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SEEDLING GROWTH AND MORTALITY OF FOUR SHADE-TOLERANT CANOPY TREE SPECIES IN THE RAIN FOREST OF PUERTO RICO FOLLOWING HURRICANE HUGO

A Thesis

Presented for the

Master of Science

Degree

The University of Tennessee, Knoxville

William H. Petty

May 1993

ACKNOWLEDGMENTS

Numerous individuals have made my research possible. I would first like to thank my major professor, Dr. J. Frank McCormick, for providing me with the opportunity to conduct my research in the rain forest of Puerto Rico and for valuable guidance in the formulation of my research ideas. I also extend my gratitude to members of my committee, Dr. Dewey Bunting, Dr. Clif Amundsen, and Dr. Sandy McLaughlin, for valuable discussion and input. For assistance in the field, I am deeply indebted to Fred Scatena, Alejo Estrada, Carlos Estrada, Angel Colon, Bill Lawrence, Cheng Xia You, Larissa Montfort, John Bell, Madheva Joshi, and Win Everman. For valuable discussion and use of microclimate equipment, I thank Dr. Joanne Logan and Dr. David Coffy. Many thanks go to my fellow degree-seeking colleague Dr. Nicholas McLetchie, who was especially supportive and helpful during the writing phase of this research. I would also like to thank several people who graciously read and edited the final version of this thesis, including Deborah Awl, Eric Pauley, and my mom, Anne Marie (van Wagtendonk) Petty. For their patience and support while I overlapped degree programs I thank Drs. Paul and Hazel Delcourt. For additional help in the field, extensive editing of the text, and unfailing love and support while I finished my ecology degree, I give my heartfelt appreciation to Rebecca A. Young.

This research was performed under grant BSR-8811902 from the National Science Foundation to the Terrestrial Ecology Division, University of Puerto Rico, and the International Institute of Tropical Forestry as part of the Long-Term Ecological Research Program in the Luquillo Experimental Forest. Additional support was provided by the Forest Service (U. S. Department of Agriculture)

and the University of Puerto Rico. Support for travel was provided by Oak Ridge Associated Universities, Oak Ridge, Tennessee.

DEDICATION

For my father,

Robert Owen Petty,

who first showed me the woods
and taught me by example to embrace
that which nourishes both my mind and my heart.

ABSTRACT

Hurricane Hugo struck the rain forest of Puerto Rico on September 18, 1989. Three months after the hurricane, permanent transects were established to measure post-hurricane microenvironments, growth, and survival of seedlings of four shade-tolerant canopy tree species (*Dacroydes excelsa, Sloanea berteriana, Manilkara bidentata,* and *Buchenavia capitata*). Transects were placed on slopes in or near the Bisley Watersheds of the Luquillo Experimental Forest. Microenvironmental conditions in the post-hurricane environment were characterized by solar irradiance levels 5 to 47 percent full sunlight. Air (@ 25 cm) and soil (@ -2 cm) temperatures ranged between 19.3 - 33.5 °C and 19.4 - 30.7 °C, respectively. Vapor pressure deficit ranged from 0.07 kPa to 1.1 kPa. Microenvironmental measurements indicate that Hurricane Hugo created canopy openings on slopes equivalent to gaps in the forest canopy ranging from slightly less than 200 m^2 to greater than 400 m^2.

Initial population sizes of small and large seedlings (0-15 cm and >15-50 cm in height, respectively) and saplings (>50-200 cm in height) varied significantly between species. For large seedlings of all species, positive correlations were found between monthly height growth increment and solar exposure index. Mean growth rates for large seedlings ranged from 0.83 cm mo^{-1} for *Sloanea* to 5.87 cm mo^{-1} for *Buchenavia*. Limited gas exchange measurements suggest that seedling growth rate is influenced more by dark respiration than by photosynthesis. Seedling mortality from 3 to 15 months after the hurricane ranged from 23% for *Sloanea* to 81% for *Dacroydes*. Despite high mortality, all species increased sapling densities by at least 100 stems ha^{-1} during the first 16 months following Hurricane Hugo. Where data were available for comparison,

recruitment rates were greater than those measured under pre-hurricane conditions.

Significant differences in growth and mortality were found among species. There was no consistent pattern, however, with regard to growth and mortality. Resource partitioning with respect to light was not evident, based on the fact that all species increased sapling densities under near identical light conditions. Species did, however, demonstrate different survival strategies in the post-hurricane microenvironment. *Sloanea* exhibited a "conservative" strategy with slow growth rates and low mortality. *Dacroydes* and *Buchenavia* showed a "maximal performance" strategy, compensating for high mortality with either fast growth rates (*Buchenavia*) or high initial seedling densities (*Dacroydes*). Relatively rapid growth rates were crucial for *Buchenavia* which had the lowest initial seedling densities of the four species. *Manilkara* combined intermediate growth and mortality with moderate initial seedling densities resulting in a "moderate" strategy. Recruitment ratios (number of stems recruited into next larger size class per initial number of stems) were inversely proportional to initial population size, suggesting possible density-dependent factors influencing seedling and sapling recruitment.

Refoliation of surviving canopy trees, along with rapid growth of pioneer species, reduced the amount of solar radiation reaching the forest floor. Growth of shade-tolerant species, diminished during the study, but, was still two and a half to eight times greater than under pre-hurricane conditions for *Manilkara*. Over the course of the study, mortality increased for some size classes (*Sloanea*, *Manilkara* and *Buchenavia* small seedlings and *Dacroydes* and *Buchenavia* large seedlings) and decreased for others (*Sloanea* and *Manilkara* large seedlings and *Dacroydes* small seedlings).

Disturbance caused by Hurricane Hugo created microenvironment conditions which facilitated accelerated regeneration of these four shade-tolerant rain forest species. Measurements of microenvironment and shade-tolerant seedling performance indicate that the impacts of Hurricane Hugo on slopes of the Bisley Watersheds are similar to those of large gaps.

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CHAPTER I

BACKGROUND

A. Introduction

Disturbance plays an important role in structuring ecological communities (Richards 1952, Pickett 1983, Pickett and White 1985). It disrupts autogenic processes and leads to altered patterns of resource distribution. In forests, disturbance creates temporal resource gradients (*e.g.* light, water, nutrients) which are predicted to "favor a succession of plant species, each adapted to exploit a particular range of resource concentrations, along the gradient" (Tilman 1982). These gradients change over time, leading to changing pressures on those species that survive the disturbance and are able to adapt to the new environment.

In tropical rain forests, disturbance may contribute to maintenance of species diversity (Ricklefs 1977, Denslow 1987). Some theories which propose mechanisms for the maintenance of diversity by disturbance (*i.e.* "regeneration niche," Grubb 1977; "niche partitioning," Denslow 1980) rest on the idea that species partition resources in the rain forest environment. This phenomenon has been demonstrated in temperate annuals by Wieland and Bazzaz (1975) who showed that three codominant herbs apparently coexist by partitioning soil moisture. The root systems of *Setaria faberii, Abutilon theophrasti,* and *Polygonum pensylvanicum* exploit different soil depths and thus, different moisture resources (Wieland and Bazzaz 1975). The theory of resource partitioning has been countered with the assertion that chance and history are more important in maintaining species diversity (Hubbell and Foster 1986, Clark and Clark 1992).

If resource partitioning is important in tropical rain forests, it might be found with respect to light. Plants of the wet tropics are often light limited (Pearcy and Robichaux 1985, Chazdon 1988, Denslow *et al.* 1990) and may, therefore, partition light resources. This partitioning could lead to species occurring under different light regimes which vary either spatially or temporally. Because of differences in species specific life cycle characteristics, one might expect to observe differential survival and growth of shade-tolerant species in the post-disturbance environment. The existence of these different strategies may have some bearing on the ability of species to coexist. Shade-intolerant pioneer species demonstrate differential performance in gaps of varying sizes (Brokaw 1987), however, the vast majority of species in tropical rain forests exhibit some degree of shade tolerance. Thus, the question of how these shade-tolerant species coexist in the forest becomes important for understanding the maintenance of species diversity in tropical moist forests. Although Chazdon (1988) reports that understory shrubs of the genus *Piper* are distributed in microenvironments receiving different amounts of solar radiation in the form of sunflecks, relatively little work has been done on light resource partitioning in shade-tolerant canopy species.

The major goal of the Long Term Ecological Research Project of the Luquillo Experimental Forest, Puerto Rico is to determine the relative impact of different scales of disturbance on forest structure and dynamics (Waide and Lugo 1988). Treefalls, landslides and hurricanes are the three major types of disturbance which occur in the LEF. Because treefalls and hurricanes both leave soil relatively undisturbed compared with landslides, pre-established individuals of shade-tolerant species which survive the disturbance will have an opportunity to directly regenerate the pre-disturbance forest composition.

