

11 Future Weed, Pest, and Disease Problems for Plants

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11.1 INTRODUCTION

Recently, the global human population surpassed 6 billion. Increasing populations require increasing resources, particularly with respect to energy and food. As the global demand for power and agricultural land intensifies, fossil fuel burning and deforestation will continue to be human-derived sources of atmospheric carbon dioxide. Since the mid-1950s, records of carbon dioxide concentration [CO_2] obtained from the Mauna Loa observatory in Hawaii have shown an increase of about 20% from 311 to 375 parts per million (ppm) (Keeling and Whorf 2001). The current rate of [CO_2] increase ($\sim 0.5\%$) is expected to continue with concentrations exceeding 600 ppm by the end of the 21st century (Schimel et al. 1996). Interestingly, because the observatory at Mauna Loa and other global monitoring sites (cdiac.esd.ornl.gov/home.html) sample air at high elevations, away from anthropogenic sources, actual ground-level [CO_2] may be significantly higher. For example, urban areas in Phoenix and Baltimore show [CO_2] values exceeding 500 ppm, and suburban values near Washington, D.C. and Sydney, Australia, report [CO_2] above 420 ppm (Idso et al. 1998, 2001; Ziska et al. 2000). This suggests that while the Mauna Loa data may reflect [CO_2] for the globe as a whole, regional increases in [CO_2] may already be occurring as a result of urbanization.

Overall, the documented increases in atmospheric [CO_2] are likely to change the biology of agricultural weeds, insects, and diseases in two fundamental ways. The first is related to climate stability. The observed change in atmospheric [CO_2] has been accompanied by documented increases in other radiation-trapping gases such as methane (CH_4) (0.9% increase per year), nitrous oxide (N_2O) (0.25% per year), and chlorofluorocarbons (CFCs) (4% per year). Recent evaluations by the Intergovernmental Panel on Climate Change (IPCC) based, in part, on an assessment by the U.S. National Academy of Sciences has indicated that the rise of [CO_2] and associated *greenhouse gases* could lead to a 3 to 12°C increase in global surface temperatures, with subsequent consequences on precipitation frequency and amounts.

The second likely impact is the [CO_2] *fertilization effect*. That is, plants evolved at a time when the atmospheric [CO_2] appears to have been four or five times present values (Bowes 1996). Because CO_2 remains the sole source of carbon for plant photosynthesis (and, hence, 99% of all living terrestrial organisms), and because at present [CO_2] is less than optimal, as atmospheric [CO_2] increases, photosynthesis will be stimulated accordingly. Elevating [CO_2] stimulates net photosynthesis in plants with the C_3 photosynthetic pathway by raising the CO_2 concentration gradient from air to leaf and by reducing the loss of CO_2 through photorespiration. Specifically, because oxygen competes with CO_2 for active sites of the enzyme, ribulose-bisphosphate carboxylase/oxygenase (Rubisco, the principle enzyme that incorporates carbon into the plant), elevating the concentration of CO_2 (relative to O_2) increases net carbon uptake by stimulating photosynthesis and reducing CO_2 lost via photorespiration. Because the competition between O_2 and CO_2 for active sites is temperature sensitive (favoring O_2 with increasing temperature), the stimulation of net photosynthesis by elevated CO_2 should increase as the temperature increases. While some studies have suggested that the photosynthetic response to [CO_2] is

limited by nutrients (Diaz et al. 1993), this seems less likely in managed agroecosystems where nitrogen, phosphorus, and so forth are likely to be optimal for crop growth. Thus, for plants that rely solely on the C_3 photosynthetic pathway, (~95% of all plant species), increasing $[CO_2]$ and temperatures associated with climate change should be favorable for increased growth.

Alternatively, plants with the C_4 photosynthetic pathway (~4% of all known plant species) have an internal mechanism for concentrating CO_2 around Rubisco; therefore, increases in external CO_2 concentration should have little effect on net photosynthesis in C_4 plants (for reviews, see Bowes 1996; Ghannoum et al. 2000, Ghannoum et al., Chapter 3, this volume). However, one of the most consistent responses of both C_3 and C_4 species to elevated $[CO_2]$ is a decrease in stomatal conductance (Morison 1985; Eamus 1991). The decrease in stomatal conductance can result in significant increases in leaf transpiration efficiency (CO_2 assimilated/ H_2O transpired) or water use efficiency (dry matter obtained/ H_2O transpired). Hence, under water-limiting conditions, elevated CO_2 should result in significant increases in photosynthesis and biomass for both C_3 and C_4 plant species.

At the whole plant level, the $[CO_2]$ -induced stimulation of photosynthesis is associated with an decrease in Rubisco investment and an increase in the ratio of C:N (Bowes 1996). Enhanced $[CO_2]$ also can result in increased growth, leaf area, tillering, and total biomass as well as allometric shifts between plant organs (Kimball et al. 1993, Poorter 1993). In addition, enhanced $[CO_2]$ can alter germination (Heichel and Jaynes 1974; Ziska and Bunce 1993), flowering times (Reekie et al. 1997), pollen output (Ziska and Caulfield 2000), seed yield (Allen et al. 1987), and the onset of senescence (Sicher 1998).

For weeds, insects, and diseases, what are the consequences of a direct CO_2 fertilization effect, and how are these consequences likely to be altered by concurrent changes in temperature or precipitation? Are these changes likely to increase or decrease crop production in agroecosystems? Surprisingly, while the detrimental effects of the above pests are well recognized, most research to date has focused on how individual crop species will respond to $[CO_2]$ and climate (for reviews, see Kimball et al. 1993; Poorter 1993; Curtis and Wang 1998). This may be due, in part, to the complex nature of ecological systems (even managed ones), and the challenge of implementing ecologically relevant experiments that address spatial and temporal interactions between organisms. Yet, not understanding these complex interactions and deriving suitable responses to avoid or mitigate their resulting impacts will certainly have critical and potentially damaging consequences with respect to crop productivity and global food security.

To that end, we are beginning to address the probable impacts of climate change and atmospheric $[CO_2]$ on pest biology. These impacts are multifaceted and include the direct effects of CO_2 and concomitant changes in climate on weed growth and weed-crop competition; secondary CO_2 -induced effects on crop hosts (digestibility, chemical defenses, canopy microclimate), which may affect insect fecundity and pathogen success, and temperature and precipitation changes that directly alter where and when pathogen or insect outbreaks occur. While providing a tentative mechanistic basis for both the direct and indirect consequences of $[CO_2]$ and climate, we also hope to determine, in part, how current pest management efforts might fare in

a future climate. We recognize that given the scarcity of available data, any review is likely to be problematic; however, our overall goal is to begin a synthesis of what is known and to derive a preliminary set of key climatic questions to address in the context of pest biology and agroecosystems.

