CEER-T-205: SUCCESSION AT THE EL VERDE RADIATION SITE - A 17-YEAR RECORD BY SUSAN SILANDER, MARCH 1985, CENTER FOR ENERGY AND ENVIRONMENT RESEARCH

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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 known as 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 lower montane rain forest by Beard, 1955). The dominant species is tabonuco (Dacryodes excelsa) and other important species include motillo (Sloanea berteroana), 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 Location

"El Verde" in the Caribbean National Forest (Luquillo Experimental Forest).

The 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). The total density of canopy trees (>10 cm DBH) was 870/ha and of all trees greater than 4.5 ft (1.8 m) in height (i.e., stems with diameter at breast height-DBH) was 8120/ha.

The dominant canopy species were Dacryodes excelsa, Prestoea montana, Croton poecilanthus, and Sloanea berteriana. Dominant understory species included Palicourea riparia, Drypetes glauca, and Cordia borinquensis. The most abundant climbers or vines were Rourea glabra, Philodendron krebsii rectifolia, and Heteropterys laurifolia. Total density of climbers was 133/m². Dichanthelium pallens (Graminae) and Pilea krugii (a herb) composed over 50% of the ground flora.

The total density of herbs and ferns was 1.48/m² and of arborescent seedlings, it was 2.72/m². Plant biomass in the mature tabonuco forest was estimated to be 27.2 kg/m² and was distributed in the following manner: 939 g/m² as leaves; 7230 g/m² as roots; and 19.0 kg/m² as bole and branch wood (Odum, 1970). Above ground plant biomass was 19.9 kg/m².

Table 1 - Size class distribution of the species found in a 2 ha sample of tabonuco forest (from Wadsworth, 1951). The number of trees by species are as follows:

Carita recemifora: 2
Micvepels purcinolio: 0
Colscoronim sysumulerum: 3
Mopnoli planters Urban: 2, 7, 6
Croton pecionthus Urban: 3, 26
Tebebuevigita Cirtan: 0
Deryede excelsa Vat: 71, 2, 8
Ter ida (ab) Masia: 6
Inge luring tS) Wil: 2
Sopium lureceraiue Dest: 3, 5, 1, 8

'Sloanea berteriana Chow & Mtasta sumingensis (OC) Pad, Evgen tah (Liaersh) Krag, Oba, and Homelum racemes. Linecieva demingeneas (Lass) Koh and Didymeponas mesctoroni (AUB!) Dene, Corda tormguenis Urban, Ovsiee morehave (Paven) Met, Aioersea lente, Trott oposa Pere, Ficus eripeto Vabs, Fraxinus saronii War, and Other species.

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

Table 2 cont.

METHODOLOGY

For vegetation sampling purposes a 676 m2 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 throughout the years. Among these were Carl Jordan, Jerry Kline, Barbara Cintrén, Miguel Canals, Elvi Cuevas, Alejo Estrada, and Susan Silander. Data collected prior to 1975 were organized by Elvira Cuevas and Richard Clements. Each m2 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 m2 were identified by growth habit (vine, herb, or grass and sedge) and by species, sprout, sapling, seedling, fern, etc. The percent cover of each m2 was estimated for each grass species. The basal diameter of seedlings and sprouts under 4.5 feet (1.4 m) in height were measured. The 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 (SSS). The following relationships (Jordan, 1968) were utilized to estimate biomass (y-biomass in grams dry weight).'

Weight; x-basal diameter in x/128 of an inch and the number of samples:

1) Tree-shaped species (< 2 inches or 5 cm basal diameter) y = .0289x - .2025x + 13.4557 (n = 50)

ZONE I

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

2) Sprouts (< 2 inches or 5 cm basal diameter) y = .0203x7 + .7657x - 28.40 (n = 35)

3) Grasses and sedges y = 826 (& coverage of $1m^2$) (n = 10)

The following biomass regression (Doyle et al., 1982) was utilized in order to estimate the biomass of stems for which the diameter at breast height (DBH) was measured: B = .1568 (07-7337) where B = biomass in kg dry weight and diameter at breast height (DBH) in cm. This was derived from biomass-diameter data presented by Ovington and Olson (1970).

Summary of Previous Studies on 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 increased 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 8 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 5.78% in the irradiated area and 27.8% in the cut area. By 1968, the forest floor in the cut center was similar in composition and environmental conditions to that of the 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 the availability of seed sources. Stem and root resprouting in the irradiated area was limited (1.78%) and restricted to the side away from the source, whereas by early 1966 in the cut area, 21.8% of the trees cut had resprouted (Smith, 1970).

