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SUCCESSION AT THE EL VERDE RADIATION SITE

A 17 YEAR RECORD

SUSAN SILANDER

MARCH 1985

CENTER FOR ENERGY AND ENVIRONMENT RESEARCH
UNIVERSITY OF PUERTO RICO   U.S. DEPARTMENT OF ENERGY

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A 10,000-curie cesium source was placed in the tabonuco forest at El Verde, Puerto Rico for a period of 92.8 days from January 19, 1965 to April 26, 1965. The objectives of this study were to evaluate the effects of this irradiation upon the forest and to add to the understanding of the structure and function (processes such as nutrient cycling, energy flow, and regeneration) of the rain forest. This disturbance and the consequent creation of a canopy gap provided an ideal opportunity to examine the successional process, for which there exist few data in the tropics, on a long-term basis, to compare an irradiated to a cut-over area and to evaluate the effects, if any, the irradiation had upon regeneration. This document provides an overview of data collected to date, background material for future censuses, and successional trends observed. Many statistical analyses remain to be applied to the census data.

The El Verde study site is located at an elevation of 450 m in the Luquillo Experimental Forest (also Caribbean National Forest) of northeastern Puerto Rico and lies within the subtropical wet forest life zone (Ewel and Whitmore, 1973; Figure 1). The mature vegetation of the site has been described as the tabonuco forest type by Wadsworth (1951; also as lower montane rain forest by Beard, 1955). The dominant species is tabonuco (*Dacryodes excelsa*) and other important species include motillo (*Sloanea berteriana*), yagrumo hembra (*Cecropia peltata*), caimitillo (*Micropholis garciniaefolia*), and the sierra palm (*Prestoea montana*). In a 4 ha sample of mature forest Wadsworth (1951) found that *D. excelsa* had the greatest number of stems in the largest size class whereas the

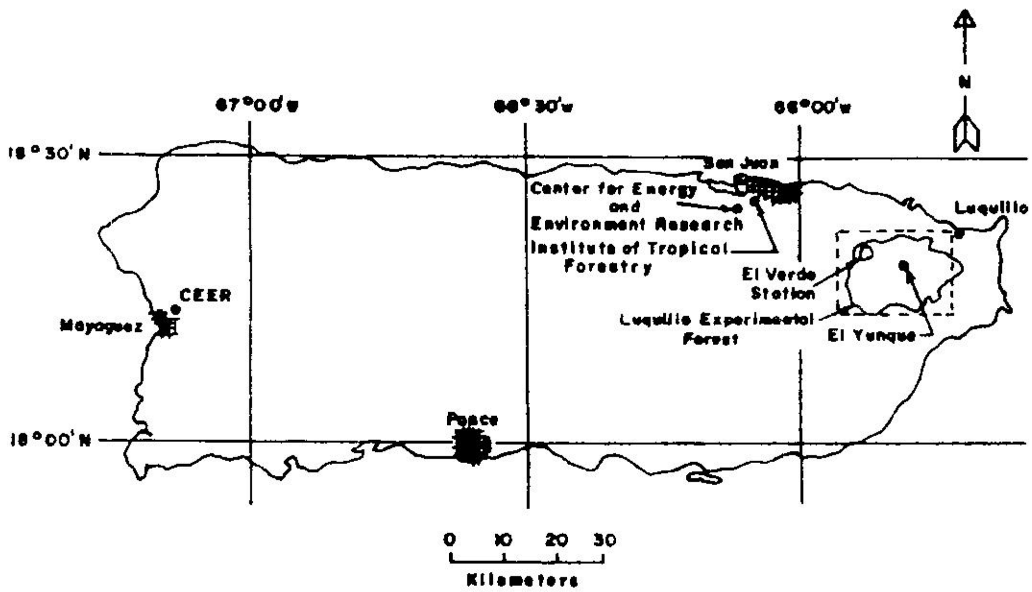


Figure 1. Location of El Verde in the Caribbean National Forest (Luquillo Experimental Forest).

majority of stems of *P. montana*, the most numerous species, were in the smallest size class (Table 1).

Prior to the initiation of radiation, preliminary studies of species composition by synusiae and of plant density were carried out in the El Verde site (Table 2). In a sample area of 2 ha a total of 214 species from all synusiae (canopy, understory, climbers, stranglers, epiphytes, herbs, saprophytes, and semi-parasites) were reported (Smith, 1970). Total density of canopy trees ($>$ 10 cm DBH) was 870/ha and of all trees greater than 4.5 ft (1.4 m) in height (i.e. stems with diameter at breast height-DBH) was 8120/ha. The dominant canopy species included *Dacryodes excelsa*, *Prestoea montana*, *Croton poecilanthus*, and *Sloanea berteriana* and dominant understory species were *Palicourea riparia*, *Drypetes glauca*, and *Cordia borinquensis*. The most abundant climbers or vines were *Rourea glabra*, *Philodendron krebsii*, *Marcgravia rectiflora*, and *Heteropteris laurifolia*. Total density of climbers was $.133/m^2$. *Ichnanthes pallens* (Graminae) and *Pilea krugii* (a herb) composed over 50% of the ground flora. Total density of herbs and ferns was $1.44/m^2$ and of arborescent seedlings $2.72/m^2$.

Plant biomass in the mature tabonuco forest was estimated to be 27.2 kg/m^2 and was distributed in the following manner: 939 g/m^2 as leaves; 7230 g/m^2 as roots; and 19.0 kg/m^2 as bole and branch wood (Odum, 1970). Above ground plant biomass was 19.9 kg/m^2.

Table 1 - Size class distribution of the species found in a 4 ha sample of tabonuco forest (from Wadworth, 1951).

Species	Number of trees by dbh (cm)				
	10–15	20–25	30–35	40+	Total
Cyrilla racemiflora L.	29	22	43	82	176
Micropholis garcinifolia Pierre	228	120	111	15	474
Calycogonium squamulosum Cogn.	239	122	81	3	445
Euterpe globosa Gaertn.*	873	12	...	...	885
Micropholis chrysophylloides Pierre	165	79	51	4	299
Cecropia peltata L.	47	12	9	...	68
Magnolia splendens Urban	22	7	6	11	46
Croton poecilanthus Urban	210	36	3	...	249
Ocotea spathulata Mez	62	33	17	1	113
Tabebuia rigida Urban	27	10	13	...	50
Dacryodes excelsa Vahl.	7	7	10	2	26
Ilex nitida (Vahl) Maxim	29	6	10	1	46
Inga laurina (Sw.) Willd	18	2	8	...	28
Sapium laurocerasus Desf.	13	7	4	1	25
Sloanea berteriana Choisy	14	5	3	...	22
Matayba domingensis (DC.) Radlk.	22	5	2	...	29
Eugenia stahlii (Kiaersk) Krug & Urban	7	10	2		19
*Homalium racemosum** Jacq.	4	...	5	...	9
Linociera domingensis (Lam.) Knobl.	11	4	3		18
Didymopanax morototoni (Aubl.) Dcne.	9	7	2	...	18
Cordia borinquensis Urban	39	1		...	40
Ocotea moschata (Pavon.) Mez.	2	1	1	1	5
Alchornea latifolia Sw.	19	4	...	...	23
Hirtella rugosa Pers.	14		1	...	15
Ditta myricoides Griseb.	17	2	...	...	19
Ficus laevigata Vahl	5	3	1	...	9
Ficus sintenisii Warb	7	1	...	...	8
30 other species	159	30	22	1	212
Totals	2,298	548	408	122	3,376

**Prestoea montana*

Table 2 - Species composition of tabonuco forest at the El Verde by relative density (from Smith, 1970).

Name	Relative density %*
CANOPY TREES—Species with dbh > 10 cm	
Total area sampled: 1.57 ha	
Total absolute density: 0.087 tree/m²	
Dacryodes excelsa Vahl	18.2
Euterpe globosa Gaertn.	11.4
Croton poecilanthus Urban	9.5
Sloanea berteriana Choisy	8.1
Manilkara bidentata (A. DC.) Cher.	6.4
Miconia tetrandra (Sw.) D. Don	5.5
Cecropia peltata L.	4.6
Ormosia krugii Urban	3.1
Matayba domingensis (DC.) Radk.	3.0
Inga fagifolia (L.) Willd.	2.7
Linociera domingensis (Lam.) Knobl.	2.0
Alchornea latifolia Sw.	1.9
Alchorneopsis portoricensis Urban	1.8
Sapium laurocerasus Desf.	1.7
Tabebuia pallida Miers	1.7
Buchenavia capitata (Vahl) Eichl.	1.7
Micropholis garciniaefolia Pierre	1.6
Ocotea leucoxylon (Sw.) Mez	1.1
Calycogonium squamulosum Cogn.	1.1
Guarea trichilioides L.	1.1
Didymopanax morototoni (Aubl.) Decne. & Planch.	1.0
Inga vera Willd.	1.0
Eugenia stahlii (Kiaersk.) Krug & Urban	0.9
Cyrilla racemiflora L.	0.9
Guettarda laevis Urban	0.9
Ocotea spathulata Mez	0.7
Casearia sylvestris Sw.	0.6
Homalium racemosum Jacq.	0.5
Casearia arborea (L.C. Rich.) Urban	0.5
Cordia sulcata DC.	0.5
Ocotea moschata (Meisn.) Mez	0.5
Casearia bicolor Urban	0.5
Byrsonima coriacea (Sw.) DC.	0.5
Tetragastris balsamifera (Sw.) Kuntze	0.4
Miconia prasina (Sw.) DC.	0.3
Symplocos sp.	0.3
Magnolia splendens Urban	0.3
Meliosma herbertii Rolfe	0.2
Henriettella fascicularis (Sw.) C. Wright	0.2
Myrcia deflexa (Poir.) DC.	0.1
Eugenia jambos (L.) Millsp.	
Roystonea borinquena O. F. Cook	
Beilschmiedia pendula (Sw.) Benth. & Hook. f.	
Cyathea arborea (L.) J. E. Smith	
Antirhea coriacea (Vahl) Urban	
Micropholis chrysophylloides Pierre	
Citharexylum caudatum L.	
Pisonia subcordata Sw.	
Byrsonima wadsworthii Little	
Haenianthus salicifolius var. *obovatus* Knobl.	
Andira inermis (W. Wright) H. B. K.	
Coccoloba swartzii Meisn.	
Ilex sideroxyloides (Sw.) Griseb.	
Nectandra sintenisii Mez	
UNDERSTORY TREES—Species that flower under the main canopy and low shrubs of secondary forests	
Total area sampled: 0.28 ha	
Total absolute density: 0.224 tree/m²	
Total density including all plants from 1.4 m tall to 10 cm dbh: 0.725 tree/m²	
Palicourea riparia Benth.	41.5
Drypetes glauca Vahl	19.4
Cordia borinquensis Urban	10.7
Hirtella rugosa Pers.	7.4
Psychotria berteriana DC.	3.8
Myrcia leptoclada DC.	3.6
Trichilia pallida Sw.	3.3
Ixora ferrea (Jacq.) Benth.	2.9
Lasianthus lanceolatus (Griseb.) Urban	1.9
Cassipourea guianensis Aubl.	1.5
Myrcia splendens (Sw.) DC.	0.9
Guarea ramiflora Vent.	0.7
Comocladia glabra (Schultes) Spreng.	0.7
Ocotea portoricensis (Mez)	0.6
Daphnopsis philippiana Krug & Urban	0.3
Ardisia glauciflora Urban	0.3
Wallenia pendula (Urban) Mez	0.3
Guatteria caribaea Urban	0.3
Piper treleaseanum Britton & Wilson	0.3
Piper blattarum Spreng.	0.2
Chlorophora tinctoria (L.) Gaud.	0.1
Ditta myricoides Griseb.	0.1
Samyda spinulosa Vent.	0.1
Urera baccifera (L.) Gaud.	
Piper aduncum L.	
Palicourea crocea (Sw.) R. & S.	
Psychotria maleolens Urban	
P. patens Sw.	
P. brachiata Sw.	
P. uliginosa Sw.	
Rondeletia portoricensis Krug & Urban	
Brunfelsia portoricensis Krug & Urban	
Hedyosmum arborescens Sw.	
Mecranium amygdalinum (Desr.) C. Wright	
Laplacea portoricensis (Krug & Urban) Dyer	
Oxandra laurifolia (Sw.) A. Rich.	
Cestrum macrophyllum Vent.	
Rheedia acuminata (Spreng.) Planch. & Tr.	
Malpighia fucata Ker.	
Myrcia berberis DC.	
Coccoloba pyrifolia Desf.	
Miconia racemosa (Aubl.) DC.	
Miconia sintenisii Cogn.	
Miconia guianensis (DC) Cogn.	
Maytenus sp.	
Piptocarpha tetrantha Urban	
Tabernaemontana oppositifolia (Spreng.) Urban	
CLIMBERS—Individuals that had leaves in the main canopy	
Total area sampled: 0.28 ha	
Total absolute density: 0.133 plant/m²	
Rourea glabra Griseb.	28.4
Philodendron krebsii Schott	18.0
Marcgravia rectiflora Tr.	14.0
Heteropteris laurifolia (L.) Juss.	13.7
Schlegelia brachyantha Griseb.	4.9
Neorudolphia volubilis (Willd.) Britton	4.0
Securidaca virgata Sw.	4.0
Paullinia sp.	3.4

Table 2 cont.

