

# REGROWTH OF CLEARCUT SUBTROPICAL DRY FOREST: MECHANISMS OF RECOVERY AND QUANTIFICATION OF RESILIENCE

By

Vicki L. Dunevitz

#### A THESIS

.

Submitted to Michigan State University in partial fulfillment of the requirements for the degree of

# MASTER OF SCIENCE

Department of Botany and Plant Pathology

#### ABSTRACT

## REGROWTH OF CLEARCUT SUBTROPICAL DRY FOREST: MECHANISMS OF RECOVERY AND QUANTIFICATION OF RESILIENCE

By

Vicki L. Dunevitz

The degree of recovery and mechanisms of regeneration were investigated on a one ha 13-year-old cut-over dry forest site near Guanica, Puerto Rico. Recovery was relatively rapid, with leaf area index 64% and basal area and mean plant height 40% of adjacent mature forest values. Fifty-nine percent of mature forest species occurred in the Cut Site. Species diversity was higher in the 13-year-old site than in one-year-old or mature forest sites, with pioneer species contributing 46% of stem density and 28% of species. Half the plants with stems > 1 cm originated as sprouts from roots or cut stems, the remainder as seedlings. Numbers of woody seedling origin plants varied with distance from the forest edge, but not significantly. Quantities of VA mycorrhizae did not differ in three different-aged dry forest sites. Significant effects of 1969 recut/herbicide treatments still persisted in 1982.

#### ACKNOWLEDGEMENTS

I would like to thank Dr. Peter Murphy for financial support through NSF Grant DEB-8110208 and for his advice and guidance. Thanks are extended to my other committee members, Dr. Deborah Goldberg and Dr. John Beaman, and to Dr. Ariel Lugo, for helpful suggestions and critical comments. Alice Murphy provided invaluable assistance with seed bank studies, species identification, and field work. Baudilio Hernandez, Eusebio Santiago, and Roberto Santiago provided inestimable help with field work. I am grateful to Dr. Gene Safir for the use of his laboratory equipment and for technical advice on mycorrhizal analyses. I thank Dr. Robert Jansen and Dr. Cheryl Crowder for taxonomic assistance, and Dr. Jay Harman for advice and friendship.

Colleagues who have supplied unflagging support as well as advice and critical comments include Maureen Mulligan, Terese Hart, Martha Tilmann, Susan Gibbons, John Hart, Leni Wilsmann, Dan Nepstad, Helen Kuhn, and Barbara Wilber. This thesis would not have been possible without the energetic support and enlightening analyses provided by the Women in Science group (WEBS) and the Thursday night volleyball league.

ii

# TABLE OF CONTENTS

List of Tables	iv
List of Figures	vi
Introduction Theoretical Background Objectives and Hypotheses	.1 .2 .5
Forest Recovery Dry Forest Ecology	.9 12
The Study Area	17
Methods Vegetation Structure and Composition Seed Banks Mycorrhizae	24 24 31 <b>34</b>
Results Site Description Vegetation Structure and Composition	36 36
Species Diversity Structure Mechanisms of Regeneration Mycorrhizae Effects of Ewel's Recut/Herbicide Treatments	39 41 54 66 70
Discussion. Temporal Patterns of Succession. Mechanisms of Regeneration. Mycorrhizae. Recovery and Resilience.	72 72 79 83 84
Summary	91
Appendix	93
Literature Cited	99

# LIST OF TABLES

Table	Page
1.	Importance values for plant species with DBH > 1 cm in Cut Site and adjacent forest plots42
2.	Structure of Cut Site and adjacent forest vegetation43
3.	Leaf area index and percent cover in the Cut Site43
4.	Structure of woody vegetation in Cut Site, in adjacent forest, and on Cut Site before it was cut
5.	Comparison of herbs in Cut Site and adjacent forest between dry season (March) and wet season (August)53
6.	Effect of distance from forest edge on seedling species and densities in Cut Site 2 x 2 m plots60
7.	Total seed densities in soil and litter samples in September and March62
8.	Densities of seed species < 2.38 mm germinating from soil and litter samples under greenhouse conditions63
9.	Densities and species of seeds > 2.38 mm collected from soil and litter samples64
10.	Viability and germinability of fresh seeds collected in August 198267
11.	Effects of scarification treatments on Leucaena leucocephala seed germination68
12.	Mean mycorrhizal ratings of species in three different-aged sites69
13.	Structure of vegetation in the portion of the Cut Site which had recut/herbicide treatments in 1969 and in the portion which was cut only71

-

14.	Degree of recovery of structural parameters in thirteen-year-old dry forest
Al.	Characteristics of all species occurring in plots
Α2.	Structural parameters of all stems > 5 cm DBH on the study site before it was cut in 196996
A3.	Importance values for woody plant species with DBH > 5 cm on the study site before it was cut in 196997
λ4.	Multivariate comparisons of structure in the Cut Site and forest 2 x 10 m plots using the Hotelling T test

•

.

# LIST OF FIGURES

Figure	Pa	age
1.	Location of the Guanica Commonwealth Forest	18
2.	Monthly distribution of annual rainfall in two Puerto Rican dry forest sites	19
з.	Location of the thirteen-year-old Cut Site, adjacent forest study area, and forest plots studied by Murphy and Lugo	22
4.	Location of 2 x 10 m Cut Site and forest plots	26
5.	Location of 2 x 2 m Cut Site and forest plots	28
6.	Leaf area index sampling locations	30
7.	Appearance of Cut Site vegetation in 1982, 13 years following cutting	37
8.	Appearance of adjacent forest vegetation in 1982	38
9.	Species area curves for Cut Site and forest 2 x 2 m sampling plots	40
10.	Comparison of structure in Cut Site and adjacent forest	14
11.	Leaf litter biomass in forest and Cut Site in September and March	16
12.	Numbers of plants in height interval classes in Cut Site and forest	17
13.	Vertical stratification of Cut Site vegetation using vegetation area index readings	48
14.	Size class distribution in the 2 x 10 m plots in forest (N=30) and Cut Site (N=10)	51
15.	Percentages of woody stems > 1 cm DBH originating as vegetative sprouts and as seedlings in Cut Site and forest plots!	56

16.	Percentages of woody plants with stems > 1 cm DBH with stems originating as vegetative sprouts and as seedlings in Cut Site and forest plots
17.	Height class distribution of woody plants in Cut Site and forest originating as vegetative sprouts and as seedlings58
18.	Relationship between numbers of woody seedling-origin plants in Cut Site and distance to the forest edge61
19.	Species diversity changes relative to succession in the Guanica forest
20.	Patterns of structural change in long-term dry forest succession

•

-

#### INTRODUCTION

The widespread human impact on many of the world's forests has resulted in a great deal of interest in and concern with the ability of forested ecosystems to recover following disturbance. Because of the constraints on obtaining data on long-term forest recovery, the most formidable being the long time period involved (sometimes up to several hundred years), rates and processes of natural forest regeneration remain incompletely understood.

Especially lacking are studies of succession in tropical and subtropical dry forest (sensu Holdridge 1967). Since this community type constitutes an estimated 42% of the world's tropical and subtropical forests (Brown and Lugo 1982), and is subjected to a myriad of land uses causing various degrees of disturbance (Tosi 1980), it is a topic that gravely needs addressing.

In 1981, a detailed study of dry forest dynamics and succession in the Guanica Commonwealth Forest in Puerto Rico was undertaken by P. Murphy and A. Lugo to begin to address that need (Murphy and Kephart 1981, Murphy and Lugo 1983,1985). A nearby one ha stand of forest which had been clearcut in 1969 by John Ewel (Ewel 1971) provided an ideal opportunity to study the degree of longer-term recovery of the forest. This study was

undertaken in 1981 to attempt to elucidate the mechanisms and measure the degree of recovery of a cry forest thirteen years following clear-cutting.

#### Theoretical Background

The study of ecosystem recovery rates involves several components of successional change. One that is of prime importance is ecosystem resilience. Much confusion has persisted regarding the use of the terms "stability" and "resilience" and their components (e.g. see discussions in Margalef 1975 and Westman 1978). Stability is used here to mean the pattern of fluctuation in a relatively unimpacted ecosystem over time (sensu Westman 1978), with low and/or predictable amounts of fluctuation equating with high stability. Whittaker (1975) identified nine aspects of stability. The first eight are described as the application of four variables to both the community and the abiotic environment: 1) relative amplitude of regular fluctuation, 2) relative irregularity of fluctuation, 3) presence of zero values in fluctuation, and 4) the duration of this pattern in evolutionary time. The ninth aspect is the one addressed in this study: resilience, defined here as the ability of a system to return to its initial, predisturbance condition after a

disturbance or stress period.

Degree of resilience can be expressed in empirical studies as 1) the time required to restore a particular characteristic of an ecosystem (e.g. biomass, basal area, etc.) to a given percentage of pre-impact level, or 2) the percent similarity of the disturbed ecosystem to the undisturbed ecosystem after a particular period of time.

Cairns and Dickson (1977) developed a recovery index for aquatic ecosystems based on subjective ratings of six parameters. Ewel (1980) proposed a less subjective index calculated with 12 structural measurements: stem density, biomass, four measures of foliage density, three measures of height, and three measures of species richness. He compared relative resilience of five sites by expressing each variable as a percentage of the maximum value obtained at any of the five sites studied, and then averaged the percentages for each site. This method is limited to studies with comprehensive data from equal-aged sites, and, more importantly, does not take into account predisturbance structure.

There has been much discussion regarding potential causes of variation in resilience among ecosystems. Clapham (1971) suggested that resilience is maximized in regions in which productivity, "niche breadth", and environmental fluctuations are high, though he provided no mechanisms for the effects of these factors on resilience.

He predicted that the tropical rainforest has a relatively low resilience despite the small amplitude of environmental fluctuation and high productivity because organisms are adapted to narrow, highly specialized niches, making them extremely vulnerable to perturbations. He suggested that temperate deciduous forests, characterized by moderate fluctuation, productivity, and "niche breadth", have relatively high resilience values. Lacking in this theory are predictions of the relative contribution of each of the 3 variables; it is doubtful that they are weighted equally. Other hypothesized causes of high relative resilience include low species diversity (Loucks 1970) and small size of disturbed area (Hill 1975). Additional factors affecting resilience are disturbance history (Holling 1975), abiotic properties (Holling 1973), and spatial organization (Hill 1975).

Cairns and Dickson (1977) developed a recovery index for aquatic ecosystems based on subjective ratings of 6 parameters. Ewel (1980) proposed a less subjective index calculated with 12 structural measurements: stem density, biomass, four measures of foliage density, three measures of height, and three measures of species richness. He compared relative resilience of 5 different sites by expressing each variable as a percentage of the maximum value obtained at any of the five sites studied, and then averaged the percentages for each site. This method is

limited to studies with comprehensive data from equal-aged sites, and does not take into account predisturbance structure.

## Objectives and Hypotheses

The fundamental objectives were to assess the degree and some of the mechanisms of recovery of 13-year-old dry forest vegetation, and to quantify the forest's resilience. To accomplish this, structural measurements of the one ha site in Guanica, Puerto Rico are compared with measurements made in adjacent older secondary forest, representative of the most mature stands in Guanica. Additionally, data collected on the site before and one year after it was cut (Ewel 1971, 1977, and unpublished data) are summarized to provide information on early site recovery. Several hypotheses guided the research. The first addresses resilience of dry forest vegetation in relation to other forest ecosystems. The next four make predictions regarding aspects of the dry forest recovery process, and the last addresses the effects of multiple disturbance on dry forest recovery. The hypotheses were as follows:

## A. Resilience

Dry forests are more resilient than tropical humid to

wet forests, and equivalent in resilience to temperate deciduous forests. Clapham (1971) and Ewel (1980) suggested that ecosystems in intermediate-stess environments, such as temperate and tropical deciduous forests, may be more resilient than those of more benevolent (e.g. tropical rain forest) or more harsh (e.g. montane rain forest or tundra) environments. Clapham argued that intermediate-stress environments may possess higher fluctuation and organisms with greater phenotypic plasticity than benevolent environments, and higher productivity than harsh environments. The lack of recovery data from sites with age and disturbance history comparable to that of the study site makes absolute comparisons of relative ecosystem resilience impossible at this time. In this study, dry forest resilience is quantified and discussed in relation to short-term recovery data from other forest types, and suggestions for further study of resilience are made.

B. Diversity

Plant species diversity in successional dry forest vegetation is higher than in mature forest stands. Margalef (1963) postulated that diversity in ecosystems tends to peak following a spurt of productivity such as that occurring in young successional vegetation, and then declines as the system matures and productivity lessens, but he did not present empirical data to support this. In

this study, diversity of vegetation from 1-year-old, 13-year-old, and mature dry forest sites are compared to determine whether this pattern holds true during dry forest recovery.

C. Mechanisms of Regeneration

(1) Vegetative sprouting, rather than seed germination, is the dominant mode of regeneration in the dry forest. Sprouting is known to be of importance in cut-over dry forest recovery (Ewel 1977, Murphy and Lugo 1983). Seedling emergence and survival, on the other hand, may be inhibited in dry forests due to lack of sufficient soil moisture (Ewel 1977). Relative proportions of sprouted stems and seedling-origin stems are examined in the 13-year-old site and in mature forest to determine whether there were more plants which had orirginated as seedlings following the 1969 clearcut than those which had originated as sprouts.

(2) Distance to the forest edge is inversely related to species distribution and density of seedlings in a 1 ha successional dry forest site. It appears from the few studies available that the size of area disturbed is a major determinant of the rate and pathway of succession. When very large vegetated areas are disturbed, the invasion of propagules must necessarily take place from the edge of the plot, resulting in a possible delay of full species reestablishment (Gomez-Pompa et al. 1974).

The edge effect on species distribution of seedling-origin plants is measured on the one ha site.

D. Mycorrhizae

Vesicular-arbuscular mycorrhizal associations are not appreciably impacted by the cutting of a dry forest. All of 33 plant species in the Guanica forest examined for presence or absence of mycorrhizae were infected to some degree (Dunevitz et al. 1983), indicating that VA mycorrhizae are important components of the dry forest ecosystem. Janos (1980) predicted that cutting a tropical forest would not greatly affect mycorrhizal populations when tree roots are left intact and soils remain in place, since the primary impact is on the aboveground structures. This hypothesis is tested by comparing mycorrhizal quantities in 1-year-old, 13-year-old, and mature dry forest sites.

# E) Multiple Disturbance

Multiple cutting and disturbance treatments applied to dry forest for one year following cutting will result in less site recovery 12 years later than will cutting alone. The findings of Isensee et al. (1973), Ewel (1971), and Ewel et al. (1981) supported the idea that increasing intensity of disturbance generally results in slower rates of recovery. A 6000 m<sup>2</sup> portion of the Guanica study site received a mosaic of repeated cutting and herbicide

treatments for one year following cutting; structural variables there are compared to those on the remainder of the site.

Literature Review

Forest Recovery

The essential components for estimating resilience include predisturbance data, comprehensive measurements of a number of structural variables following disturbance, and documentation of the time and extent of disturbance. A review of the forest succession literature reveals that there are few published reports which include all of these components.