Shade-tolerant canopy species are often described as small gap specialists (Denslow 1980) and as such, are predicted to perform poorly under large gap conditions (Bazzaz 1979, Denslow 1987). The size of light gaps created by hurricanes may be large when compared with treefalls and as a result, may create microenvironments which are substantially different. Hurricanes not only cause treefalls but extensive defoliation and branch falls of trees that remain standing (Walker 1991, Basnet *et al.* 1992). Can seedlings of shade-tolerant species acclimate to post-hurricane conditions which are similar to, if not more extreme than, large gaps? Yih *et al.* (1991) suggest that regeneration of shade-tolerant species from seedlings established prior to disturbance (*i.e.* advanced regeneration) was important in the recovery of Nicaraguan rain forest after Hurricane Joan. Canopy openings caused by Hurricane Joan were described as a "super gap," (Yih *et al.* 1991) but levels of solar irradiance and seedling survival in the post-hurricane environment were not reported. Spurr (1956) found substantial advanced regeneration in central New England forests after the 1938 hurricane. Species diversity was unaffected on sites where no salvage of timber was conducted. Where salvage operations took place advanced regeneration was intermixed with pioneer species due to increased soil disturbance.

In Puerto Rico, hurricanes have had a site recurrence interval of 50-60 years for at least the past 300 years (Scatena 1989). Although infrequent compared to treefalls and landslides, hurricanes effect large areas and create environments that may vary significantly in their impact on forest structure. On September 18, 1989, Hurricane Hugo struck the Luquillo Experimental Forest of Puerto Rico, radically altering forest structure and resulting in a substantial increase in the amount of light reaching the forest floor (Walker

et al. 1992). This study investigates the growth and survival of seedlings of four shade-tolerant tree species following this disturbance.

B. Site Description

This study was conducted in and near the Bisley Watersheds of the Luquillo Experimental Forest (LEF) on the island of Puerto Rico (Fig. 1), the easternmost Caribbean island of the Greater Antilles. The Corderean mountains which run the length of the island rise in the eastern third of Puerto Rico to an elevation of 1075 m. Due to orographic effects, precipitation in the Bisley Watersheds averages 350 cm/year (Lugo 1986), with high variation from year to year and little seasonality (Scatena 1989). The forest fits the classification of a subtropical moist forest as defined by Holdridge (1967). Soils of this area have recently been reclassified as belonging to the humatus-zarzal-cristal complex (Scatena 1989). The Bisley Watersheds (261-450 m a.s.l.) (Scatena 1989, Brown *et al.* 1983) were severely damaged by Hurricane Hugo (Walker *et al.* 1992).

C. Study Species

Species were selected on the basis of three criteria: shade-tolerant canopy tree species status (Crow and Weaver 1977), importance in the mature forest, and extent of previous study. Four species were chosen for this study: *Dacroydes excelsa* Vahl (Burseraceae), *Sloanea berteriana* Choisy (Elaecarpaceae), *Manilkara bidentata* (A. DC.) Chev. (Sapotaceae), and *Buchenavia capitata* (Vahl) Eichl. (Combretaceae). Each of these shade-tolerant species has been included in previous studies (Table 1). All of these

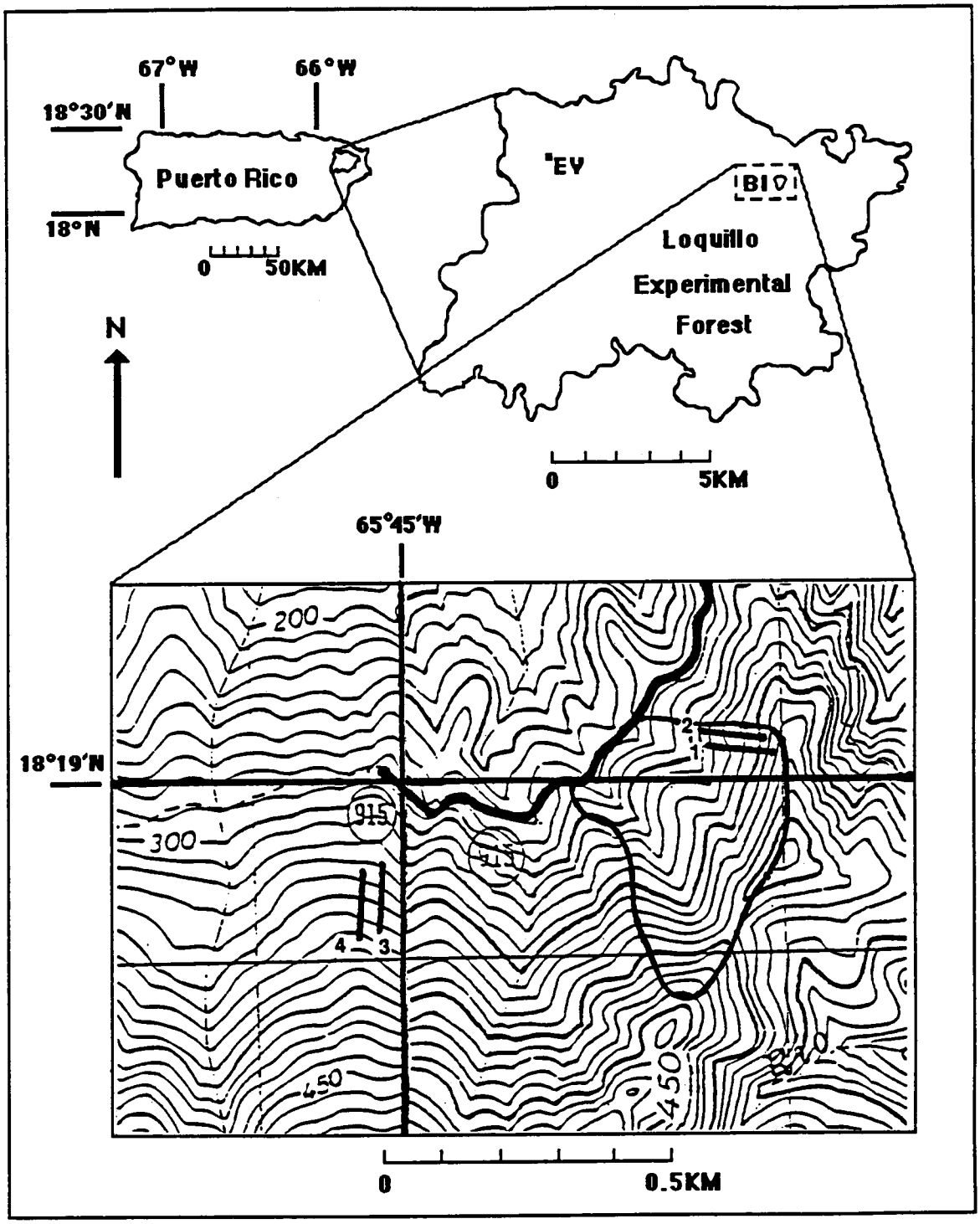


FIGURE 1. Map of Puerto Rico showing location of study site. Shown are: the Luquillo Experimental Forest (LEF), research areas within the LEF at El Verde (EV) and Bisley (BI), and the location of four study transects established within (transects 1 and 2) and near (transects 3 and 4) the Bisley Watersheds. Transects shown on enlarged sections of 7.5' topographic quadrangles (El Yunque and Fajardo quadrangles). Elevation contours are in meters. Contour interval is 10 m.

TABLE 1. Summary of life cycle characteristics for each species based on previous research. Table modified from McCormick (in press).

STAGES	*Dacroydes excelsa*	*Sloanea berteriana*	*Manilkara bidentata*	*Buchenavia capitata*
Seed	Large (1x0.5") oblong fleshy brown fruit[1]	Large (1.25"), elliptic brown, thick walled[1]	Large (1"), round, oval,[1] few, short viability, infected by fungi[2]	Large (0.7-0.9"), elliptic, greenish fruit[1],few, high predation[3].
Seedling	uniform size, shallow roots[8], depend on mycorrhizal assoc. for establishment[10]	variable size, deep roots[8]	Long lived, very shade tolerant[2]	High mortality (86%),deciduous[3]
Juvenile	assoc. w/ridges and slopes[6]	assoc. w/ valleys[6]	Low mortality, slow constant growth[2]	High mortality, (2-10m ht.) light limited[3]
Mature	Long lived, avg. ht= 100'[1], specific gravity= 0.53[7]	Long lived, avg. ht.=100'[1], specific gravity= 0.80[7]	Long lived, avg. ht.= 100'[1] specific gravity= 0.82[7]	Long lived, avg.ht.=60-80'[1], low mortality beyond 10m, deciduous[3]
PROCESSES				
Germination	greater on steep slopes[8], and in shade (42%) rather than in open (25%)[4]	no data	About 40%, fast[2]	Dry season, high light, under parent tree[3]
Growth	Mature mean annual DBH increase=0.36 cm (2.2%)[7] Seedlings: do not respond to sunflecks, sat. psn= 1.39 µmol $m^{-2}s^{-1}$, rsp= 1.34 µmol $m^{-2}s^{-1}$ [8]	Mature mean annual DBH increase=0.22 cm (1.5%)[7] Seedlings: respond to sun-flecks, sat. psn = 3.24 µmol $m^{-2}s^{-1}$, rsp= 0.92 µmol $m^{-2}s^{-1}$ [8]	Mature mean annual DBH increase=0.32 cm (3.4%)[7] Slow variable, light limited, high seedling growth in small and large gaps[2]	Mature mean annual DBH increase = 0.83-1.83 cm[12] Wide crown, rapid in gaps, light dependent[3]
Reproduction	no data	no data	late maturation, few ripened fruits[2]	Prolific flowering, few fruits[3]
Dispersal	no data	no data	poor, bats, gravity[2]	very poor, gravity or water[3]
Survival	relatively low for seedlings in shade, higher in light[8]	high for seedlings in shade[8]	good, long lived, long seedling persistence, lower under parent[2]	Influenced by hurricanes, poor for juvenile[3]
Phenology	summer and fall flowering, fall and winter fruit drop[5]	Spring flowering, fruiting almost continuously[5]	Flower and fruit all year, variable in pop. and on branches of single ind.[2]	April and May at end of "dry" season, fruit fall after one year.[3]
Special Adaptations	Sprouting from roots common[11]	Abundant sprouting from stem[11]	bat dispersal, 40x seedling growth with increased light[2]	deciduous[3]
Habitat preferences	Ridges and upper slopes[6]	Upper slopes and valleys[6]	Forest slopes[2]	Mesic sites, slopes and plateaus[3]

