). According to his assessment, the view that *C. laricinellae* detracted from biological control neglected to attribute on the plus side to *C. laricinellae* the additional fraction of the host population parasitized by its previous generation(s) but not by *A. pumila* (Quednau 1970a); *C.laricinellae* thus adds mortality to the casebearer generation that *A. pumila* cannot. Quednau concluded that, on balance, *C. laricinellae* contributed positively to biological control. Although *A. pumila* was clearly the dominant species in biological control in many areas, *C. laricinellae* was an important contributor and, in fact, seemed to dominate in certain situations, particularly in the Maritime Provinces of Canada.

In addition to his life-table work in the field, Quednau (1967b and c, 1970b) added detailed biological knowledge on the casebearer and the two established parasites through laboratory rearings. He also renewed efforts to establish the particularly promising species, *D. laricinellum*, that had not been established in the first phase (Otvos and Quednau 1984). His approach was to establish a laboratory culture for studying its interaction with *A. pumila* and which would serve as a source of inoculum for the eventual release of *D. laricinellum* (Webb and Quednau 1971). However, the parasite proved as elusive to collect as before and few were released. Inability to culture continuous generations of the host in the laboratory also indicated that a parasite that spends almost a year in the host larvae could likewise not be cultured. Quednau's research on the larch casebearer was terminated in 1974 by administrative reorganization and reallocation of effort within the Canadian government.

The long-distance dispersal of the insect pest onto western larch in Idaho in the late 1950s (Denton 1958) ushered in the third phase of larch casebearer biological control -- the parasite introduction effort in the West. The U.S. Forest Service's Intermountain Forest Research Experiment Station (INT) initiated research on the new pest in 1960. There were several studies of its biology, natural enemies, and effect on the larch resources of the West (Denton 1965, 1979; Andrews 1966; Andrews and Geistlinger 1969; Bousfield and Lood 1970, 1973; Denton and Tunnock 1972; Ciesla and Bousfield 1974; Ross 1976; Denton and Theroux 1979).

The INT's then Chief of Forest Insect Research, D.E. Parker, cognizant of the successful biological control in the East, seized the research opportunity to see what *A. pumila* could do in the West without having to interact with *C. laricinellae* (Anonymous 1960). Arrangements were made with Dowden, who collected parasitized casebearers from the Northeast, reared out *A. pumila*, and shipped adults to R.E. Denton, at the INT station in Missoula, MT, who made the first releases in northern Idaho in 1960 (Denton 1972). Other species were not released. Recoveries were made in 1963 (Denton 1972). Forest Pest Management of the Northern Region headquartered in Missoula, MT, then became involved in further releases to spread more rapidly the establishing *A. pumila*. Entomologists in State and Private Forestry in the Northeast made additional collections of parasitized larch casebearers in Massachusetts and Vermont and shipped them to northern Idaho for rearing of overwintering larvae to obtain adult *A. pumila*. The rearing effort over the next several years was the combined effort of INT and Forest Pest Management. Whole-tree cages were used to obtain parasitism of the Idaho larch casebearer population with parasites from the East (Denton 1979). Between 1965 and 1969, parasitized overwintering casebearers were distributed by Forest Pest Management to approximately 400 sites in Idaho, Montana, and, with entomologists from Region 6 and British Columbia, to many sites in those areas as well, virtually blanketing the then-infested larch stands in the U.S. Subsequent evaluation revealed that *A. pumila* had become widely established (Bousfield et al. 1974).

By about 1970, the expected collapse of the larch casebearer population failed to occur in the West and there was still widespread and severe defoliation, although green pockets of undefoliated trees were noted to surround some release sites. Nevertheless, widespread disappointment with the results

of biological control led foresters to fear that larch, an important timber tree in the West (Schmidt et al. 1976), may be lost due to this pest in much the same way that white pine apparently was lost due to white pine blister rust. Some research on chemical control was going on at the time (Denton 1967; Denton and Tunnock 1968; Lyon and May 1970), but biological control research seemed to have stalled. Indications were that the larch casebearer would continue to be a serious problem (Tunnock et al. 1969). Indeed, larch was temporarily omitted from management plans.

INT Assistant Director C.A. Wellner convened a strategy meeting in January 1971. It was decided that an all-out Research and Development (R&D) effort was called for. INT spearheaded a proposal to the Forest Service Washington Office to back and obtain funding for a "big bug" program on larch casebearer. The proposal called for expanded research on biological and chemical control and almost every other conceivable research area. In the next several years there was a flurry of effort in many areas, both inside and outside the Forest Service (Amman and Tunnock 1971; Tunnock et al. 1972; Ciesla and Bousfield 1974; Miller and Finlayson 1974, 1977a and b; Ryan 1974a and b; Hansen 1977, 1980, 1981; Long 1977; Moody 1977; Washburn et al. 1977; Crabtree et al. 1978; Theroux and Long 1978; Denton and Theroux 1979; Flavell 1979; Hard et al. 1979; Long and Theroux 1979; Pettinger and Johnsey 1979; Page et al. 1980, 1982; Ismail 1981; Niwa and Hard 1981; Ismail and Long 1982; Niwa 1982; Nathanson et al. 1985; Niwa et al. 1986). However, as it turned out, the "big bug" proposal was shelved to allow an expanded biological control effort to bear fruit.

At the Pacific Northwest Forest Research Experiment Station's (PNW) Corvallis Laboratory, R.B. Ryan drafted a study plan that called for the introduction of parasite species in addition to *A. pumila*. Because of the considerable time already invested in the single-species parasite introduction approach, additional species were to be added to some plots while maintaining the *Agathis*-only character of others. That would permit a few establishment foci from which additional parasite species could spread and assist in biological control, while at the same time allow data to be gathered on the single-species vs. multiple-species polemic. Those two types of plots plus a check plot (with no introduced parasites) were to be established in each infested state. Participants in the study agreed to gather the appropriate data from the three plots, constituting a block, in their area of responsibility, i.e. INT in Idaho, Region 1 Forest Pest Management in Montana, Region 6 Forest Pest Management in Washington, and PNW in Oregon. It was difficult in Idaho, Washington and Montana to establish check plots to conform to the arbitrary 50 miles between plots because of the widespread releases in those states of *A. pumila* in the 1960s. Nevertheless, check plots were established as far from previous releases as possible. Distance to previous release plots was not a problem in Oregon, because it had not been infested at the time and no releases of *A. pumila* had been made in that state.

In addition to stock of *A. pumila* and *C. laricinellae* from the eastern U.S., releases in the western infestation originated from collections in numerous localities in Europe and Japan. Adults were received through the Canadian Quarantine Stations at Belleville, Ontario (1971-72) and Ottawa (1973), and the USDA-ARS station at Newark, DE (1974-80). Between 1971 and 1982, releases included the four species previously released in the eastern U.S., namely *A. pumila, C. laricinellae, D. westwoodii*, and *D. laricinellum*, plus two other parasites from Europe, *Elachertus argissa* and *Necremnus metalarus*, and one from Japan, *Dicladocerus japonicus* (Denton 1972, 1979; Ryan and Denton 1973; Ryan et al. 1975, 1977; Ryan 1979c, 1981; Otvos and Quednau 1984; Coulson et al. 1988). The following table lists the total numbers of each species released in the West from 1960-83:

Agathis pumila	42,344
Chrysocharis laricinellae	19,111
Dicladocerus westwoodii	4,610
D. japonicus	8,426
Diadegma laricinellum	11,068
Elachertus argissa	6,196
Necremnus metalarus	13,184

These totals do not include the prodigious numbers of *A. pumila* and *C. laricinellae* redistributed from initial establishment sites (Bousfield et al. 1974; Ryan et al. 1977; Valcarce and Lowe 1980; Ebel et al. 1982; Thier 1982).

Aside from the field-cage rearing to obtain adult *A. pumila* in 1964 and 1965, all releases in the West were direct releases of adults obtained through quarantine or from laboratory cultures established from those adults. The latter was possible once the difficulties of culturing larch casebearer in the laboratory had been solved by learning how to manipulate its complex larval diapause and the availability of the deciduous larch foliage (Ryan 1975, 1979a and b). Culture of the parasites and further experimentation were then relatively easy (Ryan and Yoshimoto 1975; Ryan 1980). Because many of the releases were from laboratory cultures, they could be timed appropriately. There were recoveries soon after release of all of the species except *N. metalarus*. *Elachertus argissa* was recovered 15 miles from the nearest release after at least two field generations (Pettinger and Johnsey 1979). However, only *C. laricinellae* spread and increased significantly to supplement the control value of *A. pumila* already established. *Chrysocharis laricinellae* was found at release sites, but also at other sites, suggesting an earlier establishment (Ryan et al. 1974; Ryan and Theroux 1981).

The numbers of adults released were deemed adequate for *E. argissa* and *N. metalarus* which are uniparental (Ryan 1980). However, larger numbers of *D. westwoodii, D. japonicus*, and *D. laricinellum*, may have made establishment of those species more likely. Unfortunately, laboratory cultures of those species had to be terminated when Ryan was transferred in 1983 from Corvallis to La Grande, OR.

Data were gathered for several years from the single-species vs. multiplespecies study. However, an epidemic of Douglas-fir tussock moth in the 1970s caused a change in priorities, and larch casebearer plots were neglected for several years in Washington and completely in Montana after 1974. In addition, the *Agathis*-only plot in Oregon was sprayed in 1974 with DDT to control Douglas-fir tussock moth and the population of *A. pumila* established there disappeared. Plots in Idaho were studied by Denton (1972-73) and R.F. Schmitz (INT) (1974-76) until Schmitz transferred out of the region in 1976. Several Idaho plots were studied for several more years by G.E. Long (Washington State University) and his students (Ismail 1981; Ismail and Long 1982; Long 1988, 1990; Ramsay and Long 1988). However, the original study design was abandoned. In Oregon, parasite evaluation continues to be a major focus, both in the original and in additional plots, but by using "before and after" and life-table methods (Ryan 1983, 1985a, b, and c, 1986, 1988, 1990; Ryan et al. 1987, 1989). Population dynamics and modeling research has been a large part of the larch casebearer research elsewhere as well (Brown and Kulhavy 1978a and b; Long 1988, 1990).

Evaluation of the Oregon population published to date (1993) spans 18 years. The emphasis on evaluation of biological control of the larch casebearer represents a significant departure from some past biological control efforts in which evaluation was neglected. Populations of the larch casebearer are now (1993) much below what they were in the 1960s and 1970s, indicating successful biological control. In the years before casebearer populations decreased, feeding damage caused tree-growth losses in the western states estimated to equal a stumpage value of $3 million per year. With the reduced populations normal tree growth has returned (Ryan et al. 1989). Detailed analysis of life-table data from the Blue Mountains of Oregon identified the introduced parasite, *A. pumila*, as the key factor associated with the reduced populations there (Ryan 1990). In Montana and Idaho, where *C. laricinellae* appears to be much more important than in Oregon (Tunnock and Ryan 1985), the situation may have been somewhat different. However, no life-table work was conducted there.

Research on the larch casebearer has furnished at least one valuable spin-off result. *Chrysocharis laricinellae*, although introduced for control of larch casebearer, parasitizes some other casebearer species as well. It became a key factor in the population dynamics of the pistol casebearer (LeRoux

et al. 1963; LeRoux 1971; Paradis and LeRoux 1971). Overall, the larch casebearer stands as one of the most successful and one of the most well-documented cases of biological control.

9. Larch sawfly, *Pristiphora erichsonii* (Hartig) (Hymenoptera: Tenthredinidae). By Mary Ellen Dix

The larch sawfly, one of the most serious pest of larch in North America, is native to Europe and Asia (Ives 1976). This sawfly has few native enemies in North America and most of these are not effective at managing sawfly damage. In 1910, an ichneumonid parasite from England, *Mesoleius tenthredinis*, was successfully introduced and established in Manitoba and Minnesota (Hewitt 1912). This parasite develops internally in the sawfly larvae and prepupae. In 1944, sawflies resistant to *M. tenthredinis* were discovered in Manitoba (Muldrew 1953; Lejeune and Hildahl 1954). The same apparent "resistance" and low parasitism rate was observed in larch sawfly from northern Minnesota during 1947 to 1949. In 1952, A.T. Drooz found sawfly cocoons from Minnesota containing encapsulated eggs of the parasite (Drooz 1953). Between 1957 and 1973, Drooz documented the change in the distribution of resistant and susceptible sawflies in Minnesota, Wisconsin, Michigan, Illinois, Maine, Maryland, New York and Pennsylvania (Drooz 1957, 1975).

During the early 1970s, a second ichneumonid parasite from Europe, *Olesicampe benefactor*, was released in Minnesota and Canada (Kulman et al. 1974). *Oleisicampe benefactor* was known to be effective in suppressing larch sawfly populations in Europe (Turnock and Muldrew 1971; Kulman et al. 1974). In April 1975, approximately 2,000 parasitized cocoons were shipped from Minnesota to North Carolina. The wasps were allowed to emerge and mate before they were released in Pennsylvania to control a severe larch sawfly outbreak. *Oleiscampe benefactor* parasitized 5% of the sawflies after four years; parasitism doubled annually for the next three years and reached 59% by the eighth year after release (Drooz et al. 1985b).

10. Spruce budworm, *Choristoneura fumiferana* (Clemens), and western spruce budworm, *C. occidentalis* Freeman (Lepidoptera: Tortricidae). By Mary Ellen Dix and Leah S. Bauer

Several species of budworms (*Choristoneura* spp.) are native to North America and over centuries have periodically caused extensive defoliation in spruce-fir and pine forests (Baskeville 1975; Harvey 1985). Two species, the spruce budworm (SBW; often called "eastern spruce budworm") and western spruce budworm (WSBW), are of major economic importance in both the U.S. and Canada (Blais 1985; Harvey 1985; Shepherd 1985). Research on the biological control of budworms was conducted by both federal and university scientists and can generally be divided into three phases: pre-CANUSA, CANUSA, and post-CANUSA.

Pre-CANUSA. The pre-CANUSA (1943-1976) era of budworm biological control research emphasized identification of natural control agents, documentation of biological aspects, and microbial control trials. Before 1953, USDA Bureau of Entomology and Plant Quarantine (BEPQ) scientists identified natural enemies, determined their impacts, and documented aspects of their biologies in New York (Dowden et al. 1948; Dowden and Carolin 1950), Maine (Jaynes and Drooz 1952; Dowden et al. 1953), and Colorado (Dowden et al. 1948). George and Mitchell (1948) estimated that birds ate 3.5 to 7.0% of the SBW. Dowden et al. (1953) analyzed the stomach contents of red squirrels, and was able to demonstrate that birds ate larger quantities of budworms than do red squirrels. In a Michigan survey, Mattson et al. (1968) and Mattson (1974) also demonstrated that birds were more important predators than mammals in regulating budworm populations. Several of the scientists who worked for BEPQ in Maine, New York, and Colorado later joined the Forest Service and formed the core of the spruce budworms research effort.

