CEER-T-205

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SUCCESSION AT THE EL VERDE

RADIATION SITE

AIT YEAR RECORD

SUSAN SILANDER

MARCH 1985

CENTER FOR ENERGY AND ENVIRONMENT RESEARCH

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SUCCESSION AT THE EL VERDE RADIATION SITE:

A17 YEAR RECORD

?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 understand-ing 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 @ canopy gap provided an ideal opportunity to examine the successional process, for which there exist few data in the tropics, on long-term basis, to compare an irradiated to 9 cut-over area and to evaluate the effects, if any, the irradiation had upon regeneration. This document provides an overview of data collected te dete, 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 &50 m in the Luquitlo Experimental Forest (also Caribbean National Forest) of north=

eastern Puerto Rico and fies within the subtropical wet forest life zon

(Enel 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 bert jana), yagrumo hembra (Cecropie peltata), caimitillo (Wiicropholis gorcinieefolia), and the sierra palm (Prestoes montana). In 2 4 ha sample of mature forest Wadsworth (1951) found that D. excels hhad the greatest number of stems in the largest size class whereas the

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Figure

Location of El Verde in the Caribbean National Forest

(Luquitio Experimental Forest).

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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). tn 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 then 4.5 ft (1.8 m) in height (i.e. stems with diameter at breast

tuded

height-DBH) was 8120/ha. The dominant canopy species

Dacryodes excelsa, Prestoca montana, Croton poecilanthus, and Sloanea

berteriana and dominant understory species were Palicourea riparia,

Drypetes glauca, and Cordia boringuensis. The most abundant climbers

Maregravia

- Total density of climbers was

or vines were Rourea glabra, Philodendron kreb:

rectifiora, and Heteropteris laurif

-133/m?,Jchnanthes pallens (Graminae) and Pilea Krugii (a herb) composed over 508 of the ground flora. Total density of herbs and ferns was 1.48/m? and of arborescent seedlings 2.72/m?.

Plant blomass in the mature tabonuco forest was estimated to be 27.2 kg/m? and was distributed in the following manner: 939 gin? as leaves; 7230 g/m? as roots; and 19.0 kg/m? as bole and branch wood

(Odum, 1970). Above ground plant biomass was 19.9 kg/m?.

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Table 1 - Size class distribution of the species found in 2 & ha sample of tabonuco forest (from Wadworth, 1951).

Number of trees by abhfom)

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Croton pecionthus Urban aw 3 26

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Homelum racemes 390 4 5 °

Linecieva demingeneas (Lass) Koh a ? 5 6

Didymeponas mesctoroni (AUB!) Dene ° ? 2 ae

Corda tormguenis Urban 2 ! °

Ovsiee morehave (Paven) Met 2 : a 1 :

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Ficus eripeto Vabs $ a 1 °

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Bother specie a om

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Table 2 - Species composition of tabonuco forest at the El Verde by rela~

tive density (from Smith,

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coset Oo,

1970).

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Table 2 cont.

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METHODOLOGY

For vegetation sampling purposes a 676 m? 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 Cintrén, Miguel

Canals, Elvi

Cuevas, Alejo Estrada, and Susan Silander. Data col-

lected prior to 1975 were organized by Elvira Cuevas and Richard

Clements. Each m? quadrant (1 through 676) was considered @ sampling

unit, Two soil types were identified within the sampling grid, @ 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? were identified by growth habit (vine,

herb, or grass and sedge) and by spe-

sprout, sapling, seedling, fern,

cles. Percent cover of each m? was estimated for each grass species.

Basal diameter of seedings 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

(sss)

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

?snumber of samples):

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

y=.0289x? - .2u25x ~ 13.4557 c

50)

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ZONE I

Figure 2. Vegetation sampling grid showing original location of

cesium source ($) in the Center.

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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?) (N=10)

The following biomass regression (Doyle et al., 1982) was utilized in

order to estimate biomass of stems for which @ DBH was measured:

B= .1568 (07-7337)

where B=biomass in kg dry weight and

ameter at breast height

{OBH) in em. This was derived from biomass-diameter data presented

by Ovington and Olson (1970).