1 Perez (1988) 4 Quarterman (1970) 7 Murphy (1970) 10 Guzman-Grajales (1991)
2 You (1991) 5 Pinto (1970) 8 Lugo (1970) 11 Jordan (1970)
3 Sastre-De Jesus (1979) 6 Basnet (1992) 9 Crow (1980) 12 Crow and Weaver (1977)

species are found outside of Puerto Rico (Crow and Weaver 1977). References to these species in future sections of this paper will be by genus only. Previous studies include Little and Wadsworth 1964, Odum and Pigeon 1970, Crow and Weaver 1977, Sastre-De Jesus 1979, Crow 1980, Perez 1988, Guzman-Grajales and Walker 1991, You 1991, Basnet 1992, and McCormick in press.

D. Objectives and Hypotheses

Impacts of Hurricane Hugo provide an excellent opportunity to study the importance of advanced regeneration of shade-tolerant species following disturbance in the LEF and the role of hurricanes in structuring the forest community. The purpose of this study is to characterize the post-hurricane light environment and to examine the growth, mortality, and recruitment of seedlings of four shade-tolerant tree species in the LEF following Hurricane Hugo. The following hypotheses are to be tested:

H1: Hurricane Hugo opened the forest canopy resulting in micro-environmental conditions more severe than those associated with large gaps (>400 m^2).

H2: Seedlings of shade-tolerant species thrive in the post-hurricane environment.

H3: Seedlings of each species differ in growth and mortality in the post-hurricane microenvironment due to species specific life cycle characteristics.

H4: The contribution of shade-tolerant species to forest regeneration is dependent upon accelerated recruitment of seedlings into larger size classes.

CHAPTER II

METHODS

A. Field Methods

In November of 1989, an initial trip was taken to the study site to assess damage caused by Hurricane Hugo and to photograph damage. One month later, four transects, 100 meters long and 2 meters wide, were established on north to northwest facing slopes, oriented perpendicular to slope to avoid valley and riparian habitats. These habitats were avoided to maintain consistency in substrate and soil type between transects (see Basnet 1992). Along each transect, microenvironment and seedling demography were measured. Microenvironment was characterized by photosynthetically active radiation (PAR), air and soil temperature, vapor pressure deficit (VPD), canopy openness, and solar exposure index (SEI). Seedling demography was characterized by seedling distribution, growth, mortality, and recruitment. Table 2 shows the collection interval (designated as H + n months after Hurricane Hugo) for each type of data.

Microclimate

Each transect was divided into ten 2 x 10 meter plots. In a randomly selected plot of each transect, three microclimate stations were placed at 5 meter intervals to measure the following microclimate variables: PAR, air temperature, soil temperature, and VPD. Each station, consisting of a quantum sensor (LiCor, Inc.), thermocouples, and a wet/dry bulb

TABLE 2. Time-table of data collection expressed in months following Hurricane Hugo in September 1989.

Type of Data Collected	Time (Hurricane + n months)			
	H+2	H+3-4	H+9-10	H+15-16
Microclimate				
PAR[1]		X	X	
Air and Soil Temperature		X		
Vapor Pressure Deficit		X		
Canopy Openness / PPFD[2]	X	X	X	X
Solar Exposure Index (SEI)		X	X	X
Seedling Demography				
Distribution		X	X	X
Growth				
Height Increment			X	X
Gas Exchange				X
Mortality			X	X
Recruitment			X	X

[1] PAR = Photosynthetically Active Radiation

[2] Canopy Openness / PPFD (photosynthetic photon flux density) predicted from hemispherical photographs.

psychrometer, was left in place for 3 to 14 days in each plot. PAR, air temperature, and VPD were measured at 25 cm above the forest floor. Soil temperature was measured at 2 cm depth. Data from all sensors were recorded by a datalogger (Campbell Scientific 21x) powered by a 6-volt battery.

Following Anderson (1964), several researchers have used hemispherical photographs to evaluate varying forest light conditions (Lasko 1980, Chazdon and Field 1987a, Turner 1990, Canham *et al.* 1990). In this study, hemispherical photographs were used to, 1) measure changes in canopy openness over time, 2) estimate total daily photosynthetic photon flux density (PPFD), 3) estimate reduction in PPFD due to cloud cover, and 4) calibrate a solar exposure index (SEI) measured for each seedling. Hemispherical photographs were taken 25 cm above ground surface in the middle of each plot and above each PAR sensor. A random selection of these photographs were printed and then digitized using the computer software Apple Scan (Apple Computer Co. Cupertino, CA). Each digitized image was then analyzed for canopy openness and PPFD using the computer program Solarcalc 5.41 written by Chazdon and Field (1987). Strong correlations between measured PPFD and predicted PPFD based on hemispherical photographs have been demonstrated by Chazdon and Field (1987b)(r=0.89) and Becker *et al.* (1989)(r=0.99). Chabot *et al.* (1979) found that integrated photon-flux density had a larger influence on leaf acclimation than did peak photon-flux density. For this reason, total daily PPFD was used in this study. Percent of full sun for predicted and measured PPFD was based on above canopy measurements of PPFD by Fernandez and Fetcher (1991) at the El Verde field station (Fig. 1) during the study period.

To quantify the light environment of individual seedlings a solar exposure index (SEI) was calculated. This index, calculated from a method modified from Riechert *et al.* (1986), characterizes the amount of light reaching a seedling by first measuring the amount of obstruction to light, then subtracting this from the total potential exposure based on the solar arc of the sun. SEI was measured by holding a 1.4 meter stick divided into ten 14 cm segments (numbered from zero to nine) above each photographic site and seedling, then recording the presence of any light obstructions within 2 meters above each site or seedling along a two-meter, east-west axis (Fig. 2). The 'microenvironment stick' was held at a 45° angle above the horizontal to lessen weight given to light obstructions farther away and closer to the ground since these obstructions would have relatively little effect on the amount of light reaching the seedling. The 90° angle within which obstructions were recorded corresponds to the path of the sun from 0900 to 1500 hours, or a total of 360 minutes of potential solar exposure. The recorded obstruction index was converted into a solar exposure index by, 1) estimating the number of degrees each idealized obstruction would occupy, 2) multiplying by 4 minutes per degree (360 min/90°) , 3) summing these values into total minutes of solar obstruction and then, 4) subtracting this value from 360 to obtain the total minutes of solar exposure or Solar Exposure Index. SEI for each photographic site was correlated with predicted PPFD to establish the degree to which SEI was reflective of the true light environment.