Name	Relative density %*
Ipomoea repanda Jacq.	3.2
Dolicocarpus calinoides (Eichl.) Gilg.	2.0
Philodendron lingulatum (L.) C. Koch.	1.4
Cissus sicyoides L.	1.2
Hippocratea volubilis L.	0.9
Smilax coriacea Spreng.	0.6
Forsteronia corymbosa (Jacq.) G.F.W. Meyers	0.3
Cissampelos pareira L.	
Rajania cordata L.	
Mikania fragilis Urban	
M. pachyphylla Urban	
Marcgravia sintenisii Urban	
Tournefortia maculata Jacq.	
Cissus sycyoides L.	
Marcgravia sintenisii Urban	
Philodendron giganteum Schott	
Hippocratea volubilis Sw.	
STRANGLERS	
Ficus laevigata Vahl	
F. sintenisii Warb.	
Clusia gundlachii Stahl.	
C. rosea Jacq.	
EPIPHYTES	
Total ground area sampled: 0.04 ha	
Total absolute density (expressed as plants/m² if the epiphytes were brought vertically to the ground): 0.47 plant/m²	
Hymenophyllum polyanthos Sw.	40.1
Guzmania berteroniana (R. & S.) Mez	28.0
Nephrolepis rivularis (Vahl) Mett.	8.5
Elaphoglossum rigidum (Aubl.) Urban	5.8
Polypodium lycopodioides L.	3.7
Epidendrum corymbosum Lindl.	3.2
Elaphoglossum dussii Underw.	2.6
Polypodium chnoodes Spreng.	1.6
Vriesia macrostachya (Bello) Mez	1.6
Hillia parasitica Jacq.	1.6
Oleandra articulata (Sw.) Presl.	0.5
Elaphoglossum herminieri (Bory & Fee) Moore	0.5
Lycopodium linifolium L.	0.5
Columnea tulae Urban	0.5
Hohenbergia portoricensis Mez	0.5
Lepanthes selenipetala Rchb.	0.5
Pleurothallis ruscifolia (Jacq.) R. Br.	0.5
Guzmania lingulata (L.) Mez	
Catopsis floribunda (Brongn.) L. B. Smith	
Lycopodium funiforme Bory	
Trichomanes punctatum Poir.	
T. crispum L.	
Polypodium astrolepis Liebm.	
P. crassifolium L.	
P. aureum L.	
P. taenifolium Jenman	
P. loriceum L.	
P. polypodioides (L.) Watt	
Elaphoglossum pteropus C. Chr. Ind.	
E. apodum (Kaulf.) Schott	
Hymenodium crinitum (L.) Fee	
Cochlidium siminudum (Willd.) Maxon	
Vittaria filifolia Fee	
Asplenium serratum L.	
Jaquiniella globosa (Jacq.) Schlechter	
Ornithidium coccineum (Jacq.) Salisb.	
Polystachya extinctoria Rchb.	
Epidendrum cochleatum L.	
E. nocturnum Jacq.	
E. n. var *latifolia*	
Vittaria remota Fee	
Peperomia emarginella (Sw.) DC.	
HERBS	
Total area sampled: 0.0064 ha (64 m²)	
Total absolute density: 1.44 herbs/m²	
Total density including seedlings: 4.16 plants/m²	
Ichnanthus pallens (Sw.) Munro	32.9
Pilea krugii Urban	26.6
Dryopteris deltoidea (Sw.) Kuntze	11.4
Arthrostylidium sarmentosum Pilger	8.9
Alsophila boringuena Maxon	8.2
Polypodium duale Maxon	3.2
Selaginella krugii Hieron	1.9
Elaphoglossum flaccidum (Fee) Moore	0.6
Anthurium dominicense Schott	0.6
Adiantum cristatum L.	
Anthurium acaule (Jacq.) Schott	
Begonia decandra Pav.	
Scleria canescens Boeckl.	
Selaginella portoricensis A. Br.	
Phacosphcrion persicariaefolius (DC.) C. B. Clarke	
Pitcairnia angustifolia (Sw.) Redoute	
Heliconia bihai L.	
Gonolobus variifolia (Schlechter) Britton	
Pilea obtusata Liebm.	
P. semidentata (Juss.) Wedd.	
Trichomanes rigidum Sw.	
Danaea elliptica J. E. Smith	
Dryopteris effusa (Sw.) Urban	
D. reticulata (L.) Kaulf.	
Polybotria cervina L. Kaulf.	
Blechnum occidentale L.	
Tectaria plantaginea (Jacq.) Maxon	
Asplenium cuneatum Lam.	
Adiantum petiolatum Desv.	
Rhipidopteris peltata (Sw.) Schott	

SAPROPHYTES AND SEMIPARASITES	Flowering time
Prescottia stachyoides (Sw.) Lindl.	March
Erythrodes plantaginea (L.) Lindl.	March
Erythrodes hirtellus (Sw.) Lindl.	Spring
Spiranthes cranichoides (Griseb.) Cogn.	March
Centrogonium setaceum Schlechter	May-June
Liparis elata Lindl.	Winter
Triphora surinamensis (Lindl.) Britton	Summer-fall
Wullschlaegelia aphylla (Sw.) Rchb.	Summer
Apteria aphylla (Nutt.) Burm.	Summer-fall
Gimnosiphon portoricensis Urban	Summer-fall
Phoradendron piperoides (H.B.K.) Trel.	

*Blanks in this column indicate species present but not sampled.

METHODOLOGY

For vegetation sampling purposes a 676 m^2 grid was established in the area immediately surrounding the cesium source with the original position of the source lying in the center (Figure 2). Vegetation sampling was carried out in 1966, 1967, 1968, 1969, 1971, 1973, 1975, and 1982.

Scientists responsible for sampling varied througout the years. Among these were Carl Jordan, Jerry Kline, Barbara Cintrón, Miguel Canals, Elvira Cuevas, Alejo Estrada, and Susan Silander. Data collected prior to 1975 were organized by Elvira Cuevas and Richard Clements. Each m^2 quadrant (1 through 676) was considered a sampling unit. Two soil types were identified within the sampling grid, a well drained or oxidized soil and a poorly-drained or reduced soil. These soil types are described by Smith (1970).

All plants within each m^2 were identified by growth habit (vine, sprout, sapling, seedling, fern, herb, or grass and sedge) and by species. Percent cover of each m^2 was estimated for each grass species. Basal diameter of seedlings and sprouts under 4.5 feet (1.4 m) in height were measured. Diameter at breast height (DBH) was measured for all other sprouts and saplings. Analyses were conducted utilizing prepared and modified programs of the Statistical Package for the Social Science (SPSS).

The following relationships (Jordan, 1968) were utilized to estimate biomass (y=biomass in grams dry weight; x=basal diameter in x/128 of an inch and N=number of samples):

1) tree shaped species ($<$ 2 inches or 5 cm basal diameter)

$$y=.0289x^2 - .2425x - 13.4557 \qquad (N=150)$$

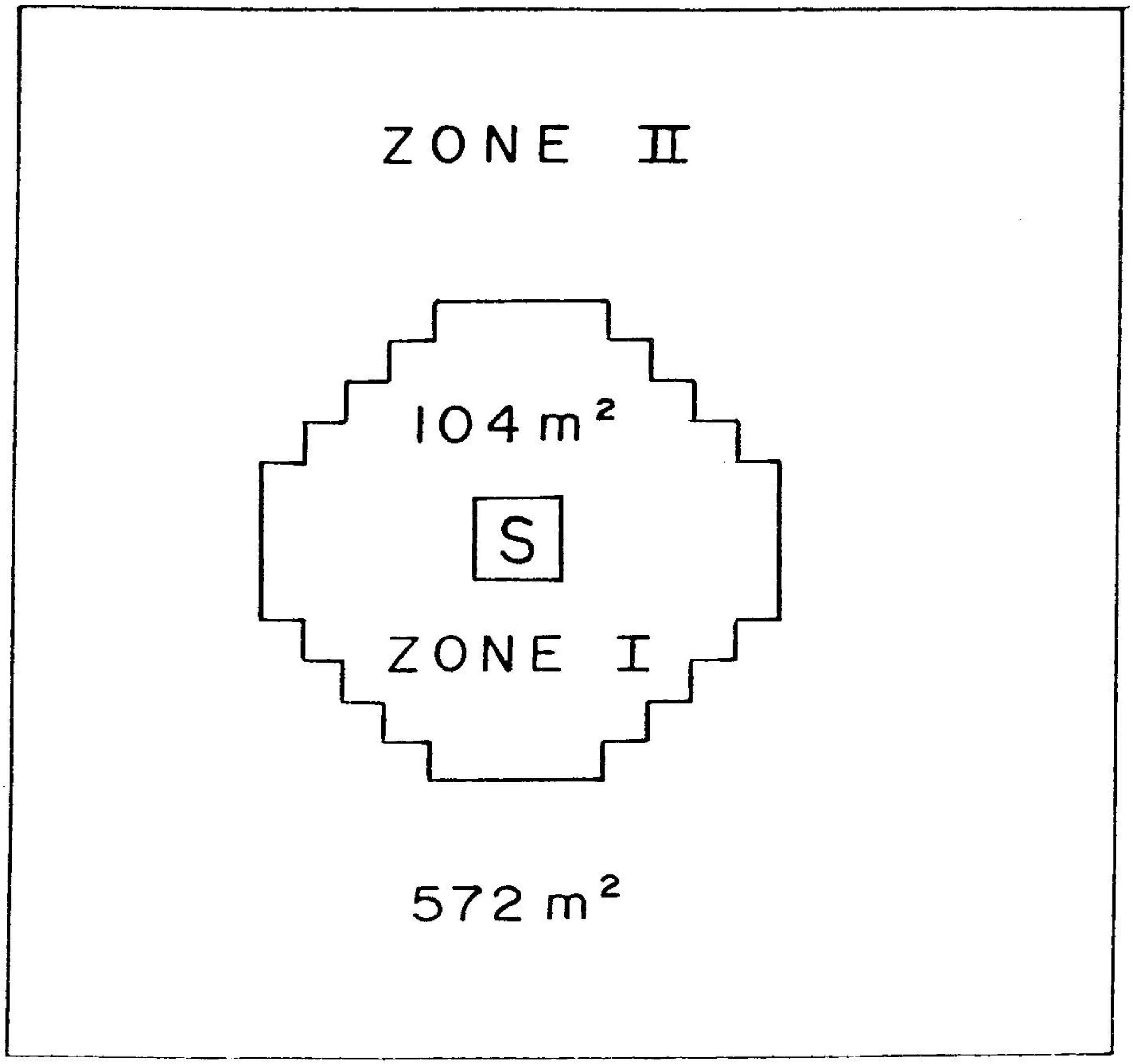


Figure 2. Vegetation sampling grid showing original location of cesium source (S) in the Center.

2) sprouts (< 2 inches or 5 cm basal diameter)

$y = .0203x^2 + .7657x - 24.40$ (N=35)

3) grasses and sedges

$y = 426$ (% coverage of 1 m^2) (N=10)

The following biomass regression (Doyle et al., 1982) was utilized in order to estimate biomass of stems for which a DBH was measured:

$$B = .1568 \, (D^{2.2337})$$

where B=biomass in kg dry weight and D=diameter at breast height (DBH) in cm. This was derived from biomass-diameter data presented by Ovington and Olson (1970).

Summary of Previous Studies

Radiation Effects and Early Secondary Succession

Changes in vegetation structure immediately following irradiation and early successional trends were examined by Jordan (1968), Odum et al. (1970), Desmarais and Helmuth (1970), Smith (1970), and McCormick (1970).

The most important effect of irradiation was defoliation and the consequent changes in the environment which occurred thereafter. Spread of radiation damage continued for 3 months following the cessation of radiation. Although plant responses occurred as far as 40 m from the cesium source, severe vegetation damage was restricted to within a 10 to 12 m radius. Environmental changes in this area included increased light levels, higher temperatures, lower relative humidities, and creased soil temperatures (Figures 3, 4, and 5; McCormick, 1970). At a distance of 10 m from the cesium source damage to seedlings consisted of the destruction of approximately half of the population during the irradiation period. Secondary species appeared to be more resistant to radiation than were primary species (Smith, 1970).

Vegetation regeneration immediately following irradiation was compared to recovery in a nearby area of similar size ("cut center") which received the following treatment: 1) pulling of all seedlings and herbs; 2) cutting of plants under 4 cm in diameter at ground level; and 3) pruning of leaf-bearing twigs off other trees. Recovery in the irradiated area was slower than that in the cut area where an explosive seedling germination, extensive sprouting, and lateral growth contributed to a rapid canopy closure. Eighteen months after irradiation, cover by new seedlings and herbs was 5.7% in the irradiated area and 27% in the cut area. By 1968 the forest floor in the cut center was similar in composition and environmental conditions to that of adjacent undisturbed forest (Odum et al., 1970). Seedling and herb regrowth in the irradiated area tended to be clumped rather than regular in distribution as is found in undisturbed forest. In both areas new seedlings were of secondary species. In the irradiated area the dominant tree seedling was roble (Tabebuia heterophylla) whereas in the cut area the dominant seedling species was Alchornea latifolia. Although both are secondary species this difference in dominance probably reflects a difference in availability of seed source. Stem and root resprouting in the irradiated area was limited (1.7%) and restricted to the side away from the source whereas by early 1966 in the cut area 21% of the trees cut had resprouted (Smith, 1970).

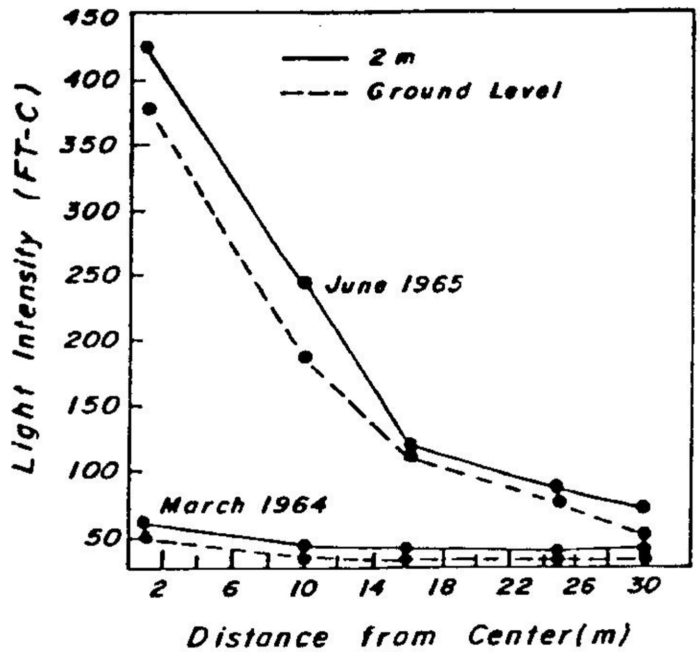


Figure 3. Light-intensity gradients in the Radiation Center before and after irradiation. Each point is an average of the measurements taken along eight different compass bearings (from McCormick, 1970).