Summary of Previous Studies

ion 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 con~ sequent changes in the environment which occurred thereafter. Spread of radiation damage continued for 3 months following the cessation of ra~ diation. Although plant responses occurred es for as 40 m from the cesium source, severe vegetation damage was restricted to within 2 10 to 12m radius. Environmental changes in this area included increased

light fevels, higher temperatures, lower relative humidities, and

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creased soll temperatures (Figures 3, 4, and 5; McCormick, 1970). At 2 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 & cm in diameter at ground level; and 3) pruning of teaf-bearing twigs off other trees, Recovery in the ir- radiated 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 278 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 ir- radiated area tended to be clumped rather than regular in distribution 3s 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 ere secondary

species this difference in dominance probably reflects 2 difference in availability of seed source. 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 218 of the trees cut had

resprouted (Smith, 1970).

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Figure 3.

Figure 4,

430

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400

350

300]

250)

200

150]

Light Intensity (FT-C)

100

50]

Distonce trom Center(m)

Light-intensity gradients in the Radiation Center before ond after irradiation. Each point is an average of the measure~ ments. taken along eight different compass bearings (from MeCormick, 1970).

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Distonce trom Center(m)

Relative humidity gradients in the Radiation Center before and after ieradiation.. Each point is an average of meo-surements taken along eight different compass bearings (from McCormick, 1970).

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Temperature (°C)

2

2 end Ground Level

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Distonce from Center (m)

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 MeCormick, 1970).

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Odum et at. (1970) stress that recovery of the irradiated area was

delayed by 6 mos to 1 yr due to elimination of the seed bank by irradi

tion 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 2 dense ground cover of herbs, grasses and seedings.

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

Results of recovery studi

carried out in 1966 and 1967 were sum- marized 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 5286

Individuals of 97 species w

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 SHY of the biomass. Grasses and sedges composed 20.08 end sprouts

19.28 of the biomass of new vegetation.

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Table 3 -

?af 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 1.68 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

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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?

1966

well-drained soi

ew vegetation 247

sprouts 69

poorly drained soil

ew vegetation 126

sprouts 6

TOTAL 196 163,656 2a"

1967

well-drained soil

new vegetation 323,256 837

sprouts 4777 123

poorly-drained soil

ew vegetation 482

sprouts 30

TOTAL 1967 519,620 768"

?mean biomass for entire area

1S

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Dominant vascular plants in 1966 which originated from seed following irradiation were Psychotria berteriana, Palicourea riparia, Cecropla peltata, Didymopanax morototonl, Ichnanthes pallens, Casearia bicolor, Alchornes Jatifolia, 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 dis~ turbance. Doyle (1981) and Doyle et al. (1982) modified @ gap succes- sion 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, lands s, etc.) on

this forest. This model simulates gaps of 1/30 ha, area, or approxi

mately 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 spe

?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 98-998 of a

seedting cohort.

Figure 6 represents 500 year simulation of the successional se~

uence beginning with an open gap and the absence of standing trees.

Leaf area index (LAI) increases rapidly during the first 50 years to @

m?/m? but later declines to approximately 6.5 m?/m?.

maximum of 7,

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Figure 6.

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?Mean values for 120 simulated 1/30-ha plots throygh 500 year:

of model simulation: (a) leaf area index (m* of leoves/nv

of land area); (b) total biomass (metric ton/ha): (c) total

number of trees (Individual trees greater than 1.3 cm dia~

meter at breast height, or dbh). (from Doyle, 1981)

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Above ground biomass increases during the first 125 years, fluctuating

thereafter between 175 and 250 metric tons per hectare. Stem density

Geclines 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 spe~

cies: Cecropia peltata, Didymopanax morototoni, Buchenavia capitata,

Sloanea ber

and Dacryodes excelse (Figure

7). Biomass of the first two, typically secondary, species peaks eround

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 @ 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 2 very low fevel.

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? in 1967

(Figure 8). Density decreased slightly in 1968, increased to 3 peak of

approximately 15 individuals / m? In 1973, but by 1982 had declined to

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Figure 7.