Many forest succession studies have relied on the reconstruction of historical changes using aerial photographs, tree-ring analyses, fire scar analyses, or comparisons of different-aged old-growth stands (Kittredge 1934, Martin 1959, Vogl 1969, Auclair and Goff 1971, Day 1972, Henry and Swan 1974, Taylor 1980, Sprugel and Bormann 1981, Romme and Knight 1981, Romme 1982, Agee and Smith 1984). These studies were limited by the availability of historical information, and studies using different-aged stands are further complicated by site-to-site variability. A number of reports of tropical forest succession are largely descriptive and lack quantitative information (e.g. Symington 1933, Richards 1955, Nye and Greenland 1960, and Fox 1976). Studies of post-agricultural succession (e.g. Grieg-Smith 1952, Budowski 1963, 1965, Kellman 1970, Pickett 1982, Uhl and Jordan 1984) demonstrate temporal sequences which are likely to differ radically from those on cut-over forest lands, as farming practices generally modify soils, eliminate seed sources of woody vegetation, and kill stumps and rootstocks which may otherwise resprout. Forest recovery studies focusing on just one aspect of ecosystem change, such as leaf production (Covington and Aber 1980), species diversity (Shafi and Yarranton 1973, Tomkins and Grant 1977), root biomass (Berish 1982), or forest floor organic matter and nutrient content (Likens et al. 1978, Covington 1981, Binkley et al. 1982) are too limited to be useful in comparisons of ecosystem resilience. Early studies of regeneration of American northern hardwood stands following cutting (Leak and Wilson 1958), fire (Larsen 1925), or hurricanes (Spurr 1956) focused only on measuring the restocking of desirable tree species, while other floristic elements were ignored.

More comprehensive studies (e.g. Ross 1954, Odum and Pigeon 1970, Webb et al. 1972, Malmer et al. 1978, Ewel et al. 1981, Uhl 1982, Hibbs 1983) either lacked information on pre-disturbance forests or measured only

short-term recovery. Perhaps the most detailed published forest succession study to date (Bormann and Likens 1981) reported only the first six years of regeneration following cutting and herbicide application. Marks and Bormann (1972) measured revegetation on 1 to 14-year-old cut-over northern hardwood stands dominated by *Prunus pensylvanica*, but reported only limited data on climax associations.

While the studies cited above demonstrate a limited amount of data on temperate and wet tropical forest recovery, even less is known about tropical dry forests, despite their large areal extent. Opler et al. (1977) compared the rate of recovery on a one-year-old cut and burned dry forest to that of one to three-year-old wet forest in Costa Rica, relying primarily on mean seed weight data and making the assumption that lighter seeds are found in younger sites. They predicted full recovery times of 150 and 1000 years for dry and wet forests, respectively. Van Riper (1980) suggested that in Hawaiian dry forests, tree species composition and distribution have been appreciably impacted by human disturbance, browsing by feral mammals, and changes in seed dispersal due to the presence of introduced avian species. Ewel (1971, 1977, 1980) examined regrowth for one year using various combinations of cutting and herbicide treatments in five tropical forests ranging from the dry forest site

of this study (880 mm rainfall) to tropical wet forest (4800 mm rainfall). Lowland wet forests grew the fastest, exhibiting the maximal values of species richness, leaf area index, biomass, and average height of the 3 tallest plants per plot. The 2 dry forest sites showed lower recovery rates, and a tropical montane rain forest was least recovered (Ewel 1980).

## Dry Forest Ecology

Old world dry forest formations include the African miombo (reviewed and described by Malaisse 1978), dry deciduous forests (Bourliere 1983), and Australian semiarid woodlands (described by Pressland 1975). Water relations of these and other areas were discussed by Doley (1981).

Recent ecological studies demonstrate the variety of species associations which fall under the category of New World dry forest. Costa Rican dry forest (Hubbell 1979, Opler et al. 1980) has structure and diversity similar to Puerto Rican dry forest, but supports a very different species association. Hubbell found that all dry forest tree species were either clumped or randomly dispersed, and that clumping was related to seed dispersal. Goldberg (1982) found that soil factors strongly affected the distribution of Lysiloma divaricata-dominated Mexican dry forest and adjacent evergreen oak-woodland. Dry evergreen

forests in Jamaica (described by Loveless and Asprey 1957) had many species in common with Puerto Rican dry forests, while Jamaican dry slope and dry limestone scrub forests (studied by Grubb and Tanner 1976) were guite different.

Lugo et al. (1978) measured structure, productivity and transpiration in the Guanica forest near the study site of this investigation, and emphasized the role of low soil moisture availability in determining structural and functional aspects of the formation. Murphy and Lugo (1983, 1985) are collecting comprehensive data on the dynamics and succession of the Guanica forest. Their study site includes a 1.4 ha plot located 1.0 km east of the site used in this investigation. They found a total of 59 vascular plant species, including 33 species with a minimum diameter at breast height (DBH) of 2.5 cm. Stem density and basal area for stems > 2.5 cm were 14,007/ha and 19.8  $m^2/ha$ , respectively. Tree heights were small, with fewer than 3% exceeding six m, and the tallest tree sampled reaching only 8.5 m. The live-plant biomass was 89.9 t/ha, with about 50% occurring below ground.

Dry forest phenological studies have demonstrated a distinct seasonality in leaf flushing, flowering, and fruiting. In Costa Rican dry forests, where rainfall is generally > 1500 mm/year, Daubenmire (1972) reported two flowering seasons correlating with major and minor seasons of drought. His work was substantiated by Frankie et al.

(1974), Janzen (1967), and Opler et al. (1980), who also demonstrated a predominance of dry-season flowering in Costa Rican dry forests. Malaisse (1974), in a study of Zambezian miombo (mean rainfall 1270 mm/yr) found a preponderance of flowering and leaf flushing in the warm dry season just before the onset of the rainy season. In areas with less rainfall than the Costa Rican and Zambezian sites, phenological activity is apparently largely limited to wetter seasons. Lieberman (1982) found that flowering and fruiting in West African dry forest (rainfall of 1100 mm/year) reached a peak during wet periods, and the size of the fruit crops appeared to be greatest following periods of abundant rainfall. Murphy and Lugo (1983 and unpublished data) found that in the Guanica forest, flowering tended to peak in May-July, a period when precipitation is fairly high. Fruiting followed a more sporadic, possibly bimodal pattern, with peaks in January and in June-July. Of the 48 tree species observed, there were never more than 32% flowering or 52% fruiting at any one time. Leaf senescence in dry forests, generally corresponding with the dry season, appears to be triggered by drought stress more than by daylength (Daubenmire 1972, Frankie et al. 1974, Lieberman and Lieberman 1984, Murphy and Lugo 1985).

Data on seed dispersal, storage, and germination in dry forests are sparse. Aristeguieta (1968) and

Daubenmire (1972) noted that animals and wind are important vectors of seed dispersal in dry forests, but did not quantify numbers of species which were gravity dispersed. Cheke et al. (1979) found 40 seeds per .25  $m^2$  and 16 species of seeds in 5 cm deep soil samples from dry dipterocarp forest in Thailand. Hall and Swaine (1980), in a study of seed banks from 3 different dry forest types in Ghana, found that 107 to 696 seeds/m<sup>2</sup> germinated from 4 cm deep soil samples. All seeds were from secondary forest species except the 0.3 to 11.2% which were primary forest species.

Endomycorrhizae have been shown to be important components of Tanzanian miombo (Hogberg 1982) and of the Guanica forest (Dunevitz et al. 1983), corroborating other reports of the prevalence of mycorrhizae in arid zones such as deserts (e.g. Miller 1979, Diem et al. 1981).

Herbivory patterns and rates are potentially important factors in vegetative recovery. Herbivore damage to leaves in Costa Rican dry forest was greater than that of nearby riparian forest (Stanton 1975). Lieberman and Lieberman (1984) reported that herbivory in African dry forest was most common in newly flushed leaves and found severe herbivore damage to leaves in 25% of the 59 species studied. Forty-three per cent of the species had some form of protection from herbivores. Janzen (1981) found

that folivory varied "enormously" from year to year in Costa Rican dry forest.

#### THE STUDY AREA

The 4000 ha Guanica Commonwealth Forest is located on the southern coast of Puerto Rico at latitude 18 N (Figure 1). The low annual rainfall, ranging from about 600 to 1100 mm, is partially due to the forest's position in the orographic rain shadow of Puerto Rico's Central Cordillera. The monthly distribution of mean annual rainfall in a dry forest site near Guanica (Figure 2) illustrates a severe dry season, from January through March, and a secondary moisture-limited period in mid to late summer. The forest is classified as subtropical dry forest by Holdridge's life zones classification system (Holdridge 1967), based on mean annual precipitation, biotemperature, and humidity.

The soil is derived from limestones of Miocene and Oligocene age which surface in many places (Monroe 1976). Soil types vary depending on the hardness and depth of the limestone. Much of the Guanica forest is underlain by a mollisol (Calciustoll: Aquilita series) which consists of a 15-18 cm dark brown clay loam or clay surface layer (bulk density = 0.7 g/cc), high in organic matter, which grades into a soft, porous, mottled, white limestone (bulk density = 1.3 g/cc) by 40-50 cm depth<sup>1</sup>. This soft

<sup>1</sup>Unpublished data collected by Daniel Nepstad, 1982.







Figure 2. Monthly distribution of annual rainfall in dry forest at Santa Isabel, Puerto Rico (after Ewel and Whitmore 1973).

limestone has, in some areas, produced a layer of indurated caliche above it. The remainder of the area is underlain by shallower, redder soils, apparently derived from harder limestone formations. Crevices in the rock in the Guanica forest are sometimes filled by soils of  $\geq 200$ cm depth (Ewel 19171). Forest soils (measured at depths of 5 and 15 cm) were found to be fertile in terms of total nitrogen (9100 kg/ha), phosphorus (1820 kg/ha), and potassium (7460 kg/ha) (Lugo and Murphy 1985). The high exchangeable calcium (>4000 ppm) and high pH (7.3-7.6) cause only 1.3% and 25% of total phosporous and potassium, respectively, to be exchangeable.

The vegetation of the region was described by Gleason and Cook (1926) and was labelled dry limestone forest by Little and Wadsworth (1964). Wadsworth (1950) described the climax dry forest of the southern coast of Puerto Rico as being very dense, with tree heights from 40 to 60 feet, and consisting of 2 tree layers, each with distinct species. At present only old-growth secondary forest is extant; all primary forests have been logged. Lugo et al. (1978) distinguished three upland plant associations in the Guanica forest based on soil and floristic differences; they included scrub, deciduous, and semi-evergreen forest. The deciduous association, which includes the sites of this study, occupies about 58% of the Guanica forest.

The one ha site of this study is located 1.9 km from the south coast of Puerto Rico, on a southwest-facing 5% slope at 180 m elevation (Figure 3). The vegetation occurring on the site before it was cut in 1969 had been free from grazing and fire for about 40 years, but had been subjected to some cutting (Ewel 1971). The vegetation consisted of about half deciduous and half evergreen species, with emergent trees on the site about 10-12 m tall (Ewel 1971).

Data collected on the study site previous to the 1969 cut were provided by J. Ewel. The sampling included three 100 x 10 m transects across the site, in which the species and DBH of each stem  $\geq$  5 cm and the total stem density were recorded. The data are summarized in Tables Al and A2. Ewel identified 16 species with stems  $\geq$  5 cm DBH and noted there were about 2 additional unidentified species in each transect (Table A3), compared to 30 species/1500 m<sup>2</sup> in that size class in the site studied by Murphy and Lugo (1983). The three most important species in the Ewel site accounted for about half the total importance value.

The mean density of 1127 stems  $\geq 5$  cm DBH per ha was about half the density of 2307/ha in the site measured by Murphy and Lugo (1983). Similarly, basal area on the 1 ha site was about half the basal area in the site measured by Murphy and Lugo: 4.9 m<sup>2</sup>/ha compared to 9.4 m<sup>2</sup>/ha. Though



Figure 3. Location of the thirteen-year-old Cut Site, adjacent forest study area, and forest plots studied by Murphy and Lugo (1983, 1985).

some density and growth increases probably occurred in the 12 year interim between the two sets of measurements, the small annual dry forest tree diameter growth of 0.12 mm (Murphy and Lugo 1983) and relatively low dry forest seedling survival (Ewel 1980) would not account for the differences between the two sites. Rather, environmental site differences such as soil texture and structure, elevation, and disturbance history probably account for most of the differences in the vegetation.

#### METHODS

The one hectare study site was relocated and a trail cut around the perimeter in July 1981 (Murphy and Lugo 1982). The field work for this study was conducted during 3 trips to the site in March 1982, August-September 1982, and March-April 1983.

Statistical analyses were performed on the Michigan State University Cyber 750 mainframe computer. Statistical procedures used included SPSS BREAKDOWN (Nie, Bent, and Hull 1975), which calculates means, sample size, variance, standard deviation, and standard error for data classified according to a number of variables; SPSS ONEWAY and SPSS ANOVA (Kim and Kohout 1975), which calculate one-way and more complex analyses of variance, respectively, and provide a priori and a posteriori contrasts; SPSS REGRESSION (Kim and Kohout 1975), which calculates regression statistics; and BMDP3D ONE-SAMPLE AND TWO-SAMPLE T-TESTS (Dixon, 1981), which performs a Hotelling T Square multivariate test.

#### Vegetation Structure and Composition

Structural characteristics of woody vegetation in the Cut Site were measured in twenty 2 x 10 m plots placed randomly in the Cut Site in March 1982. Ten plots were in

the portion of the site which received a mosaic of cutting and herbicide treatments following the 1969 clearcut (hereafter referred to as the "recut/herbicided" portion), and 10 were in the portion of the site which was merely clearcut ("cut only" portion) (Figure 4). For comparative purposes, 30 plots were randomly placed in adjacent forest. Species area curves and graphs of running mean of basal area for each set of plots (in each site) indicated that sample sizes were adequate. All stems ≥ one cm DBH were included in analyses, and epiphyte species and numbers in the plots were tabulated. Measurements of woody plants included density of stems per plant, plant density, stem DBH, and origin of stems (stem sprout, root sprout, or seedling). Stem origin was determined quite easily in most cases by examining the stem bases.

Measurements of herbs and smaller woody plants as well as larger diameter trees in the Cut Site were conducted in 2 x 2 m plots established in March 1982. Twenty-four plots were placed at regular intervals along the diagonals of the site (Figure 5) for an examination of the effect of the distance from the forest edge on structural parameters. Eight plots were in the "cut only" section of the site, and the remaining 16 in the "recut/herbicided" section. Trails were cut parallel to and 2 m away from the diagonals for access to the plots. Six additional 2 x 2 m plots were randomly placed in the "cut only" portion



Figure 4. Location of 2 x 10 m Cut Site and forest plots.

of the site in March 1983. Twenty 2 x 2 m plots were randomly placed in adjacent forest and analyzed for comparison in August 1982 (Figure 5). All plants with cover in a plot were identified and measurements of height, crown area (computed from the average of two diameter measurements), number of stems, origin of each stem, and diameter at ground height (DGH) of each stem were made. In the case of grasses, clumps (which were generally < 0.2 m in diameter at ground level) were tallied rather than stems. The plots were censused in August 1982, and seasonal differences were examined by remeasuring herbs in March 1983. When the field work was completed, all plot stakes except those marking the 4 corners of the 1 ha site and the 24 Cut Site 2 x 2 m plots were removed.

I identified all taxa to the species and variety level. Nomenclature of trees follows Little and Wadsworth (1964) and Little, Woodbury, and Wadsworth (1974); that for all other species follows Britton and Wilson (1924), except where noted. Species occurring primarily in disturbed sites such as roadsides were considered pioneer species, and those which were regular components of mature forest were considered persistent species.