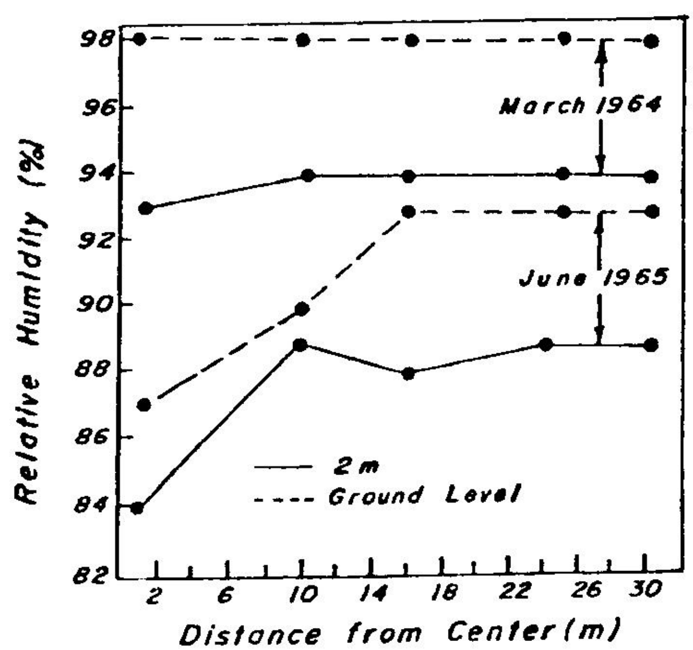


Figure 4. Relative humidity gradients in the Radiation Center before and after irradiation. Each point is an average of measurements taken along eight different compass bearings (from McCormick, 1970).

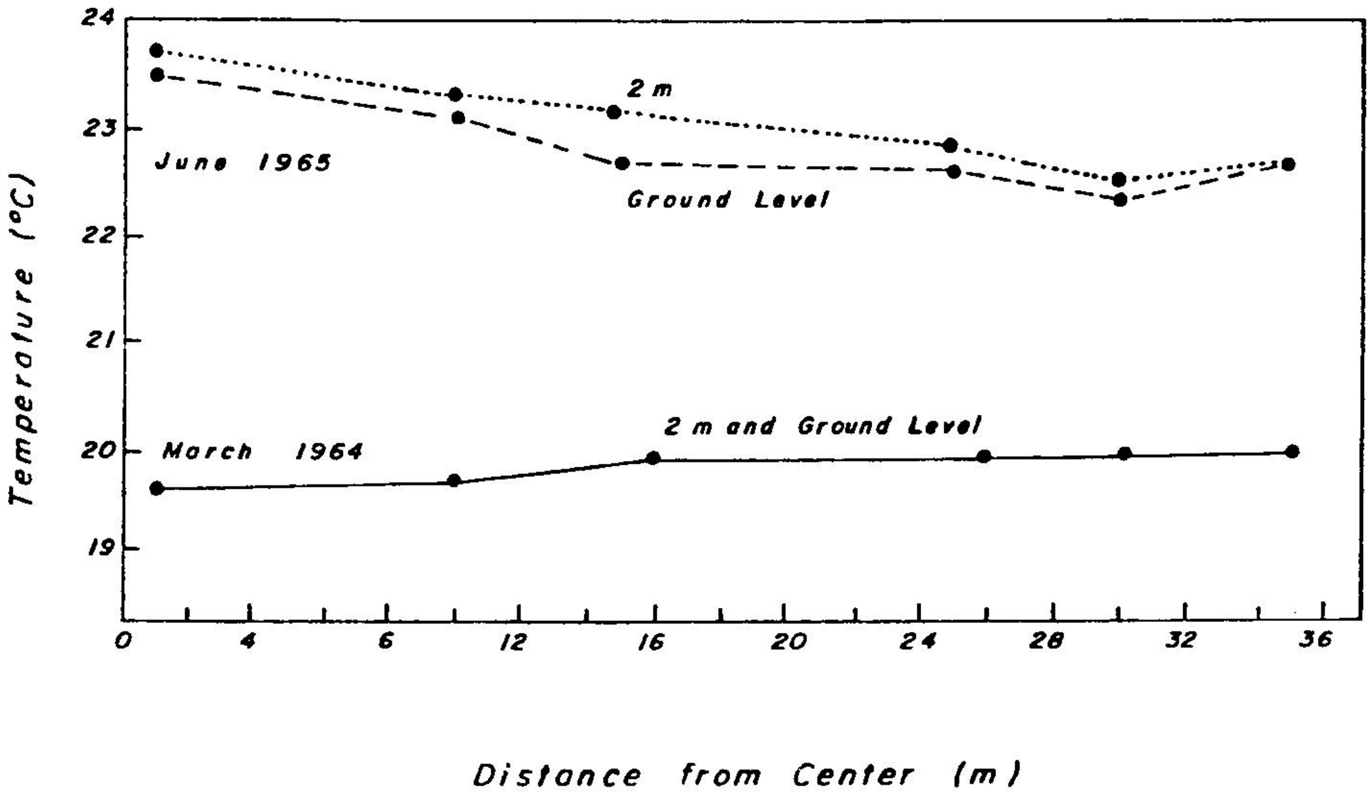


Figure 5. Temperature in the Radiation Center before and after irradiation. Each point is an average of measurements taken along eight different compass bearing (from McCormick, 1970).

Odum et al. (1970) stress that recovery of the irradiated area was delayed by 6 mos to 1 yr due to elimination of the seed bank by irradiation and that therefore seed rain or introduction probably played the primary role in recovery of the area. By 1968, in contrast to the cut area, the irradiated area supported a dense ground cover of herbs, grasses and seedlings.

Immediately following irradiation seedling species diversity was reduced in zones receiving greater radiation exposure. Seedling density, with the exception of a disproportionate increase in density in the zone which received the greatest radiation, was found to be proportional to distance from the source. Within a 10 m radius <u>Palicourea riparia</u> became much more abundant due to the changes in microclimatic conditions which occurred in this zone (McCormick, 1970).

Results of recovery studies carried out in 1966 and 1967 were summarized by Jordan (1968). Leaf area indices (LAI) were measured in 1966, 1967, and 1968 (Table 3). In the irradiated area LAI of new vegetation increased from .96 in August, 1966, to 3.26 in February, 1968, whereas LAI of old vegetation remained the same. Leaf area index of new vegetation in the cut-over area, however, remained the same during this same time period and LAI of old vegetation increased slightly, an indication of regrowth of the canopy. A total of 5246 individuals of 97 species were encountered in 1966 and 8,671 individuals of 121 species in 1967. Total biomass of new vegetation and sprouts was 163,656 grams dry weight in 1966 and 519,620 grams dry weight in 1967 (Table 4). Biomass tended to be greater on the well-drained soil in both years. In 1966 seven species, most secondary, composed approximately 54% of the biomass. Grasses and sedges composed 20.0% and sprouts 19.2% of the biomass of new vegetation.

Table 3 - Leaf area indices of new and old vegetation in the irradiated and cut areas (from Jordan, 1968)

	LEAF AREA INDEX			
	Aug. 1966	Feb. 1967	Aug. 1967	Feb. 1968
Irradiated area, new vegetation	.96	1.64	2.90	3.26
Cut area, new vegetation	1.51	1.65	1.63	1.45
Irradiated area, old vegetation	2.20	2.10	2.21	2.25
Cut area, old vegetation	2.53	2.73	2.82	3.02

Table 4 - Biomass of new plants and sprouts in the irradiated area in 1966 and 1967 (from Jordan, 1968)

	Total g dry weight in area	g dry wt/m^2
1966		
well-drained soil		
new vegetation	95,388	247
sprouts	26,678	69
poorly drained soil		
new vegetation	36,691	126
sprouts	4,899	16
TOTAL 1966	163,656	242*
1967		
well-drained soil		
new vegetation	323,256	837
sprouts	47,727	123
poorly-drained soil		
new vegetation	139,893	482
sprouts	8,744	30
TOTAL 1967	519,620	768*

*mean biomass for entire area

Dominant vascular plants in 1966 which originated from seed following irradiation were Psychotria berteriana, Palicourea riparia, Cecropia peltata, Didymopanax morototoni, Ichnanthes pallens, Casearia bicolor, Alchornea latifolia, and Tabebuia heterophylla, the majority of which are secondary species. In 1967 these same species remained predominant, however, Tabebuia heterophylla increased in relative abundance as did sprouts of Palicourea riparia.

Secondary Succession in Tabonuco Forest

Outside although of the irradiated area a number of studies have examined various aspects of vegetation recovery following forest disturbance. Doyle (1981) and Doyle et al. (1982) modified a gap succession model (FORET) in order to adapt it to characteristics of the tabonuco forest (FORICO) and thereby investigate the effects of major and minor disturbances (hurricanes vs. treefalls, landslides, etc.) on this forest. This model simulates gaps of 1/30 ha, area, or approximately half the size of the gap caused by radiation. Model assumptions include, among others, the presence of the gap within a closed or intact forest which provides an adequate and equitable seed source from all species, the selection of species and seedling numbers as a stochastic process, the reduction of optimum growth by factors such as shading, competition, and climate, and an intrinsic mortality rate of 98-99% of a seedling cohort.

Figure 6 represents a 500 year simulation of the successional sequence beginning with an open gap and the absence of standing trees. Leaf area index (LAI) increases rapidly during the first 50 years to a maximum of 7.8 m^2/m^2 but later declines to approximately 6.5 m^2/m^2.

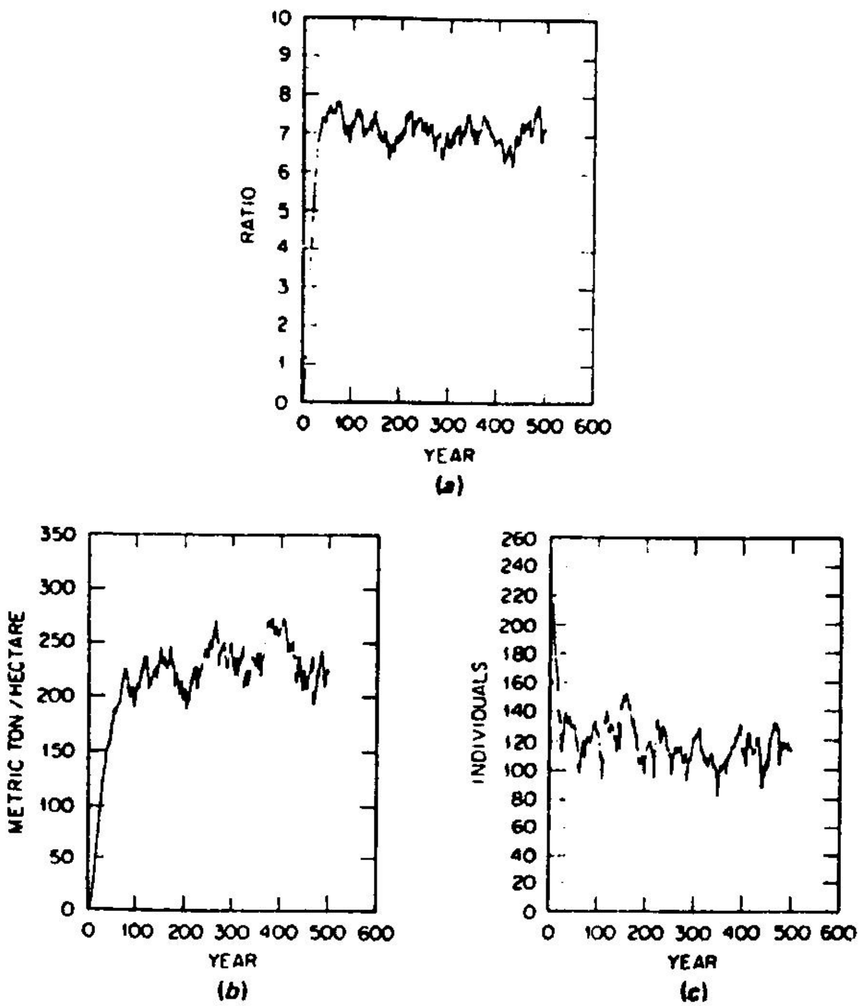


Figure 6. Mean values for 120 simulated 1/30-ha plots through 500 years of model simulation: (a) leaf area index (m^2 of leaves/m^2 of land area); (b) total biomass (metric ton/ha); (c) total number of trees (individual trees greater than 1.3 cm diameter at breast height, or dbh). (from Doyle, 1981)

Above ground biomass increases during the first 125 years, fluctuating thereafter between 175 and 250 metric tons per hectare. Stem density declines rapidly during the first 50 years stabilizing thereafter at an average of 110 trees per plot (3,300/ha).

Doyle (1981) also modelled dynamics of the individual dominant species: Cecropia peltata, Didymopanax morototoni, Buchenavia capitata, Manilkara bidentata, Sloanea berteriana, and Dacryodes excelsa (Figure 7). Biomass of the first two, typically secondary, species peaks around 15-30 years but by 60 years they have virtually disappeared. Biomass of the last three, dominant primary species of the tabonuco forest, increases steadily reaching a peak after 100 to 200 years and thereafter declining slightly. Biomass of Buchenavia capitata, a late secondary species, increases to a peak after 200 years, then declines but shows a secondary peak after 300 years and thereafter decreases to a very low level.

Various studies have examined individual species and their roles in succession: Palicourea riparia (Lebron, 1977); Cecropia peltata (Silander, 1979), Didymopanax morototoni (Nieves, 1979), and Buchenavia capitata (Sastre, 1979).

RESULTS

Plant Density and Species Composition

Total plant density (including seedlings, sprouts, saplings, vines, herbs, and ferns) in the irradiated area was 10.9 individuals/ m^2 in 1967 (Figure 8). Density decreased slightly in 1968, increased to a peak of approximately 15 individuals / m^2 in 1973, but by 1982 had declined to

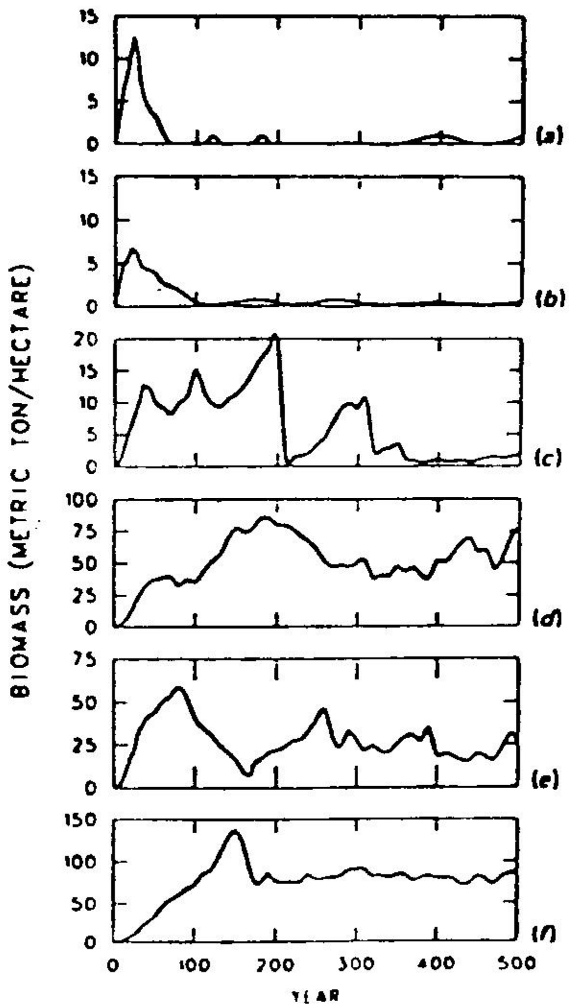


Figure 7. Successional dynamics of six dominant species of the tabonuco forest as simulated by the FORICO model: (a) Cecropia peltata; (b) Didymopanax morototoni; (c) Buchenavia capitata; (d) Manilkara bidentata; (e) Sloanea berteriana; (f) Dacryodes excelsa.