11.2 RISING [CO₂] AND WEED BIOLOGY

11.2.1 CO₂ FERTILIZATION

Weeds are an anthropogenic classification given to plants that are generally recognized as objectionable or undesirable to human activities. However, there are biological similarities among such plants, including colonization of disturbed environments, vigorous growth, prodigious seed production, and seed longevity (see Baker 1974). Historically, one of the earliest accepted classifications of weeds was recognition of those plant species that interfered with crop production. Human selection of agronomically desirable species has led to inadvertent selection for other undesirable plant species that mimic the biology of the crop (e.g., commercial and wild oat, sorghum, and Johnson grass). Therefore, while numerous studies have shown that crop species will demonstrate enhanced photosynthesis, growth, and yield with increasing atmospheric [CO₂] (Kimball 1983; Kimball et al. 1993; Poorter 1993; Curtis and Wang 1998), similar benefits are likely for weedy competitors as well. David Patterson, a weed specialist at North Carolina State University has classified the relative responses of a range of crops and weeds to a projected increase of ~300 ppm [CO₂] for plants with the C₃ and C₄ type of photosynthesis. He found that C₃ and C₄ crops showed a range of responses from 1.10 to 2.34x and 0.98 to 1.24x, while C₃ and C₄ weeds showed a range of response from 0.95 to 2.72 and 0.7 to 1.61x, respectively (Patterson and Flint 1990; Patterson 1993; Patterson et al. 1999). Recent data on the specific response of noxious weeds to recent increases in atmospheric [CO₂] during the 20th century (284 to 380 ppm) shows a much stronger response: 1.77 to 2.78x relative to 1.15 to 1.55 in other plants (Sage 1995; Ziska 2003a). Overall, the greater range of responses observed for weeds with increasing atmospheric [CO₂] is consistent with the suggestion of Treharne (1989), that weeds have a greater genetic diversity and, hence, physiological plasticity, relative to crop species.

11.2.2 CO₂ FERTILIZATION AND CLIMATIC INTERACTIONS

Because increasing temperatures result in greater photorespiratory carbon loss, the impact of increasing [CO₂] on net carbon uptake should increase with increasing temperature (see Long 1991 and earlier discussion); however, this is not always observed. For example, increasing day and night temperatures with a doubling of [CO₂] can either decrease leaf area and biomass (Ackerly et al. 1992, Coleman and Bazzaz 1992) or have no effect (Tremmel and Patterson 1993) in velvetleaf (*Abutilon theophrasti*), a common agronomic weed. Similarly, CO₂ enrichment and temperature did not interact for two C₄ weed species (*Echinochloa crus-galli* and *Eleusine indica*) (Potvin and Strain 1985). Alternatively, spurred anoda (*Anoda cristata*)

biomass increased at 700 ppm when day and night temperatures increased from 26/17 to 32/23°C (Patterson et al. 1988). At present, there is little unequivocal evidence for significant differences in response to $[\text{CO}_2]$ with increasing temperatures. Overall, theoretical limitations based on biochemical models have generally assumed no growth temperature effects on carboxylation kinetics (V_{Cmax}) and no limitation on the potential rate of electron transport (J_{max}) (Long 1991); however, more recent studies indicate that long-term adaptation to growth temperature may adjust both parameters, lowering the temperature sensitivity of CO_2 -induced photosynthetic stimulation (Bunce 2000; Ziska 2001a).

Potential increases in global temperature may be accompanied by changes in the pattern and amount of precipitation. However, because of the indirect effect of CO_2 on stomatal aperture, elevated CO_2 can still stimulate plant photosynthesis and growth even if water is limiting (Patterson 1986; Chaudhury et al. 1990). For some C_4 weeds, increased photosynthesis and growth at elevated $[\text{CO}_2]$ may only occur under dry conditions, presumably due to increased water use efficiency (WUE, the ratio of carbon gained to water lost) and reduced water stress. Although water shortages should not limit the response to elevated $[\text{CO}_2]$, no assessment on CO_2 response under flooded conditions is available for weedy species.

11.3 RISING $[\text{CO}_2]$ AND WEED-CROP COMPETITION

11.3.1 CO_2 FERTILIZATION

Any resource that affects the growth of an individual alters its capacity to compete with individuals of the same or different species (Patterson and Flint 1990). Consequently, induced changes in competition can be associated not only with limited resources, but with resource enhancement as well. For example, in weed-crop competition it was thought that the addition of nitrogen would reduce crop losses due to weeds by increasing the availability of a resource (Vengris et al. 1955). However, because weeds utilize nitrogen more efficiently than crops, weed competition was actually favored when additional nitrogen was applied (Appleby et al. 1976; Carlson and Hill 1985). Analogous to the nitrogen response, differential responses of weeds relative to crops are likely as atmospheric $[\text{CO}_2]$ increases.

If differential responses to increasing $[\text{CO}_2]$ occur between crops and weeds, will crop losses due to weedy competition increase or decrease? Early, subjective classification of "worst" weeds by Holm et al. (1977) indicated that a majority (14 out of 18) of the world's worst weeds are C_4 , whereas of the 86 crop species that make up 95% of the world's food supply, only five are C_4 (Patterson 1995a). As a consequence of this observation, many initial experiments analyzed C_3 crop- C_4 weed competition (Alberto et al. 1996; Bunce 1995; Carter and Peterson 1983; Patterson et al. 1984). These studies uniformly reported that increasing $[\text{CO}_2]$ resulted in a greater ratio of crop-to-weed vegetative biomass ($\text{C}_3:\text{C}_4$), which is consistent with the known carboxylation kinetics of the C_3 and C_4 pathways. Hence, some global models have suggested less crop loss due to weedy competition as atmospheric $[\text{CO}_2]$ increases (e.g., Rosenzweig and Hillel 1998).

However, the general perspective that weeds are C_4 and crops C_3 is somewhat misleading. For example, it can also be stated that 4 of the top 10 producing crops globally are C_4 (Maize, *Zea mays*; Millet, *Sorghum prostratum*; Sorghum, *Sorghum bicolor*; and Sugarcane, *Saccharum officinarum*), and that of the 33 most invasive weeds globally (which can certainly be considered among the worst weeds categorically), only two are C_4 (*Spartina anglica* and *Imperata cylindrica* L. Beauv) (www.issg.org/database). In reality, crop–weed competition varies significantly by region; consequently, depending on temperature, precipitation, soil, and so forth, C_3 and C_4 crops will interact with C_3 and C_4 weeds (Bridges 1992). In addition, a C_3 crop vs. C_4 weed interpretation does not address weed–crop interactions where the photosynthetic pathway is the same (e.g., Bunce 1995; Potvin and Vasseur 1997). Yet many of the worst, most troublesome weeds for a given crop are genetically similar and frequently possess the same photosynthetic pathway (e.g., sorghum and Johnson grass [*Sorghum halapense*], both C_4 ; oat and wild oat, both C_3).