Figure 3. Figure 4. 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 5. 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 6. Temperature gradients at ground level in the Radiation Center.

Figure 5 shows the temperature in the radiation center before and after irradiation. Each point represents an average of measurements taken along eight different compass bearings (McCormick, 1970).

Odum et al. (1970) stressed that the recovery of the irradiated area was delayed by 6 months to 1 year due to the elimination of the seed bank by irradiation. Therefore, seed rain or introduction probably played the primary role in the 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 most radiation, was found to be proportional to the distance from the source.

Within a 10m radius, Palicourea Hiparia became much more abundant due to the changes in microclimatic conditions which occurred in this zone (McCormick, 1970). Jordan (1968) summarized the results of recovery studies carried out in 1966 and 1967.

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. In the cut-over area, however, leaf area index of new vegetation remained the same during this same time period and LAI of old vegetation increased slightly, indicating regrowth of the canopy.

In 1966, a total of 5286 individuals of 97 species were encountered and in 1967, 8,671 individuals of 121 species were found. The 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 of them secondary, composed approximately 50% of the biomass. Grasses and sedges were also found.

Composed on 20.08, end sprouts make up 19.28% 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)

	Aug. 1966	Feb. 1967	Aug. 1967	Feb. 1968
Irradiated area, new vegetation	96	1.68	2.90	3.26
Cut area, new vegetation	1st	1.65	1.63	14s
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	247
1966 sprouts	69
1966 poorly-drained soil new vegetation	126
1966 sprouts	6
TOTAL 1966	163,656
1967 well-drained soil new vegetation	323,256
1967 sprouts	4777
1967 poorly-drained soil new vegetation	482
1967 sprouts	30
TOTAL 1967	519,620
Mean biomass for entire area	1S

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.

Outside 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

The text provides an adequate and equitable seed source from all species. The selection of species and seedling numbers is a stochastic process. Factors such as shading, competition, and climate reduce optimum growth. There is 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. The Leaf Area Index (LAI) increases rapidly during the first 50 years to its peak but later declines to approximately 6.5 m^2/m^2.

Figure 6. The figure below is a representation of the average 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). This is 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 modeled dynamics of the individual dominant species: Cecropia peltata, Didymopanax morototoni, Buchenavia capitata, Sloanea berteroana, 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, including Palicourea riparia.

(Lebron, 1977); Cecropia peltata (Silander, 1979), Didymopanax morototoni (Nieves, 1979), and Buchenavia capitata (Sastre, 1979). Results indicate that plant density and species composition, including seedlings, sprouts, saplings, vines, herbs, and ferns, in the irradiated area was 10.9 individuals/m^2 in 1967 (Figure 8). The density decreased slightly in 1968, increased to a peak of approximately 15 individuals/m^2 in 1973, but by 1982 it had declined.

Figure 7 illustrates the 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) Bidentata; e) Styrax berteriana; f) 19.

Figure 8 shows the overall plant density (not including grasses) in the radiation center. The data for 1973 does not include sprouts.

Density in the area immediately surrounding the source (Zone 1) was somewhat lower than in the outlying area (Zone 2) 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. 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. The 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, the density of vines was consistently greater in the study area following irradiation than that reported by Smith (1970), at 0.133 individuals per m^2, for the undisturbed El Verde. Dominant species in 1967 were Securidaca.

Virgata, Rourea glabra, Mikania fragilis, Heteropteris laurifolia, and Maregravia rectiflora are outlined in 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 significant species in 1982.

As for herbaceous plants, their total density remained relatively constant throughout the study period (refer to Figure 9). However, the density in the area immediately surrounding the source (Zone 1) increased between 1967 and 1969 and was greater than that in the outlying area (Zone 11) throughout the other census years (refer to Figure 10b).

Dominant species in 1967 included Desmodium spp., Neptunia aquatica, Solanum spp., and Phytolacca icasandra (refer to Table 6). Species of Solanum, characteristic of hillsides, banks, thickets, or open areas (Britton and Wilson, 1927), were significant 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 significant 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 in 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 less prominent 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 the area.