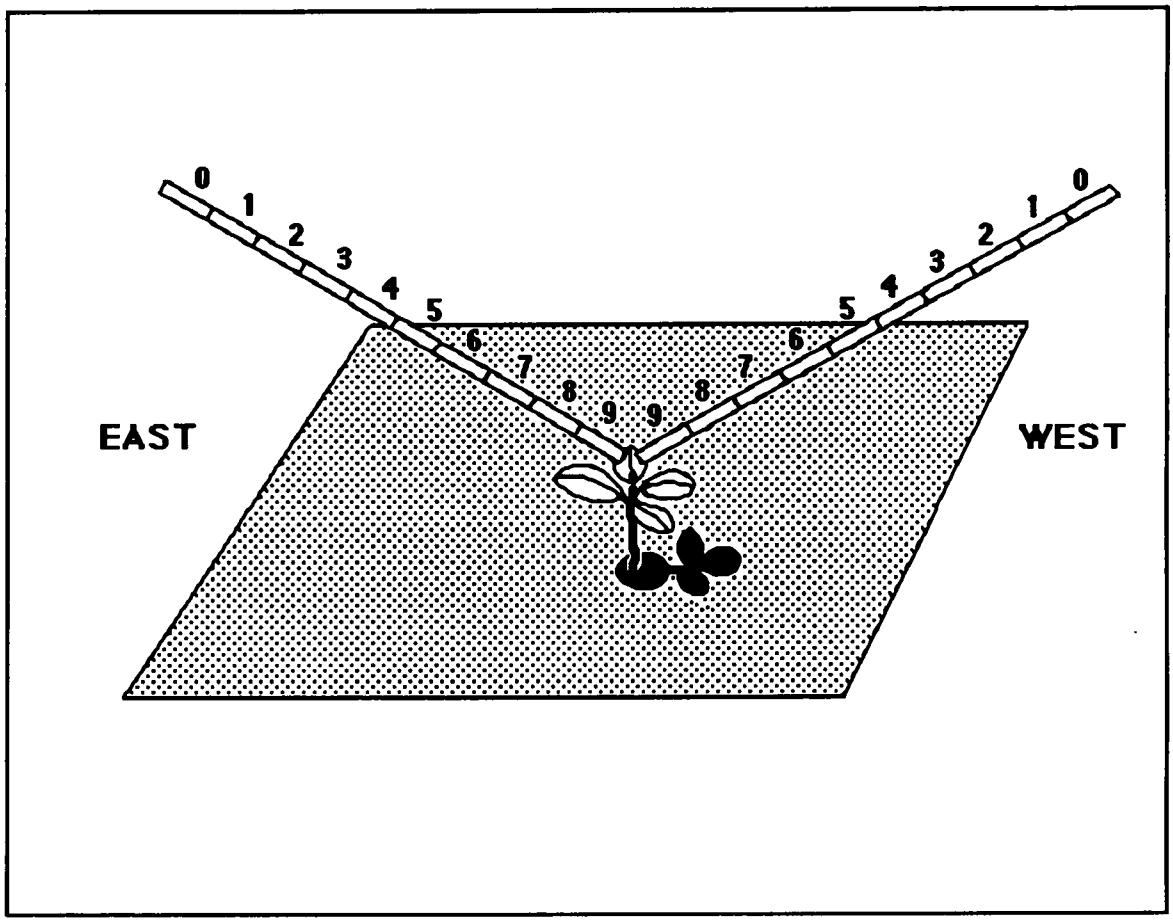


FIGURE 2. Illustration of solar exposure measurement along an east-west transect using a 'microenvironment stick.' All obstructions (leaves/branches) above the angled microenvironment stick were categorized by numbers 0 through 9. These numbers were transformed into estimated minutes of solar obstruction, summed and then subtracted from the total possible minutes (360) to obtain minutes of solar exposure expressed as a solar exposure index(SEI).

Seedling Demography

Species Distributions

Spatial distribution. Within each plot, all identifiable seedlings and saplings less than two meters tall were recorded and tagged. Seedlings were identified using a seedling key (Duke 1970) and with the help of Alejo Estrada Pinto, the El Verde field station manager. Height and SEI were measured for all individuals taller than 25 cm in height and for the first five individuals of each species less than 25 cm in each plot. Due to very low frequency of *Buchenavia* seedlings, additional individuals were located outside transects within the general study area. Since these additional seedlings were not found within a defined area, they were used only in calculations of growth rates. Seedling densities of each species were calculated for each transect for spatial comparisons.

Size class distribution. Beginning 3 months after Hurricane Hugo (H+3) all stems were divided into three size classes following You (1991). These size classes were: small seedlings (0 – 15cm), large seedlings (>15 – 50cm), and saplings (>50 – 200cm).

Growth

Height increment. Transects were censused again at 9 and 15 months after Hurricane Hugo (H+9 and H+15)(Table 2). Growth was measured as an increase in height by measuring overall height from the base of the stem to the tallest shoot. A new solar exposure index (SEI) was measured at each census and was taken from the apex of the tallest shoot. Seedlings which were bent over or sprouting from the lower portion of their stems were not included in calculations of growth.

Gas exchange. One large seedling of each species was selected for gas exchange measurements based on its overall good condition (no herbivory, sunburn, or mechanical damage) and high growth rate (> average). Photosynthesis was measured in μmol CO^2 m^{-2} s^{-1} using a portable photosynthesis system by LiCor Inc. (LI-6200). Using methods modified from McLaughlin *et al.* (1990), one fully expanded leaf was exposed for 10 minutes to a PPFD of 1000 μmol m^{-2} s^{-1} using an incandescent lamp (12 V, 75 W General Electric EYF bulb) powered by a 12-volt battery. A 1-liter leaf chamber was then placed on the leaf, enclosing a set leaf area, and two consecutive gas exchange samples were recorded. Each sample consisted of three, 30-second gas exchange measurements.

Dark respiration rates were measured by first placing a heavy double-sided cloth bag (white on the outside and black on the inside) around the seedling for >5 minutes, after which the leaf chamber was placed on the same leaf as above and two samples were recorded. Respiration was measured in μmol CO^2 m^{-2} s^{-1}.

A second fully expanded leaf on the same plant was chosen as a replicate and the above procedure was repeated. Within a single sample (three, 30 second measurements) any value greater than three times the standard deviation of the other two values was considered an outlier and was not included in the final analysis. During all measurements, care was taken to maintain leaf temperature to within 3°C of initial value and relative humidity to within 10% of initial value by continual monitoring of the system display panel.

Mortality

Individuals were considered dead if they no longer had leaves at the time of census. Individuals that could not be found at the 9-month census were marked as missing until the next census. If missing individuals were not found at the 15-month census, they were recorded as dead. Only one previously missing individual was found alive at the 15 month census.

Recruitment

Tagging of stems allowed the recording of recruitment of small seedlings into the large seedling size class and large seedlings into the sapling size class at the time of each census. From these data, recruitment cost (number of stems dying per successful recruit into the next larger size class) and recruitment ratio (number of stems recruited into a larger size class per number of initial stems) were calculated for each size class of each species.

B. Data Analyses

Distributions of all variables were tested for normality using the Shapiro-Wilk test (SAS Institute 1989). For data sets which did not meet assumptions of parametric tests (normality and equal variance), or had very small N values (<10), non-parametric tests were used. While some data could be transformed into a near normal distribution, others could not be, and for consistency non-parametric tests were used. Spearman rank-order correlation (Sokal and Rohlf 1981) was used to determine association between species growth and solar exposure index. Kruskal-Wallace Rank-Sums test

(Sokal and Rohlf 1981) was used to test significant differences among populations and between pairs. Log likelihood ratio test (Sokal and Rohlf 1981) was used to test for differences among percent mortalities. Due to error in both PPFD and SEI, reduced major axis (RMA) regression methods (geometric mean, Sokal and Rohlf 1981) were used to determine the structural relationship between the two variables, following the recommendations of McArdle (1988). All statistical tests were performed using the statistical program JMP® (SAS Institute 1989).

CHAPTER III

RESULTS

A. Microclimate.

Prior to Hurricane Hugo, typical microenvironment near the forest floor in the Luquillo Experimental Forest (LEF) was characterized by low light availability interrupted by brief, spatially limited sunflecks (Odum, *et al.* 1970). Total daily insolation ranged from 3 to 8% of that above the canopy. Air temperature ranged between 21 and 24° C, soil temperature from 18.5 to 22.5° C, and relative humidity ranged from 89 to 97% (Odum *et al.* 1970). The post-hurricane microenvironment for H+4 months after Hurricane Hugo was characterized by higher solar irradiance, air temperature, soil temperature and vapor pressure deficit with large variability for each (Table 3). Average PPFD was 5.53 mol m^{-2} d^{-1} (25% full sun). Measurements of soil moisture using a Boyucous meter were consistently at 100%; however, the duration of measurement (two 2-week samples) may have been too short to detect post-Hugo drops in soil moisture (see Steudler *et al.* 1991).

Predicted PPFD was significantly correlated with SEI (r_s= 0.78) ($P<0.01$)(Fig. 3). The RMA regression equation ($y = 0.089x - 5.28$, $R^2=0.57$, $P<0.01$) gives the structural relationship between SEI and PPFD. Average SEI and PPFD equal 240 SEI and 15.8 mol m^{-2} d^{-1} PPFD, respectively.

Analysis of hemispherical photographs assumes a clear sky, free of any cloud cover and, therefore, overestimates actual PPFD received at any given location. Actual measurement of PPFD includes effects of clouds. Differences between measured and predicted PPFD can largely be explained by cloud cover. Based on same-site measurements of total daily PPFD using quantum

TABLE 3. Summary of microenvironment data from 20 slope sites in and near the Bisley Watersheds, January 1990, four months after Hurricane Hugo.