Even within crops and weeds of the same photosynthetic pathway, it is unclear how CO_2 -induced variations in reproduction could alter competitive outcomes or persistence within the seed bank. Reproduction is often increased in response to rising CO_2 as additional carbon is allocated both to flowers and to increased nodes and branches (see Ward and Strain 1999 for a review). In common ragweed (*Ambrosia artemisiifolia*), time to reproduction was shortened, in part, by faster growth rates (Ziska et al. 2003), although for other species, elevated CO_2 may alter the size at which plants initiate reproduction (Reekie and Bazzaz 1991). However, no clear distinction between flowering times between weeds and crops is evident in response to $[CO_2]$. Furthermore, while seed yield is easy to determine in cultivated crops, it is difficult to assess seed production, particularly *in situ*, for weeds given that seed shattering (e.g., lambsquarters, *Chenopodium album*) is endemic to such species. Consequently, meta-analyses comparing the reproductive output of crop and “wild” species may only include a handful of common agronomic weeds (e.g., velvetleaf, sicklepod [*Cassia obtusifolia*], barnyard grass [*Echinochloa glabrescens*], and ladysthumb [*Polygonum persicaria*], see Appendix 1, Jablonski et al. 2002). In addition, comparisons of weed–crop reproductive success do not consider many invasive weeds, such as Canada thistle (*Cirsium arvense*), which may reproduce asexually from belowground structures, which, in turn, may be particularly sensitive to rising $[CO_2]$ (Ziska 2003a).

Overall, data regarding vegetative or reproductive competition between crops and weeds as a function of increasing $[CO_2]$ remain scarce. The studies that are available fall into two general categories, one where crops and weeds have the same photosynthetic pathway, and another where the pathway differs. The majority of studies involving different photosynthetic pathways have focused on a C_3 crop in competition with a C_4 weed (Table 11.1). In this comparison, increasing CO_2 increased the crop-to-weed biomass ratio, consistent with the known biochemical response. However, it is interesting to point out that biomass and yield of grain sorghum (C_4 crop) was reduced when grown in the presence of either velvetleaf or cocklebur (*Xanthium strumarium*), both C_3 weeds (Ziska 2001b, 2003b). Most comparisons with the same photosynthetic pathway for crops and weeds resulted in significant increases in weed-to-crop biomass when weed and crop emerged simultaneously (Table 11.1). In a study comparing

TABLE 11.1
Summary of Studies Examining Whether Weed or Crops Were Favored as a Function of Elevated [CO₂]

Crop	Weed	Increasing [CO ₂] Favors?	Environment	Reference
A. C₃ Crops/C₃ Weeds				
Soybean	<i>Chenopodium album</i>	Weed	Field	Ziska 2000
Lucerne	<i>Taraxacum officinale</i>	Weed	Field	Bunce 1995
Pasture	<i>Taraxacum and Plantago</i>	Weed	Field	Potvin & Vasseur 1997
Pasture	<i>Plantago lanceolata</i>	Weed	Chamber	Woodward 1988
Sugarbeet	<i>Chenopodium album</i>	Crop*	Chamber	Houghton & Thomas 1996
B. C₄ Crops/C₄ Weeds				
Sorghum	<i>Amaranthus retroflexus</i>	Weed	Field	Ziska 2003b
C. C₃ Crops/C₄ Weeds				
Fescue	<i>Sorghum halapense</i>	Crop	Glasshouse	Carter & Peterson 1983
Soybean	<i>Sorghum halapense</i>	Crop	Chamber	Patterson et al. 1984
Rice	<i>Echinochloa glabrescens</i>	Crop	Glasshouse	Alberto et al. 1996
Pasture	<i>Paspalum dilatatum</i>	Crop	Chamber	Newton et al. 1996
Lucerne	Various grasses	Crop	Field	Bunce 1995
Soybean	<i>A. retroflexus</i>	Crop	Field	Ziska 2000
D. C₄ Crops/C₃ Weeds				
Sorghum	<i>Xanthium strumarium</i>	Weed	Glasshouse	Ziska 2001b
Sorghum	<i>Albutilon theophrasti</i>	Weed	Field	Ziska 2003b

Notes: Favored indicates whether elevated [CO₂] produced significantly more crop or weed biomass. Pasture refers to a mix of C₃ grass species. The asterisk (*) refers to earlier emergence of the crop relative to weeds at elevated [CO₂].

lambsquarters to sugarbeet (*Beta vulgaris*), the competitive advantage of sugarbeet at elevated [CO₂] was attributed to late emergence of the weed species within the experiment (Houghton and Thomas 1996).

Although these studies have reported changes in the ratio of crop and weed biomass, only two studies have actually quantified changes in crop yield with weedy competition as a function of rising [CO₂] (Ziska 2000b, 2003). In these studies, two crop species, one C₃ (soybean), and one C₄ (dwarf sorghum) were grown with lambsquarters (C₃) and redroot pigweed (*Amaranthus retroflexus*, C₄) and velvetleaf (C₃) and redroot pigweed, respectively, at a density of two weeds per meter of row. Although, soybean yield losses were less from pigweed, all other crop–weed interactions resulted in increased yield loss at elevated [CO₂]. Interestingly, the presence of any weed species negated the ability of the crop to respond either vegetatively or reproductively to additional [CO₂]. This is significant because CO₂ enhancement studies and crop modeling efforts rarely consider crop–weed competition. However, additional field-based studies are needed to confirm and amplify the results presented here.

11.3.2 CO₂, ENVIRONMENTAL INTERACTIONS, AND COMPETITION

As with field evaluations of crop loss, almost no data has examined how crop weed competition will be altered by simultaneous increases in [CO₂] and climate. Only a single study has evaluated the interactions among temperature, [CO₂], and crop-weed competition (Alberto et al. 1996). In this experiment, competition between rice (*Oryza sativa*, C₃) and a weedy competitor, barnyard-grass (*Echinochloa glabrescens*, C₄) was assessed at two different [CO₂] (ambient and ambient +200 ppm) and two different temperatures (day and night of 27/21 and 37/29°C). This study confirmed that at 27/21°C, increased [CO₂] favored the crop (the C₃ species); however, with concomitant changes in both [CO₂] and temperature, the C₄ weed was favored, primarily because higher temperatures resulted in increased seed yield loss for rice (Alberto et al. 1996).