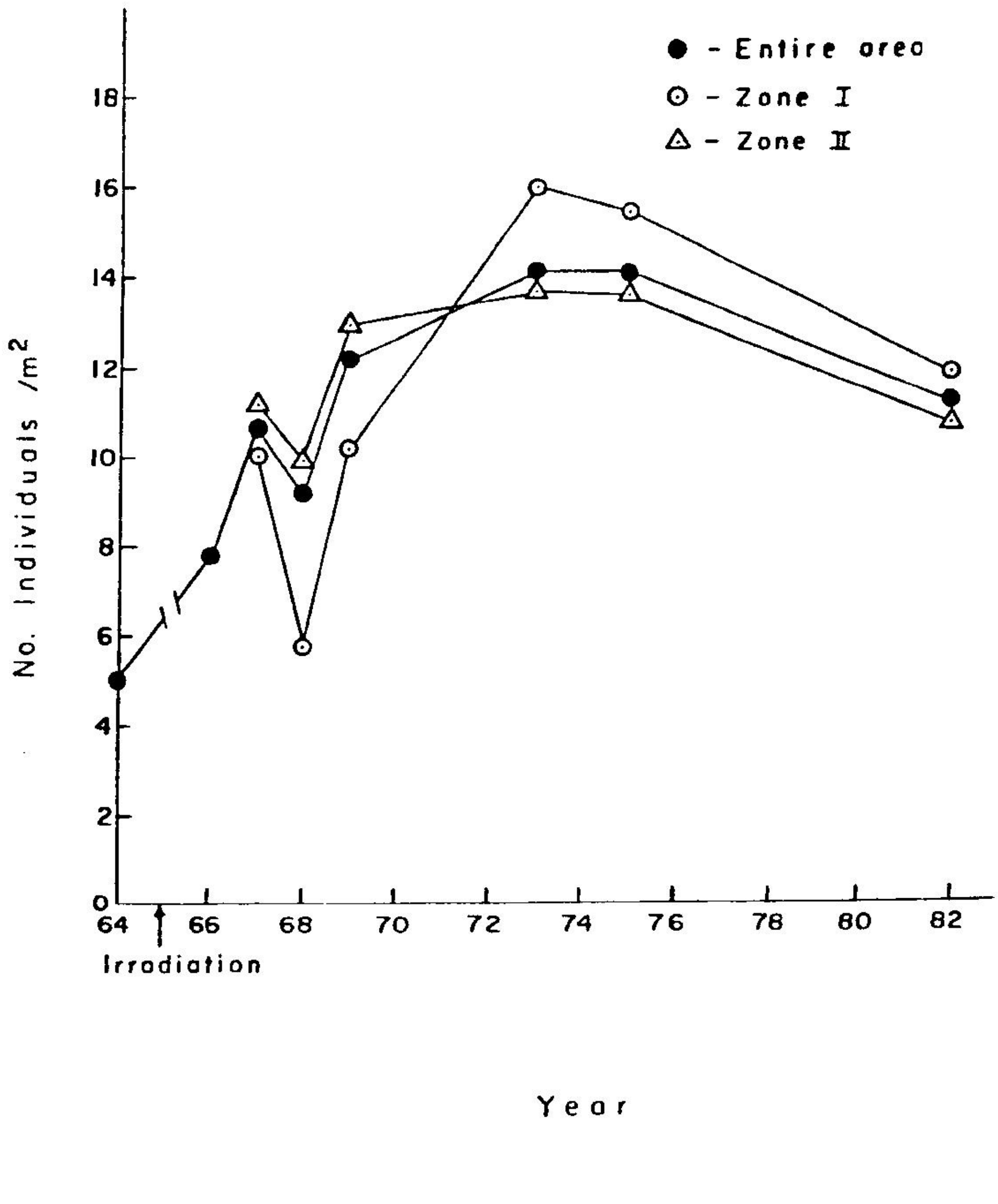


Figure 8. Overall plant density (not including grasses) in the radiation center. Data for 1973 does not include sprouts.

11 individuals $/m^2$. Density in the area immediately surrounding the source (Zone I) was somewhat lower than in the outlying area (Zone II) in the early years following irradiation, but by 1973 this trend had been reversed. Smith (1970) reported a density of approximately 5 individuals per m^2 (including similar plant groups) in the undisturbed study area prior to irradiation. By 1982 total plant density was still greater than that of the undisturbed forest.

Vines

Total density of vines increased between 1967 and 1975 but showed a slight decrease in 1982 (Figure 9). The number of vine species present remained similar through 1975 but decreased substantially in 1982 . Density was lower in all years in the zone immediately surrounding the radiation source (Figure 10a). Dominant vine species were similar before and after irradiation. However, density of vines was consistently greater in the study area following irradiation than that reported by Smith (1970), .133 individuals per m^2, for the undisturbed El Verde site. Dominant species in 1967 were *Securidaca virgata*, *Rourea glabra*, *Mikania fragilis*, *Heteropteris laurifolia*, and *Marcgravia rectiflora* (Table 5). These species remained dominant throughout the study period with the exception of *Mikania fragilis* which by 1982 was not present in the study area. *Ipomoea repanda* and *Rajania cordata* were also important species in 1982.

Herbaceous plants:

Total density of herbaceous plants remained relatively constant throughout the study period (see Figure 9). However, density in the area immediately surrounding the source (Zone I) increased between 1967 and 1969 and was greater than that in the outlying area (Zone II)

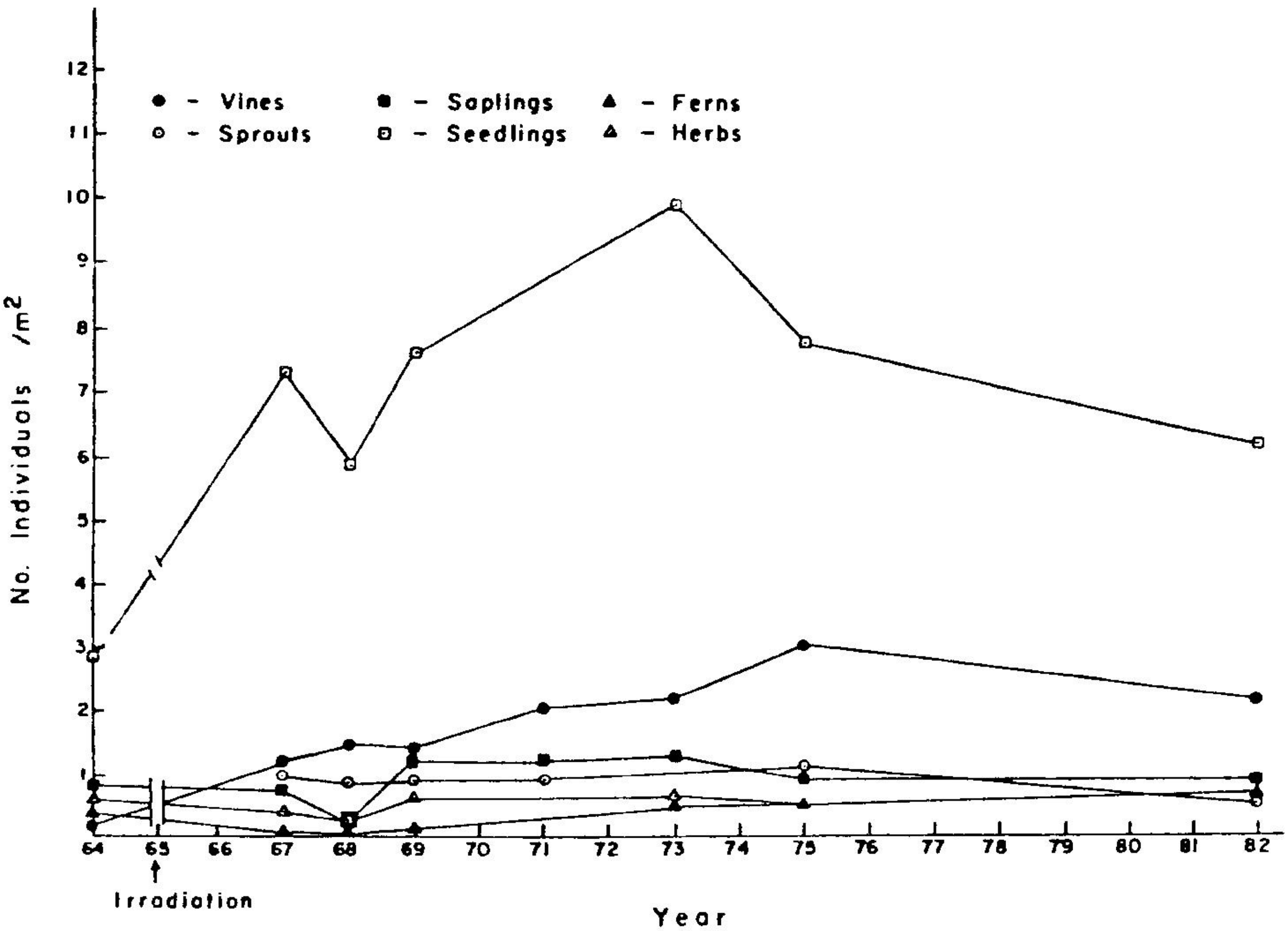


Figure 9. Density of the six plant groups included in censuses in entire 676m^2 sampling area before and after irradiation. Data for sprout density prior to irradiation not available.

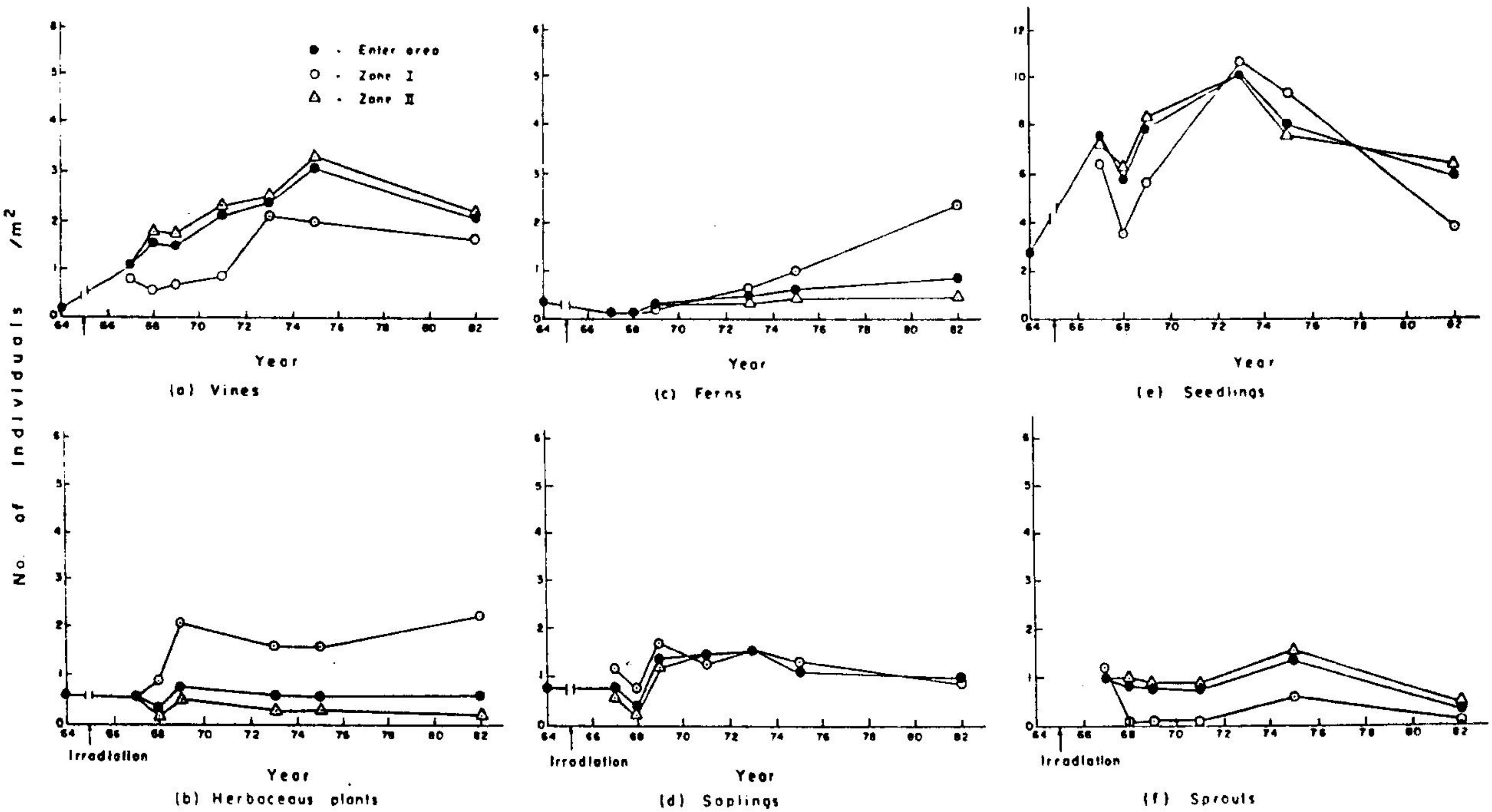


Figure 10 (a-f). Density of the various plant groups in Zone I, II, and the entire $676m^2$ before and after irradiation. Preirradiation data not available for sprouts.

Table 5 - Relative density of vines or climbers in the irradiated area.