Importance values for all woody species in the 2 x 10 m Cut Site plots were determined using the equation


Figure 5. Location of 2 x 2 m Cut Site and forest plots.

## IV = RF + RD + RDom

where IV= importance value, RF= relative frequency, RD= relative density, and RDom= relative dominance (calculated from basal area) (Brower and Zar 1977).

Vegetative cover on the Cut Site was measured with an extendable pole which supported a taut vertical rope. Measurements were made from trails so that the pole could be easily maneuvered. Three cover indices were calculated from 120 samples throughout the site (Figure 6), measured in August 1982, March 1983, and May 1983. (A sample consisted of one drop of the rope into the vegetation.) The first, horizontal cover, was the number of ropes encountering any vegetation, divided by the total number of samples and expressed as a percentage. The second, which I call vegetation area index (VAI), guantifies the amount of plant tissue on a vertical plane over the site, and is the number of times the rope intersected any plant tissue (including herbaceous and woody) each time it was dropped into the vegetation. The third, leaf area index (LAI), was the number of times the rope encountered foliar tissue each time it was dropped into the vegetation. In August, VAI was assessed in 0.5 m vertical intervals to quantify vegetation stratification.

Spatial and temporal (within-year) variability in leaf litter biomass were investigated by removing all litter from 10 round 0.25 m<sup>2</sup> sampling areas in the Cut Site



Figure 6. Leaf Area Index sampling locations.

(located next to 2 x 2 m plots) and 10 in adjacent forest (randomly located) on September 1, 1982 and March 24, 1983. Wood, insect, and rock components were removed from the samples, and visible seeds were set aside for seed bank studies. The foliage portion of each sample was oven dried (105 C for 24 hours) and weighed.

Persistent treatment effects from Ewel's 1969 site manipulations were estimated by comparing all measured structural variables in the plots on the "cut only" and "recut/herbicided" sections of the site.

## Seed Banks

Assessments of densities and species of seeds in the Cut Site and adjacent forest were made by collecting soil and litter samples on September 1, 1982, and on March 24, 1983. Seeds were collected from the litter biomass samples and from the soil beneath each litter sample to a depth of 5 cm. The soil samples were each divided into two fractions using a 2.38 mm mesh screen. Seeds from the large particle fraction were separated out by hand, and each small particle fraction was sprinkled over sterilized soil in trays which were placed in a greenhouse (with constant 12 hour/day light regime, 15-29 C temperature, watered 3-4 times/week) and monitored for seed germination. Seeds were removed from the litter collections by different methods in August and March. In August, visible seeds were removed by hand, and no quantification of small seeds in litter was made. In March, litter samples were divided into two size fractions using the 2.38 mm mesh screen. Visible seeds were removed from the large fraction, and the small fraction was weighed for addition to litter biomass measurements, then sprinkled over sterilized soil and germinated under the same greenhouse conditions described above for soil samples.

Seed germination in all greenhouse trays was monitored weekly for 9 months. Species were identified when they were large enough to be recognizable, then seedlings were tallied and pulled. If seedlings died before identification was possible, they were recorded simply as "dicot" or "monocot". There was some contamination in the trays by local weed seeds, but these were easily identified and removed.

The seeds separated by hand from soil and litter samples were identified using plant specimens from the Michigan State University herbarium and a reference seed collection compiled with seeds from fruits collected in the field. Several seeds from half the plots were subjected to standard Tetrazolium tests to determine what percentages were viable. Seeds were soaked in water overnight, then covered with a 1% Tetrazolium solution (1

gm 2,3,5 Triphenyl Tetrazolium in 100 ml water, pH 6.7) for six hours. Seeds were observed under a dissecting microscope for stain indicating viability.

Fresh fruits were collected from several tree and shrub species in August 1982 to determine whether fresh seeds had viability and germinability similar to soil and litter seeds. A subsample was tested for viability using the standard Tetrazolium test, and subsamples of 200 seeds of each of seven of the species were planted in sterile soil in trays in the greenhouse. To determine whether some seeds may require scarification to germinate, mature fruits of Leucaena leucocephala were also collected in March 1983, subjected to various scarification treatments, and measured for germinability. Forty-five seeds were used for each treatment; the treatments were: soaking in sulphuric acid for 4 and 10 minutes, respectively, soaking in boiling water for 2 minutes, and a control. Following treatment, seeds were placed between moistened filter papers in petri dishes in a growth chamber at 26 C with 76% relative humidity and 12 hours of light per day, for 21 days.

Mechanisms of seed dispersal of all species occurring in the 2 x 10 m sampling plots were assessed with a literature survey (using Little and Wadsworth 1964, Little et al. 1974, and Tomlinson 1980) combined with field observations. When dispersal agents were not known, it

was assumed that seeds surrounded by fleshy fruits were animal-dispersed and winged seeds were wind-dispersed, and all others were gravity-dispersed.

## Mycorrhizae

The effect of age of site on VA mycorrhizal quantities was investigated in August 1982. Root samples from 5 common dry forest species were collected from 3 different-aged sites: mature forest, the Cut Site, and one-year-old "regeneration plots" established by P. Murphy and A. Lugo 1 km east of the Cut Site (Murphy and Lugo 1983). The 5 species were Thouinia portoricensis, Exostema caribea, Croton humilis, Gymnanthes lucida, and Coccoloba diversifolia (all canopy trees except Croton, which is a shrub).

Field collections and laboratory procedures were identical for the 2 sampling periods. Root samples were collected from surface soils to a depth of 5 cm. The entire root systems of seedlings and herbs were collected; for larger woody plants, enough of the finest roots available per plant were collected to fill a 25 cm<sup>3</sup> vial. Samples were collected from 3 individuals per species when possible, stored in distilled water, and refrigerated until laboratory procedures were begun (within 3 weeks of the collection date).

Laboratory methods for staining mycorrhizae were modified from Philips and Hayman (1970). Root samples were placed in test tubes with 10 percent KOH and heated in a water bath at 85 C for 90 minutes. The samples were then washed in distilled water to remove KOH and acidified in 0.1 M HCl for one hour. Roots were stained in 0.1 percent acid fuchsin in lactophenol for 2 days and destained in clear lactophenol (2 changes over a 24 hour period), in which they were stored. Ten 1 cm root segments per plant were mounted on a glass slide and examined for infection. The samples were rated with a score of 0 to 4, defined as follows: (0) no evidence of infection, (1) light infection with occasional, isolated infection points, (2) a few hyphae spread throughout, or less than 1/3 of root with clumped hyphae, (3) continuous hyphal strands throughout without clumping, or clumped hyphae covering from 1/3 to 2/3 of the root, and (4) heavily infected, with clumped hyphae throughout the root. Vesicles and/or arbuscules were considered to be part of the hyphae for quantification purposes, and their presence was noted for each sample in which they occurred.



Figure 7. Appearance of Cut Site vegetation in 1982, 13 years following cutting.



Figure 8. Appearance of adjacent forest vegetation in 1982.

#### RESULTS

#### Site Description

The thirteen-year-old site had a markedly different appearance from the adjacent forest in 1981 (Figures 7 and 8). Prominent features in the Cut site included emergent Bucida buceras trees up to 12 m in height scattered throughout the area and a high density of the common tropical weedy legume species, Leucaena leucocephala. Also immediately obvious were the tangle of vines covering much of the site and a predominance of grasses in much of the understory, with Panicum maximum the tallest and most prominent.

Cursory measurements of relative humidity and air temperature in the site and in adjacent forest (unpublished data) indicated that microenvironments were similar in the 2 areas on at least the 4 days sampled. Soil nutrient contents, pH, organic matter content, and bulk density in the Cut Site were comparable to values of those parameters for nearby forest (Murphy and Lugo, unpublished data).

#### Vegetation Structure and Composition

Species Diversity

Species diversity was 36% higher in the Cut Site (76 species/80 m<sup>2</sup>) than in forest (49 species/80 m<sup>2</sup>), with 39 species common to the two sets of plots. The value of Sorenson's coefficient of community (Brower and Zar 1977) of 62.4% demonstrates a rather high similarity between the two sites. When plots in the mature forest were randomly divided into two groups, the coefficient of community between the two groups was 76.1%, just 14% higher than that between the Cut Site and forest.

The higher diversity of the younger site is largely due to the presence of species classified as pioneer, many of which were herbs or vines; 28% of Cut Site species were pioneer species, compared to only 4% in forest plots (Table Al). Pioneer species comprised 46% of the density of stems in the Cut Site and only 3% of those in the forest. The slow continual ascendance of species area curves for Cut Site and forest plots (Figure 9) indicates additional species occur in the sites. I recorded 10 species in the Cut Site and 13 in adjacent forest that did not fall into sampling plots.

Species diversity of stems  $\geq$  1 cm DBH (including trees, shrubs, cacti and vines) was similar in the two sites (36 and 39 species/400 m<sup>2</sup> in Cut Site and forest,



Figure 9. Species area curves for Cut Site and forest 2 x 2 m sampling plots.

respectively), although species composition differed somewhat (Sorenson's coefficient of 66.7%) (Table 1). Of the 41 tree and shrub species in forest plots, 59% also occurred in Cut Site plots. Several of the dominant adjacent forest tree species also were dominants in the Cut Site. Most notably, *Bucida buceras*, a fast-growing, copious sprouter, was important due to its high relative dominance in both sites, with percent of total importance values of 20 (Cut Site) and 9 (forest). *Exostema caribaeum* and *Thouinia portoricensis* were also among the 10 most important species in both sites (Table 1). A major difference between the two sites is the relative importance of *Gymnanthes lucida*, which comprises 11% of the total importance value in the forest but less than 1% in the Cut Site.

#### Structure

Relationships between structural variables in the two sites are summarized in Table 2 and Figure 10. Stem density in the Cut Site was nearly 3 times that in adjacent forest; herbaceous, woody, and vine stems all were significantly (p<.001, ANOVA) denser in the younger site. Epiphytes were the only life form found in lesser numbers in the Cut Site, although differences were not significant due to a high variance between forest plots (Table 2). Especially notable were the high Cut Site

Table 1. Importance values for plant species with DBH  $\geq$  1 cm in Cut Site and adjacent forest plots'. NP = not present in sampling plots. \* = species classified as pioneer.

		FOREST		(	CUT SITE	
Species	IV	<b>%</b> of Total	Rank	IV	<b>%</b> of Total	Rank
Gymnanthes lucida	32.40	10.80	1	2,12	0.71	18
Bucida buceras	27.36	9,12	2	58.93	19.64	10
Coccoloba diversifolia	24.54	8.18	3	1.84	0.61	20
Exostema caribaeum	22.61	7.54	Ĩ.	29.24	9.75	2
Pictetia aculeata	21.53	7.18	5	NP	2.12	-
Thouinia portoricensis	19.02	6.34	6	15.80	5.27	6
Amyris elemifera	16.77	5.59	7	3.59	1.20	17
Cephalocereus royenii	16.46	5.49	8	NP		• •
Eugenia foetida	15.04	5.01	9	2.02	0.67	19
Bursera simaruba	12.23	4.08	10	8.47	2.82	12
Samyda dodocandra	9.91	3.30	11	9.08	3.03	11
Pithecellobium unguis-cati	7.38	2.46	12	20.42	6.81	5
Guettarda krugii	6.33	2.11	13	4.51	1.50	16
Eugenia rhombea	5.94	1.98	14	NP		
Pisonia albida	5.67	1.89	15	20.89	6.96	4
Krugiodendron ferreum	5.38	1.79	16	1.48	0.49	24
Savia sessiliflora	5.11	1.70	17	12.65	4.22	7
Coccoloba microstachya	4.75	1.58	18	11.40	3.80	8
Coccoloba krugii	4.08	1.36	19	NP	•	
Leptocereus quadricostasus	3.49	1.16	20	NP		
*Helicteres jamaicensis	3.16	1.05	21	24.17	8.06	3
Guaicum sanctum	2.98	0.99	22	NP		2
Tabebuia heterophylla	2.86	0.95	23	NP		
Jatropha hernandiifolia	2.48	0.83	24	NP		
*Sabinea florida	2.35	0.79	25	10.64	3.55	10
Antirhea acutata	2.24	0.65	26	1.48	0.49	22
Bumelia obovata	2.16	0.72	27	NP		
Cassine xylocarpa	1.57	0.52	28	1.43	0.48	29
Randia aculeata	1.39	0.46	29	5.06	1.69	15
Croton rigidus	1.21	0.40	30	5.10	1.70	14
Bernardia dichotoma	1.17	0.39	31	NP		
Colubrina arborescens	0.73	0.24	32	NP		
Guettarda elliptica	0.64	0.21	33	NP		
*Leucaena leucocephala	0.60	0.20	34	6.14	2.05	13
Plumeria alba	0.59	0.20	35	1.45	0.48	25
*Lantana involucrata	0.48	0.16	36	11.00	3.67	9
Unknown trees (5 species)	4.66	1.55	37	NP		
Unknown vines (2 species)	2.62	0.87	38	NP		
Reynosia guama	NP			1.55	0.52	21
Clusia rosea	NP			1.48	0.49	23
*Unknown shrub	NP			1.45	0.48	26
Comocladia dodonea	NP			1.44	0.48	27
Wedelia lanceolata	NP			1.44	0.48	28
Unknown vine sp.	NP			1.43	0.48	30

<sup>1</sup>Data are from 2 x 10 m plots in Cut Site (N=10) and adjacent forest (N=30).

Table 2. Structure of Cut Site and adjacent forest vegetation. All stems included in analyses. Standard errors are in parentheses.

Parameter	Cut Site	Forest	<b>p</b> <sup>2</sup>
Species per 4 m2	17.0 (1.2)	9.0 (0.8)	<.001
Plant height (m)	0.7 (0.1)	1.6 (0.1)	<.001
Basal area (m2/ha)	19.7 (5.0)	52.8 (8.5)	<.01
Stem density/m2 of:			
Total stems	26.4 (3.7)	9.8 (1.6)	<.001
Pioneer species	12.7 (2.7)	0.3 (0.2)	<.001
Woody	19.2 (3.0)	6.5 (0.8)	<.001
Herbaceous	6.9 (1.6)	0.5 (0.2)	<.001
Cacti	0.04 (0.02)	0.04 (0.02)	NS
Epiphytes	0.3 (0.1)	2.8 (1.3)	NS
Vines	5.7 (1.1)	0.8 (0.2)	<.001
Mean crown area	2115.9	201.5	<.05
of vines (m2/ha)	(547.6)	(89.1)	-

<sup>1</sup>Data are from 2 x 2 m plots in Cut Site (N=20) and forest 2(N=20). Significance in ANOVA. NS = not significant at p<.1.

Table 3. Leaf area index and percent cover in the Cut Site. LAI is the mean number of foliar intersections per vertical rope in  $m^2/m^2$ . Percent cover is the number of times the rope encountered vegetation divided by the total number of counts. (N=120).

Date	Leaf Area Index	Percent Cover
September 2-4, 1982	1.8	100.0
March 23-24, 1983	2.2	99.2
May 30, 1983	3.9	100.0



Figure 10. Comparison of structure in Cut Site and adjacent forest.

.

densities of herbs and vines (14 and 7 times the densities in adjacent forest, respectively). Vine cover was 10 times higher in the younger site.