This area had Desmodium spp. as a predominant herb, and its importance was consistent in all census years, peaking in 1982. On the other hand, Nepsera gradually decreased in relative abundance throughout the study period and was absent by 1982. There were a few which increased in relative importance throughout the study period, including Elephantopus mole cimoides and Triphora suraminesis. Classified here as a herb, Triphora is a terrestrial orchid which usually flowers in the summer or fall (Smith, 1970), and is characteristic of woodlands or forested areas (Britton and Wilson, 1927). Pilea krugil, 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.

Ferns' total density increased slightly throughout the study period (Figure 9). A more significant increase was evident in Zone 1, the area immediately surrounding the radiation source (Figure 10c). The dominant species in 1967 were Dryopteris deltoid, and Alsophila borinquena (Table 7). The relative abundance of both Dryopteris and Alsophila declined throughout the study period, while that of Nephrolepis increased until 1973 and then decreased.

Both Dryopteris and Alsophila were also important species in the ground flora prior to disturbance. By 1982, the dominant fern species was Blechnum occidentale, a species not present until the 1973 census. Britton and Wilson (1927) describe Blechnum occidentale as a species characteristic of dryish shrubby banks, open situations, and moist forest slopes. In 1982, this species was more abundant in the zone immediately surrounding the source than in the outlying area (Zone).

The cover of grasses and sedge species was estimated rather than their density. The mean percent cover per m² for the entire sampling area decreased from approximately 80% in 1967 to less than 58% in 1982. However, the cover by grasses in the area immediately surrounding the radiation source (Zone 1) decreased to only 20% in 1982, as opposed to 38% in the outlying area (Figure 11).

Dominant grass species throughout the study period included Hes Pallens, Paspalum Conjugatum, and Panicum Microcarpa. The mean percent cover per square meter was greater in all years on wet or poorly drained soil than on dry or well-drained soil types.

GRASSES
Mean % Cover
MEAN % COVER per square meter in Year
Figure 11, Mean percent cover per square meter by grasses in total area (676m²) and zones band I

Saplings

The total density of saplings slightly decreased in 1968, gradually increased to a peak in 1973, but slightly decreased in 1975 (Figure 9). This pattern was similar in both the area close to the source (Zone 1) and the outlying area (Zone II) (Figure 10d). The density was initially similar to that reported by Smith (1970), .812 per square meter, for the undisturbed El Verde site, but increased to approximately 1.2 per square meter in 1969.

Dominant species in the early years following irradiation were Psychotria La Riparia, Cecropia Peltata, Didymopanax Morototoni, Tabebuia Heterophylla, Miconia Racemosa, and Casearia

Bicolor (Table 8). The 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 41.58% 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 P. Heterophylla, Casearia Arbore. The latter was a dominant canopy species prior to irradiation (relative S. Berteri density 8.18) and along with E. Stahlli is classified as a primary forest canopy species (Smith, 1970).

Seedlings

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

In subsequent years, the number declined (Figure 9). In all years, the 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 1 and 11 as in the entire sampling area, although density in Zone 1 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 dominicana. 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.

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, the density was less in Zone 1, 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 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. The biomass of grasses in Zone 1, the area immediately surrounding the source, was similar to that in the outlying area in 1967 but in all subsequent years, it was less.

The biomass in 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. Biomass of saplings (those stems with @ OBH) in the entire sampling area increased between 1967 and 1973, decreased slightly in 1975, but by 1982 had reached approximately 6 kg dry weight/m² (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 1, in contrast to that in Zone 2 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 m² and zones 1 and 2.

Figure 13 - Biomass of saplings (kg dry wt/m²) in entire 676m² and zones 1 and 2.

Primary vs. Secondary Species

Primary and secondary species were grouped utilizing the criteria of Smith (1970).

Twelve species represent each group:

Primary:
1. Tetragastris balsamifera
2. Eugenia stahili
3. Sloanea berteriana
4. Ocotea moschata
5. Guarea trichilioides
6. Linociera domingensis
7. Ormosia krugii
8. Inga tauring
9. Micropholis garciniaefolia
10. Matayba domingensis
11. Dacryodes excelsa
12. Prestoea montana

Secondary:
1. Cecropia peltata
2. Miconia tetandra
3. Cyrilla racemiflora
4. Alchorneopsis portoricensis
5. Casearia bicolor
6. Cordia sulcata
7. Sapium laurocerasus
8. Tabebuia heterophylla
9. Croton poecilanthes