	1967	1968	1969	1971	1973	1975	1982
Heteropteris laurifolia	6.71%	5.04%	6.56%	----	3.08%	2.96%	4.24%
Cissampelos pariera	.13	.20	.10	.28	.86	.91	.35
Clusia gundlachii	1.48	.10	.50	.56	.29	.29	----
Dolicarpus calinoides	.81	.40	.40	.21	.12	.10	----
Dioscorea polygonoides	1.21	.79	4.24	1.82	8.49	5.48	----
Ipomoea repanda	1.61	.40	2.12	8.87	6.34	6.39	12.80
Securidaca virgata	41.61	16.90	29.67	29.61	38.09	47.38	32.39
Foresteronia corymbosa	----	.49	.20	.14	.49	1.14	1.34
Mikania cordata	----	4.45	----	----	----	----	----
M. fragilis	16.38	3.75	10.80	7.82	4.86	1.33	----
Marcgravia rectiflora	4.43	50.30	4.54	9.50	8.98	5.43	1.84
Philodendron giganteum	----	.10	----	.07	.06	.43	----
P. krebsii	----	.10	.61	.07	----	----	----
P. lingulatum	.13	.59	.50	.21	.43	.43	----
Paullina pinnata	.40	.30	.20	.07	.37	.19	.57
Rourea glabra	20.54	15.12	33.40	38.62	24.98	26.41	41.23
Smilax coriacea	2.28	.20	.81	.49	.24	.24	1.70
Schlegelia brachyantha	----	.79	.30	.21	.55	.24	----
Spigelia anthelmia	----	----	----	----	----	.05	----
Unknown species (R)	----	----	3.23	----	----	.43	----
Neorudolphia volubilis	.54	----	1.11	1.40	.74	.43	----
Rajania cordata	1.48	----	.50	----	----	----	3.54
Vanilla inodora	----	----	.10	.07	.06	.10	----
Cayaponia americana	.27	----	----	----	.06	----	----
Hippocratea volubilis	----	----	----	----	.06	.10	----

throughout the other census years (Figure 10b). Dominant species in 1967 included Desmodium spp., Nepsera aquatica, Solanum spp., and Phytolacca icosandra (Table 6). Species of Solanum, characteristic of hillsides, banks and thickets or open areas (Britton and Wilson, 1927), were important only in 1967 and 1968, the early years following disturbance, and by 1975 were absent from the census area. Phytolacca, a roadside weed (Edmisten, 1970), was important in the herbaceous flora only in 1967. Edmisten (1970) reported that Phytolacca or pokeweed appeared in both the cut-over and irradiated areas, but not the control or undisturbed area, approximately 6 months after disturbance. Experimental manipulation of seed germination indicated that elevated soil temperatures and slight scarification, events which may accompany canopy opening, enhanced germination. Phytolacca was of less importance in the irradiated area than in the cut-over area possibly due to irradiation induced seed damage and the excessive trampling, causing heavy scarification and thus reduced germination, which occurred in this area. Desmodium spp. remained important in all census years and was the predominant herb in 1982. Nepsera decreased gradually in relative abundance throughout the study period and was absent by 1982.

Increasing in relative importance throughout the study period were Elephantopus mollis, Borreria ocimoides, and Triphora suraminesis. Classified here as a herb, Triphora is a terrestrial orchid which flowers in the summer or fall (Smith, 1970) and is characteristic of woodlands or forested areas (Britton and Wilson, 1927). Pilea krugii, reported as a dominant herb species in the undisturbed El Verde site (Smith, 1970), did not appear in the herbaceous flora in any of the census years.

Table 6. Relative density of herbs in the study area following irradiation treatment.

	1967	1968	1969	1971	1973	1975	1982
Bidens pilosa	.57	.41%	.63%		----	----	----
Desmodium sp.	1.99	47.35	26.60		----	2.20	60.90
Elephantopus mollis	2.85	17.14	27.77		27.99	25.82	8.40
Hedychium coronarium	1.14	8.57	.63		.94	.27	----
Nepsera aquatica	22.22	15.51	7.31	N/A*	.63	.27	----
Pothomorphe peltata	----	4.49	3.55		----	----	----
Solanum rugosum	5.31	5.31	----		.31	----	----
Solanum sp.	1.14	.41	.63		----	----	----
S. torvum	1.14	.82	.21		----	----	----
Aeschynomene americana	----	----	2.51		----	----	----
Borreria ocimoides	3.13	----	3.55		1.89	.82	21.95
Cranichis muscosa	----	----	2.51		2.52	.82	----
Desmodium ovalifolium	49.57	----	7.72		----	12.64	----
Eupatorium odoratum	.85	----	1.88		----	----	----
Spigelia anthelmia	.29	----	2.92		----	.82	----
Spiranthes elata	----	----	.42		1.57	.82	----
Triphora suranimensis	----	----	9.19		61.95	31.87	3.25
Commelina sp.	2.56	----	----		----	----	5.15
Phytolacca icosandra	4.84	----	----		.63	----	----
Sauvagesia erecta	1.99	----	----		----	----	----
Heliconia bihai	.57	----	----		.31	.55	----
Clidemia hirta	----	----	----		.31	.27	----
Centrogonium setaceum	----	----	----		.63	4.12	----
Erythrodes hirtellus	----	----	----		.31	17.86	----
Spermacoce tenuoir	----	----	----		----	.27	----
Guzmania monostachia	----	----	----		----	.27	----
Anthurium dominicense	----	----	----		----	.27	----

*Data not available for this year.

Ferns

Total density of ferns increased slightly throughout the study period (Figure 9). A greater increase through time was evident in Zone I, the area immediately surrounding the radiation source (Figure 10c). Dominant species in 1967 were Dryopteris deltoides, Nephrolepis rivularis, and Alsophila borinquena (Table 7). The relative abundance of Dryopteris and Alsophila declined throughout the study period whereas that of Nephrolepis increased until 1973 and thereafter decreased. Both Dryopteris and Alsophila were also important species in the ground flora prior to disturbance. By far the dominant fern species in 1982 was Blechnum occidentale, a species not present until the 1973 census. Britton and Wilson (1927) describe B. occidentale as a species characteristic of dryish shrubby banks, open situations, as well as moist forest slopes. In 1982 this species was much more abundant in the zone immediately surrounding the source than in the outerlying area (Zone II).

Grasses

Cover rather than density was estimated for grass or sedge species. Mean percent cover per m^2 for the entire sampling area decreased from approximately 40% in 1967 to less than 5% in 1982. However, cover by grasses in the area immediately surrounding the radiation source (Zone I) decreased to only 20% in 1982 as opposed to 3% in the outerlying area (Figure 11). Dominant grass species throughout the study period included Ichnanthes pallens, Paspalum conjugatum, Panicum bolivense, and Scleria microcarpa. Mean percent cover $/m^2$ was greater in all years on the wet or poorly drained soil than on the dry or well drained soil type.

Table 7. Relative density of ferns in the irradiated area.

	1967	1968	1969	1971	1973	1975	1982
Alsophila borinqueña	15.48%	17.20%	13.37%		5.56%	4.27%	.18%
Adiantum petiolatum	.91	1.08	1.60		2.16	1.76	1.47
Dryopteris deltoides	63.64	80.65	61.50		41.67	39.70	15.78
D. sprengelii	----	1.08	1.07		.31	----	----
Nephrolepis rivularis	17.27	----	19.25	N/A*	36.73	28.89	16.88
Polypodium aureum	----	----	.53		.31	.25	2.02
P. loriceum	----	----	1.60		.93	.50	----
P. lycopioides	2.73	----	1.07		----	.25	----
Cyathea arborea	----	----	----		----	.50	1.28
Blechnum occidentale	----	----	----		11.42	20.60	62.39
Dryopteris chaerophylloides	----	----	----		.62	1.01	----
Adiantum cristatum	----	----	----		.31	.25	----
Elaphoglossum fermum	----	----	----		----	1.01	----
E. flaccidum	----	----	----		----	1.01	----

*Data not available for this year.

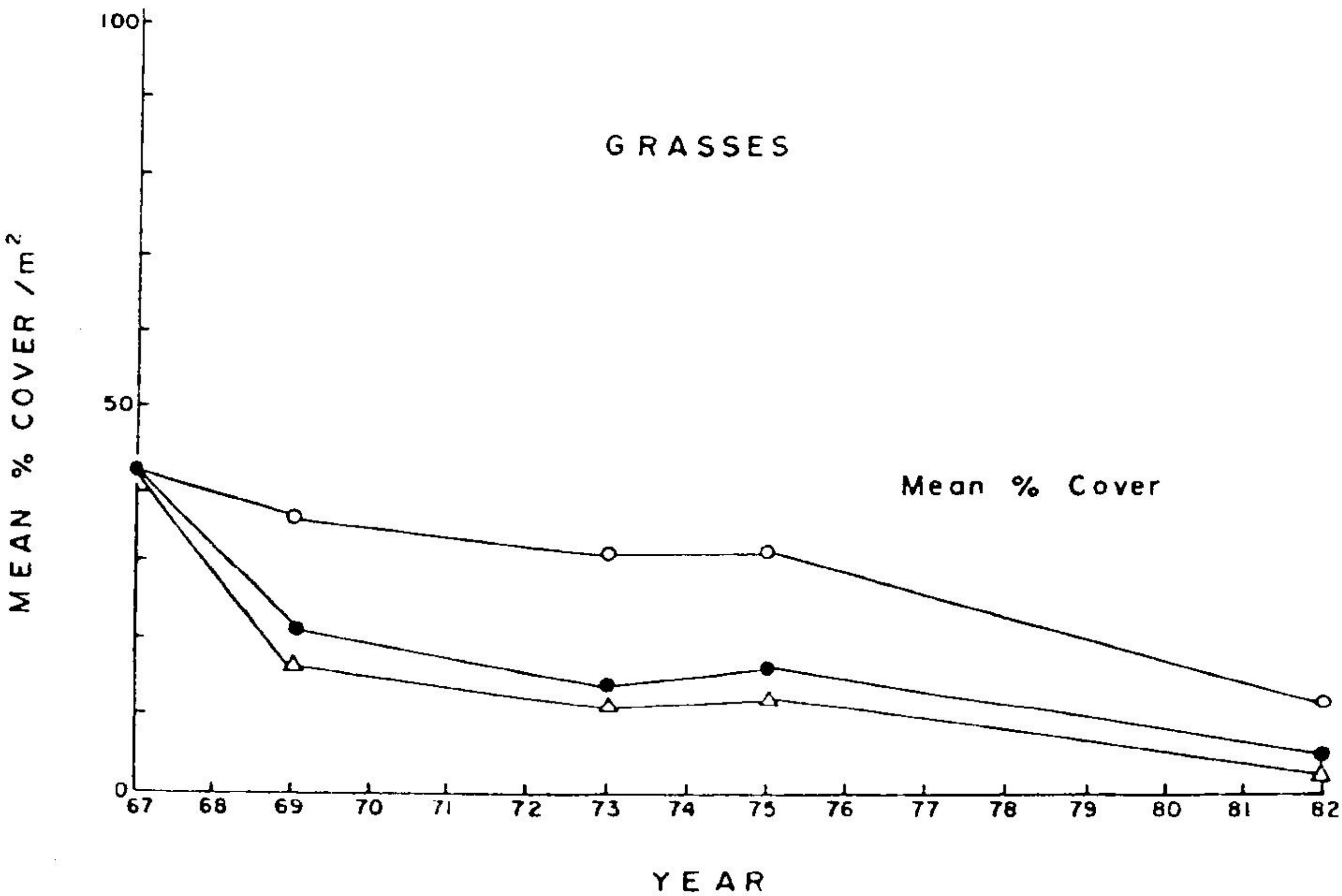


Figure 11. Mean percent cover /m^2 by grasses in total area (676m^2) and in zones I and II.

Saplings

Total density of saplings decreased slightly in 1968, increased gradually to a peak in 1973 but decreased slightly in 1975 (Figure 9). This pattern was similar in both the area close to the source (Zone I) and the outerlying area (Zone II) (Figure 10d). Density was initially similar to that reported by Smith (1970), .812/m^2, for the undisturbed El Verde site, but increased to approximately 1.2/m^2 in 1969. Dominant species in the early years following irradiation were *Psychotria berteriana*, *Palicourea riparia*, *Cecropia peltata*, *Didymopanax morototoni*, *Tabebuia heterophylla*, *Miconia racemosa*, and *Casearia bicolor* (Table 8). Relative density of *Palicourea riparia* increased throughout the study period whereas that of *C. peltata*, *D. morototoni*, and *P. berteriana* decreased. *P. riparia* is an important species in disturbed or open areas, responding to canopy opening and the resulting microclimatic changes with increased germination and growth (McCormick, 1970). However, it is also a dominant understory species in the undisturbed El Verde site where it composed 41.5% of the understory. The latter three species are characteristic of disturbed or open areas (Smith, 1970; Little and Wadsworth, 1964).

By 1982 dominant species included *Palicourea riparia*, *Tabebuia heterophylla*, *Casearia arborea*, *Sloanea berteriana*, and *Eugenia stahlii*. *S. berteriana* was a dominant canopy species prior to irradiation (relative density 8.1%) and along with *E. stahlii* is classified as a primary forest canopy species (Smith, 1970).