Location[1]	Julian Day	Tot.al Daily PPFD[2]	Avg. Air Temp.[3]	Max. Air Temp.	Min. Air Temp.	Avg. Soil Temp.[4]	Max. Soil Temp.	Min. Soil Temp.	Avg. VPD[5]	Max. VPD
T1,0m	13	3.37	23.79	27.22	20.22	22.17	22.82	21.53	0.24	0.66
T1,0m	14	2.91	23.59	27.80	20.15	22.82	26.35	21.44	0.19	0.51
T1,5m	13	9.03	24.33	28.62	20.12	22.21	22.99	21.38	0.34	0.87
T1,5m	14	8.42	23.90	28.66	19.89	22.28	23.13	21.23	0.30	0.97
T1,10m	13	8.71	24.80	29.58	20.35	22.57	23.48	21.86	0.22	0.54
T1,10m	14	6.68	24.25	28.19	19.94	22.51	23.32	21.78	0.28	0.71
T2,20m	3	8.44	24.46	30.98	20.64	23.21	24.79	21.37	0.24	1.01
T2,25m	3	8.19	24.88	33.48	20.66	23.24	25.00	21.88	0.20	0.83
T3,20m	5	7.79	23.56	28.97	19.64	21.97	22.99	21.30	0.32	0.66
T3,25m	5	5.46	22.85	26.69	19.02	21.01	21.88	20.31	0.54	1.13
T3,30m	5	6.05	23.47	27.98	19.33	21.41	21.96	20.83	0.32	0.59
T4,0m	9	1.10	22.18	24.22	20.05	22.25	22.58	21.94	0.06	0.17
T4,0m	10	1.15	22.27	24.22	19.69	22.30	22.64	22.05	0.07	0.16
T4,0m	11	1.43	22.40	24.64	20.16	22.35	22.76	21.93	0.05	0.13
T4,5m	9	4.30	22.82	26.62	20.10	22.45	25.82	19.52	0.19	0.51
T4,5m	10	4.10	22.80	25.32	19.55	22.46	25.08	19.35	0.26	0.59
T4,5m	11	6.47	23.23	27.44	20.12	23.27	30.74	19.81	0.20	0.53
T4,10m	9	4.89	23.27	28.53	20.00	22.17	22.88	21.59	0.19	0.51
T4,10m	10	5.18	23.28	26.34	19.72	22.11	22.82	21.55	0.25	0.54
T4,10m	11	6.96	23.61	28.83	20.19	22.48	23.26	21.87	0.20	0.61
Average		**5.53**	**23.49**	**27.72**	**19.98**	**22.36**	**23.86**	**21.23**	**0.23**	**0.61**
St. dev.		**2.59**	**0.80**	**2.26**	**0.40**	**0.55**	**2.04**	**0.83**	**0.11**	**0.27**

[1]Location given as transect (T#) and distance in meters along transect (#m).
[2]Total daily PPFD measured as mol m^{-2} d^{-1}. PPFD, air temperature, and vapor pressure measured at 25 cm above the ground.
[3]All temperatures are reported in degrees Celsius.
[4]Soil temperature measured at 5 cm below the soil surface.
[5]VPD=Vapor Pressure Deficit, reported in kilopascals

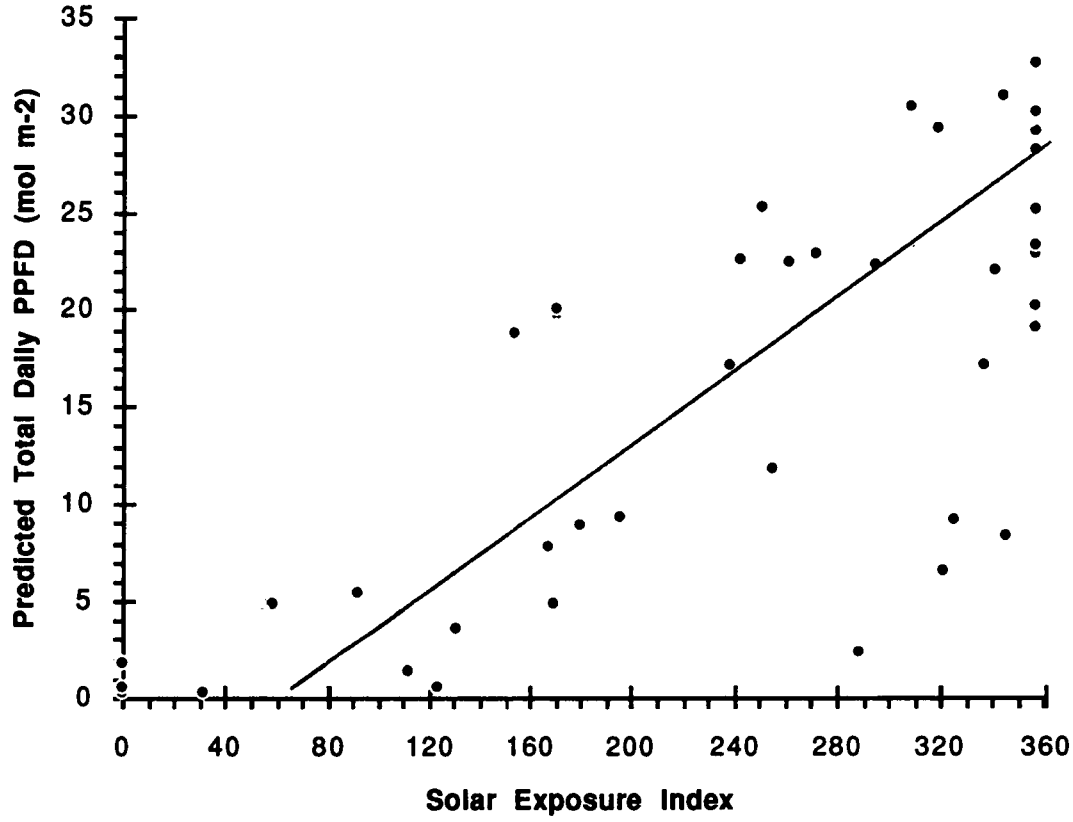


FIGURE 3. Solar exposure index vs. total daily photosynthetic photon flux density (PPFD). PPFD determined from randomly selected digitized hemispherical photographs. (r_s=0.78, N=42, P<0.01). Reduced major axis regression equation is y=0.089x-5.28, R^2=0.57.

sensors and hemispherical photographs, it was estimated that cloud cover reduced actual PPFD from predicted total daily PPFD by approximately 42% (Table 4). Thus, the effect of cloud cover would reduce the predicted average value of PPFD to 9.16 mol $m^{-2} d^{-1}$ (20% full sun). The difference between average predicted PPFD (9.16 mol $m^{-2} d^{-1}$) and average measured PPFD (5.53 mol $m^{-2} d^{-1}$) can be explained by higher solar angle and thus greater solar irradiance in July when compared to January. The percent of full sun values are in closer agreement. Regardless, both values of PPFD are within the range for those of a 400 m^2 treefall gap reported by Chazdon and Fetcher (1984)(Table 5).

Over the course of the study re-foliation of surviving canopy trees gradually reduced the degree of canopy openness (Fig. 4). This steady decline in canopy openness was accompanied by a reduction in predicted total daily PPFD (Fig. 5). Relatively higher PPFD at H+9 months is due to increased solar irradiance during summer months.

B. Seedling Demography

Species Distribution

Spatial Distribution

Distribution of species at the beginning of the study was similar for transects 1, 2, and 4 (Fig 6a) with the order of relative density being *Dacroydes, Sloanea, Manilkara,* and *Buchenavia.* In transect 3 the relative density of *Sloanea* and *Manilkara* were reversed with *Manilkara* being more dense. Order of relative densities did not change for *Sloanea, Manilkara,* and *Buchenavia* from the beginning to the end of the study along any transect (Fig. 6b). *Dacroydes,* in contrast, decreased in relative density going from most

TABLE 4. Estimated reduction in solar irradiance due to cloud cover.

Site condition	Hemispherical photograph (predicted PPFD)	Quantum sensor (measured PPFD)[a]	Estimated cloud effect[b] (percent reduction)
Open	29.1	16.37 (36%)[c]	44
Moderate	7.86	3.98 (9%)	49
Closed[d]	0.25	0.17 (0.4%)	32
		Average=	42

[a]Average measured daily PPFD based on nine consecutive days in July 1990, 10 months after Hurricane Hugo.

[b]Cloud effect calculated as (predicted - measured) / predicted *100.

[c](#)= percent of PPFD in the open based on a median value of 45.2 mol m^{-2} d^{-1} for July 1990 measured by Fernandez and Fetcher (1991).

[d]Measurement made under dense saw grass (genus *Sclerea*).

TABLE 5. Total daily photosynthetic photon flux density (PPFD) (mol m^{-2} d^{-1}) in rain forest gaps.