10. Catocoryne squamulosum

Seedlings Density of secondary

The density of secondary seedlings was initially greater than that of primary seedlings, but by 1969, five years after irradiation, the density of primary seedlings had increased and was greater than that of secondary seedlings (Figure 14). The density of secondary species continued to decrease until 1975, but showed an increase in 1982, apparently 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 a large number 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 cecropia peltata, and Alchorneopsis portoricensis. The density of saplings of primary species was less than that of secondary species. Dominant secondary saplings of Casearia bicolor were considered separately (Figures 16 and 17). However, the density of secondary saplings was greater in Zone I, the area receiving the greatest radiation exposure. Density here reached a peak in 1971 and thereafter decreased due to mortality of both C. bicolor and T. heterophylla.

Dominant primary saplings were Eugenia axillaris, 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, the biomass of secondary species was greater than that of primary species in both Zones I and II. Although the biomass of secondary saplings decreased after 1973 in Zone I, it continued to gradually increase in Zone II, the outer portion of the study area.

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 shows the density of primary and secondary individuals per 7 square meters per year.

Figure 16 illustrates the number of primary and secondary saplings in the entire 676 square meters area.

Figure 17 displays the density of primary and secondary saplings in Zones I and II.

Figure 18 presents the biomass of primary and secondary saplings in the entire 676 square meters area.

Figure 19 demonstrates the biomass (kg dry weight per square meter) of primary and secondary saplings in Zones I and II.

The biomass of Alchorneopsis portoricensis and Miconi primary saplings was extremely low in all years but among the more important species were Lineciera 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 outlying 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, the density of vines, sprouts, seedlings, and

The density of saplings increased until 1973 or 1975 and then decreased. The density of ferns increased gradually throughout the study period, while the density of herbaceous plants seemed to stabilize somewhat after 1963 (see Figure 9). In contrast, grass cover showed a continual decrease over time. Both patterns and densities of certain plant groups differed in the two zones considered: the area within a 5 m radius of the source and the outlying region. The density of ferns in the area close to the source increased dramatically between 1973 and 1982. The density of herbs was greater in this area, as was the cover by grasses and sedges. Conversely, the density of both vines and sprouts was consistently greater in the outlying area, whereas seedling and sapling densities were similar in the two areas (see Figure 10 a-f).

The density of plant groups varied throughout the study period as did species composition. Two important herbaceous species, Phytolacca, were secondary species in 1967 and 1968. 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 Psychotria and Didymopanax. Due to microclimatic conditions 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 after 1969. 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.

The density of Tabebuia seedlings markedly decreased. This abundance was responsible for the increase in secondary seedling density observed in Figure 4 in 1982, and was most important in the outerlying region of the sampling area (see Figure 15). The density of seedlings for particular species may depend upon the time of the year when the census is conducted. Estrada (1970) reported that fruit fall for Tabebuia occurred between July and September. The 1982 census was carried out in late September and October.

Even by 1982, saplings of primary species were of minor importance. Due to slow growth and high mortality resulting from continuous unfavorable microclimatic conditions, few "primary" seedlings had reached the sapling stage during the first seventeen years of succession. The density of saplings of secondary species was greater than that of primary species throughout the study period (see Figure 16). A continued gradual increase in the density of primary saplings might be expected.

The 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 the mortality of secondary species Cecropia and Didymopanax, both of which have short lifespan. Doyle (1981) reports that the biomass of these species peaks from 15 to 30 years following disturbance. Both species are often considered "gap opportunists" as 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 the regeneration by Cecropia. Palicourea is also a factor to consider.

Riparia, although present in undisturbed forest, may also be considered a "gap opportunist" as growth is stimulated by open canopy conditions (Lebrén, 1977). The 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 drier, 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/m² (or 60 mt/ha) by 1982, seventeen years following disturbance. Odum (1970) reported on aboveground plant biomass of 19.9 kg/m² 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 the 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/m² and 3568.6 g/m² 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...

The possibility of a slower accumulation of biomass in this successional area, when compared to other similar areas, might be 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 the mortality of secondary short-lived species. It is expected to increase again as primary or late successional species reach the sapling stage.

The 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. It also includes the initial invasion of late secondary and primary seedlings, but the continued presence of denser ground vegetation, such as seedlings, grasses, and sedges.

Future censuses will continue to be conducted periodically in the irradiated area. Sampling in the "cut-over" and "control" or undisturbed area may provide a basis for additional comparative studies.

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