It is, of course, difficult to generalize based on a single experiment. Hypothetically, there are a number of additional potential interactive effects related to temperature, [CO₂], and weed-crop competition. Weeds of the tropics show a large stimulation to small air temperature changes (Flint et al. 1984; Flint and Patterson 1983), but it is unknown if a greater synergy with rising [CO₂] would be anticipated for these weeds relative to tropical crops. It is likely that such potential changes in competition will be species specific.

No studies are available on the interactions among drought, rising CO₂, and weed-crop competition. Empirically, crops and weeds have similar responses to drought; consequently, the overall impact of weeds may be reduced because of decreased growth of both crops and weeds in response to water availability (Patterson 1995b). Although competition was not determined directly, the proportion of weed biomass increased with [CO₂] to a similar extent in wet and dry treatments in a pasture mixture (Newton et al. 1996).

11.4 CLIMATIC EFFECTS ON WEED BIOLOGY AND COMPETITION

In addition to the direct CO₂ fertilization effect, climatic change, particularly precipitation and temperature, will have significant effects on weed biology. Temperature and precipitation remain primary abiotic variables that control vegetative distribution (Woodward and Williams 1987), and as such will impact the geographical distribution of weeds with subsequent effects on their growth, reproduction, and competitive abilities.

Increasing temperature may mean expansion of weeds into higher latitudes or higher altitudes. High-latitude temperature limits of tropical species are set by accumulated degree days (Patterson et al. 1999), while low-latitude limits are determined in part by competitive ability at low temperatures (Woodward 1988). Many of the weeds associated with warm-season crops originated in tropical or warm temperature areas; consequently, northward expansion of these weeds may accelerate with warming (Patterson 1993; Rahman and Wardle 1990). For example, detailed studies of itchgrass (*Rottboellia cochinchinensis*) indicate that a warming of 3°C (day night temperature increase from 26/20 to 29/23°C) increased biomass and leaf

area by 88 and 68%, respectively (Patterson et al. 1979). Empirically, based on its temperature response, itchgrass could effectively increase its percent of maximum growth from 50 to 75% in the Middle Atlantic states to 75 to 100% (Patterson et al. 1999). Northward expansion of other weeds, such as cogongrass (*Imperata cylindrica*) and witchweed (*Striga asiatica*), is also anticipated (Patterson 1995b), although warming may restrict the southern expansion of some exotic weeds such as wild proso millet (*Panicum miliaceum*) due to increased competition (Patterson et al. 1986).

One of the more intriguing examples of potential northward expansion is that of kudzu (*Pueraria lobata*), a ubiquitous invasive weed. Approximately 15 years ago, a seminal work by Tom Sasek and Boyd Strain at Duke University noted that the current latitudinal distribution of kudzu was limited to areas south of the Ohio Valley and the Mason-Dixon line by low winter temperatures (see Figure 7, Sasek and Strain 1990). Interestingly, recent observations have noted kudzu populations near the Chicago area (www.chicagobotanic.org) and in northwestern Massachusetts (www.cyberonic.com). How much of this distribution is due to increasing winter temperatures is unclear, but the northward spread is consistent with the Sasek and Strain predictions.

Changes in weed distribution and the resultant changes in weed-crop competition remain unclear. If temperature changes the ranges of both agronomic and noxious weeds, such changes could indirectly alter weed-crop competition by changing the ratio of C₄ weeds to C₃ crops. For example, estimated crop losses due to weeds without the use of herbicides are substantially larger in the south than in the north in both corn (22 vs. 35%) and soybeans (22 vs. 64%) (Bridges 1992). This may be associated with the occurrence in the South of some very aggressive weeds whose presence is limited in the northern states by low temperatures (see Table 2, Bunce and Ziska 2000). Alternatively, greater increases in nighttime relative to daytime temperatures projected with global warming (McCarthy et al. 2001) could decrease seed production to a greater extent in crop relative to weed species (cowpea, *Vigna unguiculata*, Ahmed et al. 1993) with subsequent competitive effects. Differential responses of seed emergence to temperature could influence species establishment and subsequent weed-crop competition (Houghton and Thomas 1996).

Response to drought in agronomic conditions is dependent on species and cultural conditions. In general, decreased water availability may favor the crop by reducing the competitive impact of the weed (see Table 1 in Patterson 1995b). That is, when potential yield is already limited by water, weed competition for other resources has less impact. Water availability may also affect the duration of weed-free periods during crop development. Coble et al. (1981) demonstrated that in competition with common ragweed, a critical period to avoid competitive effects was 2 weeks in a dry year and 4 weeks in a wet year. However, the duration of the critical period varied by weed and crop (Harrison et al. 1985; Jackson et al. 1985).

11.5 RISING [CO₂] AND INSECTS

Although increasing [CO₂] can result in narcoleptic and behavioral changes in insects, projected concentrations of atmospheric [CO₂] up to 1000 ppm are unlikely

to affect insects directly (Nicolas and Sillans 1989). Rather, it is more probable that insect biology will be impacted by the direct physiological effects of $[\text{CO}_2]$ on host plant metabolism. Specific $[\text{CO}_2]$ -induced changes in plant metabolism include increased C:N ratios, altered concentrations of defensive (allelopathic) compounds, increased starch and fiber content (Coble et al. 1981), and increased water content. Overall, these metabolic changes are likely to impact insect-crop interactions in two principal ways: First by altering feeding behavior, and second, by altering plant defenses (Newman, Chapter 10, this volume).

11.5.1 FEEDING TRAITS

Because of qualitative changes at the leaf level, insect feeding behavior and mortality can be affected both positively and negatively by elevated $[\text{CO}_2]$ (Lincoln et al. 1993, Bezemer and Jones 1998). For example, increased growth and development were observed for larvae of *Polyommatus icarus* (Lepidoptera) feeding on *Lotus corniculatus* (Goverde et al. 1999). This was due in part because increased $[\text{CO}_2]$ resulted in both increased leaf digestibility and carbohydrate concentration. In contrast, larvae of Colorado beetle (*Leptinotarsa decemlineata*) feeding on potato (*Solanum tuberosum*), southern army worm (*Spodoptera eridania*) feeding on peppermint (*Mentha piperita*), cabbage looper (*Trichoplusia ni* Hubner) feeding on lima bean (*Phaseolus lunata*), and buckeye butterfly (*Junonia coena*) feeding on plantain (*Plantago lanceolata*) demonstrated increased feeding rates but lower growth and increased mortality associated with $[\text{CO}_2]$ -induced changes in leaf quality, specifically N concentrations (Fajer et al. 1989, Lincoln and Couvet 1989, Miglietta et al. 2000, Osbrink et al. 1987). Overall, higher C:N ratios associated with increasing $[\text{CO}_2]$ may result in compensatory increases in foliar consumption rates by insects. These increased consumption rates are often accompanied (but not always, see Watt et al. 1996) by a decrease in the efficiency of plant tissue conversion to body mass, reduced larval growth rate, and reduced pupal mass.