During the pre-CANUSA period, budworms also severely defoliated Canadian forests. Consequently, most Canadian biological control research also focused on identification of parasites, parasitoids (parasites that kill their hosts), predators, and microbial pathogens, and related studies on the biologies, life cycles, alternate hosts, and impacts of these natural enemies (McKnight 1968). During the 1960s, the focus of Forest Service biological control research shifted toward the use of microbials, and away from other natural controls. Canadian research continued to focus on parasites and predators.

McKnight (1971) studied WSBW outbreaks in the central and southern Rocky Mountains and reported that natural controls appeared to regulate most WSBW populations. Insect parasites of the WSBW were identified and their abundance and distribution determined for Colorado (McKnight 1974), Montana (Williams et al. 1969), and Oregon (Carolin and Coulter 1959). Carolin and Coulter (1959) also evaluated the impact of parasitism and hyperparasitism on WSBW outbreaks. Entomologists in the Pacific Northwest Experiment Station (PNW) used the greater wax moth as a host for intensive laboratory studies of *Ephialtes* (as *Apechthis) ontario* and *Itoplectis quadricingulata*, two solitary ichneumonid pupal parasites of WSBW and hemlock looper. These studies determined that photoperiod affected parasite diapause, higher host densities were more favorable to parasite abundance, and that a silken cocoon increased parasite larval survival (USDA, Forest Service 1968).

CANUSA. The Canada-United States Spruce Budworms Research and Development Program (CANUSA) was formed in 1977, when Robert Berglund (U.S. Secretary of Agriculture) and Romeo LeBlanc (Minister of Environment Canada) signed a six- year expanded and accelerated research and development effort. The broad objective of the cooperative agreement was to design and evaluate tactics and strategies for not only controlling spruce budworms, but also managing budworm-infested forests in an economically and environmentally acceptable manner (Grimble and Lewis 1985; Winget 1985). This agreement expanded research on microbial control of spruce budworms and increased research efforts on parasites. Melvin E. McKnight was the Program Leader for the U.S. The Forest Service program was coordinated by an Eastern Region Program Manager, Dan M. Schmitt at Broomall, PA, and a series of Western Region Program Managers at Portland, OR (Max W. McFadden, Ronald Stark, and James Colbert) (Buckner and McKnight 1985). Although much of CANUSA research focused on the development and demonstration of management techniques including pesticides, considerable research was also conducted on natural enemies of both SBW and WSBW. In the Northeast, D.T. Jennings, an entomologist, and H.S. Crawford, a wildlife biologist, organized SBW natural enemy research for the Northeastern Forest Experiment Station (NE), Orono, ME. In the Pacific Northwest, T.R. Torgersen and R.R. Mason, entomologists at the PNW station at LaGrande, OR, led research on the WSBW. Because much of this research continued after CANUSA, the discussion is summarized in separate sections below on parasite, predator, and pathogen research.

One goal of CANUSA was to catalogue all available information on spruce budworms including their natural enemies. Literature was compiled and a bibliography and several supplements were published (Jennings et al. 1979, 1981, 1982; McKnight et al. 1988). These bibliographies included publications on biological control research on SBW and WSBW throughout North America. The University of Maine and the Canadian Forest Service at Fredericton, New Brunswick, are continuing these efforts (White 1992). In September 1984, at the end of CANUSA, a CANUSA Budworms Research Symposium was held in Bangor, ME. The symposium brought together all budworm researchers and produced a summary publication describing their research advances (Sanders et al. 1985). Also, a comprehensive summary of available information on all predators and potential predators of each stage of SBW was published (Jennings and Crawford 1985).

Post-CANUSA. Although special funding for budworm research ceased after 1983, research on predators and pathogens continued in the Northeast and Pacific Northwest. Jennings and Crawford continued to lead research efforts on SBW in the Northeast, while Torgersen, Mason, and R.W. Campbell worked on the WSBW in the Northwest. In the northeast, long-term research goals were directed toward development of techniques for the conservation and enhancement of key natural enemies (Jennings et al. 1984, 1986, 1990a and b, 1991). These included studies on the roles of birds, ants, trap-nesting wasps, phalangids, small mammals, parasitic and predaceous mites, and spiders in the population dynamics of the SBW to develop effective techniques for manipulating predator populations (Crawford 1985; Crawford and Jennings 1985, 1986; Houseweart et al. 1980; Jennings and Crawford 1983, 1985, 1989; Jennings and Houseweart 1978; Jennings et al. 1984, 1986, 1990a and b, 1991). Other researchers in the PNW designed studies to develop more effective pathogens and delivery systems. In 1988, funding for research on arthropod predators of SBW ceased at Orono, ME, and Jennings was transferred to Morgantown, WV, to work on gypsy moth predators.

In the late 1980s and early 1990s, Campbell synthesized research results from studies on SBW and WSBW, and developed a comprehensive model of budworm population dynamics. The role of natural enemies, especially avian and ant predators, was discussed in his compendium (Campbell 1993).

Parasite research. The chalcidoid *Trichogramma minutum* parasitizes eggs of both SBW and WSBW shortly after the eggs are laid on the host tree foliage in early summer. Generally, less than 15% of the eggs are parasitized, and hence this species has not been considered an important factor in regulating budworm populations (Miller 1953, 1963; McGugan and Blais 1959; Neilson 1963; Thomas 1966). However, some scientists believe that *Trichogramma* spp. have good potential as augmentative biological control agents and have inundated agroecosystems with species of this egg parasitic genus (DeBach and Hagen 1964; Ridgway et al. 1981). Researchers have successfully released *Trichogramma* spp. in Canada. Papers that describe these releases can be found in the White (1992) supplement to the SBW bibliography.

In Maine and Canada, both U.S. and Canadian Forest Service scientists and their cooperators collected data needed to develop a mass-release program for *T. minutum*. This parasite was mass-reared on eggs of Angoumois grain moth. Parasites emerging from grain moth eggs were found to be smaller than those reared from SBW eggs (either laboratory- or field-reared). The size difference rapidly reversed when the parasites were subsequently reared on SBW eggs (Southard et al. 1982). However, mean daily production of the parasite on the grain moth was higher than on SBW (Houseweart et al. 1983), and the parasite also developed faster in grain moth than on SBW eggs. Because of the parasite's short development time, parasite progeny could be released early in the SBW's oviposition period (Lawrence et al. 1985). Houseweart et al. (1982) evaluated the acceptability and availability of SBW eggs to the parasites and found that female *T. minutum* preferred SBW eggs that were one to three days old. Jennings and Houseweart (1983) found that the parasite preferred budworm egg masses that were already parasitized by *T. minutum*.

Between 1977 and 1981, Houseweart et al. (1984) conducted a series of field releases of *T. minutum* in Maine. The commercially-reared California strain of *T. minutum* was released in 1977. However, this commercial strain was not as successful a control agent as Maine-reared *T. minutum* that were released in 1978, 1979 and 1981. Broadcast and multiple releases from the ground in 1979 were slightly more effective than the four-point releases in 1978. Three closely- timed aerial releases of *T. minutum* in 1981 were the most effective releases; however, none were successful in regulating epidemic populations of the SBW (Houseweart et al. 1984).

The ichneumonid *Glypta fumiferanae*, an important larval endoparasite of WSBW, diapauses in overwintering second-instar host larvae. Shon and Shea (1976) successfully reared one generation of

non-diapausing male progeny on non-diapausing hosts. Rappaport and Page (1985) developed a technique for rearing *G. fumiferanae* on five successive generations of non-diapausing WSBW in the laboratory.

In order to determine the effects of insecticides on budworm parasites, Schmid (1981) evaluated the distribution of the parasites within the tree. He found that parasitism did not differ among sides of the tree or crown levels of the host. Thus, sampling at levels or sides of the tree could be used to estimate total parasitism. Total percentage parasitism for most parasite species changed insignificantly during the two years following insecticide application, but percentages for each species varied with site and year.

The CANUSA Spruce Budworms program also supported research on the role of parasites in WSBW population dynamics in the western U.S. and Canada. Torgersen et al (1984b) examined the relationships of parasitism to variation in budworm survival rates over a range of population densities in widely scattered areas. They found that parasitism contributed little to the variation in survival rates from fourth-instar larvae to adults or within generations. Parasites were slow to respond to increases in available hosts. They concluded that parasitization played a smaller role in budworm population dynamics than previously suspected (Campbell and Torgersen 1983a; Torgersen, et al. 1984b).

Predator research in the Northeast. In 1976, Crawford, Jennings and cooperators initiated a series of studies to identify vertebrate predators of SBW and determine their distribution and impact on SBW populations in the Northeast (Crawford and Jennings 1985). A literature review and annotated bibliography on relationships between birds and SBW, and a summary of available information on predators of each SBW life stage were published (Crawford and Jennings 1982; Jennings and Crawford 1985).

Jennings, Crawford, and cooperators identified birds commonly found in SBW outbreaks and determined their diet through visual observation and gut analyses. For example, they observed pine siskins consuming SBW egg masses (Jennings and Crawford 1983) and calculated that birds ate 2.4% of large SBW larvae and pupae in Maine and New Hampshire (Crawford et al. 1983). Crawford and Titterington (1979) found that forest stands composed primarily of balsam fir had an impoverished avifauna and that mixed stands of spruce and fir supported increased bird populations. Furthermore, abundance of canopy-frequenting warblers and golden-crowned kinglets varied with changes in composition of the spruce-fir stand (Crawford and Titterington 1979; Titterington et al. 1979). Unmanaged even-age fir stands of pole or small sawlog size balsam fir were found to be poor bird habitat and were usually more susceptible to SBW infestation and damage than non-homogeneous stands. Conversely, management of uneven-age stands enhanced habitat for birds that prey on SBW (Crawford and Jennings 1986). Based on these results, silvicultural practices were recommended for increasing avian populations of budworm predators by manipulating tree species and stand diversity (Crawford and Titterington 1979; Titterington et al. 1979).

During the 1980s, research efforts continued to target the role of birds in regulating SBW populations. The bird species that preyed on SBW in sparse, transitional and outbreak SBW populations were evaluated (Crawford and Jennings 1985), and the hypothesis that birds may restrict expansion of low-density SBW populations was examined (Crawford and Jennings 1989). However, Campbell (1985) found that birds had little or no effect on sparse SBW populations in New York. Crawford et al. (1990) suggested that early increases in SBW populations could be detected by the number of SBW larvae in the stomach contents of red-breasted nuthatches.

During the bird studies, the digestive tracts of red squirrels were also examined; it was found that less than 6.7% of the squirrels ate budworms indicating that squirrels were minor predators of SBW (Jennings and Crawford 1989).

Spiders, ants, phalangids (Opiliones), eumenine wasps, mites, carabids, and other invertebrates that prey on SBW also may play a role in regulating the SBW populations. However, in the mid-1970s, the identity of the predaceous species, and their impact and biologies, were unknown or poorly understood. In 1976, Jennings and his CANUSA cooperators initiated a series of studies to identify invertebrate predators in the different northeastern forests, determine their distribution and densities, and assess their impacts. Visual observations of actual feeding and prey capture in webs, stomach-content analyses, and examination of provisions in trap-nesting blocks, were all used to document predation. Jennings and M.W. Houseweart (University of Maine, Orono) reported egg predation by male jumping spiders (Jennings and Houseweart 1978). Jennings and Crawford (1985) and Jennings and Collins (1987) identified web-spinning spiders that prey on SBW by visually observing prey in their webs. Web-spinners were found to be more abundant than hunting spiders on red spruce (Jennings and Collins 1987) and were the most abundant spider species caught in malaise traps deployed in the spruce-fir forests of west-central Maine (Jennings and Hilburn 1988). By 1989, Jennings and Houseweart had identified 15 species of spiders in 12 genera of six families that prey on SBW moths. Nine of those species appeared to prefer male moths to females (Jennings and Houseweart 1989); it was speculated that this sex-biased predation was due to sex-pheromone mimicry, uneven prey densities, accidental captures, moth behavior, and moth-flight activity.

Because first, second and later instar larvae of the SBW often drop to the forest floor, spiders living on the forest floor are also potential SBW predators. Jennings and cooperators used formalin to extract spiders from sublitter habitats on the forest floor. They found that most spiders were associated with one or two forest-stand types (Jennings et al. 1990b) and represented species that had been collected previously in pitfall traps deployed in spruce-fir forests (Jennings et al. 1988; Hilburn and Jennings 1988).

Jennings and Dimond (1988) described the arboreal spider fauna associated with balsam fir and spruces in Maine, compared spider-SBW densities among sampling sites, and explored possible relationships between spiders, budworms, and forest stand parameters. They found dissimilarities among sites and between foraging strategy (web-spinner, hunter) and that host tree species affected spider densities. Spider densities per m^2 of foliage area generally were greater on spruces than on balsam fir. They further hypothesized that because the percentage of particular tree species in a stand affects overall estimates of spider densities, spider densities could perhaps be managed through silvicultural manipulation of tree species composition.

Jennings et al. (1984) identified the phalangid fauna of strip-clearcut and dense spruce-fir forests infested with SBW, and determined their relative abundance among replicated forest conditions, seasonal activities, and species richness and diversity. They found significantly more phalangid individuals and species in uncut residual stands and in dense stands than in clearcut strips.

Jennings et al. (1986) identified ant species associated with strip-clearcut and dense forests of northern Maine, and found that the ants were not more or less abundant in any particular forest type, and that ant species density varied between years and sites.

Jennings and cooperators at the University of Maine identified the solitary trap-nesting vespid wasps of the subfamily Eumeninae that provisioned nesting blocks with SBW in strip-clearcut and dense spruce-fir forests of northern Maine (Jennings and Houseweart 1984; Collins and Jennings 1987a and b). The preferred nest height of the wasps was also determined. Among provisioned lepidopteran prey, SBW accounted for 3 to 94% of the stocked larvae, with SBW stocking levels in the nests

apparently dependent on local SBW abundance (Jennings and Houseweart 1984; Collins and Jennings 1987a). Some eumenine predators from the western U.S. were released in Maine in 1983 (Coulson 1994).

Mites are both predators and parasites of SBW in northeastern spruce-fir forests (Houseweart et al. 1980; Jennings and Crawford 1985; Welbourn and Jennings 1991). Welbourn and Jennings (1991) described two new species of erythraeid mites. Houseweart et al. (1980) found mites on up to 28% of the male moths collected in pheromone traps and on similar percentages of free-flying moths, and concluded that parasitism by mites could affect moth flight behavior.

Many species of carabid beetles are known to prey on arthropods, and many carabid species were common in northeastern spruce-fir forests. Krall and Simmons (1978) identified nine species preying on SBW larvae by tagging the SBW larvae with phosphorus-32 and tracing the radioisotope to the carabid predators; the carabid *Pterostichus adstrictus* accounted for most of the predation in Maine. Reeves et al. (1983) used barrier-pitfall traps and tree bands to identify carabid beetles in forests of northern New Hampshire.