Researcher	Gap Size (m^2)	PPFD (range or average)	% of PPFD in the open
Torquebiau (1988)	320	6.6-7.8	18-21
Chazdon and Fetcher (1984)	200	1.52-3.07	5-11
	400	3.86-13.6	20-35
Denslow *et al.* (1990)	275	4.1	9
	285	9.7	21
	335	11.3	23
This study	post-hurricane	1.1-9.03	5-47
		5.53	25

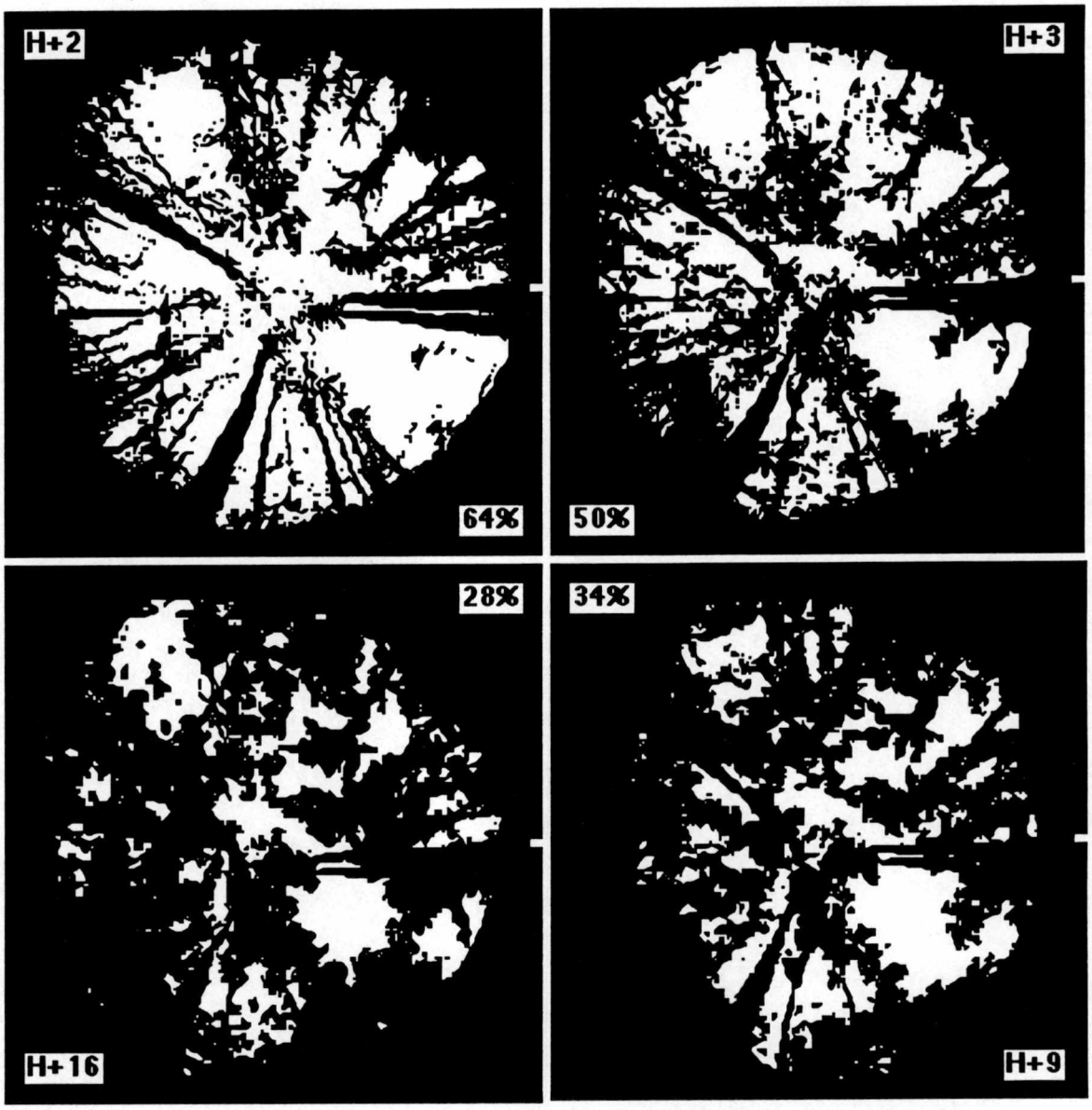


FIGURE 4. Digitized hemispherical photographs from one site over time. Each photograph was taken H+n months following Hurricane Hugo, corresponding to 11/89, 12/89, 6/90, and 1/91, respectively. Percent canopy openness is shown on the inside corner of each image.

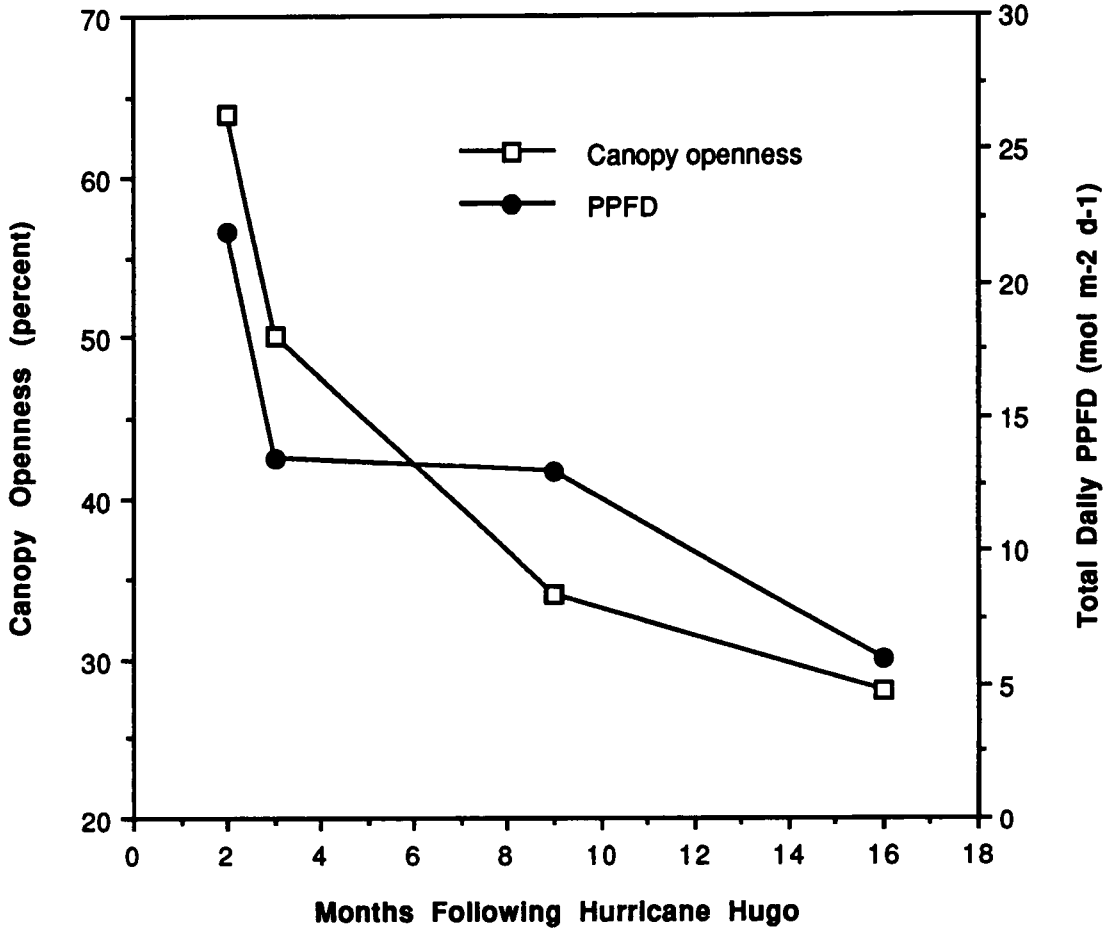
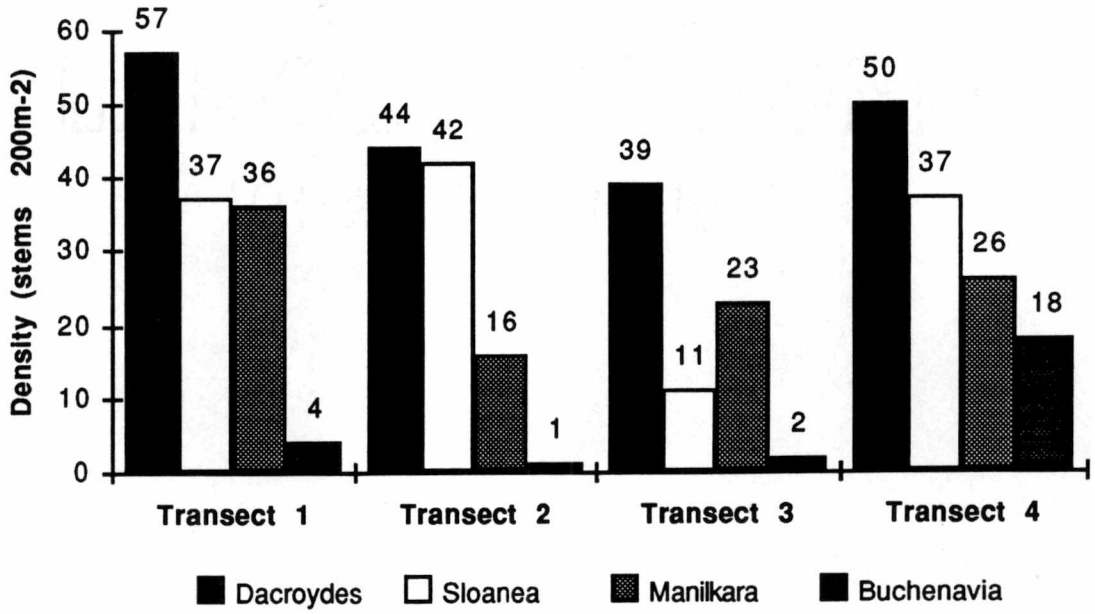


FIGURE 5. Changes in canopy openness and total daily PPFD based on hemispherical photographs taken 2, 3, 9, and 16 months following Hurricane Hugo (9/89).