Structural parameters which were significantly smaller in the Cut Site included basal area (determined from diameter at ground level measurements) and mean plant height; both were 40% of adjacent forest values (Table 2).

Horizontal cover was 100% in the Cut Site (Table 3), compared to values of 77 to 93% in nearby mature forest (Murphy and Lugo 1983). Leaf area index in the Cut Site (Table 3) was 57 to 65% of that measured by Murphy and Lugo (1983) in mature forest. Leaf litter biomass did not differ significantly between the Cut Site and adjacent forest (p>.1, ANOVA) (Figure 11).

The stratification of plant heights in height interval classes demonstrates that lower mean heights in the Cut Site are due to the presence of more seedlings and fewer tall shrubs and trees in the younger site (Figure 12). The smallest height class (1-25 cm) made up 52% of Cut Site woody plants and 30% of those in forest. Densities in intermediate height classes were similar in the two sites, while plants in height classes > 2 m contributed larger percentages in forest plots. The vertical stratification of vegetation area index (Figure 13) demonstrates the concentration of plant tissues close to the ground: 84% of VAI counts occurred below a height of 1



Figure 11. Leaf litter biomass in forest and Cut Site in September and March.



Figure 12. Numbers of plants in height interval classes in the Cut Site and forest plots. Data are from  $2 \times 2 m$  plots.



Figure 13. Vertical stratification of Cut Site vegetation using vegetation area index readings.

m, with the remaining 16% between 1 and 5 m heights.

The Cut Site supported fewer plants with stems > 1 cm DBH than adjacent forest (8600/ha versus 10,452/ha). Cut Site trees supported more stems/individual, however; this was reflected in the comparative stem densities of (27,000/ha versus 25,155/ha in forest). Many of the stems in the younger site were small in diameter. When distributed according to size class, 86% fell into the smallest category (1-2.5 cm DBH) compared to 51% in that category in adjacent forest (Figure 14). In all the larger size classes, forest plots possessed a higher mean number and higher percentage of stems than Cut Site plots. Basal area of stems > 1 cm DBH in the Cut Site (8.88  $m^2/ha$ ) was 29% of that in adjacent forest (30.75  $m^2/ha$ ) (Table 4). The two values differed significantly (ANOVA, p<.001). Fewer than 1% of the total number of stems in the Cut Site were dead, compared to 9.7% mortality in forest plots (Table 4). An examination of composite differences between the 2 sites using 4 variables measured for stems > 1 cm DBH revealed that differences were highly significant (Hotelling T test, p<.001) (Table A4).

Summaries of density and basal area of stems  $\geq 5$  cm DBH in the Cut Site and adjacent forest were compared to pre-cut measurements made by Ewel on the one ha site in 1969 (consisting of diameter measurements of trees  $\geq 5$  cm DBH in three 1000 m<sup>2</sup> transects) (Table 4). The adjacent

Table 4. Structure of woody vegetation in Cut Site, in adjacent forest, and on Cut Site before it was cut<sup>2</sup>. Values are means per ha. (\*\*\* = significantly\_different from adjacent forest value in ANOVA at p<.001)<sup>3</sup>.

Parameter	Cut Site	Forest	"Cut Site" in 1969
Live stems > 1 cm DBH			
Plant density	8600	10452	
Stem density	27000	25155	
Basal area (m2)	8.877***	30.751	
Dead stems > 1 cm DBH			
Stem density	150	2717	
Live stems > 5 cm DBH			
Stem density	400	3433	1127
Basal area (m2)	1.237***	18.574	4.950
Dead stems > 5 cm DBH			
Stem density	0	283	

<sup>1</sup>Data are from 2 x 10 m plots in Cut Site (N=10) and in adjacent forest (N=30). Data are summarized from data collected by J. Ewel in 31969 on the one ha site before it was cut. Where there are no asterisks, values did not differ significantly between sites at p<.1.</p>



DIAMETER CLASS (cm)

Figure 14. Size class distribution in the 2 x 10 m plots in forest (N=30) and Cut Site (N=10).

forest in 1982 possessed stem densities and basal areas which were 3.0 and 3.8 times higher, respectively, than the pre-cut one ha site in 1969 (Table 4). This large difference indicates the Cut Site probably began with less structure than the adjacent forest. The Cut Site in 1982 supported only 400 stems  $\geq$  5 cm DBH/ha which contributed 1.24 m<sup>2</sup>/ha of basal area; these values were 1/3 and 1/4 of those values, respectively, for pre-cut vegetation.

Seasonal Variation

Comparisons of Cut Site structural parameters between sampling periods revealed seasonal differences (although not always significant ones) in leaf litter biomass, leaf area index, and herbaceous density and cover (Figure 11 and Tables 3 and 5). Leaf litter biomass was significantly (p<.05, ANOVA) higher in both sites in March than in September (Figure 11).

Leaf area index values, summarized in Table 3, nearly doubled in the interval between the March and May measurements, reflecting the leafing out of many species following the onset of the rainy season (Figure 2). LAI in September was slightly lower than in March, probably as a result of a brief dry spell in August 1982 that caused many plants to wilt and/or lose their leaves (Murphy and Lugo, unpublished rainfall data).

Herbs in both Cut Site and forest showed no

Table 5. Comparison of herbs in Cut Site and adjacent forest between dry season (March) and wet season (August). Values are means per plot. Standard errors are in parentheses.

	Number of species	Density	Mean height (cm)	Mean crown area (cm2)
Cut Site	2			
August	4.0 (0.4)	23.5 (4.3)	39.3 (7.7)	4075.9 (1588.2)
March	5.5 <sup>2</sup> (0.5)	28.1 (5.2)	26.3 (4.9)	3529.2 (807.4)
Forest				
August	0.7 (0.2)	1.6 (0.9)	10.8 (3.7)	480.0 (202.2)
March	0.9 (0.3)	2.1 (1.0)	7.5 (2.4)	294.0 (144.3)

<sup>1</sup> <sup>2</sup>Data are from 2 x 2 m plots in Cut Site (N=24) and forest (N=19). <sup>2</sup>These two values differ significantly at p<.05 in ANOVA. The other month-to-month comparisons do not differ significantly.

•

.

significant differences in density, mean height, or mean crown area between the August and March sampling dates. Mean number of herbaceous species in the Cut Site was significantly higher in March (p<.05, ANOVA) than in August, possibly reflecting seasonal patterns of more species germinating in March. The trend of higher densities coupled with lower mean heights (i.e. more seedlings than taller plants) in both sites in March supports this explanation. Mean herbaceous cover was somewhat lower in both sites in March, the drier season.

# Mechanisms of Regeneration

Proportions of sprouts and seedlings were analyzed from the perspectives of both the number of plants and the number of stems. The proportion of plants which were seedlings yields information about the prevalence of seed regeneration in the site. The examination of the number of stems in each category allows one to analyze sprouting in such a way that decisions regarding how a particular individual is defined (e.g. as a plant or as part of a plant) are avoided. The latter method is especially helpful when considering the case of root sprouts, since without excavating root systems, it is impossible to determine which plants root sprouts are connected to.

Seedlings constituted an important portion of plants

supporting stems  $\geq$  1 cm DBH in both sites. Fifty-one percent of Cut Site plants and 68% of forest plants had seedling origins (i.e. did not possess any sprouts) (Figure 15).

From the standpoint of stems, 81% of Cut Site stems  $\geq$ 1 cm DBH originated as sprouts from cut stumps, 3% as root sprouts, and 16% as seedlings (Figure 16). The adjacent forest possessed 49% stem sprouts, 23% root sprouts, and 28% seedling-origin stems. Stems  $\geq$  1 cm DBH in the adjacent forest were primarily persistent species (98 to 99% of stem density) regardless of origin. In the Cut Site, pioneer species comprised 32% of seedling origin stems, 35% of root sprouts, and 15% of stem sprouts. Every woody species occurring in the sampling plots in the two sites produced vegetative sprouts, except the small tree species *Plumeria alba*, which did produce sprouts in another cut-over Guanica site (A. Murphy, pers. comm.).

A height class analysis of all woody stems in the Cut Site plots demonstrates that stems originating as sprouts were generally the taller plants in the site, while stems of seedling origin were shorter (Figure 17). Of stems in height classes  $\geq 1.5$  m, 54 to 100% were stem sprouts, while in height classes < 1 m, 52 to 81% were of seedling origin. Stems between 1 and 1.5 m heights were primarily root sprouts (47%) or of seedling origin (41%). It appears that either vegetative sprouts have faster height



Figure 15. Percentages of woody plants with stems  $\geq$  1 cm DBH with stems originating as vegetative sprouts and as seedlings in Cut Site and forest plots.



Figure 16. Percentages of woody stems  $\geq$  1 cm DBH originating as vegetative sprouts and as seedlings in Cut Site and forest plots.



Figure 17. Height class distribution of woody plants in Cut Site and forest originating as vegetative sprouts and as seedlings.

.

growth rates than seedlings, or seedling regeneration was at some point suppressed in the Cut Site, giving the sprouts a temporal advantage.

An examination of the effect of distance from the forest edge on seedling species and densities indicates that seed dispersal has not been a limiting factor to seedling success in the Cut Site. The 24 2 x 2 m plots examined for an edge effect revealed no significant differences (ANOVA, p > 0.5) in all parameters measured (Table 6). There was a trend toward decreasing numbers of woody seedling origin plants toward the center of the site (Figure 18). Coefficients of determination ranged from .002 to .115 (Table 6), indicating that distance from the forest edge accounted for only 0 to 12% of variation in plant density and species richness of herbs, woody plants, persistent species densities, and pioneer species densities.

The present-day seed bank in the Cut Site consists of a broad array of species throughout the site, including those classified both as pioneer and as persistent forest species (Tables 7, 8, and 9). The combined densities of species of seeds in September and March collections from plots at varying distances from the forest edge demonstrates that species were broadly distributed throughout the sites (unpublished data).

Half of the 94 plant species identified in the Cut

Table 6. Effect of distance from forest edge on seedling species and densities in Cut Site 2x2 m plots. N=4 plots per distance. Values are means per plot.

•

	Distance from forest edge (m)				•			
	1.4	10	20	30	40	48	∠ ★R	**Sig.
Number of species		_						
Total	12.0	10.8	13.0	8.8	11.5	9.3	.036	NS
Herbaceous	3.5	4.0	4.5	2.5	4.0	4.8	.010	NS
Woody	8.5	6.8	8.5	6.3	7.5	4.5	. 103	NS
Density								
Total	36.8	85.0	57.5	27.8	69.5	36.8	.008	NS
Herbaceous Herb.	8.8	38.5	22.0	5.0	43.0	24.3	.014	NS
persistent sp Herb.	. 4.8	5.5	5.3	1.3	16.5	9.5	.044	NS
pioneer sp.	4.0	33.0	16.8	3.8	26.5	14.8	.002	NS
Woody Woody	28.0	46.5	35.5	22.8	26.5	12.5	.115	NS
persistent sp. Woody	15.0	18.3	20.3	6.0	9.5	5.3	.101	NS
pioneer sp.	13.0	28.3	15.3	16.8	17.0	7.3	.052	NS

\*Coefficient of determination, calculated from regression.
\*\*Significance in ANOVA. NS = not significant at p < .1.</pre>



Figure 18. Relationship between numbers of woody seedling origin plants in Cut Site and distance to the forest edge.

Table 7. Seed densities in soil and litter samples  $(N=10.25 \text{ m}^2 \text{ samples per site per sampling date})$ . Pt=persistent species seeds, Pi=pioneer species seeds, Total is the sum of Pt + Pi + unidentified species. Percent of total for each fraction is in parentheses.

		Seeds ≥ 2.38 mm	Seeds < $2.38$ mm		
	<b># seed</b> s/m2	<pre># seeds tested for viability</pre>	<pre>*percent viability</pre>	★★ # seeds germinated/m2	
September col	lection				
Cut Site					
Pt	500.4 (64.0)	64	1.6	4.3 (8.8)	
Pi	248.0 (31.7)	51	37.3	40.8 (83.3)	
TOTAL	782.4	115	17.4	49.0	
Forest					
Pt	1249.6 (80.6)	168	1.2	3.8 (40.0)	
Pi	208.8 (13.5)	32	62.5	3.9 (41.1)	
TOTAL	1550.4	228	11.0	9.5	
March collec	tion				
	728 1 (58 2)	F(		1 - ()	
Pt	/30.4 (50.3)	50	/.1	4.2 (3.3)	
P1	500.8 (39.8)	39	66./	64.0 (49.9)	
TOTAL	1265.6	95	17.4	128.3	
Forest					
Pt	1537.6 (88.8)	74	0	0	
Pi	127.2 (7.3)	21	42.9	8.8 (16.2)	
TOTAL	1732.4	<b>9</b> 5	9.5	54.2	

\*Viability tests were performed on May 21, 1983 for samples collected on September 1, 1982, and on June 1, 1983 for samples collected on March 24. Tests were based on non-randomly selected small samples, thus should be considered estimates.

\*\*Seed germination was measured from soil and litter samples sprinkled over sterilized soil and placed in a greenhouse. Germination experiments were initiated 6 months following the September collection date and 2 months following the March collection date, with samples stored at room temperature in the interims. Table 8. Densities of seed species < 2.38 mm germinating from soil and litter samples under greenhouse conditions (N=10 .25 m<sup>2</sup> samples per site per sampling date).

Germinated seeds per m2

	*September		March		
Species	Cut Site	Forest	Cut Site	Forest	
Commelina erecta	0.7	0	0	0	
Croton humilis	0	0	2.0	0	
Echinochloa colonum	0	0	0	0.4	
Eupatorium sinuatum	0	0	0.4	0	
Galactia dubia	0	1.9	0	0	
Helicteres jamaicensis	0	1.4	2.2	0	
Jacquemontia pentantha	20.5	0	31.1	2.1	
Lasiasis divaricata	0	1.9	0	0	
Scleria lithosperma	3.6	0	2.2	0	
Setaria setosa	9.3	0.6	6.7	0	
Sida acuta	8.7	1.9	1.9	3.9	
Spermacoce tenuoir	0	0	16.5	1.2	
Stachytarpheta strigosa	a 0	0	3.6	0	
Wedelia lanceolata	0	0	1.6	1.2	
Unidentified	3.9	1.8	60.1	45.4	
TOTAL	49.0	9.5	128.3	54.2	

\*In September, samples were from soil collections only
 (not litter).