Leaf-sucking insects would also be affected by qualitative leaf changes associated with enhanced $[\text{CO}_2]$. For mites, increased epidermal or leaf thickness could reduce infestation (Joutei et al. 2000). However, positive effects of $[\text{CO}_2]$ on mite infestation have been observed and were associated with an increase in the concentration of nonstructural carbohydrates (Heagle et al. 2002). Ostensibly, phloem feeders such as aphids should be less responsive to $[\text{CO}_2]$ -induced changes in leaf quality as they avoid the majority of plant-derived secondary metabolites. However, increases in population density were observed for aphids (*Myzus persicae*) on groundsel (*Senecio vulgaris*) and annual blue grass (*Poa annua*) (Bezemer et al. 1998), and increases in the daily rate of nymph production were observed for the aphid *Aulacorthum solani* on bean (*Vicia faba*) (Awmack et al. 1997). The basis for the increased performance of these aphids at elevated- $[\text{CO}_2]$ -grown plants is unclear; presumably, if all other limiting factors on aphid populations remain unchanged, then aphid damage and diseases carried by aphids could be more severe as atmospheric $[\text{CO}_2]$ increases.

Whether the response observed at the leaf or plant level is consistent with the community response is undetermined. Certainly there are compensatory changes,

particularly in leaf production, that could overcome insect related damage (Hughes and Bazzaz 1997), but whether the production of new tissue could stimulate additional feeding is unknown. For scrub oak and marsh ecosystems, less infestation of leaf eaters was observed at the higher $[\text{CO}_2]$ concentration (Thompson and Drake 1994; Stiling et al. 2002). Whether this is related to leaf qualitative changes (e.g., N), or more complex community level processes is unknown. Certainly, preferential herbivore feeding on one species may have a positive benefit on another plant species less affected by $[\text{CO}_2]$. Overall, however, most data to date have focused on single insect-host crop interactions, making a more complex assessment of insect risks to agroecosystems with increasing $[\text{CO}_2]$ tentative.

11.5.2 $[\text{CO}_2]$ AND PLANT DEFENSES

Because increasing atmospheric $[\text{CO}_2]$ alters C:N ratios, nutritional quality, and photosynthate supply, the production of secondary compounds will be affected. It has been widely observed that herbivore feeding is strongly influenced by leaf allelochemicals as well as by leaf nutritional quality (Lincoln and Couvet 1989). The carbon to nutrient balance hypothesis (Bryant et al. 1983) predicts that the increase in internal C availability will activate the synthesis of C-based secondary defense chemicals, with subsequent reductions in leaf quality for leaf-feeding insects. A number of studies have shown that the level of secondary (carbon-based) products tends to increase with enhanced $[\text{CO}_2]$ (Lavola and Julkunen-Titto 1994; Lindroth 1996; Lindroth and Kinney 1998; Lindroth et al. 1993, 1997), although this response is not universal (Kerslake et al. 1998). However, even if no increase in secondary compounds was observed, a decline in leaf protein levels under CO_2 enrichment would result in an increase in the ratio of allelochemicals per unit of protein, with subsequent negative effects on insects due to higher consumption rates and increased exposure.

11.6 CLIMATE AND INSECTS

11.6.1 WARMING

Although high temperature stress could increase crop vulnerability to insects directly, temperature is widely recognized as the principle abiotic factor controlling insect growth and development. Porter et al. (1991) hypothesized that climate warming could alter geographical distribution, increase overwintering, and lead to a subsequent reduction in generation time and increased generational number. Patterson et al. (1999) provides an extensive list of climatic thresholds, associated phenological responses, and potential shifts in the expansion of insect ranges. They suggest that for temperate regions, warming may lead to increased winter survival, while at northern latitudes, warming would speed up growth and increase fecundity. However, range expansion of insects will be dependent on plant host expansion as well, and it is likely that such expansion is species specific. Gutierrez (Figure 5, 2000) has suggested that predator and insect herbivores are likely to respond differently to increasing temperature, with possible reductions in insect predation. The

synchronization between crop and insect may also be affected if increased temperature alters photoperiod sensitivity. Increased invasion by migratory exotic pests has also been hypothesized because pests could colonize crops present at distant locations. This was suggested by Cannon (1998), who examined the spread of nonindigenous species in northwestern Europe, and the implications for insect invasion in the United Kingdom. Overall, most of these projected changes are likely to be detrimental to crop production. However, given species-specific adaptation (Bale et al. 2002) and the complexity of ecosystem interactions and human mitigation responses, long-term predictions regarding temperature remain conditional.

11.6.2 WATER AVAILABILITY

Precipitation extremes such as droughts or floods are associated with changes in insect herbivory and projected shifts in availability will have significant impacts on agricultural ecosystems (Fuhrer 2003). Intense precipitation has been shown to act as a deterrent to the occurrence and success of oviposition by insects (e.g., European corn-borer, Davidson and Lyon 1987). Flooding may also have a negative impact on soil-dwelling insects (Watt and Leather 1986) or indirect effects on pathogens, predators, and parasites, as has been shown for *Helicoverpa zea* pupae in a corn system (Raulston et al. 1992). Conversely, drought, which concentrates carbohydrates or sugars at the leaf level, may make the host plant more attractive to insect pests, particularly phytophagous insects (Mattson and Haack 1987). As with temperature, projected changes in extreme precipitation events are likely to shift the occurrence and frequency of insect outbreaks. For example, Drake (1994) demonstrated that increased variability in precipitation was one factor in determining the size and quality of insect populations in Australia. Increased precipitation from the El Niño event of 1997 and 1998 was hypothesized as one factor in the spread of the little fire ant (*Wasmannia auropunctata*), an alien species in the Galapagos Islands (Roque-Albelo and Causton 1999).