Seedlings

With the exception of a slight decrease in 1968 total density of tree (both canopy and understory) seedlings increased to a peak in 1973 and

Table 8. Relative density of saplings in Radiation Center ($676 m^2$)

	1967	1968	1969	1971	1973	1975	1982
Alchornea latifolia	1.19	.338	1.06	----	.89	1.01	1.75
Alchorneopsis portoricensis	1.39	.99	1.59	----	1.09	.88	.15
Casearia arborea	.79	.99	1.38	----	1.78	2.02	4.22
Casearia bicolor	3.57	1.32	3.29	2.22	1.68	1.77	1.60
Cecropia peltata	15.08	21.05	8.61	7.37	6.32	6.70	3.06
Cyathea arborea	----	3.95	.64	.20	.20	----	----
C. portoricensis	----	.66	----	----	----	----	----
Didymopanax morototoni	14.29	17.11	8.61	8.68	7.50	7.59	2.91
Eugenia stahlii	----	.33	.11	.20	.99	.76	3.20
Henrietta fascicularis	.79	.99	.21	----	.20	.13	----
Inga vera	.99	.66	.74	1.11	1.40	1.26	.58
Manilkara bidentata	----	.66	.64	.61	.49	----	2.04
Miconia prasina	1.19	1.64	2.13	3.23	2.07	1.90	1.75
Ocotea moschata	.40	.33	1.06	----	.20	.13	----
Psychotria berteriana	30.36	31.91	22.42	23.41	17.67	16.43	3.93
Piper aduncum	.99	1.32	1.49	1.01	.69	.38	----
Palicourea riparia	15.08	7.57	23.91	33.91	36.72	36.41	35.40
Sloanea berteriana	1.19	.33	.42	.50	2.17	1.01	5.24
Tabebuia heterophylla	3.17	7.89	5.95	7.77	7.80	11.00	13.68
Byrsomina spicata	.60	----	1.06	----	1.38	1.77	1.75
Cordia borinquensis	----	----	.64	.30	.69	.51	.58
Croton poecilanthus	----	----	.64	.61	.59	1.01	.58
Casearia sylvestris	----	----	.32	.30	.20	.38	1.31
Calycogonium squamulosum	----	----	.11	----	----	----	----
Cordia sulcata	----	----	.32	.20	.10	----	.15
Dacryodes excelsa	----	----	.11	----	----	----	.15
Heterotrichum cymosum	----	----	.21	.30	----	----	----
Ixora ferrea	----	----	.32	.10	.39	.13	2.04
Inga laurina	----	----	.53	.40	.69	.63	1.75
Linociera domingensis	.40	----	.64	.71	1.10	1.01	.15

Table 8 - Continuation

	1967	1968	1969	1971	1973	1975	1982
Matayba domingensis	1.98	----	.21	----	.59	----	.73
Meliosma herberti	----	----	.21	----	.10	----	----
Miconia sp.	----	----	.11	.10	.10	.25	----
Miconia racemosum	.20	----	9.03	3.33	.39	.63	.58
M. tetandra	----	----	.21	.30	.59	1.26	2.62
Ormosia krugii	----	----	.11	----	.20	.13	.29
Piper blattarum	----	----	.21	.91	.79	.63	----
Psychotria brachiata	----	----	.11	.30	.30	.25	.29
Piper treleaseanum	.19	----	.32	.30	.10	----	.29
Sapium laurocerasus	.19	----	.32	.10	.10	.13	----
Clusea rosea	----	----	----	.10	.10	.25	.15
Cyrilla racemiflora	----	----	----	.10	.10	.13	.29
Drypetes glauca	.20	----	----	.10	.10	.13	.73
Guettarda laevis	----	----	----	----	----	----	.87
Guarea ramiflora	----	----	----	.20	.39	.13	.15
Guarea trichiloides	----	----	----	.10	----	----	.58
Homalium racemosum	----	----	----	----	.39	.13	.15
Hirtella rugosa	----	----	----	----	----	----	.44
Myrcia deflexa	----	----	----	.10	.20	.25	.29
M. leptoclada	----	----	----	----	.10	.13	1.60
M. splendens	----	----	----	.20	.10	.13	.29
Dendropanax arboreum	----	----	----	.10	.10	.13	----
Prestoea montana	----	----	----	.20	.39	----	.40
Tetrogastris balsamifera	----	----	----	----	.10	.13	.87
Trichilia pallida	----	----	----	.10	----	.13	.29
Ocotea leucoxylon	.19	----	----	.10	.10	.25	----
unknown species 1	----	----	----	.10	----	----	----
unknown species 2	5.36	----	----	----	----	----	----
# species	24	19	40	40	48	42	43

in subsequent years declined (Figure 9). In all years density was greater than that reported by Smith (1970) for the El Verde site prior to irradiation (2.72 seedlings per m^2). A similar pattern was observed in Zones I and II as in the entire sampling area although density in Zone I was initially lower and increased to a greater level in 1973 (Figure 10e). Dominant species following irradiation in 1967 included Tabebuia heterophylla, Palicourea riparia, Psychotria berteriana, Didymopanax morototoni, and Linociera domingensis. Due to the presence of an adult flowering T. heterophylla in the immediate vicinity and its profuse production of seeds, as well as the continued open nature of the canopy and the consequent favorable microclimatic conditions, seedlings of this secondary species continued to be an important component of the seedling flora in all years. P. riparia, a radiation-resistant species described as characteristic of open or disturbed areas but also present in the understory of undisturbed forest, decreased through time in relative importance. By 1982 species such as Dacryodes excelsa (a primary canopy species), Drypetes glauca (a primary understory species), and Prestoea montana (a primary canopy species) had increased markedly in relative abundance.

Sprouts

Total density of sprouts decreased slightly between 1967 and 1971, increased in 1975 and decreased again in 1982. Although the patterns were similar in all years after 1967, density was less in Zone I, the area surrounding the source, than in the outlying area (Figure 10f). Dominant sprouting species in all years included Sloanea berteriana, Palicourea riparia, Croton poecilanthus, Inga vera, and Eugenia stahlii.

Biomass

Grasses

Biomass of grasses decreased from approximately 175 g dry weight/-m^2 in 1967 following irradiation to less than 25 g dry weight/m^2 in 1982. Biomass of grasses in Zone I, the area immediately surrounding the source, was similar to that in the outerlying area in 1967 but in all subsequent years was greater (Figure 12). Grass biomass was greater in all years on the wet or poorly drained soil than on the dry or well-drained soil type.

Saplings

Biomass of saplings (those stems with a DBH) in the entire sampling area increased between 1967 and 1973, decreased slightly in 1975, but by 1982 had reached approximately 6 kg dry weight/m^2 (or 60 metric tons/ha) (Figure 13). This compares favorably to model biomass predictions made by Doyle (1981; 1982) for gap regeneration in tabonuco forest. It may, however, be an overestimate as both primary and secondary species are grouped together and secondary species generally have lighter wood.

Sapling biomass in Zone I, in contrast to that in Zone II and the area as a whole, continued to decrease after 1973, possibly due to the mortality of rapidly growing, larger stemmed secondary species such as C. peltata in this zone following 1971.

Sapling biomass was consistently greater throughout the study period on the dry or well-drained soil than on the wet or poorly-drained soil.

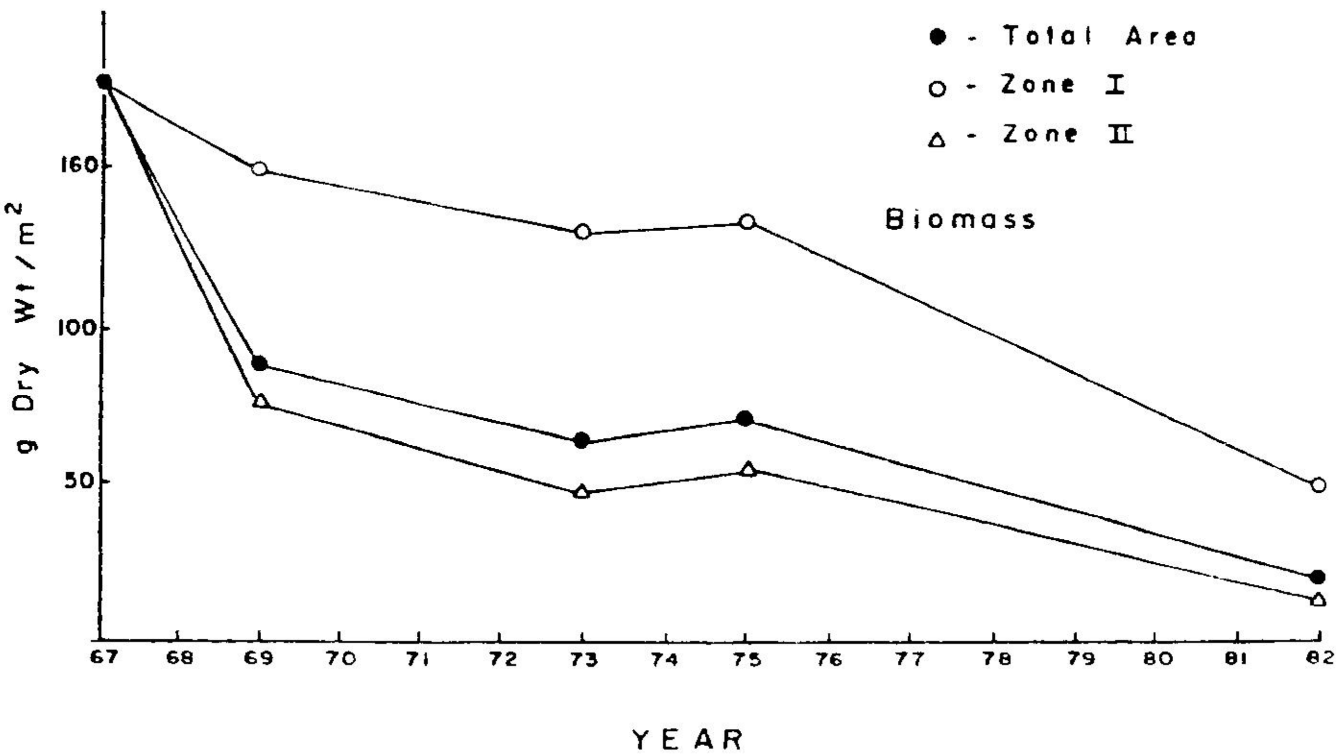


Figure 12. Biomass of grasses in entire 676 m^2 and zones I and II.

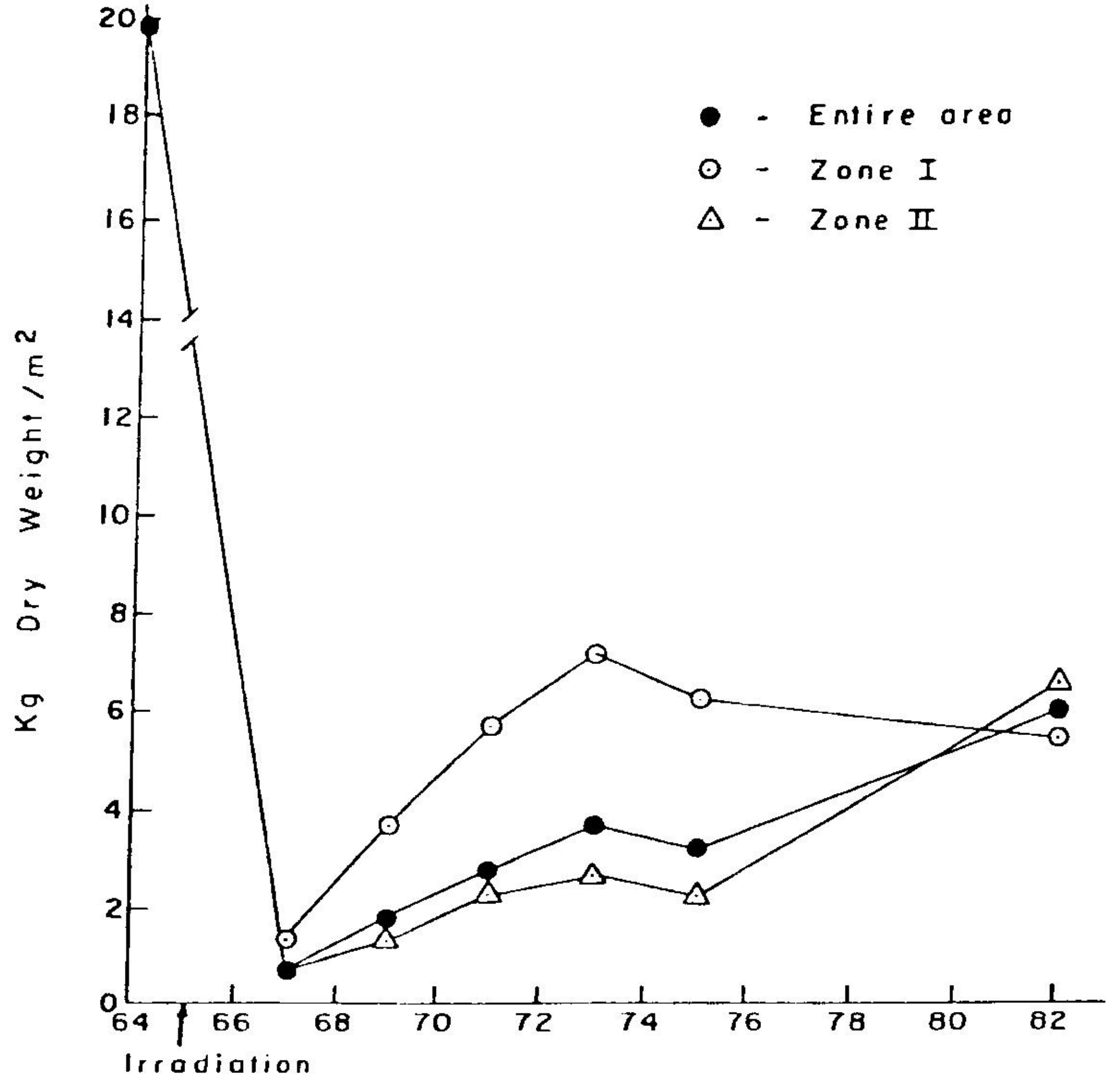


Figure 13 - Biomass of saplings (kg dry wt/m^2) in entire 676m^2 and zones I and II.