.
Table 9. Densities and species of seeds  $\geq 2.38$  mm collected from soil and litter samples. N=10 0.25 m<sup>2</sup> samples per sampling date. Numbers in parentheses are densities of viable seeds.\*

	September			March				
Species	Cut	Site	Fore	st	Cut S	ite	For	est
Bucida buceras	358.0	(19.9)	210.4	(199.1)	284.0	(0)	708.8	(0)
Bursera simaruba	0		19.2	(0)	2.0	(0)	506.8	(0)
Coccoloba diversifolia	20.8	(0)	347.6	(0)	0		88.8	(0)
Coccoloba krugii	2.4		302.8	(0)	4.0	(0)	1.2	
Coccoloba microstachya	· 0.8		214.0		329.6	(0)	27.2	(0)
Croton discolor	6.0	(0)	0		8.4	(0)	0.4	(0)
Croton humilis	32.4		4.8		0		0	
Croton sp.	0		0		1.6		5.2	
Erithalis fruticosa	0.4		0.4	(0.4)	0		Ō	
Eugenia foetida	2.8	(0)	2.8		0		77.6	
Exostema caribaea	1.2		31.2	(0)	4.0		17.6	
Galactia striata	3.6	(3.6)	0.8	• •	0		ò	
Gouania lupuloides	19.2		0		358.4	(150.9)	99.6	(8.3)
Guettarda elliptica	0.4		0		0.4		Ō	
Guettarda krugii	2.0	(0)	8.8		0.4		2.4	(0)
Helicteres jamaicensis	69.2	(48.4)	0		0		0	
Jacquinia barteri	0.8	(0)	1.2	(0)	0		0	
Jacquemontia pentantha	121.6	(9.4)	11.2		13.2		2.4	
Kramerii ixinia	0		0		0.4		0	
Lantana involucrata	0.4		0		0.4		0	
Lasiasis divaricata	5.2		3.2		92.8	(21.4)	22.0	
Leucaena leucocephala	34.0	(20.4)	196.0	(123.5)	128.8	(115.9)	23.2	(20.6)
Passiflora sp.	0	•	0		0.4		0.4	
Pisonia albida	1.6	(0)	0		0		0	
Pithecellobium								
unguis-cati	0		0.4		0		0	
Reynosia sp.	0		1.6		0		0.4	
Thouinia portoricensis	30.4	(0)	18.0	(0)	3.2		10.4	(0)
Waltheria indica	31.2	(0)	0		Ō		0	
Wedelia lanceolata	0.4		0.8		0		2.0	
Unknown species	34.0		92.0		26.4		67.6	
TOTAL	782.4		1550.4		1265.6		1732.4	

\*Viability values are based on non-randomly selected small samples of seeds, thus should be considered estimates. Where no numbers in parentheses are given, viability tests were not done. Site and forest occurred in seed bank samples, including fifteen seed species in the < 2.38 mm size class, and 30 in the  $\geq$  2.38 mm group (Tables 8 and 9). Forty-nine species either did not show up in the seed bank samples or remained unidentified.

When seed densities were averaged over sampling periods, the younger site contained 3.7 times more small seeds (< 2.38 mm) per square m and 2.4 times more seeds of pioneer species than adjacent forest. The forest supported 1.6 times more large seeds (  $\geq$  2.38 mm) and 2.3 times more seeds of persistent species (Table 7). Mean seed densities in litter and soil samples averaged over both collecting periods were  $1112.5/m^2$  in Cut Site and  $1650.9/m^2$  in forest.

Two-thirds of the 40 identified woody species in the 2x10 m plots showed adaptations for vector-assisted seed dispersal. Fifty-three percent are dispersed by animal consumption, particularly by birds; ten percent are wind dispersed; 2% can stick onto moving vectors; and 35% show no adaptations for vector dispersal.

Per cent viability of seeds from soil and litter samples (per site, per sampling period) of pioneer species was generally fairly high (21-64%) while that of persistent species was low (0-7%) (Table 7). It is likely that these figures would have been somewhat higher if viability had been measured immediately after the seeds

were collected rather than 2 to 9 months later.

Viability of fresh seeds of 11 species collected in September 1982 and March 1983 from trees and shrubs was relatively high (12-100%/species), and germination rates very low (Table 10). It is possible that scarification of seeds or some dormancy-breaking environmental effect is needed before some dry forest species of seeds can germinate. Scarification of *Leucaena* seeds collected in March 1983 by soaking in sulphuric acid (to simulate passage through a bird's digestive system) increased percent germination by as much as 80% (Table 11).

## Mycorrhizae

A comparison of 5 tree species in the Cut Site, forest, and in one-year-old "regeneration plots" yielded no appreciable differences in degree of mycorrhizal infection of tree roots in September 1982 in the different-aged sites (Table 12). Standard errors were rather high, indicating that larger sample sizes and more precise methods of quantification may be in order to elucidate small-scale patterns. Arbuscules were observed in 4 out of the 5 species, indicating that the mycorrhizae were functioning in their role of nutrient transfer in at least those 4 species in September.

Table 10. Viability and germinability of fresh seeds collected in August 1982.

	# seeds			
Species	tested for viability	<b>\$</b> viability	# seeds planted	# seeds germinated
Bucida buceras	o	0	100	0
Cactus (unknown sp.)	78	84.6	0	0
Coccoloba diversifolia	0	0	100	0
Colubrina arborescens	0	o	200	0
Desmanthus virgatus	100	69.0	0	0
Guettarda krugij	0	0	100	0
Helicteres jamaicensis	10	80.0	200	0
Herissantia crispa	27	96.3	0	0
Lantana involucrata	124	14.5	100	0
Leucaena leucocephala	10	100.0	200	7
Waltheria indica	17	11.8	o	0

Table 11. Effects of scarification treatments on *Leucaena leucocephala* seed germination (N=45 seeds per treatment).

Pretreatment	% Germination
Sulphuric acid (4 minutes)	57.8
Sulphuric acid (10 minutes)	87.4
Boiling water (2 minutes)	3.0
No treatment	7.4

	were	
aged sites.	arbuscules	
fferent-	in which	heses.
s in 3 di	samples	in parent
f specie:	Means of	ors are
ratings o	plant).	ndard err
izal	per	Sta
*mycorrh	segments	lerlined.
Mean	root	e und
12.		ed al
Table	(N=10	observ

	ō	ne-ye	ar-ol	d plots		Cut	Site			Fo	rest	
	۵.	lant	**	Mean	ē.	ant /	34.	Mean	۵.	lant	-	Mean
Species	-	7	Ś		-	7	m		-	7	Ś	
Gymnanthes lucida	1.9	1.3	ı	1.6 (0.4)	2.0	1.2	1.5	1.6 (0.4)	1.4	2.5	1.4	1.8 (0.6)
Coccoloba diversifolia	3.0	3.3	3.3	3.2 (0.2)	0	2.9	1.7	1.5 (1.5)	1.3	ο	2.2	1.2 (1.1)
Croton humilis	2.3	2.4	2.7	2.5 (0.2)	3.5	1.8	1.1	2.1 (1.2)	3.3	2.8	3.2	3.1 (0.3)
Exostema caribaeum	3.7	2.5	2.7	3.0 (0.6)	1.8	1.7	0.1	1.2 (1.0)	2.1	3.1	1.9	2.4 (0.6)
Thouinia portoricensi:	2.6	2.8	2.5	2.6 (0.2)	2.0	0.5	1.0	1.2 (0.8)	3.1	2.4	3.3	2.9 (0.5)

\*Ratings were based on a scale of 0-4, with (0) no infection, (1) occasional infection points, (2) few hyphae spread throughout or <1/3 of root with clumped hyphae, (4) clumped hyphae throughout root. (See text).

# Effects of Ewel's Recut/Herbicide Treatments

Vegetative recovery was consistently less on the "recut/herbicided" portion of the Cut Site than on the "cut only" portion (Table 13). Species richness, stem density, woody plant density, percent of pioneer species stems, and basal area were higher in the "cut only" portion of the site, the latter significantly so in the smaller plots. There were nearly three times more epiphytes in the "cut only" part of the site in both sets of plots. While the total density of trees and the density of trees supporting some stem sprouts were similar in the two portions of the site, the number of stem sprouts in the "cut only" area was almost twice that in the "recut/herbicided" area (mean values significantly different at p < .05). This indicates that trees which were repeatedly cut or treated with herbicides responded primarily by producing fewer vegetative sprouts. Hotellings T statistic calculated with mean values of species number, plant density, stem density, and DBH, showed a significant composite difference between the two sites at p < .1 (Table A4).

Table 13. Structure of vegetation in the portion of the Cut Site which had recut/herbicide treatments in 1969 and the portion which was cut only. Values are means/m<sup>2</sup> except where noted. Standard errors in parentheses.

Parameter	Cut Only	Recut & Herbicided	Significance in ANOVA
*All stems included Species/4 m2	4.3 (0.3)	3.6 (0.3)	NS
Basal area (cm2)	19.7 (5.0)	9.0 (1.6)	p<.05
Height per plant (cm)	73.4 (6.0)	77.2 (13.1)	NS
Stem density: Total	26.4 (3.7)	24.6 (4.8)	NS
Woody	19.1 (3.0)	14.8 (1.3)	NS
Herbaceous	6.9 (1.6)	4.7 (1.2)	NS
Cacti	.04 (.02)	5.0 (3.7)	NS
Epiphytes	0.3 (0.1)	0.1 (0.1)	NS
Vines	5.7	5.1	NS
Pioneer	12.7 (2.7)	10.7 (1.9)	NS
Persistent species	13.7 (2.2)	13.9 (4.9)	NS
**Woody stems > 1 cm	DBH only		
Number of species	0.4 (.04)	0.3 (.04)	p<.1
Number of plants	0.9 (0.1)	0.8 (0.2)	NS
Plants with	0.5 (.04)	0.5 (.07)	NS
stem sprouts Basal area (cm2)	8.9 (1.7)	5.3 (1.8)	NS
Stem density:			
Total	2.7 (0.3)	1.6 (1.1)	p<.05
Stem sprouts	2.2 (0.3)	1.2 (0.3)	p<.05
Root sprouts	.08 (.03)	.03 (.02)	NS
Seedling origin	0.4 (0.1)	0.4 (0.1)	NS

\* Data are from 2x2 m plots (N=14 in Cut Only portion, and N=16 in Cut and Disturbed portion). \*\*Data are from 2x10 m plots (N=10 in each portion of site).

## DISCUSSION

Temporal patterns of succession

Margalef's (1963) view that species diversity peaks in early to mid successional stages is supported by this study (Figure 19). There were 31.6 vascular species per  $18 \text{ m}^2$  in control plots one year following cutting (data summarized from Ewel 1971); this value increased to 39.7 per 16 m<sup>2</sup> 12 years later, compared to 24.0 per 16 m<sup>2</sup> in mature forest. The peak in diversity in the 13-year-old site closely matches the pattern in temperate forests, in which diversity increases rapidly in the earliest stage of succession, then drops gradually after year 10 or 15 (Bormann and Likens 1979, Hibbs 1983).

The higher mean species richness in the younger site is at least partially due to the greater density of stems. When computed as number of species per 100 stems, the mature forest has the highest value, with a nearly linear decrease with decreasing age of site (Figure 19).

The importance of pioneer species in the thirteen-year-old site is especially notable in light of generalizations made by some earlier authors regarding their relative unimportance in dry tropical forests. Ewel (1980) stated that succession in the drier tropics is floristically simpler and involves fewer seral stages than



Figure 19. Species diversity changes relative to succession in the Guanica forest.

in wetter sites. Loveless and Asprey (1957) noted that there was little or no invasion of second-growth species in disturbed Jamaican dry evergreen bushland owing to a lack of sufficient soil for seedling colonization. While it is undoubtedly true that wetter areas support more seedling regeneration and greater successional species diversity, there does exist a distinct dry site successional flora consisting of both pioneer and persistent species. Opler et al. (1977) reported that forbs and grasses followed by vines, shrubs, and small trees dominated the first 3 years of succession on cut, burned, and grazed Costa Rican dry forest. In the Guanica study site, the proximity of roadsides and fields makes pioneer species seed sources readily available. The rather large size of the opening together with the recut/herbicide treatments applied to a portion of the site just after it was cut probably created ideal conditions for pioneer species to colonize and proliferate.

Perhaps the most obvious and surprising aspect of the Cut Site's species composition is the relative unimportance of Gymnanthes, which was dominant on the site prior to cutting and is important today in mature forest adjacent to the site. It was also listed by Ewel as a dominant in the first year of recovery. It can reproduce by stem sprouting, root sprouting, or seedling

germination, though sprouting is not common. The species was not well represented in seed banks in the site and was the only species in which an insect larva was found in seeds from seed banks, so perhaps a species-specific seed predator has limited seed survival. There has apparently been plant mortality since Ewel's observations, indicating the species may be particularly intolerant of vine infestation, or requires a dense canopy cover to survive for more than one year. Further study on this matter is needed.

Patterns of temporal change in dry forest structural parameters following clearcutting vary for different vegetation components. Summaries of Ewel's data on one-year-old regrowth on the Cut Site (from Ewel 1971), this study's results for both Cut Site and forest, and measurements made by Murphy and Lugo (1985) in mature forest were combined to depict these patterns in Figure 20.

All parameters increase sharply in the first year of growth, demonstrating an immediate spurt of productivity largely due to coppicing. Between ages 1 and 13 years, only stem density and leaf area index decreased. The stem mortality in this stage is representative of the thinning stage in forest succession which follows the establishment phase; it generally lasts until a subsequent disturbance or natural thinning makes room for additional establishment (Peet and Christensen 1980). Density continues to decline in dry forest after year 13, with most of the mortality in herbs, vines, and smaller woody stems. The thinning stage in post-agricultural moist evergreen forest begins after year 7 (Aweto 1981).

The decline in LAI in the mid-successional site is unexplained, though Marks and Bormann (1972) reported a similar pattern in temperate deciduous forest, with 14-year-old sites exhibiting lower LAI than very young sites. It is possible that the decline in the dry forest simply reflects year-to-year variabiliy in timing of deciduousness resulting from varying rainfall patterns rather than a successional trend.

Horizontal cover in the 13-year-old site (100%) represents a peak between the 90% cover value 1 year following cutting and the 78% cover in mature forest. There was a shift from the initial patchy multilayered structure in the 1-year-old site (Ewel 1977) to a more horizontally homogeneous structure consisting of a profusion of vines, shrubs, coppiced trees, and spreading herbs in the 13-year-old site.

Biomass continued to increase from year one to thirteen (Murphy and Lugo 1985), and mature forest values are higher still. This pattern is similar to that shown for temperate forest biomass recovery (Kira and Shidei 1967, Woodwell 1967, Odum 1969), except a mid-successional

peak in biomass generally occurs and is followed by a slight drop and subsequent stabilization in mature forest. A similar peak may occur during dry forest recovery sometime after age 13.

Mean plant height parallelled the successional pattern of biomass. The tallest trees in the Cut Site and the adjacent forest were emergent *Bucida buceras* individuals, reaching maximum heights of about 12 m in both sites. This was close to the canopy height mentioned by Wadsworth (1950) as representing primary forest (12-18 m).

Vines are known to be an important component of tropical dry forests, with densities of 24 to 81 lianas with stems  $\geq$  2.5 cm per 1000 m<sup>2</sup> occurring in 5 different dry forest sites (Gentry 1983). The predominance of vines in the Cut Site (22% of total stem density) undoubtedly plays an important role in plant interactions on the site. Putz (1980) stated that lianas generally interfere with trees by competing for light, nutrients, and water and by causing mechanical damage. Several vine species in temperate forests have been shown to cause damage and even death of trees by wrapping so tightly around stems that the flow of assimilates in the phloem is inhibited (Lutz 1943, Trimble and Tryon 1974, Siccama et al. 1976). There were several instances when I noted damage or death of young trees in the Cut Site with abundant vines wrapped around them. Vines may also have influenced tree species

composition in the Cut Site due to differing capacities of trees to avoid them. Characteristics making trees less susceptible to liana infestation include fast growth, angles of sway differing from neighboring tree species to prevent intercrown passage, and regular shedding of branches and leaves (Putz 1980).