11.7 CO₂ AND PLANT PATHOGENS

Overall, plant pathogens are recognized as a significant limitation on agronomic productivity. As with insects, while plant pathogens can be directly affected by high levels of CO₂ (e.g., > 5%), current and anticipated atmospheric concentrations (0.03 to 0.07%) are likely to have little direct effect on these microorganisms; this is particularly true for soilborne pathogens, which are exposed to much higher concentrations of CO₂ in the edaphic environment than exist in the atmosphere (Lamborg et al. 1983). However, one factor affecting pathogenesis is the condition of the crop host. In general, any condition that promotes plant health will better enable plants to either resist or tolerate infection by pathogenic microbes. A basic concept of plant pathology is the *disease triangle* (Figure 11.1), which simplistically demonstrates that susceptible host, pathogenic microorganism, and environment interact in a variety of ways to affect infection and disease development. For example, even with a susceptible host, many fungal pathogens cannot achieve infection unless sufficient moisture is present (environment). It is not difficult to perceive that changes in

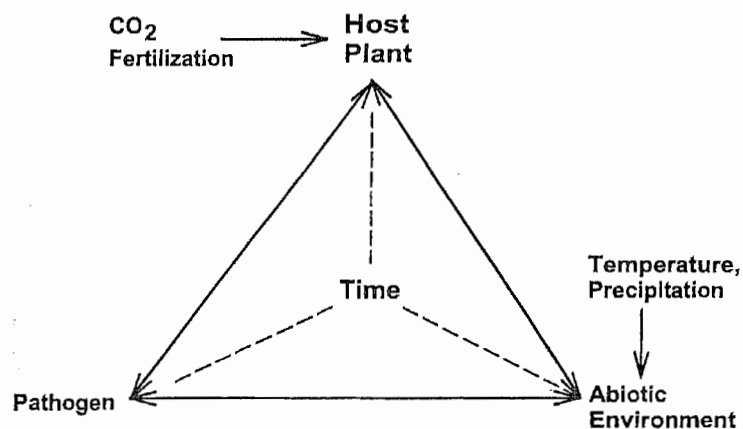


FIGURE 11.1 Interrelationships among time, pathological organisms, abiotic environment, host plant, and potential alterations as a function of climate and CO₂ fertilization.

atmospheric composition might influence disease incidence and severity; in fact, there are a number of recognized [CO₂]-induced changes that could, potentially, alter the susceptibility of crops to disease.

At the leaf level, reductions in stomatal aperture could reduce infection by stomatal-inhibiting pathogens such as rust and downy mildew fungi (Rudolph 1993). Similarly, increased epicuticular waxes, papillae, leaf surface thickness, and silicon accumulation at the sites of penetration could decrease disease incidence by pathogens that infect via direct penetration (Thomas and Harvey 1983; Hibberd et al. 1996). Improved water use efficiency and leaf water content could promote sporulation by foliar fungi (Thompson and Drake 1994; Woolacott and Ayres 1984). Increases in leaf carbohydrate content could also promote growth and reproduction of pathogens once infection occurs (Hibberd et al. 1996). Alternatively, reductions in leaf nitrogen content could reduce pathogen load and disease severity (Thompson and Drake 1994; Thompson et al. 1993). Delays in leaf senescence could increase disease severity by increasing the exposure time to the pathogen (Tiedemann and Firsching 1998) or pathogen load (Malmstrom and Field 1997), while accelerated ripening and senescence would reduce the infection period. Increased fungal fecundity (spores produced/lesion area) has also been reported to occur under elevated CO₂ (Chakraborty et al. 2000). An increase in spore numbers implies increased inoculum pressure for subsequent infection cycles and, generally, an increase in the spread and severity of disease. This could also have important implications for the functional duration of disease resistance in crop plants.

For whole plants, stimulation of plant biomass (leaves, shoots, tiller, leaves flowers, and so forth) by higher levels of atmospheric CO₂ increases the mass of host tissue for infection and use by pathogens. However, larger plants may tolerate more severe levels of infection without subsequent reductions in yield. Elevated [CO₂] can increase the production of defensive compounds (e.g., prunasin, phenolics, tannins), which could effect subsequent changes in pathogenesis (Gleadow et al. 1998, Runion et al. 1999). Although this has been studied in regard to insect performance and herbivory (Fajer et al. 1989; Lincoln and Couvet 1989), no work has addressed the impact of CO₂-altered allelochemical production on plant-microbe

interactions. This could be of critical importance because infection by pathogenic microbes often elicits phytoalexin production (Mansfield 1982), while this may or may not be the case for insect herbivory (Zangerl and Bazzaz 1992). Below ground, increased root biomass and root length may increase the proportion of host tissue available for mycorrhizal fungi, nitrogen-fixing bacteria, or pathogens; similarly, increased root exudation could stimulate both beneficial and pathogenic microflora (Manning and Tiedemann 1995).

At the community level, increased density and height could increase humidity within the crop canopy, promoting growth and sporulation of most leaf-infecting fungi (e.g., rusts, powdery mildew, anthracnose; Chakraborty et al. 2000). Increased canopy residues at the end of the growing season could also potentially improve conditions for pathogenic overwintering (Manning and Tiedemann 1995). Essentially, any condition that improves production or survival of pathogen inocula on a host in one season has crucial implications for development of disease in subsequent cropping cycles.

Overall, while there are numerous CO₂-induced mechanisms that could alter disease susceptibility in host plants, field-based observations regarding the interaction of elevated CO₂ on pathogen biology have remained scarce, although exceptions exist (Chakraborty and Data 2003; Mitchell 2003; Montealegre et al. 2000). There is little doubt that increasing atmospheric [CO₂] will elicit complex changes in plant-microbe interactions; the current challenge is to determine predictable ways in which these effects will vary (e.g., biotrophic vs. necrotrophic pathogens; Runion et al. 1994). To date, the extremely limited attention given this field of study precludes any ability to make generalized predictions with confidence; diseases may increase, decrease, or show no change (Coakley 1995). The single consistent conclusion provided from the literature is that more research is needed to fill this important and fundamental void.

11.8 CLIMATE AND PLANT PATHOGENS

The relationship between climate variation, particularly temperature and water availability, and the incidence and severity of plant disease has long been recognized (Colhoun 1973); these are principle factors in the abiotic environment portion of the disease triangle (see Figure 11.1). The effects of temperature and moisture variation on pathogenic microbes and on disease development have been researched for over a century with varying effects depending on the exact environmental conditions and the microorganism or pathosystem of interest (e.g., Lonsdale and Gibbs 1996). While these results are too detailed to discuss here, it should be noted that disease development is generally favored by warm, moist conditions. Mild winters and warmer weather have been associated with increased outbreaks of powdery mildew, leaf spot disease, leaf rust, and rizomania disease (see Patterson et al. 1999), presumably in part because overwintering results in an increase in the amount of initial inoculum present in the spring. Warm, humid conditions may result in earlier and stronger incidence of late potato blight (*Phytophthora infestans*), a devastating disease of significant historical importance (Parry et al. 1990). Warmer temperature would also be likely to shift the occurrence of disease into cooler regions (Treharne 1989).