Predator research in the West. In 1979, Torgersen, Mason and Campbell initiated a series of studies on the population dynamics of the WSBW. During the next 12 years, they used artificial stocking techniques, specialized prey-census methods, selective enclosures, and sticky barriers to identify and quantify bird and ant predation on WSBW (Torgersen et al. 1990). They found that predators killed about 95% of the WSBW (Campbell and Torgersen 1982) and that birds and foliage-foraging ants were the dominant predators of WSBW larvae and pupae in the northwestern U.S. Youngs and Campbell (1984) identified ten species of ants that prey on WSBW. Information on the identity and distribution of ants preying on WSBW in Oregon and western Montana was published (Youngs and Campbell 1984; Youngs 1985). Two species, the western thatching ant and a *Camponotus* species, were found on one-third of the trees surveyed. Shattuck (1985) developed an illustrated key to ants associated with the WSBW, which enabled pest managers to identify the common species. Based on results obtained from enclosures and traps that excluded birds (single branch exclusion cages, entire tree cages, and sticky traps), ants were the most important predator of WSBW (Campbell and Torgersen 1982). Torgersen and Campbell (1982) also used single branch enclosures to determine effects of avian predators on WSBW, and found densities of WSBW influenced levels of bird predation. Garton et al. (1985) demonstrated that forest birds consume large numbers of WSBW, and concluded that manipulating the ecosystem to increase bird diversity could be an economical method to manage WSBW.

In Montana, Carlson et al. (1984) found that infested young Douglas-fir and western larch trees had higher WSBW densities if they were protected from birds and ants during the fourth larval instar through the pupal stage of the pest. Campbell et al. (1984) found that both birds and ants reduced WSBW populations on western larch seedlings, while ants appeared to be more important on Douglas-fir seedlings. At high budworm densities, neither ants nor birds significantly reduced WSBW densities, from larvae to adults. However, at low host densities, ants alone caused about a five-fold reduction in WSBW survival, when compared to high host densities. Birds alone permitted about 8% survival of WSBW, causing about a six-fold reduction in survival, compared to WSBW survival at high densities. They concluded that ants were the more important predator (Torgersen 1985a).

Campbell and Torgersen (1983b) found that birds and ants appeared to partition the crown strata. Ants were more effective at the lower levels, while birds were effective throughout the crown. Because both bird and ant populations were influenced by availability of standing and dead wood, they recommended the retention of snags to provide habitat for ant and bird populations. Current (1993) research at the PNW Station addresses the role of standing and downed dead-wood as colony

substrate for foliage-foraging ant predators of WSBW. A related study in northeastern Oregon is assessing predation of these ants by pileated woodpeckers. A long-term study is aimed at identifying and quantifying arboreal spiders that prey on WSBW, determining spider density and diversity in different forest environments, and assessing how their effectiveness as natural enemies is affected by forest management practices.

During a 1983 WSBW-suppression project, Murphy (1985) examined the effects of aerial application of carbaryl on predaceous ants. He found that ant populations were suppressed with carbaryl use, which was potentially detrimental to overall WSBW management.

Pathogens. The bacterium *Bacillus thuringiensis* (Bt) was originally isolated from silkworms in 1901 (Cunningham 1985). In 1960, the first large-scale field tests of commercially-produced Bt were conducted against SBW outbreaks in New Brunswick, Canada (Mott et al. 1961). R.E. Denton (Intermountain Station [INT], Ogden, UT) showed that Bt was toxic to WSBW larvae in the field and laboratory, when sufficient amount of toxin was ingested (Denton 1960). In 1963, W.H. Klein (INT, Ogden, UT) and F.B. Lewis (NE, New Haven, CT) applied a new formulation of Bt with a helicopter to a SBW infestation in balsam fir-spruce stands of northern Maine. They found that Bt was not as effective as conventional pesticides in reducing SBW populations (Klein and Lewis 1966).

During the 1960s and 1970s, Bt formulations and application technology steadily improved. Between 1968 and 1980, Bt was used in operational spray projects in the Northeast, especially in Maine (Trial 1985). In 1978, the first guidelines were formulated for operational use of Bt (Morris 1980). Although Bt suppressed SBW populations, field tests and projects often had inconsistent results and were thus inconclusive. In 1972, 1973, and 1974, the effectiveness of Bt in reducing SBW populations was evaluated in northern Maine by J.B. Dimond (University of Maine). The results of the aerial application of Bt alone, combined with other insecticides, and combined with a chitinase additive were all inconclusive (Dimond 1975).

In 1975, a State and Private Forestry pilot test in western Montana evaluated impacts of aerially-applied Bt on WSBW populations, foliage damage levels in the year of treatment and the following year, and impacts on parasite abundance. M.D. McGregor and colleagues (State and Private Forestry, Northern Region, Missoula, MT) reported significant reductions in WSBW larvae, but with minimal foliage protection and disruption of parasite populations; they suggested that Bt did not impact the parasites directly but disrupted their life cycle in the host (McGregor et al. 1976). Thompson et al. (1977) reported that immatures of the WSBW parasites *Glypta fumiferanae* and *Apanteles fumiferanae* can obtain a lethal dose of Bt from infected WSBW.

In 1980, CANUSA sponsored a field test to determine the efficacy of two aerially-applied commercially-available Bt (HD-1) formulations in northern Wisconsin, New Hampshire and Maine. SBW populations and defoliation were successfully reduced in Wisconsin using Bt (Reardon et al. 1982). In 1981, R.C. Reardon (Pacific Southwest Station [PSW], Davis, CA) and K. Haissig (Wisconsin Department of Natural Resources, Rhinelander) observed lower SBW densities and less defoliation of balsam fir in treated plots in Wisconsin, even though the Bt did not persist (Reardon and Haissig 1983). Dimond (1985a) reported negative results in Maine. Another 1981 study in Wisconsin also obtained baseline data on Bt persistence at different dosages following ground applications with a mist blower. SBW were killed for up to 16 days post-spray and viable spores were collected on white spruce for up to a year post-spray (Reardon and Haissig 1984). In the mid-1980s, a cooperative study by State and Private Forestry (Northeastern Area, Durham, NH) and the Passamaquoddy Indian Tribe successfully reduced SBW populations on the Passamaquoddy reservation in Maine (McCreery and Francis 1984; McCreery et al. 1985).

Pilot tests in northern New Mexico (1981-82) and central Montana (1981) demonstrated that Bt can reduce WSBW populations and damage levels (Ragenovich 1983; Stipe et al. 1983). In 1985, Bt successfully reduced WSBW in Carson National Forest in New Mexico (Rogers 1992).

In 1984, field efficacy and persistence of the HD-1 Bt strain was compared to a new NRD-12 strain in Oregon (Beckwith and Stelzer 1987; Stelzer and Beckwith 1988). The NRD-12 strain is serologically similar to the HD-1 strain, but killed gypsy moth larvae faster than the HD-1 strain (Dubois 1985a and b; Stelzer and Beckwith 1988). Aerial application of both strains successfully reduced WSBW populations, with similar efficacy. The 30 billion International Units (BIU) in spray volume of 7.1 liters/hectare rate was more effective than a 20 BIU rate (Stelzer and Beckwith 1988).

Studies at the Univerity of Massachusetts involved screening of 402 strains of more than 18 Bt varieties. The investigators found a strong correlation between enhanced lethality to SBW and chitinase titre within the serovar; strains grown with chitinase produced a faster kill rate (Gunner et al. 1985).

Niwa et al. (1987) evaluated interactions of Bt with parasites in the field tests and found no differences in parasitism and species distribution between control and treatment plots. Although they found Bt in three parasite species, they concluded that Bt was not detrimental to the associated parasite complex (Niwa et al. 1987).

By 1985, Bt had changed from a little-used, expensive material of questionable reliability to one that could compete favorably with chemical insecticides. This was due in part to the identification of more potent strains as well as CANUSA and gypsy moth program-sponsored research aimed at improved formulations, dosage rates, and application technologies (Dimond et al. 1981; Dimond 1982, 1985a and b; Reardon et al. 1982; Walton and Lewis 1982; Morris 1982; Grimble and Morris 1983; Fast and Dimond 1984; Reardon and Haissig 1984; Gunner et al. 1985; Dubois 1985b; Beckwith and Stelzer 1987; Niwa et al. 1987; Stelzer and Beckswith 1988). Morris et al. (1984) published improved guidelines for the operational use of Bt against SBW that were based on the results of CANUSA research.

The Bt Meacham Pilot Study was initiated as part of the 1988 Western Spruce Budworm Operational Suppression Project for Washington and Oregon. This study compared ultra-low-volume (ULV) aerial applications of Dipel™ and Thuricide™ formulations with untreated controls (Torgersen et al. 1994). Mason et al. (1989) published a model using linear regressions for estimating mid-crown densities of WSBW using lower-crown samples. Entomologists of the PNW station at LaGrande, OR, assessed the relationship between late-instar WSBW larval abundance in the lower-crown and mid-crown of Bt-treated trees. They found no difference in WSBW densities between crown levels over time and concluded that lower-crown sampling was quick, inexpensive and accurate (Torgersen et al. 1994). Workers at the NE station at Morgantown, WV, are currently (1993) developing a model for converting lower-crown samples to mid-crown densities in natural populations of WSBW.

Research also is continuing on the long-term impacts of Bt on the WSBW population dynamics and the ULV Bt Meacham Pilot Study. In addition, effects of Bt on non-target Lepidoptera, food for the Townsend's long-eared bat, are being characterized in Oregon (unpublished internal Forest Service Report). With the development of plant biotechnology and molecular biology, researchers have transfered Bt δ-endotoxin genes into Douglas-fir. Tree tissue was then bioassayed for toxicity in SBW (Beckwith et al. 1988). Plant genetic engineering may be a useful tool in the development of pest-resistant transgenic trees.

Much of the developmental virus research on SBW was conducted in Canada and later applied in the U.S. Nuclear polyhedrosis (NPV) and granulosis (GV) viruses of the SBW were first reported in

Canada by Bergold (1950) and Bird and Whalen (1954), respectively. Field tests of the NPV and GV produced mortality in both 1959 and 1960 (Stairs and Bird 1962). Cunningham et al. (1972) developed a method for mass-producing two viruses of SBW in Canada and a number of Canadian researchers developed the technology for producing and applying viruses (Cunningham 1985). Aerial applications of both viruses against SBW in eastern Canada have occurred since 1971 (Cunningham et al. 1980; Cunningham et al. 1983a and b). However, in the West, the distribution of natural epizootics of NPV and GV in WSBW are limited to a few isolated patches and have been rarely reported in outbreak populations. Researchers at the PNW stations at Corvallis and Portland, OR, found that NPV and GV applied on grand fir reduced WSBW larval populations to acceptable levels by protecting 35% of the new foliage (Stelzer and Scott 1985).

Alternate hosts that are easy to study in the laboratory were needed to evaluate viruses. Stairs et al. (1981) fed an isolate of a NPV from SBW to neonate larvae of the cabbage looper and the greater wax moth. The larvae of these species were successfully infected, demonstrating that alternate hosts could be used to study the virus.

Microsporida are obligate intracellular protozoans, the causal agents of ubiquitous and somewhat chronic disease of insect and other invertebrates. *Nosema fumiferanae* is the most common microsporidan parasite found in SBW, and in the field, the prevalence of this pathogen increases in a density-dependent manner with its host (Cunningham 1985). In 1983, Leah S. Bauer (North Central Experiment Station, East Lansing, MI) in collaboration with G.L. Nordin (University of Kentucky, Lexington) began research on the importance of this indigenous pathogen in the population dynamics of SBW. Bauer and Nordin (1988a) developed a reproducible laboratory bioassay for determining the pathogenicity (median lethal dosages and times) of *N. fumiferanae* via *per os* inoculation in fourth- and fifth-instar larvae. The sublethal responses included prolonged larval development, smaller pupae, and shortened adult longevity. They also quantified the impact of larval age, microsporidan dose, and diapause conditions on the lethal and sublethal responses of SBW to *N. fumiferanae*. In a subsequent study, Bauer and Nordin (1989a) quantified a dose-dependent reduction in fecunditiy in SBW inoculated *per os*. In addition, *N. fumiferanae* was efficiently transmitted transovarially from mother to progeny. Infected progency experienced twice the larval mortality, and survivors took longer to develop and were 25% smaller than uninfected progeny. In a separate study the nutritional physiology of larvae infected with *N. fumiferanae* was quantified in an effort to determine the mechanisms of disease (Bauer and Nordin 1988b). They found suppressed rates of food consumption, relative growth rate, and production efficiencies in SBW infected with *N. fumiferanae*. However, approximate digestibility and nitrogen utilization efficiency of food in diseased larvae were higher than in healthy larvae. Moreover, the lethal and sublethal responses of infected larvae fed on diet containing 4.5% nitrogen were significantly less that cohorts reared on 2.5% dietary nitrogen. Bauer and Nordin (1989b) also determined that larvae, transovarially-infected *N. fumiferanae*, were more susceptible to Bt than healthy larvae.

Since the completion of these studies in 1988, funding and interest in SBW population dynamics waned with the outbreak itself, particularly in the U.S. However, Canadian researchers, recognizing the repressive potential of *N. fumiferanae* on SBW populations, have established long-term studies aimed at quantifying its impact and incidence during periods of low population density (L.S. Bauer, personnel observation).

In 1980, in cooperative University of California and PSW studies at Davis, CA, the nematode *Steinernema carpocapsae* with its associated bacterium *Xenorhabdus nematophilus* was applied to WSBW in the laboratory and field; results were inconsistent, probably because of the dessication and death of most of the nematodes (Kaya et al. 1981). The following year, the researchers compared four antidessicants as additives to the nematode solution. Because larval WSBW populations were still not significantly reduced, they recommended that application of nematodes be discontinued until

more effective techniques were developed for increasing nematode survival (Kaya and Reardon 1982).

E. Sap-Sucking Insects

1. Balsam woolly adelgid, *Adelges piceae* (Ratzeburg). By Gene D. Amman

The balsam woolly adelgid was accidentally introduced into the Maritime Provinces of eastern Canada and into the northeastern U.S. from Europe about 1900, presumably on infested nursery stock (Kotinsky 1916; Balch 1952). Subsequently, the adelgid was found in central California in 1928 (Annand 1928), and severe outbreaks have occurred in Oregon and Washington since 1954 (Whiteside 1955). Infestations were first seen in the Mt. Mitchell area of North Carolina in 1955 (Kulman 1964). Movement of the adelgid to these areas also probably occurred on infested nursery stock. The balsam woolly adelgid is found principally on silver fir throughout western and central Europe, where it may be native. That host is not physiologically damaged by the adelgid, apparently because it is not sensitive to bark-infesting pests. All North American firs (*Abies* species) are susceptible to this adelgid.

The balsam woolly adelgid is a very small, completely parthenogenetic homopteran. It is confined solely to true firs, unlike most adelgids which alternate between a primary spruce host and a secondary host in the family Pinaceae. Winged forms are rare, and may not exist at all in some populations. Dispersal is primarily during the first nymphal instar, when the adelgid actively searches the host tree for a suitable feeding site. The motile nymphs are frequently picked up by winds and dispersed over long distances. The adelgid has two to four generations per year, depending upon environmental conditions, and overwinters as an early first-instar nymph, which is extremely resistant to freezing.