The very low density of epiphytes in the Cut Site is typical of tropical early to mid-successional sequences (Budowski 1963, 1965). Tiny seedlings of Tillandsia recurvata (too small to be included in analyses) apppeared commonly in Cut Site trees, but reproductive-size plants were quite rare. Benzing (1980) wrote that young forest communities are relatively free of epiphytes because the rapid growth and short life of many pioneer taxa render the immature canopy too unstable for vascular epiphytes. Davis and Richards (1933) suggested that a successional sequence of epiphytes which varies with the age of the host tree may exist, and noted that in rain forests, pioneers are often of the Bromeliaceae (*Tillandsia* spp), the Araceae, and ferns, while orchids belong to later stages. Observations in the Guanica forest indicate that while Tillandsia recurvata and T. utriculata survive at low densities and small sizes in successional forest, all epiphyte species, including orchids and bromeliads, are primarily mature forest species. Epiphytes may be an accurate and easily quantifiable indicator of degree of

disturbance in dry forest. Their strong reliance on a stable support system may make them especially sensitive to the degree of stability, and therefore maturity, of a community.

### Mechanisms of Regeneration

Vegetative sprouting is an extremely important regenerative mechanism in cut-over dry forest. All tree and shrub species sampled in this study, including both pioneeer and persistent species, can survive disturbance by producing either root sprouts or stem sprouts. The height dominance by coppiced plants indicates that coppicing gives a competitive advantage to sprouted stems over seedlings in forest recovery. The well-developed root systems, complete with mycorrhizae, of cut trees undoubtedly play an important role in this competitive superiority both by their ability to reach and take up water and by serving as a source of stored energy for new sprouts. Ewel (1977) noted in a visit to the Cut Site 4 years following cutting that the area was undergoing a severe year-long drought, and that most of the plants in the site were "dead and/or leafless"; however, he indicated that a few large (up to 6 m tall) clumps of coppice appeared to be in relatively good condition.

The hypothesis of significanty more regeneration due

to sprouting than to seed germination was not upheld, however, since half of the plants with stems > 1 cm DBH had originated as seedlings since the plot was cut. Despite harsh environmental conditions, dry forest species have apparently developed adaptations to promote successful dispersal, germination, and survivorship of seeds and seedlings. The occurrence of high densities of seeds of persistent forest species throughout the Cut Site indicates that seed dispersal occurs effectively in dry forest. This is not surprising, since 65% of the species assessed for dispersal type were vector-dispersed. Another effective mechanism for dispersing seeds is the rapid flowering and fruiting of coppiced individuals, sometimes as quickly as one year following cutting (Ewel 1971 and pers. obs.). It is likely that seed banks present in the soil prior to cutting also played a large role in regeneration; numerous studies of tropical humid to wet forests have demonstrated the importance of seed banks to forest recovery (e.g. Keay 1960, Dubey and Mall 1975, Cheke et al. 1979).

The absence of a significant effect of the distance of the forest edge on seedling densities in the Cut Site is further indication that seed dispersal and seedling survival occurs effectively throughout the site. It is likely that a much larger clearcut (on the order of many hectares) would show more of an edge effect.

Authors have generally postulated that dry forest seeds can remain alive in a dormant condition for long periods of time (e.g. Budowski 1965 and Gomez-Pompa et al. 1972), but have not presented data to support this assumption. Garwood (1983) reported mean length of dormancy (time between sowing and germination) of seeds from a semideciduous forest in Panama (which has few species in common with the Guanica forest); values ranged from 2 to 370 days. She watered the seeds continuously throughout the study, however, so dormancy under field conditions may be different. How long seeds can actually survive harsh dry forest conditions such as heat and desiccation, both of which generally cause high seed mortality (Crocker 1938) has not been demonstrated. Many dry forest species have seeds covered by harad seed coats obs.), a character which generally contributes to (pers. long sseed life spans (Crocker 1938). A few seeds from litter and soil collections in this study germinated just before the study was terminated one year after the collection date, thus Guanica forest seeds may remain germinable for > one year.

Although germinability was not measured in this study, Murphy and Lugo (1983) reported that seeds  $\geq$  2.38 mm collected from soil and litter in nearby mature forest showed only 0-0.5% germination (0-1.6 seeds germinating per m<sup>2</sup>) under greenhouse conditions. It is possible that

sterile potting soil and a greenhouse environment did not provide ideal conditions for germination. It may also be that dormancy-breaking requirements inhibit germination in the greenhouse and in the field. Increased germination of scarified *Leucaena* seeds (Table 11) and seeds of 4 other species (Murphy and Lugo 1983), together with the low germinability of viable fresh seeds (Table 10), indicates that dormancy mechanisms are probably operable in at least some species.

It is also possible that many dry forest persistent species possess short-lived seeds, germinating only when conditions are favorable. It is likely that at least some species possess seeds which can survive drought, however, since a number of trees produce fruits during the dry season (Murphy and Lugo 1983).

The low viability, apparently low germinability, and desiccated appearance of many seeds from litter and soil seed banks indicate that seed mortality in the field is high over the long run. However, with soil and litter seed densities over 1000 seeds/m<sup>2</sup> and a constant input of new seeds, even very low germinability levels would be sufficient to produce the 13.1 seedling-origin plants per  $m^2$  which occur in the 13-year-old site.

#### Mycorrhizae

Janos' (1980) prediction that cutting a tropical forest would not appreciably affect mycorrhizal associations was supported by this study. Mycorrhizae may be especially important in dry forests, since they aid plants in obtaining phosphorous and water in soils which are low in available phosphorous (Safir et al. 1972, Read et al. 1976). Mycorrhizal plants have been shown to grow significantly faster than non-mycorrhizal plants in a number of tropical systems (see Janos 1980 and Bowen 1980 for reviews), rapid dry forest recovery may be partially dependent on the maintenance of intact mycorrhizal associations. In studies of severely disturbed arid communities like old roadbeds (Reeves et al. 1979). revegetated mine spoils (Miller 1979), and freshly disked farmlands (Ewel et al. 1976), where rhizospheres were heavily disturbed, nonmycorrhizal secondary species were the major invaders and mycorrhizal species became dominant only in later seral stages. If the dry forest rhizosphere were heavily disturbed by bulldozing, plowing, or heavy herbicide application following a clearcut, mycorrhizal systems would certainly be disrupted and a similar pattern of nonmycorrhizal invaders might follow, slowing down the recovery process considerably.

### Recovery and Resilience

The long-lasting effects of Ewel's recut/herbicide treatments underscores the importance of taking disturbance history into account in studies of forest recovery. The lower ratio of stem sprout to plant in the "recut/herbicided" portion of the site indicates that herbicide and repeated-cutting treatments depleted the stored energy reserves of woody plants so that fewer sprouts were produced. Basal area differences after 13 years may indicate long-lasting reduced productivity.

Differences between the pre-cut structure of the 1 ha site and the adjacent forest further emphasize the role of disturbance in dry forests. The 1 ha site was considerably more depauperate in species richness and basal area and contained more individuals of the pioneer species *Leucaena leucocephela* than mature forest in 1982, indicating that the area was probably more disturbed in the past, either naturally (e.g. by fire) or by humans (selective cutting, trampling, etc.). The latter seems likely because of the accessibility of the site; it is closer to roads and flatter than much of the surrounding forest. Evidence of past fires in the form of charcoal fragments in soil pits was found in the Cut Site as well as in mature forest stands (Murphy and Lugo, unpublished data), but no fire frequency data are available. Because

on comparisons to adjacent forest as representing the maximal measurable degree of maturity of Guanica dry forest. This inserts site-to-site variability into the study, but the immediate proximity of the forest to the Cut Site should minimize differences.

Depending on the parameter considered, recovery after 13 years was within 7 to 64% of mature forest levels (Table 14). Leaf area index and species composition were closest to mature forest values, with total basal area, mean height, and total biomass next at 40% of forest values. Basal area in larger stem size classes had recovered less, demonstrating the large contribution of smaller stems to the structure of the younger site.

The general picture of dry forest revegetation is one of relatively rapid recovery of biomass and cover. Only 13 years subsequent to cutting, the study site was completely covered by vegetation, including many woody plant species characteristic of adjacent mature forest. It may take quite a number of years for the site to obtain the structure and full species complement of mature forest, but the availability of propagules and the relatively rapid growth rate of vegetative sprouts in the site ensure that in the absence of further disturbance, the forest will continue to aggrade relatively quickly. Compared to comparable-aged sites, dry forest has recovered more rapidly than one post-agricultural northern

Table 14. Degree of recovery of structural parameters in 13-year-old dry forest.

	Parameter	Cut Site	Forest	Percent recovery
1)	Species composition: Number of mature forest tree species with stems > 1 cm DBH	17	41	59
2)	Basal area (m2/ha) All stems (from DGH)	19.7	52.8	40
	Stems > 1 cm DBH	8.9	30.8	29
	Stems > 5 cm DBH	1.2	18.6	7
3)	Mean height - all plants (m)	0.7	1.6	40
4)	Aboveground biomass (mt/ha)	2 19.1	1 44.9	43
5)	Leaf Area Index (November, m2/m2)	1.8	2.8	64
6)	Epiphyte density (plants/m2)	0.3	2.8	11

.

<sup>1</sup> <sup>2</sup>From Murphy and Lugo (1985) <sup>2</sup>From Murphy, Lugo, and Murphy (1983) temperate forest and more slowly than a post-agricultural tropical moist evergreen forest. New Hampshire 14-year-old sites supported 19% of biomass of mature northern temperate forests (Marks and Bormann 1972, Whittaker 1974), while moist evergreen sites had recovered 56% of tree height, 35% of tree diameter, and 50% of basal cover 14 years following abandonment (Aweto 1981).

The measurement of relative resilience is complicated by several factors. The first is the difficulty of obtaining accurate data on primary or mature secondary forest for estimation of recovery rates. In Guanica, there are no extant examples of primary dry forest, and the extent to which older secondary stands have reached their climax is not known.

Secondly, the constancy and rate of vegetation growth are not known for most ecosystems; the oft-made assumption that recovery is constant and logarithmic is largely unsubstantiated (Westman 1978). Patterns of recovery differ widely according to the parameter measured. Growth rates have variously been described as sigmoidal (Ewel 1983), asymptotic (Opler et al. 1977), and linear (Hibbs 1983). Dry forest recovery showed highly variable growth patterns for different parameters, as is demonstrated by the shapes of the curves in Figure 20.

Another difficulty in quantifying resilience is the assumption that a climax condition identical to the



AGE OF SITE (YEARS)

Figure 20. Patterns of structural change in long-term dry forest succession. Circles mark data points, and dotted lines are hypothetical projections of pattern. Data are from this study, Ewel (1971), and Murphy and Lugo (1983).

original will be obtained by a recovering ecosystem. Many ecologists have noted that stochastic processes are important in succession (e.g. Horn 1975), so the probability of restoration of identical structure may be small.

Finally, the degree of recovery is highly dependent on the type and intensity of disturbance, the size of the disturbed area, and the proximity of seed sources. Comparable data from different ecosystems with these 4 factors held constant are essentially nonexistent. For this reason, it is important that recovery of ecosystems under a variety of disturbance regimes be assessed with standardized measurements which can be used to compare to recovery rates from other studies. The delimitation of the most useful parameters to measure and the most important site information to collect will make possible the collection of data which can be used to make accurate assessments of relative resilience.

The measurements listed in Table 14 all provide useful information regarding resilience of dry forest. The combination of all these values into an index of resilience may simply mask the important details of recovery, and may place artificial emphasis on some of the values. For example, the exclusion of any of the three basal area values listed would leave out information regarding the sizes of stems in the site, but the

inclusion of all three in an index would heavily weight that parameter. Another example is epiphyte density, which gives a different kind of information than any of the other values, and therefore should be considered separately. It is suggested, therefore, that recovery values of each of these parameters be quantified in future studies, and reported together with available information on areal extent of the disturbance, intensity and frequency of disturbance, and relative maturity of the original forest; all of these factors considered together give a composite picture of resilience.

#### SUMMARY

In thirteen-year-old dry forest, basal area of stems l cm DBH and mean plant height were 40% of mature forest measurements. Leaf area index and epiphyte density were 64% and 11%, respectively, of values in mature forest. Structure and species richness still differed significantly from mature forest values, however (Hotelling T test; ANOVA). It is suggested that in studies of ecosystem recovery, all these parameters be measured and considered as a whole to provide a composite picture of resilience.

Cut Site species composition included a distinct pioneer species component, with 46% of stem density and 28% of species classified as pioneer as compared to 3% and 4%, respectively, in mature forest. Mature forest species were also well represented in the site, with 59% of all tree species with stems  $\geq$  1 cm DBH in mature forest plots also occuring in Cut Site plots.

Species diversity (species per unit area) was higher in the 13-year-old site than in one-year-old or mature forest sites, supporting the hypothesis of highest diversity in mid-successional sites.

The hypothesis of dominance of vegetative sprouting over seed germination was not supported. Of plants supporting stems  $\geq$  1 cm DBH in the Cut Site, half

originated as seedlings since the 1969 clearcut, and half as sprouts from roots or cut stems. High seed densities in soil and litter (780 to 1265 per m<sup>2</sup> in Cut Site in 1982) may account for high seedling densities despite low seed viability of persistent species (0-7% per species), apparent low germinability, and the many desiccated seeds.

Numbers of woody seedling origin plants decreased with distance from the forest edge in the 13-year-old site, though not significantly.

Quantities of VA mycorrhizal associations did not differ in plants occurring in one-year-old, 13-year-old, and mature forest sites, indicating that cutting did not appreciably affect mycorrhizae.

The effects of recut/herbicide treatments applied to a portion of the Cut Site in 1969 persisted 13 years later, evidenced by significant structural differences (Hotelling T test) between the "recut/herbicided" portion and the "cut only" portion. Trees in the "recut/herbicided" area possessed nearly twice as many stems and had significantly less basal area than those in the "cut only" portion.

In conclusion, recovery on the 13-year-old site has been relatively rapid. Because of the relative simplicity of mature West Indian dry forest and the potential of component species to grow and reproduce under highly disturbed conditions, the system's resilience is perhaps greater than that of tropical rain forest.

Table A1. Characteristics of all species occurring in plots. Nomenclature according to Little and Wadsworth (1964) and Little, Woodbury, and Wadsworth (1974) for trees, and Britton and Wilson (1924) for other species, except where noted. T=tree, S=shrub, H (P)=perennial herb, H (A)=annual herb, C=cactus, Ep=epiphyte, V (W)=woody vine, V (H)=herbaceous vine, Pt=persistent, Pr=pioneer, D=deciduous, E=evergreen, N=native to Puerto Rico, Ex=exotic, En=endemic to Puerto Rico.

Pt

Pt

Pr

Pt

Pt

Pt

Pt

Pt

Pr

Pt

Pr

Pt

Pr

Pt

Pt

Pt

Pt

Pr

Pt

Pt

Pt

E

-

-

D

E

D

E

D

D

E

-

-

-

Ε

Ε

Ε

Ε

Ε

Ε

-

Ε

-

Ε

-

-

-

-

-

-

-

Ε

Ε



N

Ν

N

N

N

Ν

N

N

Ν

N

N

Ν

N

N

N

N

N

N

Ν

N

N

N

N

N

N

N

?