Primary vs. Secondary Species

Primary and secondary species were grouped utilizing the criteria of Smith (1970). Twelve species represent each group:

Primary	Secondary
1. *Tetragastris balsamifera*	1. *Cecropia peltata*
2. *Eugenia stahlii*	2. *Miconia tetandra*
3. *Sloanea berteriana*	3. *Cyrilla racemiflora*
4. *Ocotea moschata*	4. *Alchorneopsis portoricensis*
5. *Guarea trichilioides*	5. *Casearia bicolor*
6. *Linociera domingensis*	6. *Cordia sulcata*
7. *Ormosia krugii*	7. *Sapium laurocerasus*
8. *Inga laurina*	8. *Alchornea latifolia*
9. *Micropholis garciniaefolia*	9. *Homalium racemosum*
10. *Matayba domingensis*	10. *Tabebuia heterophylla*
11. *Dacryodes excelsa*	11. *Croton poecilanthus*
12. *Prestoea montana*	12. *Calycogonium squamulosum*

Seedlings

Density of secondary seedlings was initially greater than that of primary seedlings but by 1969, 4 yrs after irradiation, density of primary seedlings had increased and was greater than that of secondary seedlings (Figure 14). Density of secondary species continued to decrease until 1975 but showed an increase in 1982, apparently

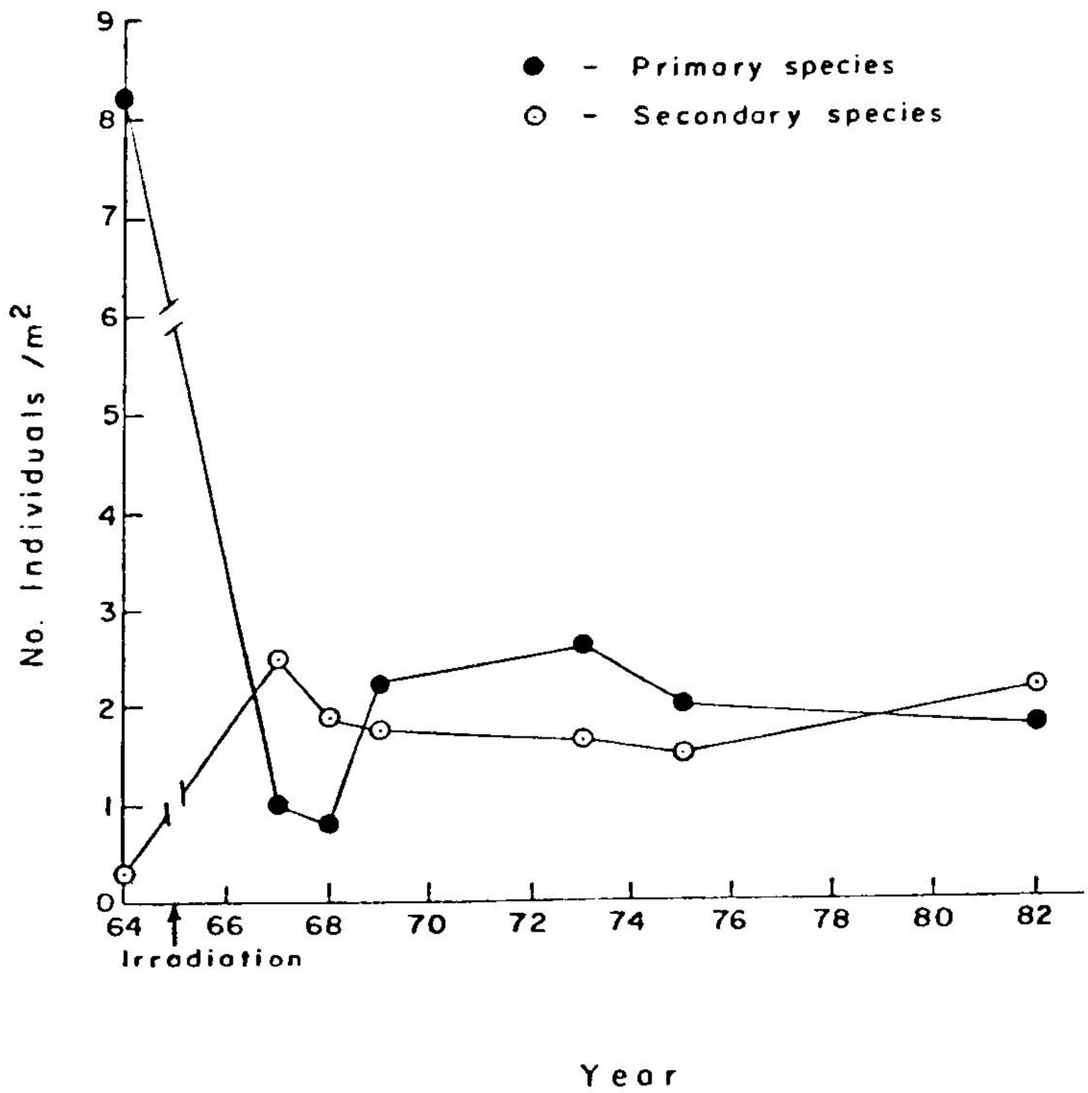


Figure 14. Density of primary and secondary seedlings in entire $676m^2$ sampling area before and after irradiation. Preirradiation data from McCormick (1970).

due to an increase in density in Zone II (Figure 15). This increase in secondary seedling density in Zone II in 1982 was due to great numbers of seedlings of Tabebuia heterophylla, a result of the presence of an adult, flowering specimen in the immediate area and continued favorable microclimatic conditions. Dominant primary seedling species included Dacryodes excelsa, Linociera domingensis, Matayba domingensis, and Prestoea montana. Dominant secondary species were T. heterophylla, Alchornea latifolia, Casearia bicolor, Cecropia peltata, and Alchorneopsis portoricensis.

Saplings

Density of saplings of primary species was less than that of secondary species when the entire area was considered as well as when Zone I and II were considered separately (Figures 16 and 17). However, density of secondary saplings was greatest in Zone I, the area receiving the greatest radiation exposure. Density here reached a peak in 1971 and thereafter decreased due to mortality of stems of both C. peltata and T. heterophylla. Dominant primary saplings were Eugenia stahlii, Linociera domingensis and Matayba domingensis. Even by 1982 few individuals of Dacryodes excelsa, a dominant primary seedling and indicator of this forest type, had reached the sapling stage.

As is evident from Figures 18 and 19 biomass of secondary species was greater than that of primary species in both Zones I and II. Although biomass of secondary saplings decreased after 1973 in Zone I it continued to increase gradually in Zone II, the outer portion of the study area. Cecropia peltata was by far the dominant secondary species with respect to biomass although by 1973 dominance was shared by several other species such as T. heterophylla, Alchornea latifolia,

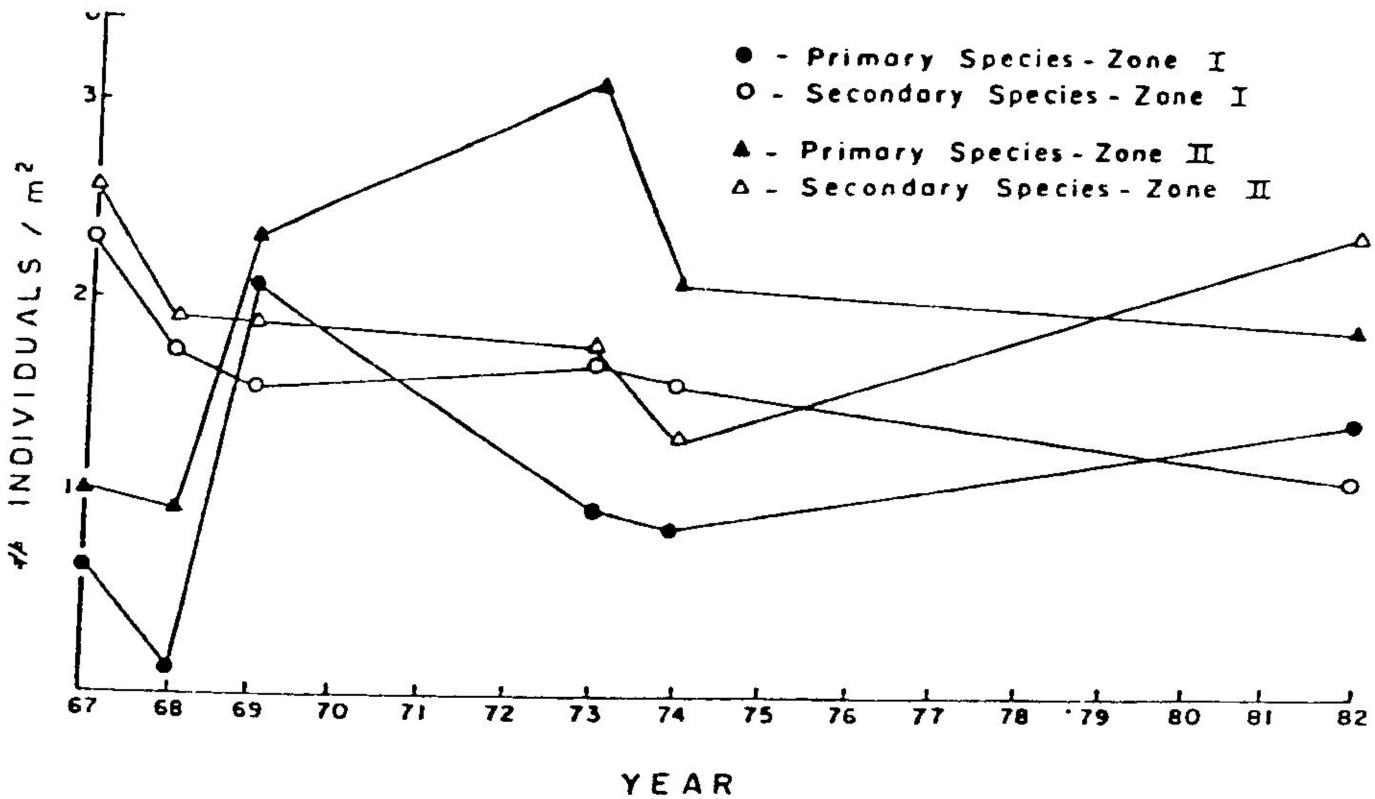


Figure 15. Density of primary vs. secondary seedlings in zones I and II.

Figure 16. Primary and secondary saplings in entire $676m^2$

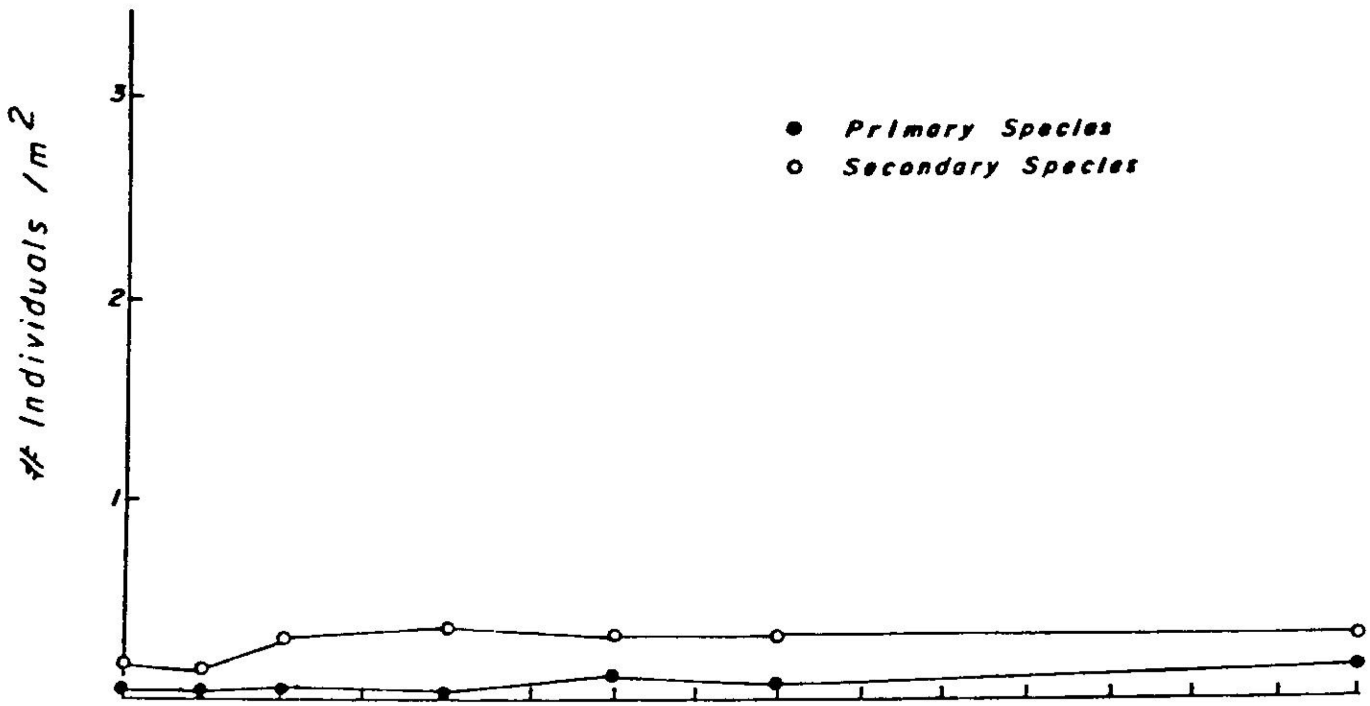
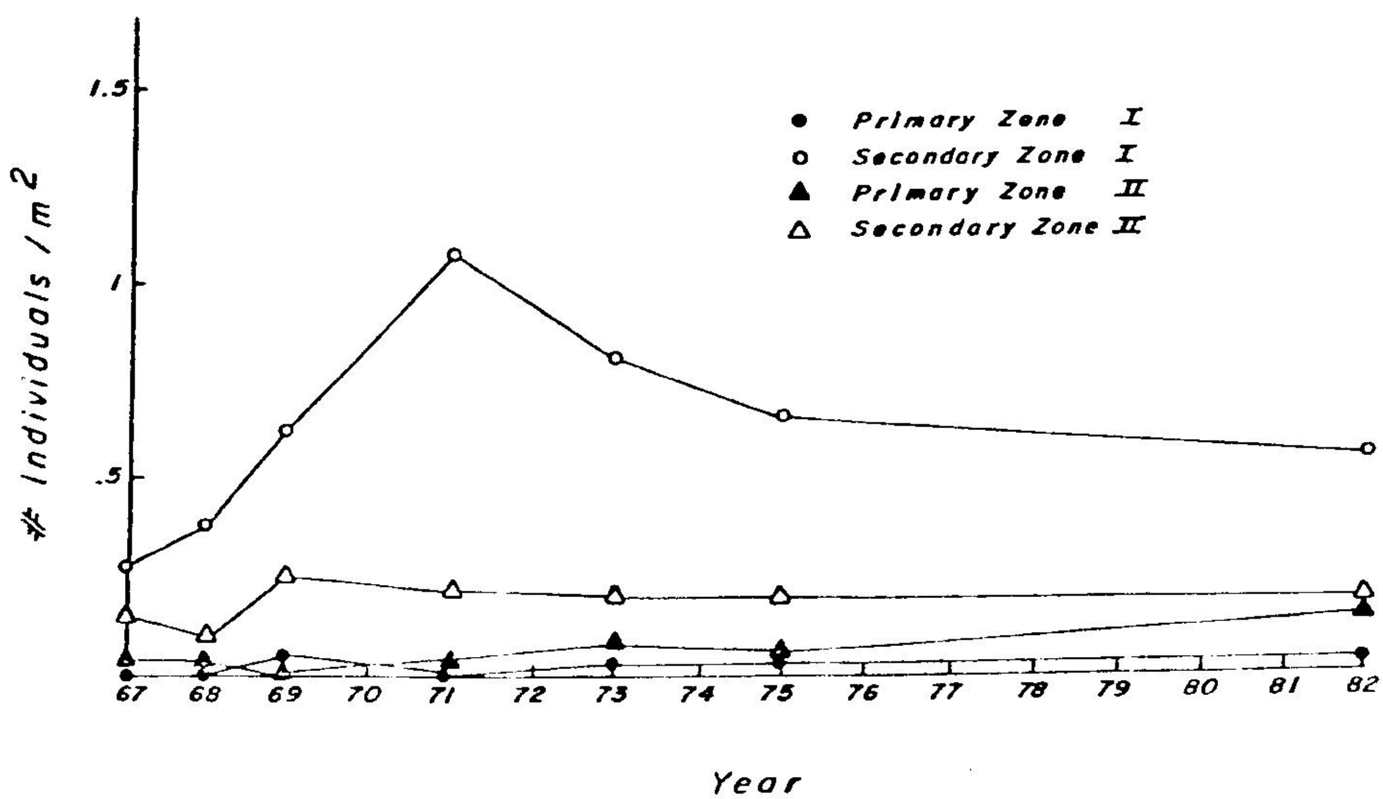