The use of chemical insecticides to control the adelgid over the large inaccessible areas infested by the pest was impractical. Therefore, the widespread mortality of trees prompted predator introduction programs to bring about some control. From 1957 through 1960, predators were collected in Europe and Australia by the Commonwealth Institute of Biological Control, and screened through the Canadian Department of Agriculture. Predators from Europe were also screened by ARS (USDA). In 1958, P.B.Dowden (Northeastern Forest Experiment Station [NE], New Haven, CT) searched for predators in Japan. After 1960, predator introductions from India and Pakistan were financed by the Forest Service through Public Law 480, and were screened by the ARS quarantine facility in New Jersey. The success of introductions into Canada was discussed by McGugan and Coppel (1962a).

New England. Predator introductions for control of the balsam woolly adelgid on balsam fir were under the overall direction of Dowden. David Crosby also participated in the work. The first introduction into the U.S. was unplanned, when the chamaemyid fly *Leucopis obscura* spread inadvertently into Maine, about 1937, from New Brunswick, where it had been introduced from England. Planned introductions of predators into the U.S. started in 1957 and continued through 1960 (Dowden 1962). A total of 21,390 specimens, representing four species of predators, were introduced into Maine, Vermont, New Hampshire and New York (Table 2). *Leucopis obscura* and the derodontid beetle *Laricobius erichsonii* became established (Dowden 1962). Following establishment, 3,175 *L. obscura* were collected and released at additional sites in New Hampshire, New York and Vermont. Effectiveness of the introductions was not determined. However, the continued mortality of balsam fir caused by the adelgid suggests that they were not very effective.

North Carolina. Predator introductions into North Carolina for control of the balsam woolly adelgid on Fraser fir in the Mt. Mitchell area were under the direction of G.D. Amman (Southeastern Forest Experiment Station [SE], Asheville, NC). Others involved with introductions and evaluations were

G.F. Fedde, C.F. Speers, and J.A. Witter. These introductions were started in 1959 and extended through 1966. The releases totaled 46,325 individuals of 22 species from Germany, Austria, Australia, New England (previously introduced from England), India, and Pakistan (see Table 3 for list of species) (Amman 1961; Amman and Speers 1964, 1971). Of this group, three species initially overwintered and reproduced successfully: the cecidomyiid *Aphidoletes thompsoni* and the beetles *L. erichsonii* and *Aphidecta obliterata*. However, in an extensive survey in 1968, only *Laricobius* was recovered (Fedde 1972). None of the predators from India and Pakistan were recovered following release.

Oregon and Washington. Predator introductions into Oregon and Washington to control the balsam woolly adelgid on the regions's true firs (subalpine fir, Pacific silver fir, and grand fir) were under the direction of R.G. Mitchell (Pacific Northwest Forest Experiment Station [PNW], Portland, OR). Others involved with introductions and evaluations were K.H. Wright and P.E. Buffam. Predator liberations began in 1957 and continued through 1964. During this period, 19 species totaling 61,785 specimens from seven countries were released (Table 4) (Mitchell and Wright 1967). These were only slightly more successful than those in the eastern U.S. Of this group, three species of flies (*A. thompsoni, Cremifania nigrocellulata*, and *L. obscura*) and two species of beetles (*L. erichsonii* and *Scymnus* [as *Pullus] impexus*) became established. Of the established predators, 1,562 *Laricobius* and 2,104 *Aphidoletes* were collected and recolonized in additional sites in Oregon and Washington. In addition to species released, four species from India and Pakistan were studied in the laboratory only. These were the coccinellids *Ballia dianae* and *Oenopia sauzeti*, and the neuropterans *Chrysopa (sens. lat.)* sp. and *Hemerobius* sp.

Conclusions. Failure of the predators to establish was probably related to much cooler temperatures in all infested areas in the U.S. than in India and Pakistan on the lower slopes of the Himalayas, and in Europe, where the predators were originally collected. Failure of the introduced predators to accept the host plant as an oviposition site or the balsam woolly adelgid as prey are other possible factors contributing to their non-establishment, because many of the predators were collected from conifers other than fir, and original prey were often not *Adelges* species. None, with the exception of the anthocorid bug *Tetraphleps* sp., oviposited freely on Fraser fir. Some of the imported predators may have become established on other types of vegetation where their microclimatic and nutritional needs (i.e., suitable prey) were met.

The established predators were considered ineffective, individually and as a group, in preventing tree mortality. Even in areas where the predators were well established, adelgid populations generally increased and trees continued to die.

For all areas infested by the balsam woolly adelgid, tree killing has slowed, probably because most of the highly susceptible trees have been killed, and, in the case of Fraser fir in North Carolina, almost all overstory trees are dead. As the next generation of fir grows to maturity, the most susceptible trees may be killed by the balsam woolly adelgid, but it is expected that selection will occur for trees that are more tolerant of the adelgid. Predators are likely to play a greater role in prolonging the lives of scattered, semitolerant trees of the next generation than occurred when thousands of highly susceptible trees were infested during the first exposure to the adelgid. With time and selection of tolerant trees, the relationship between the adelgid and its hosts is expected to emulate that found in Europe and observed in a silver fir plantation in North Carolina where the adelgid causes little or no damage (Amman and Fedde 1971; Franz 1958).

2. "Cypress aphid", *Cinara cupressi* (Buckton). By Mary Ellen Dix

In 1990, Forest Pest Management (Forest Health), International Forestry's Tropical Forestry Program, the International Institute of Biological Control (IIBC) in Great Britain, the World Bank, United

Nations Development Program (UNDP), and the United Nations Food and Agricultural Organization (FAO) initiated a cooperative project with Kenya's Forestry Department to identify potential parasites and predators of *Cinara cupressi*, an aphid from Central America that is a pest of tropical cypress in East Africa. In 1986, this aphid was discovered in Malawi. By 1991, the aphid had spread to Kenya and was severely damaging cypress, an important timber producing tree.

Dan Kucera (Northeastern Area, State and Private Forestry), was assigned to coordinate Forest Service participation in the project. In 1992, Denny Ward (Southern Region R-8, Asheville, NC) began a two-year detail to FAO in Kenya to deal with the emergency situation, initiate and monitor a research program, transfer research technology, and assist in the development of a forest pest management program in the Kenya Forestry Department. At the same time, Forest Service entomologists in the Rocky Mountain, Southwestern, Pacific Southwest, and Southern Regions, and the Northeastern Area of State and Private Forestry, searched for parasites and predators of *C. subinae*, a related pest of juniper in Colorado, Arizona, California, North and South Carolina, Virginia, Pennsylvania, and the New England states. They shipped live immatures of these natural enemies to IIBC in England for initial biological screening and host preference evaluation. Presently, the Forest Service, FAO, Canada, and IIBC are assisting the Kenya Forestry Research Institute develop facilities for mass rearing the natural enemies.

3. Scales and mealybugs of pines. By Mary Ellen Dix

During the 1980s, pyrethroid insecticides replaced organophosphates as the preferred aerially- or ground-applied insecticides for control of seed and cone insects. In 1982-83, Stephen Clarke and Gary DeBarr (Southeastern Forest Experiment Station, Athens, GA), in cooperation with C. Wayne Berisford (University of Georgia, Athens) identified parasites and predators of "striped pine scale", *Toumegella pini* and "loblolly pine mealybug", *Oracella acuta* in Georgia loblolly pine seed orchards, and evaluated the impact of two commonly used pyrethroid insecticides on their abundance. Parasitism of *T. pini* was highest on unsprayed trees after the third insecticide application. Predation of female *T. pini* was lowest on trees treated with azinphosmethyl. They concluded that aerial insecticide application in seed orchards had little effect on settling female scale insects, but can result in lower resident natural enemy populations (Clarke et al. 1989, 1990).

III. BIOLOGICAL CONTROL OF FOREST PATHOGENS

A. Forest Diseases. By Ned B. Klopfenstein, E. G. Kuhlman, Carol M. Schumann, and Mary Ellen Dix

The USDA Forest Service has traditionally played a significant role in research to understand and develop biological controls for tree diseases. This area of Forest Service research has been reviewed recently (Stewart 1989). Initial studies are aimed at identifying and characterizing potential biological control agents, including antagonists, parasites, competitors, and predators of tree pathogens. It is generally believed that the vast majority of biological control agents are yet to be identified, and thus continued efforts to identify such agents are warranted. After identification, additional studies are needed to evaluate the range of activity and develop methods for effective application and maintenance of biological control agents. Continued studies also contribute to a better understanding of the complex interactions among host tree, pathogens, biological control organisms, and other biotic and abiotic components of a forest ecosystem.

Since mycorrhizal interactions and wood-rotting organisms are covered elsewhere, other Forest Service research in biological control of tree diseases can be divided into three general categories of disease which follow.

1. Biological control of root and butt rots

Organisms that are competitive, antagonistic, parasitic, or predatory to rhizosphere and wood-inhabiting fungi offer potential for biological control of root and butt rots. However, the complex dynamics of such organismal interactions can pose significant difficulties in deploying such biological control (Shaw and Roth 1978, 1980; Shaw and Kile 1991). Several studies have investigated the interactions of *Trichoderma* spp., fungal antagonists, with *Phellinus weirii* or *Armillaria* spp., the causal agents of root rots (Nelson and Thies 1984, 1985, 1986; Goldfarb et al. 1985, 1989a and b; Nelson et al. 1987, 1988; Reaves et al. 1990). Virus-like particles in isolates of *Armillaria* sp. have been observed (Reaves et al. 1987, 1988), and may have potential for controlling these pathogens. In addition, mycophagous nematodes have shown potential for controlling Armillaria root rot (Riffle 1973).

The principles of and potential for biological control of forest nursery diseases have been recently reviewed (James et al. 1993). Biological control of root disease caused by *Rhizoctonia* sp. and *Pythium* sp. has been investigated (Burdsall et al. 1980). In addition, studies were initiated at the North Central Forest Experiment Station (NCFES) laboratory in St. Paul, MN, to evaluate seed treatments with antagonistic and other beneficial organisms to control damping off and root rot of red pine and white pine caused by *Fusarium* spp. (C. Ocamb, personal communication, NCFES, 1993). Methods to assay soil for antagonistic fungi also have been developed (Li et al. 1969).

2. Biological control of stem cankers and other stem diseases

E.G. Kuhlman (Southeastern Forest Experiment Station [SE], Research Triangle Park, NC) studied the utility of hypovirulence in *Cryphonectria parasitica* for controlling chestnut blight disease on American chestnut during 1977-89. Hypovirulence apparently is caused by double stranded ribonucleic acid (dsRNA), which normally is a component of mycoviruses. Hypovirulence reduces the vigor or virulence of the fungus so that the tree resists infection and develops callus tissue rather than cankers. Kuhlman (1979, 1981b and c) verified that hypovirulent isolates can limit the spread of virulent isolates within young cankers. Conidia from hypovirulent isolates also limited spread of young cankers. A mix of conidia from four to 11 hypovirulent isolates converted 95% of a random selection of 98 virulent isolates from the eastern U.S. to the hypovirulent condition in culture (Kuhlman 1982, 1983; Kuhlman and Bhattacharyya 1984; Kuhlman et al. 1984). However, treatment with a conidial suspension from eleven hypovirulent isolates failed to enhance the survival of American chestnuts in a West Virginia field test. Apparently the endemic inoculum level and/or the diversity of virulent isolates was too great for the hypovirulent inoculum to overcome. Other studies also have investigated the ability of hypovirulent isolates to control the establishment of virulent cankers (Double 1982). As of 1993, Forest Service researchers in Delaware, OH, were attempting therapy for chestnut blight using *Pseudomonas* spp.

During 1973-80, Kuhlman conducted a study of hyperparasitic microbes associated with *Cronartium quercuum* f. sp. *fusiforme* to determine their potential as biological control agents for fusiform rust disease. The hyperparasite *Scytalidium uredinicola* was discovered and described (Kuhlman et al. 1976); it was quite effective at reducing aeciospore numbers in some areas of a gall, although its effect was limited to one year on any localized area (Kuhlman 1981a). Other workers have investigated potential biological control and interactions of Cronartium rusts with hyperparasitic fungi such as *Tuberculina* spp. (Mielke 1933; Hubert 1935a and b; Wicker 1970, 1980, 1981; Wicker and Wells 1968, 1970). *Tuberculina maxima* demonstrated a long-term effect on aecial sporulation, but its occurrence was limited to more northerly areas where rust incidence was lowest (Kuhlman and Miller 1976). *Sphaerellopsis filum* (as *Darluca filum*) reduced the production of basidiospores by *C. q. fusiforme* on oak, but the effectiveness of this hyperparasite for controlling fusiform rust

disease is limited by the short duration of the rust life cycle that occurs on oak leaves (Kuhlman and Matthews 1976; Kuhlman et al. 1978).

Other FS research on the biological control of stem diseases includes evaluation of *Arthrobacter* sp. and *Fusarium* sp. as potential biological controls of pitch canker on Virginia and slash pines at the SE laboratory at Athens, GA (Barrows-Broaddus and Dwinell 1987a and b), and of suppressive strains of *Streptomyces* for control of the poplar leaf spot and canker pathogen *Septoria musiva* (=*Mycosphaerella populorum*) at the NCFES laboratory at St. Paul, MN (Ostry and Anderson, 1992).

3. Biological control of vascular wilts

Studies conducted by the FS on the biological control of vascular wilts have been ongoing since Shigo (1958) initiated a search for potential biological control agents associated with trees infected with *Ceratocystis fagacearum*. Subsequent studies have focused on the colonization of oak trees by endophytic *Bacillus* spp. and *Pseudomonas* spp. as potential controls for oak wilt (Brooks et al., 1988a and b; Brooks 1989; Gehring 1990; Gehring et al. 1990).

Additional research on control of oak wilt was begun at the FS laboratory in St. Paul, MN, investigating the colonization of oak trees with alternative *Ophiostoma* sp. to suppress sporulation and overland transmission of oak wilt pathogens (J. Juzwick, NCFES, St. Paul, MN, personal communication, 1993). *Streptomyces* spp. also have been assessed for their ability to control Dutch elm disease (O'Brien et al. 1984). Additionally, Forest Service researchers at Delaware, OH, initiated a program to identify bacterial and fungal endophytes of American elm that are antagonistic to the Dutch elm disease pathogen, *Ophiostoma* sp. Schreiber et al. (1988) isolated *Bacillus subtilis* FS94 from American elm xylem which produced novel antibiotics *in vitro* (Chang and Eshita 1988), but the isolate failed to protect elms in subsequent studies. Eshita and Roberto (1991) isolated a nonfluorescent *Pseudomonas gladioli*, LC_g, from American elm. This bacterium exhibited both antagonism and antibiosis *in vitro*, but failed to protect elms in greenhouse trials. The interaction of xylem-colonizing *Bacillus* spp. with Verticillium wilt of maples has also been investigated (Hall et al. 1986).

4. Role of host tree resistance to diseases in biological control

Although not classically considered a form of biological control, the genetic constitution of host trees can have an important impact on the incidence of disease and the effectiveness of other forms of biological control. Identification of disease-resistant seed sources and development of improved populations through selection and breeding have been important outcomes of Forest Service tree improvement programs. Reviewing those activities is beyond the scope of this historical perspective, but it is important to consider possible mechanisms of genetic resistance in any discussion of biological control. For example, partial resistance to pathogens conferred by elevated levels of phytoalexins might also confer "resistance" to hypovirulent strains, non-pathogenic epiphytes, or symbionts. Similarly, resistance conferred by introducing a gene with antimicrobial activity (such as chitinases, gluconases, or cecropins) can be expected to have an impact on microflora associated with that host. Alternatively, more specific types of resistance can be engineered that affect only the target pest (e.g., coat-protein mediated viral resistance).