A (H+3)



B (H+15)

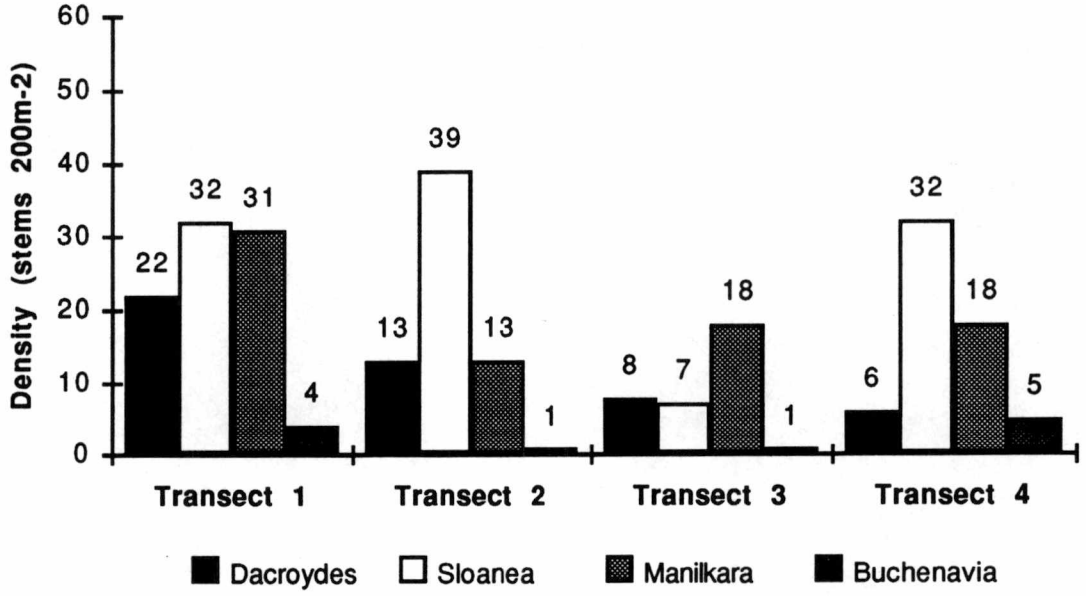


FIGURE 6. Spatial distribution of each species for all individuals less than 2 meters in height. (A) Initial distribution 3 months following Hurricane Hugo (December 1989). (B) Final distribution 15 months following Hurricane Hugo (January 1991).

dense in all transects by H + 3 to second (transect 3) or third (transect 1, 2, and 4) by H + 16 (Fig. 6b). *Buchenavia* had the lowest seedling densities in all four transects. The highest densities of *Buchenavia* were in transect 4 where an adult *Buchenavia* (DBH=70cm) occurred near the transect. Due to the lack of seed production following Hurricane Hugo (pers. observation), there was no seedling recruitment and none of the study species increased in overall density during the study period.

Size Class Distribution

By comparing changes in size class distributions it is possible to assess the relative performance of each species in the post-hurricane environment. It was assumed that seedling and sapling mortality due to the immediate physical impact of the hurricane would be species independent. Therefore, while the absolute number of stems would decrease due to Hurricane Hugo, the relative abundance of stems between species would not change. Given this assumption, it was evident that seedling size-class distributions at H+3 months were highly influenced by pre-hurricane factors (Fig. 7).

Manilkara and *Buchenavia* showed decreasing abundance from small to large size classes at the beginning of the study. *Sloanea* and *Dacroydes* both had greater numbers of large seedlings than small. Within study transects, no saplings of *Dacroydes* or *Buchenavia* were encountered during the first census in December of 1989. Over the course of the study, the small-seedling size class of all species declined due to the lack of new recruits from seed, death of individuals, and growth of individuals into the large seedling size class. By H+16 months, *Manilkara* was the only species of the four to still

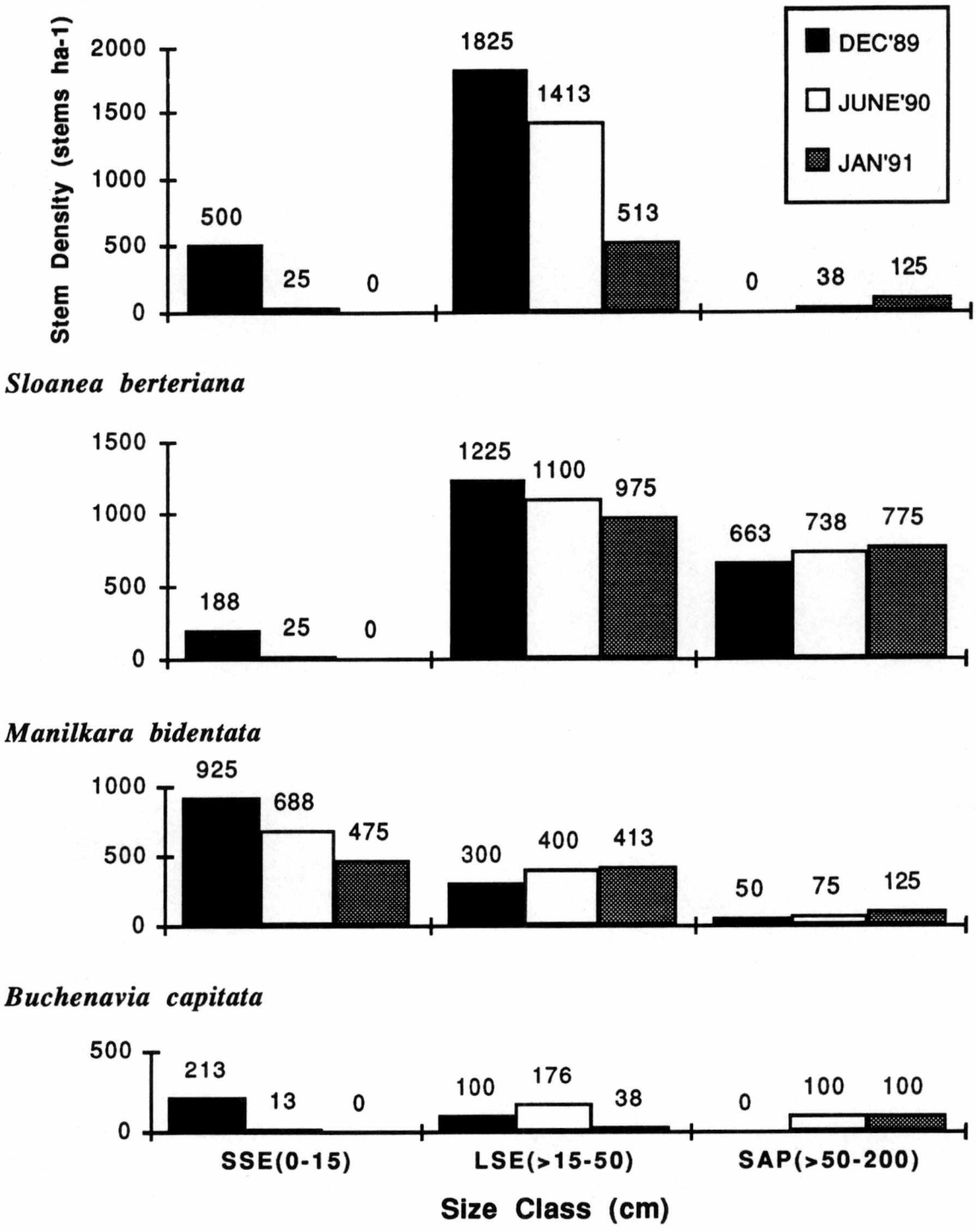


FIGURE 7. Seedling and sapling size class distributions for Dec. '89, June '90, and Jan. '91 (3,9, and 15 months after Hurricane Hugo, Sept. '89). SSE=small seedling, LSE=large seedling, and SAP=sapling.

have a small seedling population. *Manilkara* was also the only species to show an increase in its large seedling size class.