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?Successional dynamics of six dominant species of the tabonuco

forest 9s simulated ?by the FORICO model: (a) Cecropls vel tata; (b) Didymopanax morototoni; (¢) Buchenavia capitata;

> bidentata; Te) Stoanes berteriana: (1)

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18) © - Zone I

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Individuals sm?

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

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11 Individuals /m?, Density in the area immediately surrounding the source (Zone 1) was somewhat lower than in the outlying area (Zone 11)

in the early years following irradiation, but by 1973 this trend had been

reversed. Smith (1970) reported @ density of approximately 5 indi viduals per m? (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

2 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 ra- Giation 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?, for the undisturbed El Verde

Dominant species in 1967 were Securidaca virgata, Rourea glabra, Mikania fragilis, Heteropteris laurifolia, and Maregravia rectiflora (Table 5). These species remained dominant throughout the study period with

the exception of Mi

nia 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 1) increased between 1967

?and 1969 and was greater than that in the outlying area (Zone 11)

one

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© = vines 2 = Ferns

© = Sprouts © - Seedlings - He

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Figure 9. Density of the six plant groups included in censuses

in entire 676m2 sampling ares before and after irra:

diation. Data for sprout density prior to irradia

?tion noi available.

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throughout the other census years (Figure 10b). Dominant species in 1967 Included Desmodium spp., Nepsera aquatica, Solanum spp.. and Phytolacca Icasandra (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 eisturbance, and by 1975 were absent from the census area, Phyto-lacea, 2 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 dis~ turbance. Experimental manipulation of seed germination indicated that

elevated soll temperatures and slight scarification, events which may

accompany canopy opening, enhanced germination. Phytolacca was of fess importance in the irradiated area than in the cut-over area possibly ue 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 end was

absent by 1982.

Increasing in relative importance throughout the study period were

Elephantopus mol ecimoides, and Triphora suraminesis.

Classified here as a herb, Triphora is a terrestrial orchid which flowers

Bor

In the summer or fall (Smith, 1970) and is characteristic of woodlands or forested areas (Britton and Wilson, 1927). Pilea krugil, reported as 2 dominant herb species in the undisturbed Ei Verde site (Smith, 1970),

id not appear in the herbaceous flora in any of the census years.

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Ferns

Total density of ferns increased slightly throughout the study period (Figure 9). A greater increase through time was evident in Zone 1,

the area immediately surrounding the radiation source (Figure 10c). Do

and Alsophila borinquena (Table 7). The relative abundance of

minant species in 1967 were Dryopteris deltoidk

Dryopteris and Alsophila declined throughout the study period whereas

that of Nephrolepis increased until 1973 and thereafter decreased. Both

Dryopteris and Als

prior to disturbance. By far the dominant fern species in 1982 was

-ophila were also important species in the ground flora

Blechnum occidentale, 2 species not present until the 1973 census.

Britton and Wilson (1927) describe occidental

asa 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

.

Grasses

Cover rather than density was estimated for grass or sedge species. Mean percent cover per m? for the entire sampling area decreased from approximately 80% in 1967 to less than 58 in 1982. However, cover by grasses in the area immediately surrounding the radiation source (Zone 1) decreased to only 208 in 1982 as opposed to 38 in the

outerlying area (Figure 11). Dominant grass species throughout the

study period included

hes pallens, Paspalum conjugatum, Panicum

microcarpa. Mean percent cover /m? was greater in all years on the wet or poorly drained soil than on the dry or well

drained soil type.

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GRASSES

Mean % Cover

MEAN % COVER /m?