N

N

N

Ν

En

Y

No

No

No

Y

Y

Y

Y

Y

No

Y

No

No

No

Y

Y

Y

Y

Y

Y

Ν

N

Y

Y

No

No

Y

Y

No

No

No

Y

Species

CUT SITE

Amyris elemifera	Т
Antirhea acutata	Т
Argythamnia fasciculata	S
Ayenia pusilla	H (P)
Bernardia dichotoma	Т
Bourreria succulenta	Т
Bucida buceras	Т
Bumelia obovata	Т
Bursera simaruba	Т
Calliandra caracasana	Т
Cassine xylocarpa	Т
Cephalocereus royenii	C
Chiococca alba	V (W)
Cissus trifoliata	V (H)
Citharexylum fruticosum	Т
Citharexylum spinosum	Т
Clusia rosea	Т
Coccoloba diversifolia	Т
Coccoloba krugii	Т
Coccoloba michrostachya	Т
Commelina elegans	H (P)
Comocladia dodonea	Т
Corchorus hirsutus	S
Crossapetalum rhacoma	Т
Croton betulinus	S
Croton discolor	S
Croton humilis	S
Croton rigidus	S
*Dalea carthagenensis	S
Desmanthus virgatus	S
Distictis lactiflora	V (W)
Eugenia foetida	Т
Eugenia ligustrina	Т

Table Al (Cont'd)

Fuenda te abantan	-	<b>D</b> .4	-		
Eugenia rhombea	i c		Ľ	N	Y
	3 T	Pr De	-	N	NO
Exostema caribaeum		Pt	Ł	N	Y
Galactia dudia	V (H)	Pr	-	N	NO
Galactia striata	V (W)	Pr	-	N	No
Gouania lupuloides	V (W)	Pr	-	N	No
Guaicum sanctum	T	Pt	E	N	Y
Guettarda elliptica	Т	Pt	E	N	Y
Guettarda krugii	Т	Pt	E	N	Y
Gymnanthes lucida	Т	Pt	E	N	Y
Helicteres jamaicensis	Т	Pr	E	N	Y
*Herissantia crispa	V (H)	Pt	-	Ex?	Nọ
Heteropterus purpurea	V (W)	Pt	-	N	Y
Hibiscus brasiliensis	V (W)	Pr	-	N	No
Hypelate trifoliata	Т	Pt	E	N	No
lpomea arenaria	<b>V (</b> Н	Pt	-	N	Y
Jacquemontia pentantha	V (W)	Pr	-	N	No
Justicia sessilis	H (P)	Pr	-	N	No
Krugiodendron ferreum	Т	Pt	Ε	N	Y
Lantana involucrata	S	Pr	-	N	Y
Lasiacis divaricata	H (P)	Pt	-	N	Y
Leptocereus quadricostasus	C	Pt	-	N	Ŷ
Leucaena leucocephala	Т	Pr	D	N	Ŷ
Opuntia repens	Ċ	Pt?	-	En	No
Panicum maximum	H (P)	Pr	-	Fx	No
Passiflora sp.	V (W)	Pr	-	7	Y
Pictetia aculeata	т.,,,	Pt	n	N	Ŷ
Pisonia albida	Ť	Pt	n	N	Ŷ
Pithecellobium unquis-cati	Ť	Pt	n	N	v
Plumeria alba	Ť	P+	5	N	v
Randia aculeata	Ť	P+	<b>D</b>	N	v
Revosia uncinata	Ť	D+	5	N	No
*Rhyncheletrum renens	ц Ц	Pr	-	N E v 2	No
Sahinea florida	T	D+	n		v
Samyda dodocandra	' T	P+	D		v
Sawia cocciliflora	T		D		v
Sclaria lithocharma	ц (р)			N AI	T V
Setaria estesa			-		T V
Setaria selosa		Pr D-	-	N	T N.
Selaria ulowanaea	п (P)	Pr	-	N	NO
Sida acuminata	5	Pr	-	N	NO
Stigmaphylion peripiocitol		Pt	-	N	No
inouinia portoricensis	1	Pt	D	En	Y
lillandsia recurvata	E	Pt	-	N	Y
Tillandsia utriculata	E	Pt	-	N	Y
Tournefortia microphylla	V (W)	Pr	-	N	Y
Tragia volubilis	V (H)	Pr	-	N	No
Turnera diffusa	S	Pr	-	N	No
Vanilla egersii	V (H) , E	Pt	-	N	Y

Table Al (Cont'd)					
Wedelia lanceolata	S	Pr?	-	En	No
Zamia portoricensis	H (P)	Pt	-	En	Y
Unknown #87	?	?	?	?	No
OCCURRING IN FOREST ONLY					
Adelia ricinella	Т	Pt	D	N	
Colubrina arborescens	Т	Pt	E	N	
Jatropha hernandiifolia	Т	Pt	Ε	N	
Reynosia guama	Т	Ρt	Ε	N	
Tabebuia heterophylla	Т	Pt	Ε	N	
Unknown tree species (5)	Т	Pt	?	?	
Unknown vine species (4)	V (W)	Ρt	-	?	

\*Nomenclature according to Long and Lakela (1971).

Table A2. Structural parameters of all stems  $\geq$  5 cm DBH on the study site before it was cut in 1969. Data summarized from J. Ewel (unpublished data).

Value per 10 x 100 m transect

Transect	Number of species	Total DBH (cm)	Total Basal Area (cm2)	Density
1	12	795.3	5175.7	116
2	8	731.8	4653.2	102
3	10	822.2	5020.8	120
Total	18-22	2349.3	14849.8	338
Mean	10.0	783.1	4949.9	112.7
Mean/ha	-	7831	49499	1127

Table A3. Importance values for woody plant species with DBH  $\geq 5$  cm on the study site before it was cut in 1969. Data summarized from three 100 x 10 m transects measured by J. Ewel (unpublished data).

•

Species	IV	<pre>% of Total</pre>	Rel. Density	Rel. Freq.	Rel. Dominance
Gymnanthes lucida	70.45	23.48	28.99	9.7	31.76
Exostema caribaeum	57.17	19.06	30.47	9.7	17.00
Bucida buceras	24.96	8.32	8.88	3.2	12.88
Pisonia albida	20.16	6.72	5.92	6.5	7.74
Amyris elemifera	19.84	6.61	5.33	9.7	4.81
Bursera simaruba	19.66	6.55	2.37	9.7	7.59
Leptocereus quadricostasus	17.49	5.83	1.78	9.7	6.01
Leucaena leucocephala	10.63	3.54	2.07	6.5	2.06
Cephelocereus royenii	8.26	2.75	1.78	3.2	3.28
Krugiodendron ferreum	4.68	1.56	0.88	3.2	0.60
Tabebuia heterophylla	4.43	1.48	0.59	3.2	0.64
Pictetia aculeata	4.22	1.41	0.59	3.2	0.43
Jacquinia berterii	4.16	1.39	0.59	3.2	0.37
Colubrina arborescens	3.79	1.26	0.30	3.2	0.29
Comocladia dodonea	3.73	1.24	0.30	3.2	0.23
Reynosia uncinata	3.71	1.24	0.30	3.2	0.22
2-6 unknown species	22.67	7.56	8.88	9.7	4.09
TOTAL	300.01	100.00	100.02	100.0	100.00

\*It is possible that other species were included in the count of *Gymnanthes*, as some of the diameters recorded seem rather high. The similarity of the Spanish common names (used to record data) of *Gymnanthes* and *Bucida* may have caused some errors in recording. Table A4. Multivariate comparisons of structure in the Cut Site and forest  $2 \times 10$  m plots using the Hotelling T square test. Variables used were per plot values for species richness, plant density, stem density, and total DBH.

Cut Site ("Cut only" area) versus Forest plots

Hotelling T square	64.1637
Fvalue	14.7745
Significance (P value)	.0000
Degrees of freedom	4, 35

Cut Site: "Cut only" area versus "Recut/herbicide" area plots

Hotelling T square	12.2061
Fvalue	2.5429
Significance (P value)	.0830
Degrees of freedom	4, 15

#### LITERATURE CITED

- Agee, J.K. and L. Smith. 1984. Subalpine tree reestablishment after fire in the Olympic Mountains, Washington. Ecology 65(3): 810-819.
- Aristeguieta, L. 1968. El bosque cadicifolio seco de los llanos altos centrales. Boln. Soc. Venez. Cienc. Nat. 27: 395-438.
- Auclair, A.N. and F.G. Goff. 1971. Diversity relations of upland forests in the western Great Lakes area. Am. Nat. 105: 499-528.
- Aweto, A.O. 1981. Secondary succession and soil fertility restoration in south-western Nigeria. II. Soil fertility restoration. J. Ecol. 69: 609-614.
- Bazzaz, F.A. 1975. Plant species diversity in old-field successional ecosystems in southern Illinois. Ecology 56(2): 485-488.
- Benzing, D.H. 1980. The Biology of the Bromeliads. Mad River Press, Eureka, Calif. 305 pp.
- Berish, C.W. 1982. Root biomass and surface area in three successional tropical forests. Can. J. For. Res. 12(3): 699-704.
- Bormann, F.H. and G.E. Likens. 1981. Pattern and Process in a Forested Ecosystem. Springer-Verlag, New York. 253 pp.
- Bourliere, F. (ed.). 1983. Ecosystems of the World. 13. Tropical Savannas. Elsevier Scientific Pub. Co., New York. 730 pp.
- Bowen, G.D. 1980. Mycorrhizal roles in tropical plants and ecosystems. pp. 165-189 In: Mikola, P. (ed.), Tropical Mycorrhiza Research, Oxford Univ. Press.
- Britton, N.L. and P. Wilson. 1923-30. Botany of Puerto Rico and the Virgin Islands. New York Academy of Sciences, New York.
- Brower, J.E. and J.H. Zar. 1977. Field and laboratory methods for general ecology. Wm. C. Brown Co. Pub., Dubuque, Iowa. 194 pp.
- Brown, S. and A.E. Lugo. 1982. The storage and production of organic matter in tropical forests and their role in the global carbon cycle. Biotropica 14(3): 161-187.
- Budowski, G. 1963. Forest succession in tropical lowlands. Turrialba 13(1): 42-44.
- Budowski, G. 1965. Distribution of tropical American rain forest species in the light of successional processes. Turrialba 15(1): 40-42.
- Cairns, J. Jr. and K.L. Dickson. 1977. Recovery of streams and spills of hazardous materials. pp. 24-42 In: J. Cairns, Jr., K.L. Dickson, and E.E. Herricks (eds.), Recovery and Restoration of Damaged Ecosystems. Univ. of Virginia Press, Charlottesville.
- Cheke, A.S., W. Nanakorn, and C. Yankoses. 1979. Dormancy and dispersal of seeds of secondary forest species under the canopy of a primary tropical rain forest in northern Thailand. Biotropica 11: 88-95.
- Clapham, W.B. Jr. 1971. Natural ecosystems. Chapt. 7 In: Resiliency and Fitness of Ecosystems. Macmillan Publishing Co., New York.
- Covington, W.W. and J.D. Aber. 1980. Leaf production during secondary succession in northern hardwoods. Ecology 61: 200-204.
- Crocker, W. 1938. Life-span of seeds. Bot. Review 4(6): 235-274.
- Daubenmire, R. 1972. Phenology and other characteristics of tropical and semi-deciduous forest in northwestern Costa Rica. J. Ecol. 60: 147-170.
- Davis, T.A.W. and P.W. Richards. 1933. The vegetation of Moraballi Creek, British Guiana. J. Ecol. 21: 350-384.
- Day, R.J. 1972. Stand structure, succession, and use of southern Alberta's Rocky Mountain forest. Ecology 53: 472-478.
- Diem, H.G., I. Gueye, V. Gianinaazzi-Pearson, J.A. Fortin, and Y.R. Dommergues. 1981. Ecology of VA

mycorrhizae in the tropics: the semi-arid zone of Senegal. Acta Oecologica/Oecologia Plantarum 2: 53-62.

- Dixon, W.J. 1983. Comparison of two groups with t tests: BMDP3D. pp. 94-103 In: Dixon, W.J. (ed.) BMDP Statistical Software, 1983 Printing with Additions. Univ. of Calif. Press, Berkeley. 733 pp.
- Doley, D. 1981. Tropical and subtropical forests and woodlands. p. 209-323 In: T.T. Kozlowski (ed.) Water Deficits and Plant Growth. Academic Press, New York.
- Dubey, P.S. and L.P. Mall. 1975. Effect of herbicides on germination, viability and seedling growth of weed seeds. I. Digera alternifolia Aschers. Trop. Ecol. 16: 39-42.
- Dunevitz, V.L., M.F. Mulligan, P.G. Murphy, and A.E. Lugo. 1983. The occurrence of vesicular-arbuscular mycorrizae in a subtropical dry forest. Abstract of paper presented at Third International Symposium on Microbial Ecology, Mich. State Univ., August 7-12, 1983.
- Ewel, J.J. 1971. Experiments in arresting succession with cutting and herbicides in five tropical environments. PhD dissertation, Univ. of North Carolina, Chapel Hill. 248 pp.
- Ewel, J.J. 1977. Differences between wet and dry successional tropical ecosystems. Geo-Eco-Trop 1(2): 103-117.
- Ewel, J.J. 1980. Tropical succession: manifold routes to maturity. Biotropica 12 (supplement): 2-7.
- Ewel, J.J. 1983. Succession. pp. 217-223 In: F.B. Golley (ed.) Tropical Rain Forest Ecosystems. A. Structure and Function. Elsevier Scientific Pub. Co., Amsterdam.
- Ewel, J., C. Berish, B. Brown, N. Price and J. Raich. 1981. Slash and burn impacts on a Costa Rican wet forest site. Ecology 62(3): 816-829.
- Ewel, J., R. Meador, R. Myers, L. Conde, and B. Sedlik. 1976. Studies of vegetation changes in south Florida. Final report, subcontract on research agreement #18-492 with USDA-Forest Service.

- Ewel, J.J. and J.L. Whitmore. 1973. The ecological life zones of Puerto Rico and the U.S. Virgin Islands. Forest Service Res. Paper ITF-18, Institute of Tropical Forestry, Rio Piedras, Puerto Rico. 72 pp.
- Fox, J.E.D. 1976. Constraints on the natural regeneration of tropical moist forest. Forest Ecol. Manage. 1: 37-65.
- Frankie, G.W., H.G. Baker, and P.A. Opler. 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. J. Ecol. 62: 881-919.
- Garwood, N.C. 1981. Seed germination in a seasonal tropical forest in Panama: a community study. Ecol. Monog. 53(2): 159-181.
- Gentry, A.H. 1983. Lianas and the "paradox" of contrasting latitudinal gradients in wood and litter production. Tropical Ecology 24(1): 63-67.
- Gleason, H.A. and M.T. Cook. 1927. Plant ecology of Puerto Rico. Sci. Surv. Puerto Rico and the Virgin Islands. 7(1-2): 1-173.
- Goldberg, D.E. 1982. The distribution of evergreen and deciduous trees relative to soil type: an example from the Sierra Madre, Mexico, and a general model. Ecology 63(4): 942-951.
- Golley, F.B. and J.B. Gentry. 1966. A comparison of variety and standing crop of vegetation on a one-year and a twelve-year abandoned field. Oikos 15(2): 185-199.
- Gomez-Pompa, A. 1974. Recovery of tropical ecosystems. pp. 113-138 In: F. Golley (ed.) Fragile Eccosystems. Springer-Verlag, New York. 258 pp.
- Gomez-Pompa, A., C. Vazquez-Yanes, and S. Guevara. 1972. The tropical rain forest: a nonrenewable resource. Science 177: 762-765.
- Grieg-Smith, P. 1952. Ecological observations in degraded and secndary forest in Trinidad, British West Indies. J. of Ecol. 40: 283-330.
- Grubb, P.J. and E.V.J. Tanner. 1976. The montane forests and soils of Jamaica: a re-assessment. J. Arnold Arboretum 57: 313-368.