Increased precipitation per se is likely to increase the spread of diseases since rain and splash water both spread spores (Royle et al. 1986) and wet plant surfaces are necessary for spore germination and infection to proceed. Conversely, increasing aridity could lessen disease problems, although some diseases such as powdery mildew are promoted by hot, dry daytime conditions if nighttime temperatures result in dew formation (Gouk and Hill 1990). While extreme climatic conditions (drought, flood) will undoubtedly impact microorganisms directly, their effects on host plant stress are also of concern. Stressed plants are often more susceptible to pathogen attack and abiotic stresses, such as those caused by drought, and are often cited as primary contributors to disease complexes such as diebacks and declines (Manion and LaChance 1992). Drought can also effect production and concentration of plant defensive compounds; thus, these secondary plant metabolites may increase or decrease depending upon the duration and severity of the stress (Gershenson 1984).

To make matters even more complex, it is known that elevated atmospheric [CO_2] interacts with micrometeorological parameters to affect growth and health of plants. The primary example of this is the effect of increased CO_2 on water use efficiency. Increasing CO_2 generally increases photosynthesis and reduces stomatal conductance, thus increasing leaf-level water use efficiency (Rogers and Dahlman 1993). Therefore, under drought conditions, elevated CO_2 may provide a mechanism for moderation of stress. However, CO_2 -induced increases in plant growth may offset increased leaf-level water use efficiency and, thus, the ability of elevated CO_2 to ameliorate the effects of drought (Runion et al. 1999). There is little doubt that these interactions will not only impact plant growth but also interactions with pathogenic microorganisms.

Although the importance of these aspects of plant-pest interactions are recognized and beginning to be addressed (Coakley et al. 1999; Rosenzweig et al. 2000), our ability to predict the impacts of climatic changes on natural and managed ecosystems and their interactions with pathogenic microorganisms is severely hampered by a lack of rigorous scientific knowledge. Hence, our ability to determine the impact on food security is tenuous at best. It is crucial, therefore, that we further our understanding of these interactions and of the mechanisms that drive them, if we are to continue to provide adequate supplies of food and fiber to a world having a future, altered environment.

11.9 IMPLICATIONS FOR THE MANAGEMENT OF WEEDS, INSECTS, AND DISEASES

It is difficult to derive the exact cost of managing pests. The cost of herbicide alone for the United States (~US\$3 billion) is approximately equal to the value of lost crop production due to weedy competition (~US\$4 billion) for a minimum estimate of US\$7 billion (Bunce and Ziska 2000). However, the technology and associate costs of pest control vary by location and do not always include indirect environmental costs such as soil erosion or pollution.

11.9.1 CHEMICAL MANAGEMENT, CLIMATIC EFFECTS

Clearly, any direct or indirect impacts from a changing climate will have a significant effect on chemical management. Changes in temperature, wind speed, soil moisture, and atmospheric humidity can influence the effectiveness of applications (reviewed in Muzik 1976). For example, drought can result in thicker cuticle development or increased leaf pubescence, with subsequent reductions in pesticide entry into the leaf. These same variables can also interfere with crop growth and recovery following pesticide application. Overall, pesticides are most effective when applied to plants that are rapidly growing and metabolizing — those free from environmental stress.

11.9.2 CHEMICAL MANAGEMENT, DIRECT CO₂ EFFECTS

Although the effects of climate on pesticide efficacy have been well studied, can [CO₂] directly affect chemical control? There are an increasing number of studies (Ziska and Teasdale 2000; Ziska et al. 1999) that demonstrate a decline in efficacy with rising [CO₂] (Table 11.2). In theory, rising [CO₂] could reduce foliar absorption of pesticides by reducing stomatal aperture or number, or by altering leaf or cuticular thickness. In addition, [CO₂]-induced changes in transpiration could limit uptake of soil-applied pesticides. For weed control, timing of application could also be affected if elevated [CO₂] decreases the time the weed spends in the seedling stage (the time of greatest chemical susceptibility). For perennial weeds, increasing [CO₂] could stimulate greater belowground growth (rhizomes, tubers, roots), diluting the active ingredient and making chemical control more difficult and costly. At the biochemical level, [CO₂] could alter herbicide-specific chemistry in such a way as to directly reduce the efficacy of the active ingredient. For example, glyphosate inhibits aromatic amino acid production through the shikimic acid pathway; if [CO₂] reduces the protein content per gram of tissue (Bowes 1996), this would result in less demand for aromatic amino acids.

At present, little is known mechanistically regarding how [CO₂] would directly alter pesticide efficacy. For herbicides, short-term switching of quackgrass to the elevated [CO₂] condition just prior to spraying did not increase tolerance, suggesting that stomatal closure did not play a factor in efficacy (Ziska et al. 1999). Recent unpublished data for Canada thistle indicated that significant increases in belowground relative to shoot biomass (Figure 11.2) could be associated with increased herbicide tolerance (Table 11.2). This is in agreement with the idea that tolerance may be simply a dilution effect of systemic herbicides associated with the large stimulation of root relative to shoot biomass at elevated [CO₂].

It can be argued that [CO₂]-induced changes in efficacy are irrelevant given the rate of atmospheric [CO₂] increase (other pesticides will be developed in the future). However, pesticide use can persist over decades (e.g., 2-4D has been in continuous use since 1950), coinciding with significant increases in atmospheric [CO₂] (310 to 375 ppm from 1950 to 2003 for 2-4D). At present, many commercial ventures are investing in genetically modified crops specific for a given herbicide; consequently, it is likely that the use of these associated herbicides (e.g., glyphosate) would persist for decades. Furthermore, as mentioned previously, atmospheric [CO₂] is not uniform

TABLE 11.2
Changes in Efficacy Determined as Changes in Growth (g day⁻¹) Following Herbicide Application for Weeds Grown at Either Current or Projected Future Levels of Carbon Dioxide

Species (Common name)	CO ₂ p.p.m.	Environment	Herbicide	Growth g day ⁻¹
lambsquarters	365	GH	glyphosate	0.09 (death)
	723	GH	glyphosate	1.37
red-root pigweed	365	GH	glyphosate	0.04 (death)
	723	GH	glyphosate	0.18
quackgrass	388	GH	glyphosate	-0.05 (death)
	721	GH	glyphosate	1.14
Canada thistle	421	OTC	glyphosate	0.55
	771	OTC	glyphosate	1.37
Canada thistle	421	OTC	glufosinate	0.52
	771	OTC	glufosinate	1.14

Notes: Plants were followed for a 2- to 4-week period. Data for Canada Thistle (unpublished) are based on top (shoot) growth only. All weeds were sprayed with manufacturer recommended levels of the herbicide. Data for lambsquarters, red-root pigweed, and quackgrass are from Ziska and Teesdale, 2000. GH and OTC are greenhouse and open-top chamber, respectively.