Modifying host resistance through genetic manipulation can be an important tool in designing and improving the effectiveness of biological controls. However, the underlying mechanism of resistance must be considered in the context of the control system into which it is being integrated. Because host resistance is such an important interacting factor with other forms of biological control, successful management and stabilization of pathogen populations will likely involve compatible combinations of biological control strategies that include host resistance.

5. Future trends in biological control research

Because of current environmental, economic, and societal concerns with pesticide use, it seems likely that biological control will play a more prominent role in future management of tree diseases. Research will likely continue to identify biological control agents, evaluate application methods, and monitor ecological interactions. Rapidly developing techniques in molecular biology offer promise in the identification and characterization of biological control agents. In addition, molecular technology will allow the genetic engineering of biological control agents and the transfer of anti-pathogen genes from biological control agents to host trees. However, the ecological ramifications of genetic engineering for biological control will have to be thoroughly evaluated before considering deployment.

Forest Service research has demonstrated the enormous potential to develop successful biological control strategies for woody plant diseases. Considerable biological control research has been initiated on root and butt rots, stem cankers and vascular wilts. Nevertheless, it seems likely that the vast majority of potential biological control agents and other interacting factors remain unidentified. Research is noticeably lacking on diseases caused by viruses, mycoplasma-like organisms, bacteria, and nematodes. Successful development and deployment of new biological control strategies is dependent on the continuation of long-term ecological studies that determine the interaction of biological control agents with the host tree, pathogens, beneficial organisms, and other components of the forest ecosystem.

B. Mycorrhizal Symbiosis. By Randy Molina

The word mycorrhiza literally translates as "fungus root" and defines the common association of specialized soil fungi with the fine, feeder roots of plants. Mycorrhizal associations represent one of the more widespread forms of mutualistic symbioses in terrestrial ecosystems. Indeed, the plant-fungus associates have co-evolved over the millennia such that each partner depends upon the other for survival.

The mycorrhizal fungus basically serves as an extension of the plant root system, exploring soil far beyond the roots' reach and transporting water and nutrients to the roots. The uptake of phosphorus is an especially important function of mycorrhizae, and many plants depend upon the fungi to supply adequate quantities of phosphorus for healthy growth. Other plant benefits include protection of fine roots against pathogens; increased root length and branching that enhances nutrient absorption; increased root longevity; tolerance to drought stress; detoxification of soil toxins; and resistance to heavy metals. In return, the mycorrhizal fungi receive their primary energy from the plant in the form of simple sugars produced during photosynthesis and transported to the roots.

Mycorrhizal fungi not only benefit host plants. They are also key soil organisms that participate in nutrient cycling and building of soil structure. Their great mycelial biomass in the soil and reproductive structures (mushrooms and truffles) are cornerstones in the complex food webs of terrestrial ecosystems.

The importance of mycorrhizae to the productivity of trees and forest ecosystems was recognized early by the Forest Service. Indeed, Forest Service scientists have been pioneers and leaders in mycorrhiza research, publishing over 500 papers on mycorrhizae during the last 30 years. These efforts include breakthrough discoveries on the isolation and manipulation of mycorrhizal fungi; the development and application of procedures to inoculate tree seedlings with selected beneficial fungi to improve growth in the nursery as well as survival after outplanting; the taxonomic classification of major groups of mycorrhizal fungi; the ecological and physiological diversity of mycorrhizal fungi; and the functional biodiversity of mycorrhizal fungi in forest ecosystems.

Detailing the breadth of discoveries made by Forest Service scientists in mycorrhiza research is beyond the scope of this paper. What follows are historical and regional perspectives on the major thrusts and impacts by key personnel and laboratories. Selected references are provided to lead readers to the wealth of published information.

Pioneering research. USDA research on mycorrhizae began with an extensive report by McArdle (1932) on the relation of mycorrhizae to conifer seedlings. Through field observations and laboratory and greenhouse experiments, McArdle provided new evidence on the ubiquitous occurrence and beneficial aspects of mycorrhizae to conifer seedlings.

Mycorrhiza research by E. Hacskaylo and colleagues at the Forest Physiology Laboratory, Beltsville, MD, in the 1950s mark the true pioneering studies and leadership by the Forest Service. Hacskaylo studied with the grandfather of mycorrhiza research, Elias Melin, in Uppsala, Sweden, and returned with modern techniques to study the physiology of mycorrhizal fungi in the U.S. Hacskaylo and colleagues published extensively on the physiology of ectomycorrhizal fungi, including response of fungi to temperature, light, moisture stress, and pH, and developed techniques for synthesizing dual plant-fungus cultures still in use today (Hacskaylo 1953; Hacskaylo and Palmer 1955; Hacskaylo et al. 1965). Hacskaylo is considered a world authority on the physiology of ectomycorrhizal fungi and his early review on the carbohydrate physiology of mycorrhizae is a landmark reference (Hacskaylo 1973).

Hacskaylo was also very active on the international forestry scene and organized several international workshops through the International Union of Forestry Research Organizations (IUFRO). He conducted pioneering experiments on mycorrhizal inoculation of pine seedlings destined for sites where pines did not normally exist. For example, he established pines in Puerto Rico by inoculating them with mycorrhizal fungi from native pine stands in the U.S. (Vozzo and Hacskaylo 1971). His applied efforts in Puerto Rico set the stage for large-scale mycorrhizal inoculations around the world.

Forestry Sciences Laboratory, Athens, GA. The work at Athens began with C. Bryan and B. Zak who identified, isolated and studied many ectomycorrhizal fungi of southern pines (Bryan and Zak 1961; Zak and Bryan 1963). Thus began a long history of FS leadership in the characterization of ectomycorrhizae and development of fungus culture collections for use by researchers worldwide. Zak (1964) also developed novel concepts and hypotheses on the role of mycorrhizal fungi in protecting roots against root pathogens. This line of investigation was taken up by D. Marx, who experimentally demonstrated the disease protecting attributes of several ectomycorrhizal fungi. For example, he found *Leucopaxillus cerealis* produced antibiotics antagonistic to fungal pathogens in the genera *Cylindrocladium, Phytophthora, Polyporus, Poria* (=*Antrodia*), *Pythium*, *Rhizoctonia*, and *Sclerotium* (Marx 1972, 1973). Marx (1972, 1973) later synthesized all information on this subject; these reviews became the basis for current research on the disease protection aspects of mycorrhizal fungi.

In the early 1970s, Marx and colleagues began intensive research to develop practical application schemes for inoculating nursery seedlings with selected, beneficial mycorrhizal fungi. Their efforts brought worldwide attention to mycorrhiza research in forestry and paved the way for modern approaches in application of basic mycorrhiza research (Marx 1975, 1980; Marx et al. 1984).

The mycorrhiza research program in Athens centered around the ectomycorrhizal fungus *Pisolithus tinctorius* (Pt). Pt is a common pioneering mycorrhizal fungus on trees in mine spoils. Recognizing that the extremely high soil temperature reported on mine spoils might limit fungal symbionts to a few adapted species, Marx et al. (1970) explored the temperature-growth interactions of Pt. They found that Pt formed more ectomycorrhizae with *Pinus taeda* seedlings at 34° C than at lower temperatures, and that mycelial cultures grew at temperatures as high as 40° C. Marx and Bryan

(1971) found that aseptically grown *Pinus taeda* seedlings colonized with Pt survived and grew as well at 40° C as at 24° C; by comparison, nonmycorrhizal seedlings or those colonized with the fungal symbiont *Thelephora terrestris* had lower survival and no growth at 40° C. Clearly, the heat tolerance was a major factor in allowing Pt to invade coal spoils. Marx and coworkers then surveyed strip-mined lands for the presence of Pt, and found it to be the dominant and often only ectomycorrhizal fungus of pine roots growing on coal wastes in Indiana, Pennsylvania, Ohio, West Virginia, Virginia, Kentucky, Tennessee, and Alabama, and on kaolin spoils in Georgia (Marx 1975).

These findings prompted extensive investigation of ways to inoculate and establish Pt ectomycorrhizae on roots of pine seedlings for outplanting on mine spoils. Marx and Bryan (1975) developed techniques for preparing pure culture inoculum and inoculating nursery soil with Pt. They reported excellent success in establishing Pt in nurseries with doubled growth of inoculated seedlings over noninoculated controls (Marx et al. 1976). Inoculation with Pt basidiospores also succeeded. Most importantly, Pt inoculation significantly increased survival and growth of seedlings on mine spoils (Marx and Artman 1979), even on sites with a history of repeated failures of pine plantations. Pt inoculation also increased survival and growth of southern pines on routine reforestation sites (Marx et al. 1977), and the improved growth is evident today.

The work with Pt culminated with the development of commercial procedures for the production of Pt inoculum and testing of this biological product nationwide. Approximately eight million seedlings were inoculated annually (as of 1993) in the southern U.S., using Pt from a commercial source.

The often spectacular results of the Pt mycorrhiza research program at Athens and extensive efforts by Marx and colleagues to communicate their findings brought intense interest to mycorrhiza sciences worldwide. Marx traveled regularly to developing countries, promoting and initiating practical mycorrhiza research programs. His exhaustive efforts in promoting mycorrhiza research in international forestry programs was recognized in 1991 when he was awarded the Marcus Wallenberg Prize in Sweden.

Another group at Athens, under the leadership of P. Kormanik, developed practical application schemes for inoculating hardwood trees such as sweetgum with vesicular-arbuscular mycorrhizal fungi. Kormanik et al. (1977, 1981, 1982) also contributed new discoveries on the genetic interactions of mycorrhizal fungi and tree hosts.

Mycorrhiza research continues today in Athens within a newly developed Center for Tree Root Biology. Global climate change impacts on belowground ecology, belowground carbon allocation, and microbial interactions in the rhizosphere are current areas of emphasis.

Forestry Sciences Laboratory, Corvallis, OR. Mycorrhiza research at Corvallis has focused on the ecology of mycorrhizal fungi found in the diverse forest habitats of the Pacific Northwest. During the 1950s, E. Wright studied and described various types of ectomycorrhizae found on Douglas-fir and pine species in both nursery and field settings (Wright 1963). He also examined the impacts of forest disturbance on seedling mycorrhizal development. His field investigations provided early warning signs of the fragile nature of the belowground ecosystem (Wright and Tarrant 1958). Research efforts 25 years later would confirm his early observations and expand the understanding of disturbance effects on soil fungus populations.

A center of mycorrhiza expertise developed at Corvallis during the 1960s and 1970s under the leadership of J. Trappe. In a landmark publication, Trappe (1962) developed a host-fungus index for all known or suspected ectomycorrhizal associations in the world. This work continues to be a significant database for modern research on the biodiversity of ectomycorrhizal fungi. Trappe, and later B. Zak who arrived from the Athens laboratory, isolated ectomycorrhizal fungi and confirmed

their host ranges through pure culture mycorrhizal syntheses. Zak (1973) developed a modern classification scheme for ectomycorrhizae that has served as a basis for modern approaches to characterize and identify ectomycorrhizae on wild plants. During the 1970s and 1980s, R. Molina, J. Trappe, and others conducted extensive ectomycorrhizal fungus isolation work and pure culture syntheses to document the degree of host specificity found in ectomycorrhizal associations in the Pacific Northwest (Molina and Trappe 1982). They found that many ectomycorrhizal fungi are restricted to certain host genera or families while others have broader host ranges. Their work set the stage for modern studies on host-fungus recognition and patterns of host-fungus co-evolution (Molina et al. 1993). Their ectomycorrhizal fungus culture collection is one of the largest in the world and their isolates have been used in mycorrhiza research programs worldwide.

Trappe's expertise on the taxonomy of mycorrhizal fungi provided a solid mycological foundation for later studies on mycorrhiza ecology. Trappe published numerous treatises on the taxonomy of ectomycorrhizal fungi, particularly the hypogeous (subterranean) fungi called truffles. In 1974, Gerdemann and Trappe published a landmark monograph on the Endogonaceae of the Pacific Northwest. The Endogonaceae includes all fungi that form vesicular-arbuscular mycorrhizae; the most common type of mycorrhizae in terrestrial ecosystems, this occurs on nearly all important crop plants. The great explosion of world research on vesicular-arbuscular mycorrhizae during the 1970s and 1980s can be attributed partly to this publication because it provided the first classification scheme for these widespread, critically important, yet difficult to identify fungi. The taxonomic expertise on mycorrhizal fungi at Corvallis attracted many visiting scientists to Corvallis for training and cooperative research. Trappe co-authored taxonomic descriptions of mycorrhizal fungi from habitats around the world (Trappe 1979, 1982). This tradition continues today through extensive mycological cooperation with scientists in Australia, Great Britain, Spain, Canada, Argentina, Mexico, Sweden, and several other countries.

The Corvallis team also conducted research on practical applications of mycorrhiza. Trappe (1977) published a review and conceptual paper on the selection of mycorrhizal fungi for use in forestry; many of his concepts remain the basis for selecting beneficial fungi for seedling inoculation. Molina and Trappe followed leads by Marx and colleagues in Athens to develop fungus inoculum and inoculation procedures for Pacific Northwest hosts and fungi. Molina and others published extensively on the mycorrhizal fungus *Laccaria laccata*, and their isolates have been successful in improving performance of introduced Douglas-fir plantations in Europe (e.g., Molina 1982). In the 1980s, M. Castellano joined the team and began an active mycorrhizal inoculation program using basidiospores of truffle fungi in the genus *Rhizopogon*. His efforts have proven the most successful in the Pacific Northwest and approximately 14 million seedlings are inoculated annually. He found that inoculation can improve seedling productivity in the nursery by reducing the number of cull seedlings, and improve outplanting survival on severely disturbed sites. Castellano and Molina (1989) published a section of an USDA Handbook that details modern methods of mycorrhizal inoculation in container nurseries.

Reforestation failures in stressed, cut-over sites in southwestern Oregon and northern California provided impetus not only for seedling inoculation research, but also for studying disturbance effects on populations of mycorrhizal fungi. Using techniques similar to those pioneered by Wright, Corvallis scientists documented the effects of burning and organic matter depletion on fungus populations. M. Amaranthus demonstrated the positive effects of non-commercially valuable understory trees and shrubs on the maintenance of viable fungus populations following disturbance (Amaranthus and Perry 1989). From these studies, concepts of guild formation by hosts capable of forming mycorrhizae with compatible fungi have been developed (Perry et al. 1987; Molina et al. 1993); the contribution of mycorrhizal fungi in the dynamics of forest succession have also been documented (Molina and Amaranthus 1991). Amaranthus now (1990) leads a team of scientists from

various disciplines in a 200-year-long regional study on long-term ecosystem productivity, wherein the belowground ecosystem will be thoroughly integrated into the above ground ecology.