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Figure 11, Mean percent cover /m? by grasses in total area (676m") and

zones band I

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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 1)

and the outerlying area (Zone II) (Figure 10d). Density was initially

similar to that reported by Smith (1970), .812/m?, for the undisturbed

El Verde site, but increased to approximately 1.2/m? in 1969. Dominant

species in the early years following irradiation were Psychotria

1a riparia, Cecropia peltata, Didymopanax morototoni

Tabebuia heterophylla, Miconia racemosa, and Casearia bicolor (Table 8).

berteriana,

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:

12 was 2 dominant canopy species prior to irradiation (relative

S. berteri

density 8.18) and along with E. stahlli Is classified as © 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

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ln subsequent yeors declined (Figure 9). In all years density was greater than that reported by Smith (1970) for the El Verde site prior to lradiation (2.72 seedlings per m?). A similar pattern was observed in Zones | and 11 as in the entire sampling area although density in Zone 1 ?was initially lower and increased to 2 greater level in 1973 (Figure 10e). Dominant species following irradiation in 1967 included Tabebui

heterophylla, Palicourea riparia, Psychotrla berteriana, Didymopanax

morototon!, and Linociera doming 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 land the consequent favorable microclimatic conditions, seedlings of this secondary species continued to be an important component of the seed~ ling 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 (2

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

all years after 1967, density was less in Zone 1, the area Surrounding the source, than in the outlying area (Figure 10f). Domi-ant sprouting species in all years included Sloanea_berteriana,

Paticourea riparia, Croton poecilanthus, Inga vera. and Eugenia stahlii

3.

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Biomass

Grasses

Biomass of grasses decreased from approximately 175 g dry weight/-mm? in 1967 following irradiation to less than 25 9 dry weight/m? in 1982. Biomass of grasses in Zone 1, 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 soit type.

Saplings

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/m? (or 60 metric tons/ha) (Figure 13). This compares favorably to model biomass predictions made by Doyle (1981; 1982) for gap regeneration in tabonuco for-fest. 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 I and the area as 2 whole, continued to decrease after 1973, possibly due to the mortality of rapidly growing, larger stemmed secondary species such as C. peltata in this 2one following 1971.

Sapling biomes was consistently greater throughout the study

Period on the dry or well-drained soil than on the wet or poorly-drained

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Figure 12. Biomass of groeses in entire 676 m? and zones | and 1.

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Figure 13 - Biomass of saplings (kg dry wt/m?) in entire 676m? and

zones | and

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Primary vs. Secondary Species

Primary and secondary species were grouped utilizing the crite-

ria of Smith (1970). Twelve species represent each group

Primary Secondary

1. Tetragastris balsamifera 1. Cecropia peltate

: Eugenia stahili Miconia tetandra

3. Sloanea berteriana Cyrille racemifiora

4. Qcotea moschata A. Alchorneopsis

portoricensis

5. Guarea trichitioides 5. Casearia bicolor

6. Linociera domingensis Cordia suleata

7. Ormosia krugii 7. Sapium laurocerasus

8. Inge tauring 8.

9. Micropholis garciniaefo 8.

. 10. Matayba dominge: 10. Tabebuia heterophylla

11, Dacryodes excetsa 11. Groton poecitanthus

12. Prestoea montana 12. Catycagonium

-squamalosum

Seedlings

Density of secondary seedlings was initially greater than that of

Primary seedlings but by 1969, § yrs after irradiation, density of

Primary seedlings had increased and was greater than that of sec-

ondary seedlings (Figure 14). Density of secondary species continued

to decrease until 1975 but showed an increase in 1982, apparently

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© - Primory species

of © - Secondary species

No. Individuals /m@

1

tt

70 72 74 ~76~78 +80 82

Yeor

Figure 14. Densjty of primary and secondary seedlings in entire

676a¢ sampling area before and after irradiation.

Preirradiation data from NeCormick (1970).

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?due to on increase in density in Zone I! (Figure 15). This increase

in secondary seedling density in Zone II in 1982 was due to great

numbers of seedlings of Tabebula heterophylla, a result of the

Presence of an adult, flowering specimen in the immediate area and

continued favorable microclimatie conditions. Dominant primary

seedling species included Dacryodes excelsa, Linociera domingensis,

Motayba domingensis, and Prestoea montan:

species were T. heterophylla, Alchornes

Cecropia peltata, and Alchorneopsis portoricensis.