Figure 17 - Density of primary and secondary saplings in zones I and II



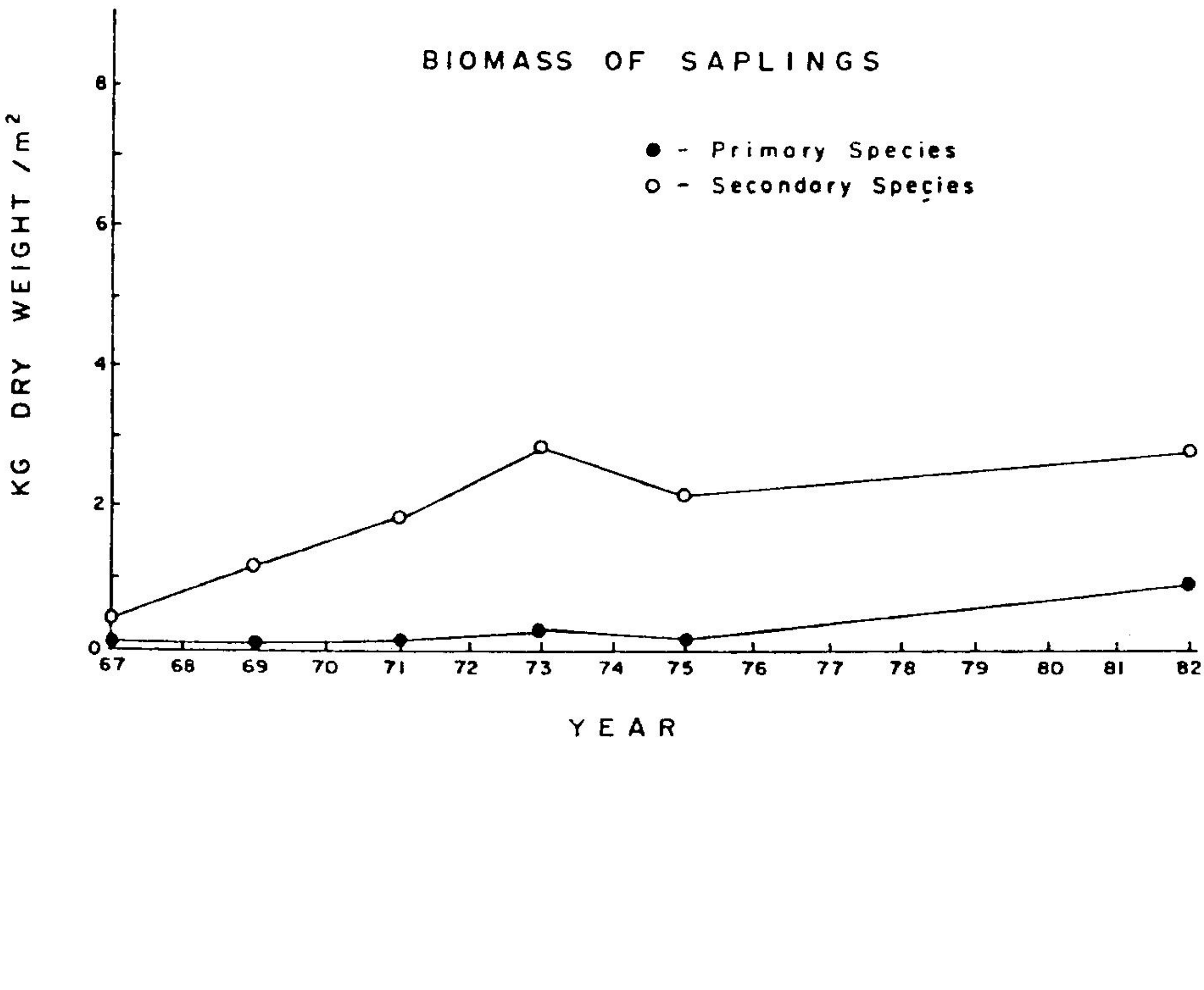


Figure 18. Biomass of primary and secondary saplings in entire 676 m^2.

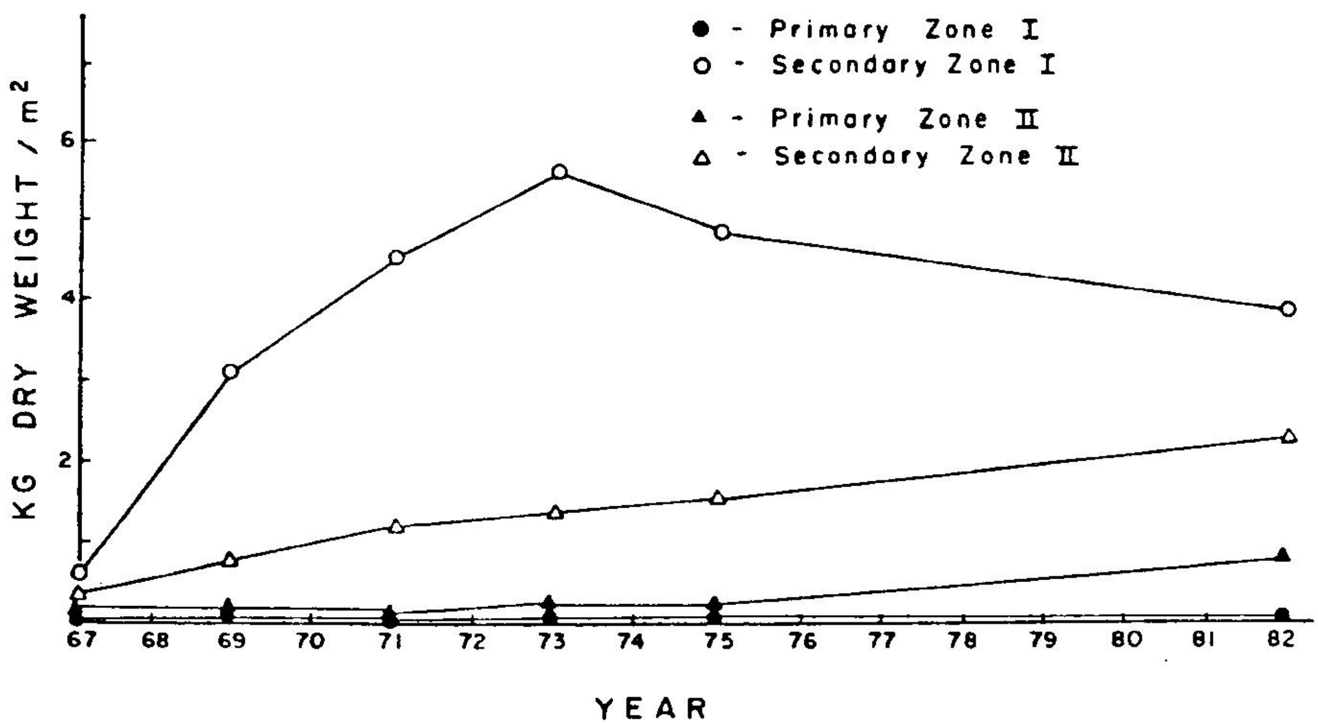


Figure 19. Biomass (kg dry wt/m^2) of primary and secondary saplings in Zones I and II.

Alchorneopsis portoricensis and in 1982, Miconia tetandra. Biomass of primary saplings was extremely low in all years but among the more important species were Linociera domingensis, Matayba domingensis, Eugenia stahlii, and by 1975, Sloanea berteriana.

DISCUSSION

Seventeen years following irradiation (1982) the canopy in the area immediately surrounding the radiation source continued to be open in nature and ground cover was dense. The outerlying area had an aspect more similar to that of the nearby undisturbed forest: a sparser ground vegetation and a closed canopy. This phenomena is evident in plant density and species composition and changes in these through time.

Overall plant density and density of the individual plant groups varied throughout the study period (1967-1982). When the entire area was considered, density of vines, sprouts, seedlings, and saplings increased until 1973 or 1975 and thereafter decreased. Density of ferns increased gradually throughout the study period whereas density of herbaceous plants appeared to stabilize somewhat after 1969 (see Figure 9). In contrast cover by grasses showed a continual decrease through time. Both patterns and densities of some plant groups differed in the two zones considered: the area within a 5 m radius of the source and the outerlying region. Density of ferns in the area close to the source increased dramatically between 1973 and 1982. Density of herbs was greater in this area as was cover by grasses and sedges. In contrast density of both vines and sprouts was consistently greater in the outerlying area whereas seedling and sapling densities were similar in the two areas (see Figure 10 a-f).

As density of plant groups varied throughout the study period so did species composition. Two important herbaceous species, Solanum and Phytolacca, in 1967 and 1968 were secondary species. By 1975 and 1982 these species were no longer present in the study area. Studies of Phytolacca indicate that germination is enhanced by increased soil temperature and some scarification, conditions which occur upon canopy opening (Edmisten, 1970). Harcombe (1977) indicates that during the first years of succession in Turrialba, Costa Rica, the most important species were of the genera Phytolacca and Solanum.

Dominant seedling species in early censuses were primarily secondary species such as Tabebuia, Palicourea, Psychotria, and Didymopanax. Due to microclimatic conditions such as those described by McCormick (1970) seedlings of primary species were relatively scarce at this time. Seedlings of primary species such as Dacryodes, Drypetes, and Prestoea became more important only following 1969. Because an adult Tabebuia in the vicinity of the study area contributed a large number of seeds in all years this species remained important throughout the study period, whereas relative abundance of other secondary species decreased markedly. This abundance of Tabebuia seedlings was responsible for the increase in secondary seedling density observed in 1982 in Figure 4 and were most important in the outerlying region of the sampling area (see Figure 15). Seedling density of particular species may depend upon the time of the year the census is carried out. Estrada (1970) reported the occurrence of fruit fall for Tabebuia between July and September. The 1982 census was carried out in late September and October.

Saplings of primary species were, even by 1982, of minor importance. Due to slow growth and high mortality as a result of continued unfavorable microclimatic conditions, few "primary" seedlings had reached the sapling stage during these first seventeen years of succession. Density of saplings of secondary species was greater than that of primary throughout the study period (see Figure 16). A continued gradual increase in density of primary saplings might be expected. Density of secondary saplings was greatest in the area closer to the source, reaching a peak in 1971 and thereafter declining. This decrease in density was due to mortality of the secondary species Cecropia and Didymopanax, the life spans of which are short. Doyle (1981) reports that biomass of these species peaks from 15 to 30 years following disturbance. Both species are often considered "gap opportunists" in that their continued existence in the undisturbed forest is dependent upon the presence of gaps or canopy openings of sufficient size. Although seedlings of Didymopanax may occasionally be found in undisturbed forest, those of Cecropia are restricted to gap situations due to the inability of the seeds to germinate beneath the forest canopy. Germination of the seed bank of Cecropia may also be inhibited by the presence of a heavy litter layer. In such areas seed rain becomes more important (Silander, 1979). The slow and continuous leaf fall which occurred for some time after irradiation may have slowed regeneration by Cecropia. Palicourea riparia, although present in undisturbed forest, may also be considered a "gap opportunist" as growth is stimulated by open canopy conditions (Lebrón, 1977). Relative abundance of this species continued to increase throughout the study period.

Statistical studies on the effect of soil type and any interaction with distance from the source are in progress. However, two preliminary observations can be made. Cover, as well as biomass, of grasses and sedges was consistently greater on the wet or poorly-drained soil than on the dryer, well-drained soil. Biomass of grasses was greatest in the area closer to the source but in both areas decreased throughout the study period. In contrast biomass of saplings was greater in all years on the well-drained soil type.

Above ground biomass of saplings had reached 6 kg dry weight/m^2 (or 60 mt/ha) by 1982, seventeen years following disturbance. Odum (1970) reported on aboveground plant biomass of 19.9 kg/m^2 from the undisturbed El Verde tabonuco forest. Doyle (1981) reported that during simulations of succession in tabonuco forest aboveground biomass increased during the first 125 years and thereafter fluctuated between 175 and 250 mt/ha. Biomass values reported here are probably overestimates due to inclusion of both primary and secondary, generally lighter species, in the same regression, particularly as secondary species tended to be dominant. Brown (1980), in a summary of tropical biomass data, states that based on available data biomass accumulates rapidly during the first 10-20 years at which time biomass may have reached 100 mt/ha. Ewel (1970) reports values of 5022.5 g/m^2 and 3564.6 g/m^2 for six year old vegetation in eastern Panama (Tropical Moist Forest, transition to Tropical Dry Forest). Snedaker (1970) found an accumulation of approximately 70 mt/ha in 9 years in subtropical wet forest at Guatemala. Harcombe (1977) reported a biomass accumulation of 1551 g/m^2 during the first year of natural regeneration. All of these figures suggest the possibility of a slower accumulation of biomass in this successional area when compared to other similar areas, perhaps a result of irradiation effects or the nature of the canopy opening. Biomass in the area closest to the source decreased after 1973 due to mortality of secondary short-lived species. It might be expected to increase again as primary or late successional species reach the sapling stage.

Various aspects of succession have been followed here for a period of 17 years, a phase which appears to include the invasion, growth, and mortality of early secondary species, the initial invasion of late secondary and primary seedlings but the continued presence of a denser ground vegetation (seedlings, grasses, and seges). Future censuses will continue to be conducted periodically in the irradiated area and sampling in the "cut-over" and "control" or undisturbed area may provide a basis for additional comparative studies.

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