Long before biodiversity became the buzzword it is today, mycorrhiza research at Corvallis recognized the need to explore the physiological and ecological diversity of mycorrhizal fungi. I. Ho published a series of papers on ecotypic variation of mycorrhizal fungi based on hormone and enzyme production (Ho and Trappe 1987). Application efforts emphasized the use of isolates adapted to diverse planting sites. Ecological research also emphasized the role of mycorrhizal fungi as belowground linkages in the complex forest foodweb. For example, Trappe and wildlife biologist C. Maser discovered the widespread phenomenon of mycophagy (fungus consumption) among forest mammals (Maser et al. 1978). Many small mammals eat the sporocarps of mycorrhizal fungi, especially truffle fungi; and the truffle fungi depend upon these mammals for spore dispersal. The relevance of mycorrhizal fungus sporocarps and mammal mycophagy in forest ecosystems becomes evident when one considers food chain linkages between trees, fungi, mammals and predators such as the endangered northern spotted owl.

As part of a regional effort to document biological diversity in Pacific Northwest forest ecosystems, the mycorrhiza research team at Corvallis is currently focusing on landscape level studies of fungus populations. For example, J. Smith is conducting studies on the ectomycorrhizal fungus community structure in various age classes of Douglas-fir forests. Research has been conducted on the ecology and productivity of commercially harvested, edible forest mushrooms (sporocarps of ectomycorrhizal fungi) (Molina et al. 1993). Commercial harvest of these special forest products provides millions of dollars to the Pacific Northwest economy. A primary goal of the Corvallis mycology team is to develop knowledge and tools to integrate the biology and function of belowground microbes into holistic ecosystem management schemes.

Forestry Sciences Laboratory, Moscow, ID. Mycorrhiza research in the northern Rocky Mountains has emphasized the influence of soil factors and harvest disturbance on natural ectomycorrhizal development on Douglas-fir, larch, and pine trees. The team of A. Harvey, M. Jurgensen, M. Larson (originally with USDA Forest Products Laboratory, Madison WI) and others have conducted numerous field studies on the seasonal distribution of ectomycorrhizae in natural forest communities (Harvey et al., 1978, 1980a and b, 1981, 1987). They found that ectomycorrhizal development was strongly related to organic matter content. A critical discovery was that the vast majority of ectomycorrhizae often occurred in buried wood, particularly on dry sites and during the driest times of the year. Their efforts clearly showed the importance of organic matter and wood in the functioning and maintenance of ectomycorrhizae, and thus the health of forest ecosystems. They also documented the effects of various disturbances to soil organic matter and subsequent effects on mycorrhizal development and tree vigor. They developed guidelines for maintenance of woody residue on harvested sites with the goal of maintaining the long-term productivity of the soil. Their research on interactions of mycorrhizal fungus populations with soil organic matter are regularly cited as pioneering efforts in forest soil biology.

Forest Service mycorrhiza research elsewhere. J. Riffle conducted several studies on ectomycorrhizae of pines planted in Nebraska (Riffle 1972, 1989). He was noted for his work on the interactions of root nematodes with mycorrhizae. F. Ponder published several papers on vesicular-arbuscular mycorrhizae of white ash and black walnut in Illinois (e.g., Ponder 1984). Ponder also studied the influence of grasshoppers and rabbits on dissemination of mycorrhizal fungus propagules into coal spoils (Maser et al. 1978).

The Forest Service has supported numerous cooperative studies of mycorrhizae with universities, private industry and other federal and state agencies. Forest Service scientists have also participated actively in university research programs around the country, sponsoring students, postdoctoral and

sabbatical fellows. They have organized many national and international meetings on mycorrhiza research. The leadership provided by Forest Service scientists and cooperators have advanced our understanding of the belowground ecosystem and provided management tools for maintaining forest productivity and healthy ecosystem functioning.

C. Fungi Attacking Wood Products. By Terry L. Highley

The potential of biological control to protect wood products against deterioration by microorganisms has been recognized for a long time, as indicated in a 1940 memorandum by Mae S. Chidester, Forest Products Laboratory (FPL), Madison, WI. In this memorandum, Chidester suggested that a better understanding of the combined effect of two or more wood-inhabiting fungi on wood would be beneficial in preventing or controlling the defects brought about by these organisms. She further suggested the possible use of *Trichoderma lignorum* (=*viride*) as a control for wood-decay fungi such as *Lenzites sepiaria* (=*Gloeophyllum sepiarium*). Evidently this proposal was not followed with experimental work, or at least nothing was published, as no reference was found in the literature.

The first published work by Forest Service scientists on the use of biological control of wood-attacking fungi appears to be that of Lindgren and Harvey (1952) at the FPL. In this work, they used fluoride pretreatment of southern pine pulpwood to enhance growth of *Trichoderma*. They observed reduced decay in the pulpwood treated with *Trichoderma*. But as recognized in a 1958 FPL problem analysis by R. Lindgren, and continuing to date, such biological control remains a young field requiring considerable exploratory work before any practical applications are developed.

Verrall (1966) made preliminary incursions into the field of microorganism associations when he commonly observed the ubiquitous mold *Trichoderma viride* as the first colonizer on rain-wetted wood in the Southeastern States, and proposed that competition from molds might possibly be an additional factor restricting the number of decayers on exterior woodwork. The effect of two isolates of *T. viride* on 41 isolates of *Gloeophyllum saepiarium*, *G. trabeum*, and *Daedalea berkeleyi* (=*Gloeophyllum mexicanum*) were studied on malt agar and in soil-block tests (Verrall 1966). All three basidiomycetes on malt agar either grew compatibly with *T. viride* or actually overgrew *Trichoderma*. *Trichoderma* did not prevent decay of pine by the basidiomycetes. In a number of cases, decay was greater in the presence of *Trichoderma* than in pure culture. These findings are important because the three basidiomycetes are the prevalent decayers of pine lumber on the exterior of buildings and of other pine products exposed off the ground but subject to rain wetting.

Following these rudimentary observations, biological control of wood-attacking fungi in wood products did not gain further attention by Forest Service scientists until the 1980s. Renewed interest was prompted by increasing environmental concerns which stimulated search for less hazardous wood preservation technology by scientists at the FPL.

Polyoxin D, one of a group of peptidyl pyrimidine antibiotics produced by *Streptomyces cacaoi* var. *asoensis* was studied by Johnson (1980, 1982, 1986; Johnson and Chen 1983) for control of wood-staining mold and decay fungi. This antibiotic is a highly specific inhibitor of the chitin-synthetase enzyme. Because chitin synthesis occurs only in lower life forms, its inhibition could be a target-specific approach to pest control with minimal effect on non-target organisms such as mammals, birds, etc. Wood decay by several white and brown rot fungi was reduced by a 10 ppm polyoxin mixture and prevented at 100-700 ppm, an appreciably lower threshold than that of pentachlorophenol. However, against mold and stain fungi, polyoxin was not so effective and is not a good candidate for protection of wood against these fungi (Johnson 1986). Although polyoxins are not themselves suitable wood preservatives, these studies have tentatively validated the concept of wood preservation via inhibition of fungal chitin synthesis.

Highley and Ricard (1988) studied the antagonistic ability of *Gliocladium virens* and various *Trichoderma* spp. against important white- and brown-rot fungi. *Gliocladium virens* and the *Trichoderma* spp. overgrew the decay fungi cultured on the malt-agar medium and in most cases killed them. In soil-block tests, pretreatment of southern pine blocks with *G. virens* prevented brown-rot decay but was ineffective against the white-rot fungi. Similarly, *Trichoderma* spp. generally prevented or reduced decay by the brown-rot fungi, except for *Gloeophyllum trabeum*, but also were generally ineffective against the white-rot fungi. Various concentrations of ammonium nitrate (NH_4NO_3) and glucose in a basal medium did not affect antagonism of *Trichoderma* spp. in wood blocks. *Gliocladium virens* did not confer residual fungistasis to wood blocks. In soil-block tests of wood blocks, *G. virens* arrested the growth of *Antrodia carbonica*, but not other decay fungi. This work suggests that *Gliocladium* and *Trichoderma* have potential as natural agents for biological control of wood decay.

Several studies were conducted by scientists at the FPL assessing the potential and application of commercial *Trichoderma* preparations for control of wood decay fungi. These preparations are mainly available as a wettable powder and as pellets both containing propagules of *Trichoderma* spp.: ATCC 20475 (T-75) and 20476 (T-76) (American Type Culture Collection). Both are produced in Toreboda, Sweden, by Bio Innovation AB(BINAB™). Looking into the mode of action of T-75 and T-76, Murmanis et al. (1988a and b) found that *Trichoderma* strains did not produce either water soluble antibiotics or exoenzymes in wood blocks but protected the wood against major brown-rot basidiomycetes. Abundant chlamydospore formation was observed. Murmanis et al. (l988b) showed, also on SEM microphotographs, that T-75 and T-76 spores became attached readily to hyphae of wood decay basidiomycetes. These spores germinated on the surface of the basidiomycete hyphae and broke through its wall.

In another study on mode of action by *Trichoderma* (Bruce and Highley 1991a), the interactive effects of *Trichoderma* strains, including T75 and T76, against a range of wood decay fungi was examined with particular attention given to the production of soluble metabolites by the antagonists. It was obvious from the results of this study that the modes of antagonism of *Trichoderma* spp. are most complex and, unlike the mode of action of most chemicals, may change with varying environmental conditions. This point is important and must be carefully considered in evaluation of control systems, particularly during screening tests for potential control agents.

To be a successful biological control agent against wood decay fungi in wood products, the antagonistic effect must last many years. The results of a study by Bruce and Highley (1989a, 1991b) showed that wood material removed from poles treated with a *Trichoderma*-based (T-75, T-76) biological control product can resist attack by active fungi seven years after first inoculated. This work suggests that the use of biological control using these *Trichoderma* species might well, with further research, be valuable as a prophylactic treatment to protect poles from internal decay. Most importantly the decay prevention observed in this experiment was achieved using material treated with *Trichoderma* under field conditions. This result indicates that at least some of the modes of antagonism attributed to this fungus during laboratory studies must still be active in the nutrient-limiting environment in wood pole interiors.

Wood products, such as poles, are commonly precolonized by a resident microflora, and any control agent must be able to either displace or coexist with a variety of mold organisms. With this in mind, Bruce and Highley (1989b) examined the direct influence that prior colonization of wood by typical mold residents from creosoted poles has on the biological control abilities of *Trichoderma* (T-75, T-76) against *Neolentinus lepideus*. The results of this study indicated that *Trichoderma* can protect wood from decay by *N. lepideus* even when the blocks are colonized with mold organisms prior to being treated with *Trichoderma*.

Trichoderma species examined for antagonistic effect against decay fungi have been rather selective in their antagonism in that they have not been able to control decay by the brown-rot fungus *Gloeophyllum trabeum*, and most white-rot fungi. In a search for antagonistic fungi with broader antagonism toward wood decay fungi, Highley (1989a and b) evaluated the antagonistic abilities of *Scytalidium lignicola* against several white- and brown-rot fungi. Pretreatment of Douglas-fir and southern pine blocks with *S. lignicola* prevented decay by all fungi. Blocks that were heated or treated with propylene oxide to kill the antagonist were not decay resistant. Thus, *S. lignicola* does not confer a residual fungistatic effect to wood. *Scytalidium lignicola* was able to eradicate all the decay fungi in wood except for *Postia placenta* and *Gloeophyllum trabeum*. Wood blocks treated with sterilized filtrates of *S. lignicola* were not decay resistant, and filtrates were not inhibitory to growth of the decay fungi in agar medium. The antagonistic effect, therefore, apparently does not involve toxins.

The interspecific interactions and antagonism among several *Scytalidium* isolates with various brown- and white-rot fungi was studied by Cease et.al. (1989). *Scytalidium* initially colonized the surface of the blocks and gradually overgrew the basidiomycetes. In individual wood blocks from 11 *Scytalidium*-basidiomycete paired treatment combinations, the basidiomycete was inhibited only in some locations in the wood block. These wood blocks demonstrated interspecific interactions and antagonism between the different fungi. The white-rot fungi responded to isolates of *Scytalidium* by occluding xylem cells with masses of hyphae, forming pseudosclerotial plates in the zone of initial interaction. *Scytalidium* appeared to gain access into portions of wood colonized by the basidiomycetes only after substantial decay had resulted by the wood decay fungus.

In several studies at the FPL, scientists examined the efficacy of bacteria as biological control agents against wood-decay fungi and sapwood-inhabiting fungi. The type of medium used in evaluation studies of bacterial-fungal interaction had considerable effect on interactions on agar and wood (Benko and Highley 1991a and b). In an initial decay test, a bacterial preparation prevented decay by a white- and brown-rot fungus when tested by an agar-block procedure (Benko and Highley 1990a). However, in further testing, using the soil-block method, the bacterial preparation was ineffective (Benko and Highley 1990b). Evidence that actively growing bacteria are needed for successful biological control by the bacterial treatment was provided by the failure of the autoclaved bacterial solution to protect wood from decay. This is discouraging from the standpoint of long-term protection against decay because there would probably be no residual fungistatic effect in the wood after death of the bacteria.

Bacterial preparations were found to be very effective in preventing stain and mold discoloration of various wood species in laboratory tests (Benko and Highley 1990a, 1991b). The greatest potential for use of bacteria, therefore, may be for protection against mold and stain in green logs or lumber where only temporary protection is needed.

An interesting observation was made by Croan and Highley (1991) who found that the blue stain fungus *Ceratocystis coerulescens* could be controlled by metabolic products released by several wood decay basidiomycetes. In this case, it might be possible to protect wood against discoloring fungi by treatment with fungitoxic metabolic products.

IV. BIOLOGICAL CONTROL OF WEEDS

A. Dwarf Mistletoes. By Ned B. Klopfenstein and Mary Ellen Dix

The name "mistletoe" is often applied to the 2,000 species of parasitic plants belonging to the families Loranthaceae and Viscaceae. Dwarf mistletoes (*Arceuthobium* spp.) are the most abundant mistletoes and they are widely distributed and cause serious damage to high value timber trees (Gill

and Hawksworth 1961). Most research on the biological control of mistletoes has been directed toward cataloguing the native fungi and insect associates of mistletoe and learning about their biology (Gill and Hawksworth 1961; Wicker and Shaw 1962, 1968; Hawksworth 1972; Knutson 1978; Knutson and Hutchins 1979). At least ten fungal pathogens of dwarf mistletoe have been identified on shoots or fruits. Three of these fungi, *Septogloeum gillii*, *Colletotrichum gloeosporioides*, and *Wallrothriella arceuthobii*, are common and widespread in North America. *Wallrothriella arceuthobii* occurs throughout much of Canada, the western U.S., and northern Mexico. It attacks only pistillate flowers of certain spring-flowering species and prevents maturation. *Colletotrichum gloeosporioides* occurs in the western U.S., and attacks the shoots and reduces the reproductive potential, while *S. gillii* causes shoot anthracnose in the western U.S. and Canada (Wicker 1967; Wicker and Shaw 1968; Hawksworth 1972). Although birds and mammals can also adversely affect mistletoe, there has been no attempt to catalogue these interactions. Results to date indicate that insects may be the most effective natural control of mistletoe (Hawksworth 1972).