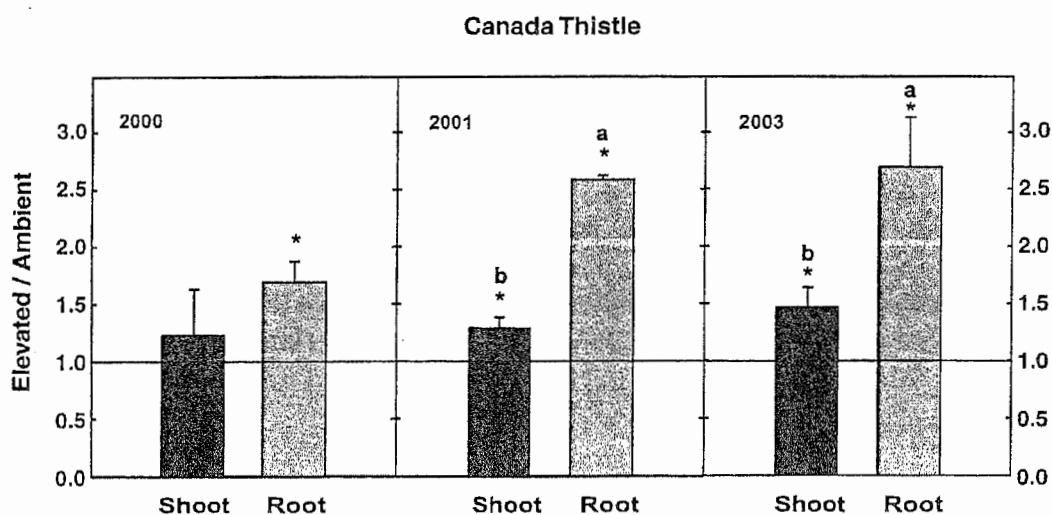


FIGURE 11.2 Shoot and root biomass at elevated (765 ppm) relative to ambient (414 ppm) CO₂ concentration for the invasive weed, Canada thistle, in 2000, 2001, and 2003 at the time of herbicide application from the unsprayed plots. Shoot biomass refers to all aboveground herbaceous material. Root biomass was obtained from soil subsamples (2.43 l in volume, to a depth of 30 cm). Bars indicate \pm SE. The asterisk (*) indicates a significant difference ($P < 0.05$) relative to unity (no [CO₂] treatment effect); different letters indicate differences in the relative stimulation of shoots and roots.

and can differ as a function of urbanization. For example, effective chemical control of ragweed in an urban setting with high $[\text{CO}_2]$ and temperature is likely to be different than in a farm setting for the same herbicide concentration (see Ziska et al. 2003). Overall, chemical control will still be possible with climatic changes or rising $[\text{CO}_2]$, but additional spraying or increasing concentrations may be necessary. How these potential changes will alter economic and environmental costs is unclear.

11.9.3 BIOLOGICAL CONTROL

Biological control of pests by natural or manipulated means is likely to be affected by increasing atmospheric $[\text{CO}_2]$ and climatic change (Norris 1982; Froud-Williams 1996). Climate as well as $[\text{CO}_2]$ could alter the efficacy of the biocontrol agent by potentially altering the development, morphology, and reproduction of the target pest. Direct effects of $[\text{CO}_2]$ would also be related to changes in the ratio of C:N and alterations in the feeding habits and growth rate of herbivores. As pointed out by Patterson (1995a), warming could also result in increased overwintering of insect populations and changes in their potential range. Although this could increase both the biological control of some weeds, it could also increase the incidence of specific crop pests, with subsequent indirect effects on crop-weed competition. Overall, synchrony between development and reproduction of biocontrol agents and their selected targets is unlikely to be maintained in periods of rapid climatic change or climatic extremes. Whether this will result in a positive or negative result remains unclear.

11.9.4 MECHANICAL CONTROL

A principal means of controlling weed populations, and the one most widely used in developing countries, is mechanical removal of the undesired plant. Tillage (by animal or mechanical means) is regarded as a global method of weed control in agronomic systems. Elevated $[\text{CO}_2]$ could lead to further belowground carbon storage with subsequent increases in the growth of roots or rhizomes, particularly in perennial weeds (see Rogers et al. 1994, for a review). Consequently, mechanical tillage may lead to additional plant propagation in a higher $[\text{CO}_2]$ environment, with increased asexual reproduction from belowground structures and negative effects on weed control (e.g., Canada thistle).

11.10 CONCLUSIONS

It is remarkable given the importance of weeds, insects, and diseases to crop production and food security, that so few experimental data are available assessing the impact of rising atmospheric $[\text{CO}_2]$ or rapid climatic change on their biology. Furthermore, most of the data that are available are based on studies in controlled environment chambers or glasshouses, usually with a single host-pest focus. This represents a significant limitation because extrapolation of such studies to field environments may differ due to light or edaphic factors (see Ghannoum et al. 1997).

How can our current knowledge base be improved? At the whole plant level, quantification of [CO₂]- and climate-induced changes in host plant performance, including a temporal and spatial analysis of secondary compounds and allelopathic effects, anatomical and qualitative changes that alter pest susceptibility, and an integrated assessment of weed and crop germination, phenology, and allometry are necessary. If possible, evaluation of these parameters should be conducted at projected extremes of temperature and water availability. At the community level, a mechanistic understanding of how [CO₂] and climate alter weed populations and associated seed banks, canopy microclimate, and pathogen load is also essential. For pathogens in particular, information on stages and rates of development and changes in the physiology of host-pathogen interactions is critical (Coakley et al. 1999). These suggestions are by no means inclusive, and given the paucity of data, there will be a number of fertile areas of inquiry. It should be emphasized, however, that hypotheses that consider multifactor responses, particularly at the ecosystem level, are highly preferable.

As has been illustrated in this review, much of what is currently known regarding the consequences of climatic change on pest biology and crop productivity is based on single-factor experiments. While useful, such experiments are limited in their ability to predict consequences for agroecosystems. We could, of course, continue to use existing knowledge to project how cropping systems might respond, but few data are available to validate whether current paradigms will accurately predict crop-pest relationships in a changing climate. There are likely to be unforeseen differences that will influence our understanding of potential impacts (e.g., temperature induced shifts in insect ranges), and subsequent mitigation and management efforts (e.g., [CO₂]-induced changes in herbicide efficacy). Overall, any accurate assessment of future threats will be dependent on modeling efforts that consider variable combinations of limiting factors while recognizing that interactions at the agroecosystem level are governed by a complex set of feedbacks among soil, plant, atmosphere, and pest populations.

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