- Hall, J.B. and M.D. Swaine. 1980. Seed stocks in Ghanaian forest soils. Biotropica 12(4): 256-263.
- Henry, J.D. and J.M.A. Swan. 1974. Reconstructing forest history from live and dead plant material - an approach to the study of forest succession in southwest New Hampshire. Ecology 55: 772-783.
- Hibbs, D.E. 1983. Forty years of forest succession in central New England. Ecology 64(6): 1394-1401.
- Hill, A.R. 1975. Ecosystem stability in relation to stresses caused by human activities. Canad. Geog. 19(3): 206-220.
- Hogberg, P. 1982. Mycorrhizal associations in some woodland and forest trees and shrubs in Tanzania. New Phytol. 92: 407-415.
- Holdridge, L.R. 1967. Life zone ecology. Tropical Science Center, San Jose, Costa Rica. 206 pp.
- Holling, C.S. 1973. Resilience and stability of ecological systems. Ann. Rev. Ecol. Syst. 4: 1-24.
- Horn, H.S. 1975. Markovian properties of forest succession. pp. 196-211 In: M.L. Cody and J.M. Diamond (eds.) Ecology and Evolution of Communities. Belknap Press, Cambridge, Mass.
- Hubbell, S.P. 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. Science 203: 1299-1309.
- Isensee, A.R., W.C. Shaw, W.A Gentner, C.R. Swanson, B.C. Turner, and E.A. Woolson. 1973. Revegetation following massive application of selected herbicides. Weed Science 21(5): 409-412.
- Janos, D.P. 1980. Vesicular-arbuscular mycorrhizae affect lowland tropical rain forest plant growth. Ecology 61(1): 151-162.
- Janzen, D.H. 1967. Synchronization of sexual reproduction of trees within the dry season in Central America. Evolution 21: 620-637.
- Janzen, D.H. 1981. Patterns of herbivory in a tropical deciduous forest. Biotropica 13(4): 271-282.
- Keay, R.W. 1960. Seeds in forest soil. Nigerian Forest Infor. Bull., New Series 4: 1-4.

- Kellman, M.C. 1970. Secondary plant succession in tropical montane Mindanao. Dept. Biogeogr. Publ. BG/2, Australian National Univ., Canberra, Australia.
- Kim, J. and F.J. Kohout. 1975. Analysis of variance and covariance: subprograms ANOVA and ONEWAY. pp. 398-433 In: Nie, N.H., C.H. Hull, J.G. Jenkins, K. Steinbrenner, and D.H. Bent (eds.) Statistical Package for the Social Sciences, Second Edition. McGraw-Hill, New York. 675 pp.
- Kim, J. and F.J. Kohout. 1975. Multiple regression analysis: subprogram regression. pp. 320-367 In: Nie, N.H., C.H. Hull, J.G. Jenkins, K. Steinbrenner, and D.H. Bent (eds.), Statistical Package for the Social Sciences, Second Edition. McGraw-Hill, New York. 675 pp.
- Kira, T. and T. Shidei. 1967. Primary production and turnover of organic matter in different forest ecosystems of the western Pacific. Japan. J. Ecol. 17: 70-87.
- Kittredge, J., Jr. 1934. Evidence of the rate of forest succession on Star Island, Minnesota. Ecology 15: 24-35.
- Larsen, J.A. 1925. Natural reproduction after forest fires in northern Idaho. J. Agr. Res. 30: 1177-1197.
- Leak, W.B. and R.W. Wilson, Jr. 1958. Regeneration after cutting of old-growth northern hardwoods in New Hampshire. USDA Northeastern Forest Exper. Station Paper 103.
- Leps, J., J. Osbornova-Kosinova and M. Rejmanek. 1982. Community stability, complexity, and species life history strategies. Vegetatio 50(1): 53-64.
- Lieberman, D. 1982. Seasonality and phenology in a dry tropical forest in Ghana. J. Ecology 70: 791-806.
- Lieberman, D. and M. Lieberman. 1984. The causes and consequences of synchronous flushing in dry tropical forest. Biotropica 16(3)): 193-201.
- Likens, G.E., F.H. Bormann, R.S. Pierce, and W.A. Reiners. 1978. Recovery of a deforested ecosystem. Science 199: 492-496.
- Little, E.L. and F.H. Wadsworth. 1964. Common trees of

Puerto Rico and the Virgin Islands. USDA Forest Service, Agr. Handbook 249.

- Little, E.L., R. Woodbury, and F.H. Wadsworth. 1974. Trees of Puerto Rico and the Virgin Islands. Vol. 2. USDA Forest Service Agr. Handbook No. 499.
- Long, R.W. and O. Lakela. 1971. A Flora of Tropical Florida. A Manual of the Seed Plants and Ferns of Southern Peninsular Florida. Univ. of Miami Press, Coral Gables, Florida. 962 pp.
- Loucks, O.L. 1970. Evolution of diversity, efficiency, and community stability. Am. Zool. 10: 17-25.
- Loveless, A.R. and G.F. Asprey. 1957. The dry evergreen formations of Jamaica. I. The limestone hills of the south coast. J. Ecol. 45: 799-822.
- Lugo, A.E., J.A. Gonzalez-Liboy, B. Cintron, and K. Dugger. 1978. Structure, productivity, and transpiration of a subtropical dry forest in Puerto Rico. Biotropica 10(4): 278-291.
- Lugo, A.E. and P.G. Murphy. 1985. Nutrient dynamics of a Puerto Rican subtropical dry forest. Submitted.
- Lutz, H.J. 1943. Injuries to trees caused by <u>Celastrus</u> and <u>Vitis</u>. Bull. Torr. Bot. Club 70: 436-439.
- Malaisse, F.P. 1974. Phenology of the Zambezian woodland area with an emphasis on the Miombo ecosystem. pp. 269-286 In: Lieth, H. (ed.) Phenology and Seasonality Modeling. Springer-Verlag, New York. 444 pp.
- Malaisse, F.P. 1978. The Miombo ecosystem. In: Tropical Forest Ecosystems. UNESCO Nat. Resour. Res. 14, UNESCO, Paris.
- Malmer, N., L. Lindgren, and S. Persson. 1978. Vegetational succession in a south Swedish wood. Vegetatio 36(1): 17-29.
- Margalef, R. 1963. On certain unifying principles in ecology. Am. Nat. 97: 357-374.
- Margalef, R. 1975. Diversity, stability and maturity in natural ecosystems. pp. 151-160 In: W.H. van Dobben and R.H. Lowe-McConnell (eds.) Unifying Concepts in Ecology. Junk, The Hague, Netherlands.

- Marks, P.L. and F.H. Bormann. 1972. Revegetation following forest cutting: mechanisms for return to steady-state nutrient cycling. Science 176: 914-915.
- Martin, N.D. 1959. An analysis of forest succession in Algonguin Park, Ontario. Ecol. Monogr. 29: 187-218.
- Mellinger, M.V. and S.J. McNaughton. 1975. Structure and function of successional vascular plant communities in central New York. Ecol. Monogr. 45: 161-182.
- Miller, R.M. 1979. Some occurrance of vesicular-arbuscular mycorrhiza in natural and disturbed ecosystems of the Red Desert. Can. J. Bot. 57: 619-623.
- Monette, R. and S. Ware. 1983. Early forest succession in the Virginia coastal plain. Bull. Torr. Bot. Club 110(1): 80-86.
- Monk, C.D. 1974. Plant species diversity in old-field succession on the Georgia piedmont. Ecology 55: 1075-1085.
- Monroe, W.H. 1976. The karst landforms of Puerto Rico. Geol. Surv. Professional Paper 899. U.S. Government Printing Office, Washington. 69 pp.
- Murphy, P.G. and S.R. Kephart. 1981. Seasonal dynamics and succession in a subtropical dry forest. Proposal to NSF, January 1981.
- Murphy, P.G. and A.E. Lugo. 1982. Seasonal dynamics and succession in a subtropical dry forest. Progress report for the period 15 June 1981 - 15 February 1982, NSF Grant DEB-8110208.
- Murphy, P.G. and A.E. Lugo. 1983. Seasonal dynamics and succession in a subtropical dry forest. Progress report for the period 1981-1983, NSF Grant DEB-8110208.
- Murphy, P.G. and A.E. Lugo. 1985. Structure and biomass of a subtropical dry forest in Puerto Rico. In press, Biotropica.
- Murphy, P.G., A.E. Lugo, and A.J. Murphy. 1983. Seasonal dynamics and recovery of a Caribbean dry forest. Bull. Ecol. Soc. Am. 64(2):113.
- Nicholson, S.A. and C.D. Monk. 1974. Plant species diversity in old-field succession on the Georgia Piedmont. Ecology 55: 1075-1085.

- Nie, N.H., D.H. Bent, and C.H. Hull. 1975. Description of subpopulations and mean difference testing: subprograms BREAKDOWN and T-TEST. pp. 249-275 In: Nie, N.H., C.H. Hull, J.G. Jenkins, K. Steinbrenner, and D.H. Bent (eds.) Statistical Package for the Social Sciences, Second Edition. McGraw-Hill, New York. 675 pp.
- Nye, P.H. and D.J. Greenland. 1960. The soil under shifting cultivation. Tech. Comm. No. 51. Commonwealth Bureau of Soils, Harpenden, England. 156 pp.
- Odum, E.P. 1969. The strategy of ecosystem development. Science 164: 262-270.
- Opler, P.A., H.G. Baker, and G.W. Frankie. 1977. Recovery of tropical lowland forest ecosystems. pp. 379-421 In: J. Cairns, Jr., K.L. Dickson, and E.E. Herricks (eds.) Recovery and Restoration of Damaged Ecosystems. Univ. Press of Virginia, Charlottesville.
- Opler, P.A., G.W. Frankie, and H.G. Baker. 1980. Comparative phenological studies of treelet and shrub species in tropical wet and dry forests in the lowlands of Costa Rica. J. Ecol. 68: 167-188.
- Peet, R.K. and N.L. Christensen. 1980. Succession: a population process. Vegetatio 43: 131-140.
- Phillips, J.M. and D.S. Hayman. 1970. Improved procedures for clearing roots and staining parasitic and vesicular-arbuscular mycorrhizal fungi for rapid assessment of infection. Trans. Br. Mycol. Soc. 55(1): 158-163.
- Pickett, S.T.A. 1982. Population patterns through 20 years of oldfield succession. Vegetatio 49(1): 45-59.
- Pressland, A.J. 1975. Productivity and management of mulga in south-western Queensland in relation to tree structure and density. Aust. J. Bot. 23: 965-976.
- Putz, F.E. 1980. Lianas vs. trees. Biotropica 12: 224-225.
- Read, D.J., J.K. Koucheki, and J. Hodgson. 1976. Vesicular-arbuscular mycorrhiza in natural vegetation systems. I. The occurrence of infection. New Phytol. 77: 641-653.
- Reeves, F.B., D. Wagner, T. Moorman, and J. Kiel. 1979. The role of endomycorrhizae in revegetation practices

in the semi-arid west. I. A comparison of incidence of mycorrhizae in severely disturbed vs. natural environments. Am. J. Bot. 66(1): 6-13.

- Richards, P.W. 1955. The secondary succession in the tropical rainforest. Sci. Prog. 43: 45-57.
- Romme, W.H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. Ecol. Monog. 52(2): 199-221.
- Romme, W.H., and D.H. Knight. 1981. Fire frequency and subalpine forest succession along a topographic gradient in Wyoming. Ecology 62: 319-326.
- Ross, R. 1954. Ecological studies on the rain forest of southern Nigeria. III. Secondary succession in the Shasha Forest Reserve. J. Ecol. 42: 259-282.
- Safir, G.R., J.S. Boyer, and J.W. Gerdemann. 1972. Nutrient status and mycorrhizal enhancement of water transport in soybean. Plant Physiol. 49: 700-703.
- Shafi, M.I. and G.A. Yarranton. 1973. Diversity, floristic richness, and species evenness during a secondary (post-fire) succession. Ecology 54: 897-902.
- Siccama, T.G., G. Weir, and K. Wallace. 1976. Ice damage in a mixed hardwood forest in Connecticut in relation to <u>Vitis</u> infestation. Bull. Torr. Bot. Club 103(4): 180-183.
- Sprugel, D.G. and F.H. Bormann. 1981. Natural disturbance and the steady state in high-altitude balsam fir forests. Science 211: 390-393.
- Spurr, S.H. 1956. Natural restocking of forests following the 1938 hurricane in central New England. Ecology 37: 443-451.
- Stanton, N. 1975. Herbivore pressure on two types of tropical forests. Biotropica 7(1): 8-11.
- Symington, C.F. 1933. The study of secondary growth on rainforest sites in Malaya. Malay. Forester 2: 107-117.
- Taylor, D.L. 1980. Biotic succession of lodgepole pine forests of fire origin in Yellowstone National Park. Nat. Geog. Soc. Res. Reports 12, 1971 Projects.

Tomkins, D.J. and W.F. Grant. 1977. Effects of herbicides

on species diversity of two plant communities. Ecology 58(2): 398-406.

- Tomlinson, P.B. 1980. The Biology of Trees Native to Tropical Florida. Harvard University, Allston, Mass. 480 pp.
- Tosi, J. 1980. Life zones, land-use, and forest vegetation in the tropical and subtropical regions. pp. 44-64 In: Carbon Dioxide Effects Research and Assessment Program: The Role of Tropical Forests of the World Carbon Cycle. Report of Symposium, Rio Piedras, Puerto Rico. 156 pp.
- Trimble, G.R., Jr., and E.H. Tryon. 1974. Grapevines a serious obstacle to timber production on good hardwood sites in Appalacia. Northern Logger 23: 22-23.
- Uhl, C. 1982. Recovery following disturbances of different intensities in the Amazon rain forest of Venezuela. Interciencia 7(1): 19-24.
- Uhl, C. and C.F. Jordan. 1984. Succession and nutrient dynamics following forest cutting and burning in Amazonia. Ecology 65(5): 1476-1490.
- van Riper, C. 1980. The phenology of the dryland forest of Mauna Loa, Hawaii, and the impact of recent environmental perturbations. Biotropica 12(4): 282-291.
- Vogl, R.J. 1969. One-hundred and thirty years of plant succession in a southeastern Wisconsin lowland. Ecology 50: 248-255.
- Wadsworth, F.H. 1950. Notes on the climax forests of Puerto Rico and their destruction and conservation prior to 1900. Carib. Forester 11(1): 38-47.
- Webb, L.J., J.G. Tracey, and W.T. Williams. 1972. Regeneration and pattern in the subtropical rain forest. J. Ecol. 60: 675-695.
- Westman, W.E. 1978. Measuring the inertia and resilience of ecosystems. BioScience 28(11): 705-710.
- Whittaker, R.H. 1975. The design and stability of plant communities. pp. 169-181 In: W.H. von Dobbe and R.H. Lowe-McConnell (eds.), Unifying Concepts in Ecology. Junk, The Hague.

Whittaker, R.H., F.H. Bormann, G.E. Likens, and T.G.

Siccama. 1974. The Hubbard Brook ecosystem study: forest biomass and production. Ecol. Monogr. 44: 233-254.

Woodwell, G.M. 1967. Radiation and the patterns of nature. Science 156(3774): 461-470.

` • • ÷ 1 . ÷