B. Hawaiian Forests and Plantings. By Mary Ellen Dix and George P. Markin

Introduced plants have long been recognized as one of the major threats to the continued existence of unique island forest ecosystems in Hawaii. Approximately half of these plants were introduced by immigrants as fruit, flowers, and ornamentals. Most others were introduced as forage plants in an effort to improve pastures or trees for reforestation or forest improvement (Neal 1965; Smith 1985). Due to lack of natural enemies that were left behind in the original homeland, these weeds can outgrow, out reproduce, and outspread native flora of Hawaii.

The Hawaiian forest weed program is a cooperative effort between five state and federal agencies: the Hawaii Department of Land and Natural Resources, USDI National Park Service, USDA Forest Service, Hawaii Department of Agriculture, and the University of Hawaii (Markin 1989). In 1982, the first foreign explorer involved in this program was sent to South America to hunt for natural enemies of Hawaii's most serious forest weed, banana poka (Gardner and Davis 1982; Markin, 1989, 1991; Smith 1990; Markin and Yoshioka 1992; Markin et al. 1992a and b). In 1983, construction began on an insect quarantine facility in the Hawaii Volcanoes National Park on the island of Hawaii specifically devoted to biological control of forest weeds. The facility was completed in 1984 and certified by both the State of Hawaii and USDA-APHIS to contain insects for study in an escape-proof environment. The first shipment of insects arrived in 1985, and the release of the first biological control agent from this facility occurred in 1987 (Markin 1991). Because Hawaii is geographically isolated, the forest weed control program has utilized the State of Hawaii's procedures and protocols for introductions and releases of biological control agents, which differ somewhat from those for mainland U.S.

Initially, all pathogen testing was conducted in the country of pathogen origin or in a converted germ-warfare facility operated by the ARS in Frederick, MD. In 1992, the first pathogen quarantine facility specifically designed and devoted to the biological control of weeds was opened in Honolulu by the Hawaii Department of Agriculture. Pathogens of forest weeds, firetree, and blackberry were the first studied in this facility (Markin 1993).

By 1993, the forest weed program was targeting banana poka, gorse, "firetree", blackberry, "strawberry guava", and "Koster's curse". The first insect release was in 1987, only six years ago, but the natural enemy populations appear to be growing and feeding damage already is visible on two of the weed species: Koster's curse and gorse. To date, seven species of insects and one pathogen have been released; see summary of this work by Markin et al. (1992). Two species of insects and two species of pathogens were in quarantine undergoing final stages of evaluation as of 1993. Ten more species of natural enemies were in various stages of study within quarantine, and 20 more were being studied in foreign countries.

These programs, however, are far from complete. Most of the targeted weeds have only one or two agents established against them, primarily insects or pathogens that attack only the foliage. The task of introducing new natural controls for the few weeds already targeted (not to mention those not yet targeted) will require the release of additional insects and pathogens, and will take five to ten more years of research (Markin 1993) and another 20 or more years before biological control becomes effective. The present program has demonstrated that biological control of forest weeds is feasible and that the technology can be developed to implement it. Nevertheless, at least 20 additional weeds must be controlled within the next 20 to 50 years if Hawaiian forest communities are to survive (Smith 1989).

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Table 1. Predators and parasites of the mountain pine beetle in lodgepole pine (DeLeon 1934b; Amman and Cole 1983)

Order	Family	Species
PHYLUM ARTHROPODA, CLASS INSECTA		
HETEROPTERA	Anthocoridae	Several species
COLEOPTERA	Cleridae	*Enoclerus lecontei* (Wolcott)
		Enoclerus sphegeus (Fabricius)
		Thanasimus undatulus Say
	Colydidae	*Lasconotus complex* LeConte
	Cucujidae	*Cucujus clavipes* Fabricius var. *puniceus* Mannerheim
	Histeridae	*Isolomalus mancus* Casey
		Platysoma punctigerum LeConte
	Nitidulidae	*Epurea inearis* Maklin
		Glischrochilus vittatus (Say)
	Pythidae	*Pytho planus* Herbst
	Rhizophagidae	*Rhizophagus procerus* Casey
	Staphylinidae	*Nudobius* sp.
		Quedius longipennis Mannerheim
	Tenebrionidae	*Corticeus parallelus* (Melsheimer)
		Corticeus substriatus (LeConte)
	Trogossitidae	*Temnochila virescens* (Fabricius) var. *chlorodia* Mannerheim
DIPTERA	Asilidae	*Laphria gilva* (Linnaeus)
	Dolichopodidae	*Medetera aldrichii* Wheeler
	Lonchaeidae	*Lonchaea viridana* Meigen
	Xylophagidae	*Xylophagus abdominalis* Loew
HYMENOPTERA	Braconidae	*Coeloides dendroctoni* Cushman
	Eurytomidae	*Eurytoma cleri* Ashmead
	Pteromalidae	*Dinotiscus acutus* (Provancher)
		Dinotiscus burkei (Crawford)
		Dinotiscus dendroctoni (Ashmead)
		Rhopalicus pulchripennis (Crawford)
		Roptrocerus xylophagorum (Ratzeburg)

Continued

Table 1. Predators and parasites of the mountain pine beetle in lodgepole pine (DeLeon 1934b; Amman and Cole 1983)--Continued

Order	Family	Species
PHYLUM NEMATA, CLASS SECERNENTIA		
APHELENCHIDA	Aphelenchidae	*Bertsenus brachycephalus* (Thorne) Massey
		Bursaphelenchus conurus (Steiner) Goodey
		Bursaphelenchus talonus (Thorne) Goodey
		Cryptaphelenchus latus (Thorne) Ruhm
		Ektaphelenchus tenuidens (Thorne)
		Parasitaphelenchus acroposthion (Steiner) Ruhm
RHABDITIDA	Diplogasteridae	*Mikoletzkya pinicola* (Thorne) Baker
	Panagrolaimidae	*Panagrolaimus dentatus* (Thorne) Ruhm
TYLENCHIDA	Sphaerulanidae	*Sphaerulariopsis hastata* (Khan) Nickle
	Allantonematidae	*Contortylenchus reversus* (Thorne) Ruhm
PHYLUM CHORDATA, CLASS AVES		
Caprimulgiformes	Caprimulgidae	prob. *Chordeiles minor* Forster
Passeriformes	Certhiidae	*Certhia americana* Bonaparte
	Corvidae	*Nucifraga columbiana* (Wilson)
	Emberizidae	*Dendroica coronata* (Linnaeus)
	Muscicapidae	*Mydaestes townsendi* Audubon
		Turdus migratorius Linnaeus
		prob. *Sialia currucoides* (Bechstein)
	Paridae	*Parus gambeli* Ridgeway
	Sittidae	*Sitta carolinensis* Latham
		Sitta pygmaea Vigors
		prob. *Sitta canadensis* Linnaeus
	Tyrannidae	*Contopus borealis* Swainson
		Contopus sordidulus Sclater
		Empidonax sp.
Piciformes	Picidae	*Picoides pubescens* Linnaeus
		Picoides tridactylus Linnaeus
		Picoides villosus Linnaeus

Table 2. Predator liberations against *Adelges piceae* (Ratzeburg) in Northeastern United States, 1954-1959

Species	Origin	Where Liberated	Year	Number Released
Coleoptera				
Coccinellidae				
Pullus impexus (Mulsant)	Europe	VT	1955	268
Derodontidae				
Laricobius erichsonii Rosenhauer	Europe	ME	1955	16,193
		NH,VT	1959	
Diptera				
Chamaemyiidae				
Leucopis obscura Haliday	Europe	NH,NY,VT	1954-56	3,744
Cecidomyiidae				
Aphidoletes thompsoni Moehn	Europe	ME	1959	1,185
TOTAL				21,390

Table 3. Predators liberated against *Adelges piceae* (Ratzeburg) in North Carolina, 1959-1966

Species	Origin	Year	Number Released
Coleoptera			
Coccinellidae			
Aphidecta obliterata (L.)	Germany/Austria	1960, 1966	2,872
Pullus impexus (Mulsant)	Germany	1960, 1966	11,606
Scymnus pumilio (Weise)	Australia	1960	3,300
Adalia tetraspilota (Hope)	Pakistan	1961	65
Adonia variegata Goeze	India	1961	15
Ballia eucharis Mulsant	India	1961	279
Calvia sp.	India	1961	55
Harmonia breiti Mader	India/Pakistan	1961	131
Oenopia sauzeti Mulsant	India	1961	90
Derodontidae			
Laricobius erichsonii Rosenhauer	Germany	1959-1962	14,006
Diptera			
Chamaemyiidae			
Leucopis obscura Haliday	New England	1960, 1962	1,508
Leucopis prob. *griseola* (Fallén)	Germany	1961	148
Leucopis spp. (3 species)	India	1962-1964	1,646
Cecidomyiidae			
Aphidoletes thompsoni Moehn	Germany	1959	8,809
Syrphidae			
Metasyrphus sp.	Germany	1961	36
Heteroptera			
Anthocoridae			
Tetraphleps (probably 2 species)	India/Pakistan	1963-1965	782
Neuroptera			
Chrysopidae			
Chrysopa (sens. lat.) (2 species)	India	1961-1962	636
Hemerobiidae			
Hemerobius sp.	India	1961-1963	341
TOTAL			46,325

Table 4. Predators liberated against *Adelges piceae* (Ratzeburg) in Oregon and Washington, 1957-1965

Species	Origin	Where Liberated	Year	Number Released
Coleoptera				
Coccinellidae				
Adalia luteopicta Mulsant	India	OR	1960	20
A. tetraspilota (Hope)	India	OR	1959-60	89
Aphidecta obliterata (L.)	Sweden/ Germany	OR,WA	1958-63	2,217
Ballia eucharis Mulsant	Pakistan	OR	1959	85
Chilocorus kuwanae Silvestri	Japan	OR,WA	1958	135
Exochomus lituratus Gorham	Pakistan	OR	1960	43
E. uropygialus Mulsant	Pakistan	OR,WA	1959-60	4,741
Harmonia breiti Mader	India	OR	1959	10
Leis dimidiata (F.)	India	OR	1959	23
Pullus impexus Mulsant	Germany	OR	1960-62	1,342
Scymnus pumilio (Weise)	Australia	WA	1959-60	2,859
Synharmonia conglobata (L.)	India	OR,WA	1959	121
Derodontidae				
Laricobius erichsonii Rosenhauer	Czechoslovakia/ Germany	OR,WA	1958-62	12,406
Diptera				
Chamaemyiidae				
Cremifania nigrocellulata Czerny	Czechoslovakia/ Germany	OR	1958-59	1,374
Leucopis obscura Haliday	Maine (ex Europe)	OR,WA	1958-59	2,785
Leucopis sp.	Pakistan	OR	1959	15
Cecidomyiidae				
Aphidoletes thompsoni Moehn	Czechoslovakia/ Germany	OR	1957-59	33,359
Neuroptera				
Chrysopidae				
Chrysopa (sens. lat.) sp.	India	OR	1961	63
Heteroptera				
Anthocoridae				
Tetraphleps sp.	India/ Pakistan	OR,WA	1964	98
TOTAL				61,785

APPENDIX IV
ABBREVIATIONS

Compiled by S. M. Braxton

ABCL .... Australian Biological Control Laboratory (ARS)
ACE ..... United States Army Corps of Engineers
Ac*M*NPV .. *Autographa californica* (cabbage looper) multiply-occluded nuclear polyhedrosis virus
AFB ..... American foulbrood (*Bacillus larvae*)
Af*M*NPV .. *Anagrapha falcifera* (celery looper) multiply-occluded nuclear polyhedrosis virus
AFRS ..... Appalachian Fruit Research Station (ARS)
AID ..... U.S. Agency for International Development
AIPM ..... Appalachian Integrated Pest Management (FS, Forest Pest Management)
AMT ..... APHIS Management Team
ANGB .... Air National Guard Base
AP-N ..... aminopeptidase-N
APHIS .... Animal and Plant Health Inspection Service (USDA)
APL ..... Asian Parasite Laboratory (BE and ARS)
ARES ..... Agricultural Research and Education Service (USDA)
ARS ..... Agricultural Research Service (USDA)
ARSEF ... Collection of Entomopathogenic Fungal Cultures (ARS)
ASHS ..... American Society for Horticultural Science
ATCC .... American Type Culture Collection
ATP ..... adenosine triphosphate
AWRL .... Aquatic Weeds Research Laboratory, Fort Lauderdale, FL
BARC .... Beltsville Agricultural Research Center (USDA)
BARD .... Binational Agricultural Research and Development Program
BATS ..... Biological Assessment and Taxonomic Support (APHIS, PPQ)
BBEP ..... Biotechnology, Biologics and Environmental Protection (APHIS)
BBII ..... Biosystematics and Beneficial Insects Institute (ARS)
BCCC .... Biological Control Coordinating Council (USDA)
BCDC .... Biological Control Documentation Center (ARS)
BCIL ..... Biological Control of Insects Laboratory (ARS)
BCIRL .... Biological Control of Insects Research Laboratory (ARS)
BCO ..... Biological Control Operations (APHIS, PPQ)
BCWRL .. Biological Control of Weeds Research Laboratory, Albany, CA (ARS)
BE ..... Bureau of Entomology (USDA)
BEPQ ..... Bureau of Entomology and Plant Quarantine (USDA)
BIIL ..... Beneficial Insect Introduction Laboratory (ARS)
BIIR ..... Beneficial Insects Introduction Research (ARS)
BIL ..... Beneficial Insects Laboratory (ARS)
BINAB™ .. Bio Innovation AB
BIRL ..... Beneficial Insects Research Laboratory (ARS)
BIU ..... billion International Units
BPDL ..... Biocontrol of Plant Diseases Laboratory (ARS)

BPI ..... Bureau of Plant Industry (USDA)
BPISAE ... Bureau of Plant Industry, Soils, & Agricultural Engineering (USDA)
BTB ..... black turpentine beetle
Bt ..... *Bacillus thuringiensis* and *Bacillus thuringiensis thuringiensis*
Bti ..... *Bacillus thuringiensis israeliensis*
BtICP .... International Cooperative Program on the Spectrum of Activity of Bt
CANUSA . Canada/United States Spruce Budworms Program
CAP ..... Customer Advisory Panel
CBC ..... classical biological control
CES ..... Cooperative Extension Service
CFRP .... Combined Forest Pest Research and Development Program (USDA)
CGA ..... *Colletotrichum gloeosporioides* f. sp. *aeschynomene*
CIBC ..... Commonwealth Institute of Biological Control (see also International Institute of Biological Control, IIBC)
CIRAD ... Centre International de Recherche Appliqué et de Développement, France
CLB ..... cottonwood leaf beetle
cm ..... centimeter
COSEPUP Committee on Science, Engineering, and Public Policy, National Academy of Sciences
CPB ..... Colorado potato beetle
CPRU .... Cotton Pathology Research Unit (ARS)
CPV ..... cytoplasmic polyhedrosis virus
CRIS ..... Current Research Information System
CSIRO ... Commonwealth Scientific and Industrial Research Organization, Australia
CSREES .. Cooperative State Research, Education and Extension Service (USDA)
CSRS ..... Cooperative State Research Service (USDA)
DDT ..... dichloro diphenyl trichloroethane
DFTM .... Douglas-fir Tussock Moth
DNA ..... deoxyribonucleic acid
dsRNA .... double stranded ribonucleic acid
EBCL .... European Biological Control Laboratory (ARS)
ECB ..... European corn borer
ECVs ..... extracellular viruses
EDB ..... ethylene dibromide
EFB ..... European foulbrood
EGT ..... ecdysteroid glucosyl transferase
ELISA .... enzyme-linked immunosorbent assay
EMF ..... ectomycorrhizal fungi
EPA ..... Environmental Protection Agency
EPL ..... European Parasite Laboratory (BE and ARS)
ERS ..... Economic Research Service (USDA)
ES ..... Extension Service (USDA)
ESCOP ... Experiment Station Committee on Organization and Policy
ESPBRAP . Expanded Southern Pine Beetle Research and Applications Program (USDA)
EUP ..... Experimental Use Permit
FAO ..... Food and Agricultural Organization (United Nations)
FAS ..... Foreign Agricultural Service (USDA)
FBCL .... Florida Biological Control Laboratory
FBS ..... fetal bovine serum
FDA ..... Food and Drug Administration
FIDM .... Forest Insect and Disease Management (FS)
FIDR ..... Forest Insect and Disease Research (FS)