Saplings

Density of saplings of primary species was less than that of secon=

Dominant secondary

fo

Casearia bicolor,

and 11 were considered separsaly (Fgures 16 and 17). However, dana

ty of secandney saplings was grants n Tora |, the ares recsivng the

arenestradatin exposure. Danaty hare caached peak nv 1971

Gheraferdcrased don to meray of stone of both C. plata and T.

hetaeghyla. Oomiant prnary suplags were Eugenis sabi, Llocara

domingensis and Matayba domingensis. Even by 1982 few indi

Dacryedes excelsa, a dominant primary seedling and indicator of this

iduals of

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 t and Il.

Although biomass of secondary saplings decreased after 1973 in Zone | it

continued to increase gradually In Zone I1, 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,

3.

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INDIVIDUALS 7 m2

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Figure 15

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10 ies

YEAR

Density of primary vs.

and It

0-

+ Primory Species- Zone I

= Secondory Species - Zone T

= Primory Species Zone I

~ Secondary Species- Zone I

a

secondary seedlings in zones 1

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Individuals /m2

Individuals sm?

Figure 16. Primary and secondary saplings in entire 676m"

© Primery Species

© Secondary Specter

»

te

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

Primary Zone =

Secondory Zone I

Primary Zone IE

Secondery Zone

Dros

o>

& 49 70 72 73 74-75 ~<76 77 79 79 ~80 BI Be

a

---Page Break---

BIOMASS OF SAPLINGS

© + Primory Species

© - Secondory Species

KG ORY WEIGHT sm?

YEAR

Figure 18. Bjomass of primary and secondary saplings in entire 676

oe

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KG DRY WEIGHT sm?

+ Primory Zone I

+ Secondary Zone I

+ Primary Zone I

+ Secondory Zone I

.

°

or eos 70 es 8 ee 79 80 8a

YEAR

Figure 19. Bionass (kg dry wt/m?) of prinary and secondary saplings

in Jones I and 11.

ae

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Biomass of

Alchorneopsis portoricensis and in 1982, 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

immedi

ly 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 1963 (see Figure

9). In contrast cover by grasses shoned 2 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 outertying 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).

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?As density of plant groups varied throughout the study period so

um and

did species composition. Two important herbaceous species, So Phytolacca, in 1967 and 1968 were secondary species. By 1975 and 1982 these species were no longer present in the study ares. Studies of Phytolacca indicate that germination is enhanced by increased soll 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 Phytolacce and Solanum.

Dominant seeding species in early censuses were primarily

Psychotria, and

Didymopanax. Due to microclimatic conditions such as those described

secondary species such as Tabebula, Palicoure:

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 mos

portant 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.

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Saplings of primary species were, even by 1982, of minor im-

portance, Due to slow growth and high mortality as a result of con-

tinued 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 @ peak in 1971 and thereafter declining. This

decrease in density was due to mortality of the secondary species

Cecropia and Didymopanax, the 1

(1981) reports that biomass of these species peaks from 15 to 30 years spans of which are short. Doyle

following disturbance. Both species are often considered "gap op-Portunists" in that their continued existence in the undisturbed forest is dependent upon the presence of gaps or canopy openings of sufficient

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 eccurred 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 (Lebrén, 1977). Relative abundance of this species continued to increase throughout the study Period,

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Statistical studies on the effect of soil type and any interaction with

Gistance 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 fon the dryer, well-drained soll. 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 yeas

on the well-drained soil type.

Above ground biomass of saplings had reached 6 kg dry weight/m? (or 60 mt/ha) by 1982, seventeen years following disturbance. Odum (1970) reported on aboveground plant biomass of 19.9 kg/m? from the undisturbed EI 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 over-

estimates due to inclusion of both primary and secondary, generally

ighter species, in the same regression, particularly as secondary species tended to be dominant. Brown (1980), in a summary of tropical biomass dota, states that based on available data biomass accumulates rapidly

during the first 10-20 years at which time biomass may have reached 100 mtyha. Ewel (1970) reports values of 5022.5 g/m? and 3568.6 g/m? 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 im? during the first year of natural regeneration. All of these figures Suggest the possibility of a slower accumulation of biomass in this,

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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

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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