FIFRA .... Federal Insecticide, Fungicide, and Rodenticide Act
FIR ..... Division of Forest Insect Research (FS)
FP ..... few polyhedra (mutant strain of LdNPV)
FPL ..... Forest Products Laboratory (FS)
FPM ..... Forest Pest Management (FS)
FS ..... Forest Service (USDA)
GCMRL .. Gulf Coast Mosquito Research Laboratory, Lake Charles, LA (ARS)
GHIPM ... Grasshopper Integrated Pest Management Project
GM ..... gypsy moth
GMLSM .. Gypsy Moth Life System Model
GMRDP .. Gypsy Moth Research and Development Program (FS)
GUS ..... glucouronidase
GV ..... granulosis virus
HIV ..... human immunodeficiency virus
HPLC .... high performance liquid chromatography
Hz*S*NPV .. *Heliothis zea* (corn earworm) singly-embedded nuclear polyhedrosis virus
IA ..... International Activities Office (ARS)
IAAT ..... Inter-agency Advisory and Action Team (USDA)
IBC ..... institutional biosafety committee
IBC^3 ..... Interagency Biological Control Coordinating Committee (USDA)
IBL ..... Insect Biocontrol Laboratory (ARS)
ICP ..... insecticidal crystal protein
IEAWL ... Insect Enemies of Aquatic Weeds Laboratory, Gainesville, FL (ARS)
IEF ..... isoelectric focusing technique
IIBC ..... International Institute of Biological Control (see also Commonwealth Institute of Biological Control, CIBC)
IIBIII ..... Insect Identification and Beneficial Insect Introduction Institute (ARS)
IIPI ..... Insect Identification and Parasite Introduction Research Section/Laboratory/Branch (ARS)
IMC ..... International Mineral and Chemical Corporation, Libertyville, IL
IMM ..... Indianmeal moth
INRA ..... Institut Nationale de Recherche Agronomique, France
INT ..... Intermountain Forest Research Experiment Station (INT)
IPD ..... International Programs Division (ARS)
IPL ..... Insect Pathology Laboratory (ARS)
IPM ..... Integrated Pest Management
IPPL ..... Insect Pathology Pioneering Research Laboratory, Beltsville, MD (ARS)
IPRU ..... Insect Pathology Research Unit (ARS)
IR-4 ..... interregional cooperative research project 4 (USDA)
IU ..... international unit(s)
IUFRO .... International Union of Forestry Research Organizations
Ld*M*NPV .. *Lymantria dispar* (gypsy moth) multiply-occluded nuclear polyhedrosis virus
MD ..... Methods Development (APHIS)
mg ..... milligram
ml ..... milliliter
MLOs .... mycoplasma-like organisms
***M*NPV** .... multiply-occluded nuclear polyhedrosis virus
MPB ..... mountain pine beetle
MSIF ..... macromolecular protein synthesis inhibition factor
mμ ..... millimicrons (wavelength unit)
NAIAD ... North American Immigrant Arthropod Database

NAL . . . . . National Agricultural Library (USDA)
NAPPO . . . North American Plant Protection Organization
NANIAD . . North American Nonindigenous Arthropod Database
NASA . . . . National Aeronautics and Space Administration
NASDA . . . National Association of State Departments of Agriculture
NBCI . . . . . National Biological Control Institute (APHIS)
NBCP . . . . National Biological Control Program (ARS)
NBCSI . . . . National Biological Control Service Institute, proposed (APHIS)
NBRF . . . . National Biomedical Research Foundation
NC . . . . . North Central Forest Experiment Station (FS)
NCFES . . . North Central Forest Experiment Station, St. Paul, MN (FS)
NCAUR . . . National Center for Agricultural Utilization Research, Peoria, IL (ARS)
NE . . . . . Northeastern Forest Experiment Station (FS)
NEFES . . . Northeastern Forest Experiment Station (FS)
NFAAT . . . Northeast Forest Aerial Application Technology Group (FS, APHIS, ARS, PA State Univ., Univ. of CT)
NGIRL . . . Northern Grain Insects Research Laboratory, Brookings, SD (ARS)
NIH . . . . . National Institutes of Health
NIS . . . . . non-indigenous species
NOV . . . . . non-occluded virus
NPL . . . . . National Program Leader (ARS)
NPS . . . . . National Program Staff (ARS)
NPV . . . . . nuclear polyhedrosis virus
NRRL . . . . Northern Regional Research Laboratory, Peoria, IL (ARS)
OB . . . . . occlusion body
OEQ . . . . . Office of Environmental Quality Activities (USDA)
OGC . . . . . Office of General Counsel (USDA)
OICD . . . . . Office of International Cooperation and Development (USDA)
OIRP . . . . . Office of International Research Programs (ARS)
Op*M*NPV . Douglas-fir Tussock Moth (*Orgyia pseudotsugata*) multicapsid nuclear polyhedrosis virus
orf . . . . . open reading frame
OTA . . . . . Office of Technology Assessment, U.S. Congress
PDV . . . . . polyhedra derived virions
P.L. 480 . . . Public Law 480; Agricultural Trade, Development, and Assistance Act of 1954
PNW . . . . . Pacific Northwest Forest and Range Experiment Station (FS)
PPDS . . . . . Program Planning and Development Staff (APHIS PPQ)
PPQ . . . . . Plant Protection and Quarantine Programs (APHIS)
PPRU . . . . Plant Protection Research Unit, Ithaca NY (ARS)
PRC . . . . . People's Republic of China
PSI . . . . . Plant Sciences Institute (ARS)
PW . . . . . Pacific Southwest Forest and Range Experiment Station (PSW) (FS)
Pt . . . . . *Pisolithus tinctorius* (a myccorhizal fungus)
RAC . . . . . Recombinant Advisory Committee
RM . . . . . Rocky Mountain Forest and Range Experiment Station (FS)
RMIS . . . . . Research Management Information System (ARS)
RNA . . . . . ribonucleic acid
ROBO . . . . "Releases of Beneficial Organisms in the United States and Territories" database
RWA . . . . . Russian wheat aphid
RWU . . . . . Research Work Unit (FS)
SAA . . . . . spotted alfalfa aphid

SABCL . . . South American Biological Control Laboratory (ARS)
SAES . . . . . State Agricultural Experiment Stations
SBDL . . . . . Soilborne Diseases Laboratory (ARS)
SBMNL . . . Systematic Botany, Mycology, and Nematology Laboratory (ARS)
SBW . . . . . spruce budworm
SBWW . . . . sugarbeet wireworm
SE . . . . . Southeastern Forest Experiment Station (FS)
SEBIIL . . . Systematic Entomology and Beneficial Insect Introduction Laboratory (ARS)
SEEBB . . . . smaller European elm bark beetle
SEL . . . . . Systematic Entomology Laboratory (ARS)
SEM . . . . . scanning electron microscopy
SERB . . . . . Simulation Environment for Research Biologists
SFC . . . . . Special Foreign Currency program (Foreign Agricultural Research Grant Program, Public Law 480)
SFCIML . . Southern Field Crop Insects Management Laboratory (ARS)
Sf*M*NPV . . *Spodoptera frugiperda* (fall armyworm) multiply-occluded nuclear polyhedrosis virus
SIBCA . . . . Subgroup on Introduction of Biological Control Agents (USDA, Office of Environmental Quality Acitivities, WGBCA)
SIML . . . . . Southern Insect Management Laboratory (ARS)
***S*NPV** . . . . . singly-embedded nuclear polyhedrosis virus
SO . . . . . Southern Forest Experiment Station (FS)
SPB . . . . . southern pine beetle (*Dendroctonus frontalis*)
SPWF . . . . sweetpotato whitefly
STEM . . . . scanning transmission electron microscopy
SUNY . . . . . State University of New York
SWG/BCV . Scientific Working Group on Biological Control of Vectors (United Nations, WHO)
SWSL . . . . Southern Weed Science Laboratory (ARS)
SY . . . . . Scientist Year
TAG . . . . . Technical Advisory Group (USDA)
TAMU . . . . Texas A & M University
TM . . . . . Terramycin, oxytetracycline hydrochloride
Tn*M*NPV . . *Trichoplusia ni* (cabbage looper) multiply-occluded nuclear polyhedrosis virus
TRV . . . . . *Trichoplusia ni* RNA Virus
UCB . . . . . University of California, Berkeley
UDP . . . . . uridine diphosphate
ULV . . . . . ultra-low-volume
UMC . . . . . University of Missouri at Columbia
UNDP . . . . United Nations Development Program
USDA . . . . . United States Department of Agriculture
USDI . . . . . United States Department of the Interior
USGMRL . U.S. Grain Marketing Research Laboratory, Manhattan, KS (ARS)
USSR . . . . . Union of Soviet Socialist Republics
UV . . . . . ultraviolet
VOs . . . . . viral occlusions
VPI . . . . . Virginia Polytechnic Institute and State University
WGBCA . . Work Group on Biological Pest Control Agents (USDA Office of Environmental Quality Activities)
WGNE . . . . Working Group on Natural Enemies (ARS)
WHO . . . . . World Health Organization (United Nations)
WO . . . . . Washington Office (FS)
WSBW . . . . western spruce budworm

INDEX OF ORGANIZATIONS AND AGENCIES

Compiled by S. M. Braxton

Units of U.S. government agencies are indexed under their respective agencies; e.g. U.S. Department of Agriculture (USDA), U.S. Department of the Interior, etc. Many reorganizations within the various USDA agencies have altered the names of many of the locations mentioned in this history. Names listed in the index for ARS laboratories are given as in the text at the time of their existence; the names of Forest Service Research Stations varied over time, and the most current names are given in this index, which may differ from those given in the text.

SUBJECT INDEX

Compiled by S. M. Braxton

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W

TAXONOMIC INDEX

Compiled by S. M. Braxton

The text contains limited taxonomic information about the species discussed. Authors and higher taxonomic affiliations were omitted, in the interest of saving space, and in many cases only common names of species were used. This index cross-references common names used in the text with current scientific names including authors, and higher taxonomic affiliations. Frequently published synonymies and alternate common names are also included. For **insect** species, we have followed various catalogs, with common names (where applicable) taken from Stoetzel et al. (1989). Insect common names not approved by the Entomological Society of America, but which are in use by USDA researchers appear in the text in quotation marks. The index includes order and family affiliations for insect species. For **nematodes**, we have followed the higher classification given in Poinar (1979). Class, order and family affiliations are given for nematode species. For **protozoans** we have followed Hutner (1978) and Burges and Hussey (1971). For **bacteria**, we have followed Skerman et al. (1980). Classification of bacteria above the generic level is de-emphasized in the above publication; however, we provide order and family affiliations where available. For **invertebrate viruses** we have followed Adams and Bonami (1991). Classification of these viruses above the family level is descriptive, based on viral structure (enveloped/non-enveloped) and mode of replication (RNA/DNA). These descriptors are provided along with family designations for invertebrate viruses. For **fungi** we have followed Farr et al. (1989) (for fungi on plants), and Humber (1992) (for entomopathogenic fungi). For many groups of fungi, order and family groups are not broadly accepted. We provide class affiliations, and orders where available. For **plant** species, we have followed Patterson et al. (1989), Terrell et al. (1986), the Germplasm Information Resources Network (GRIN) Plant Taxonomy database, and the Cronquist system of classification of the Angiosperms (as presented in Jones and Luchsinger [1976]). Order and family affiliations are given for plant species. Weed common names are taken from Patterson, et al. (1989); those common names not approved by the Weed Science Society of America are listed in quotation marks. Common names of beneficial (crop/commodity) plants are taken from the Germplasm Information Resources Network plant taxonomy database. For all groups, any disputes concerning validity of names, classifications, etc., have been settled using the appropriate ARS systematists as the final authority. For this assistance we gratefully acknowledge the contributions of the ARS Systematic Botany and Mycology Laboratory, the Systematic Entomology Laboratory and other ARS scientists, especially R.A. Humber, J.R. Adams, D.A. Knox, C.L. Wilson, K.J. Hackett, and J.J. Becnel.

C

[1] The correct taxonomic name to be used for the majority of musk thistle populations in North America, according to the rules of botanical nomenclature (J. H. Wiersema, ARS Systematic Botany and Nematology Laboratory), is *C. nutans* L. subsp. *leiophyllus* (Petrovic) Stoj. & Stef. (= *C. thoermeri* Weinm. *sensu* Kazmi [1964] or McCarty [1978]). See also Moore and Frankton (1974) and Desrochers et al. (1988). Some releases against musk thistle in Montana and Texas, and some collections from musk thistle in Italy refer to *C. nutans* L. subsp. *macrocephalus* (Desf.) Nyman.

[2] Editor's (JRC) Note: When the species *Apanteles melanoscelus* was placed in the genus *Cotesia* by Mason (1981), there was some confusion among biological control authors as to the proper gender ending for the specific epithet, and the species is given as *Cotesia melanoscela* in some subsequent publications. However, according to R.W. Carlson, ARS Systematic Entomology Laboratory, Beltsville, MD (personal communication), *Cotesia melanoscelus* is grammatically correct, as is also indicated in Mason's paper.

D

G

[3] The correct taxonomic name to be used for the majority of musk thistle populations in North America, according to the rules of botanical nomenclature (J. H. Wiersema, ARS Systematic Botany and Nematology Laboratory), is *C. nutans* L. subsp. *leiophyllus* (Petrovic) Stoj. & Stef. (= *C. thoermeri* Weinm. *sensu* Kazmi [1964] or McCarty [1978]). See also Moore and Frankton (1974) and Desrochers et al. (1988). Some releases against musk thistle in Montana and Texas, and some collections from musk thistle in Italy refer to *C. nutans* L. subsp. *macrocephalus* (Desf.) Nyman.

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NAME INDEX

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Names of many additional involved persons may be found in the references cited sections of the main text and appendices.

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T