The sapling size class of each species increased in density over the course of the study (Fig. 7). When the large seedling size class of *Dacroydes* is subdivided into five centimeter height intervals, a diminishing "wave" of recruitment can be seen over time as individuals in seedling size classes either died or were recruited into larger size classes (Fig. 8b).

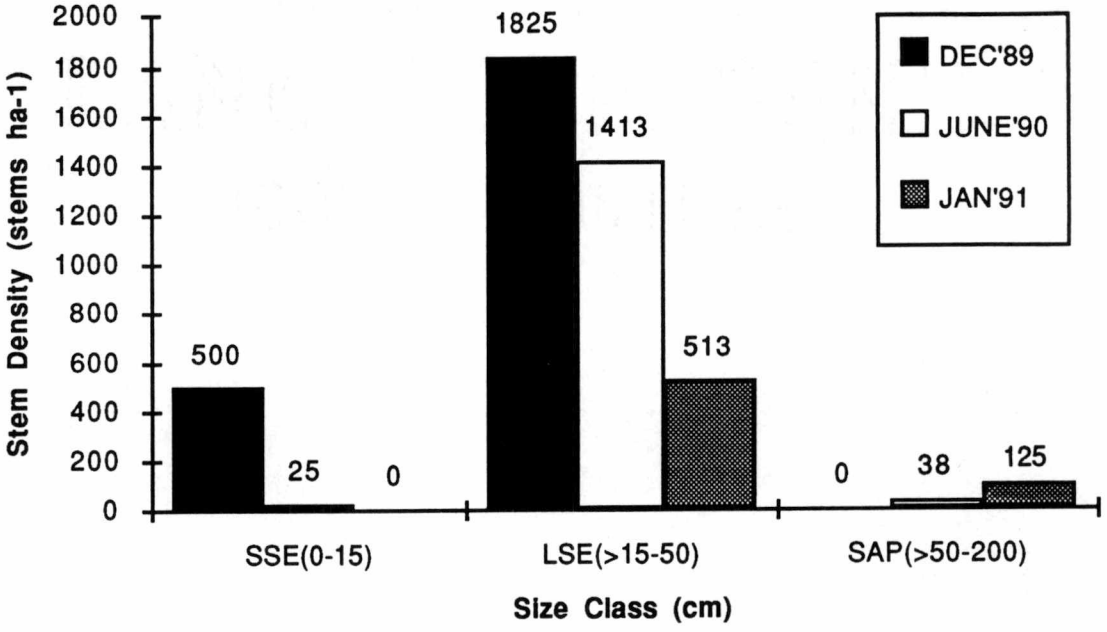
Growth

Height Increment

Average growth rates, expressed as monthly height increments, varied over an order of magnitude for small seedlings, sixfold for large seedlings, and more than fivefold overall (Table 6). For all species and size classes there was considerable variance in growth rate as evidenced by large standard deviations. This variability contributed to the lack of statistically significant differences between all species and size classes. Overall growth rates were influenced by the relative abundance of small and large seedlings of each species. *Manilkara,* for example, had the largest small seedling population with the slowest growth rate which skewed its overall growth rate to below that of *Sloanea* and *Dacroydes*. This biasing of growth rates demonstrates the importance of dividing seedling populations into small and large individuals.

Buchenavia had the highest growth rate overall and the highest growth rates for both small and large seedlings. *Dacroydes, Sloanea,* and *Manilkara* seedlings showed increased growth rates with increased size class, although differences were not significant for *Dacroydes*. Several *Sloanea*

A (*Dacroydes excelsa*)



B (*Dacroydes excelsa*)

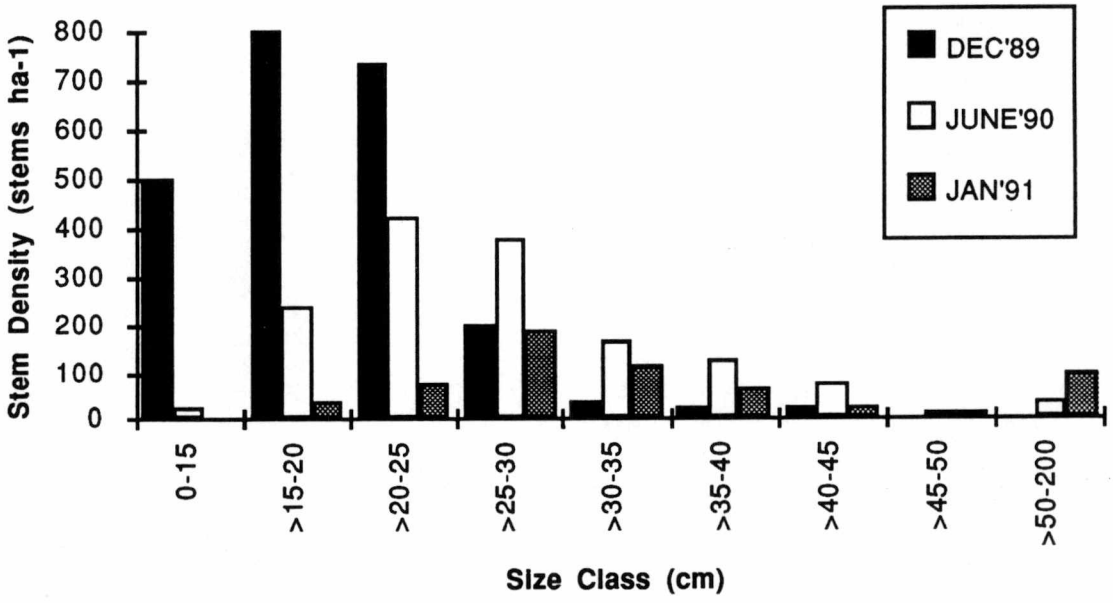


FIGURE 8. (A) *Dacroydes excelsa* seedling and sapling size class distributions for Dec. '89, June '90, and Dec. '91 (3, 9, and 15 months following Hurricane Hugo, Sept. '89). SSE=small seedling. LSE=large seedling. SAP=sapling. (B) Same as (A) with large seedling size class (>15-50cm) divided into 5 cm intervals.

TABLE 6. Small seedling (SSE), large seedling (LSE), and sapling (SAP) monthly height increments (cm mo^{-1}) for each species.

Species	Size class			
	SSE	LSE	SAP	OVERALL
Dacroydes excelsa	**0.98a*1#**	**1.19a1**	–§	**1.15a**
St. dev.¢	0.48	0.90	–	0.84
N†	8	41	–	49
Sloanea berteriana	**0.70ab2**	**0.83a2**	**1.42a3**	**0.97a**
St. dev.	0.60	0.67	1.15	0.88
N	10	67	33	110
Manilkara bidentata	**0.45b3**	**1.52a5**	**3.96b6**	**0.81b**
St. dev.	0.37	0.72	0.18	0.99
N	56	20	2	78
Buchenavia capitata	**6.50c4**	**5.87b4**	**16.13**	**6.19c**
St. dev.	3.17	1.79	–	2.58
N	19	18	1	37

*Means with the same letter are not significantly different among species ($P<0.05$).

#Means with the same number are not significantly different within a species ($P<0.05$).

§No individuals of this size class occurred within the study plots.

¢St. dev.= Standard deviation.

†Only non-sprouting individuals surviving the entire study period are included.

seedlings and saplings grew sprouts from lower portions of their stems.

The frequency of sprouting for *Sloanea* small and large seedlings and saplings was 13, 16, and 33%, respectively. These individuals were not included in calculations of growth rates as reported in Table 6, since they seldom resulted in an overall increase in height. Average growth rate of the sprouts themselves was 3.5 cm mo^{-1}. None of the other three species exhibited any seedling or sapling sprouting.

In order to determine the ability of each species to adapt to high levels of solar irradiation, average monthly height increment was correlated with average Solar Exposure Index (SEI) (Fig 9-11). Significant positive correlations between growth and SEI occurred for small *Buchenavia* seedlings, small and large *Manilkara* seedlings, large *Dacroydes* and *Sloanea* seedlings, and overall *Sloanea* and *Manilkara* seedling growth rates. Plots of individual growth rates against SEI for each species and size class show a large degree of scatter for each species overall (Fig. 9) and for large (Fig. 10) and small (Fig. 11) size classes plotted separately . Although the correlation was not statistically significant, there was a negative correlation of -0.33 between *Dacroydes* small seedlings and SEI (Fig. 11), suggesting that *Dacroydes* small seedlings are better adapted to more shaded conditions. When compared to growth under pre-hurricane conditions it is clear that for large *Manilkara* and *Buchenavia* seedlings, growth increases with increased solar irradiance in the post-hurricane environment (Fig. 12). Post-hurricane growth rates are significantly higher than pre-hurricane growth rates ($P<0.05$).

Range of growth rate increased with increased solar exposure as evidenced by visual inspection of Figures 9 - 11. Two possible explanations for this increased range are; first, something other than light is limiting for

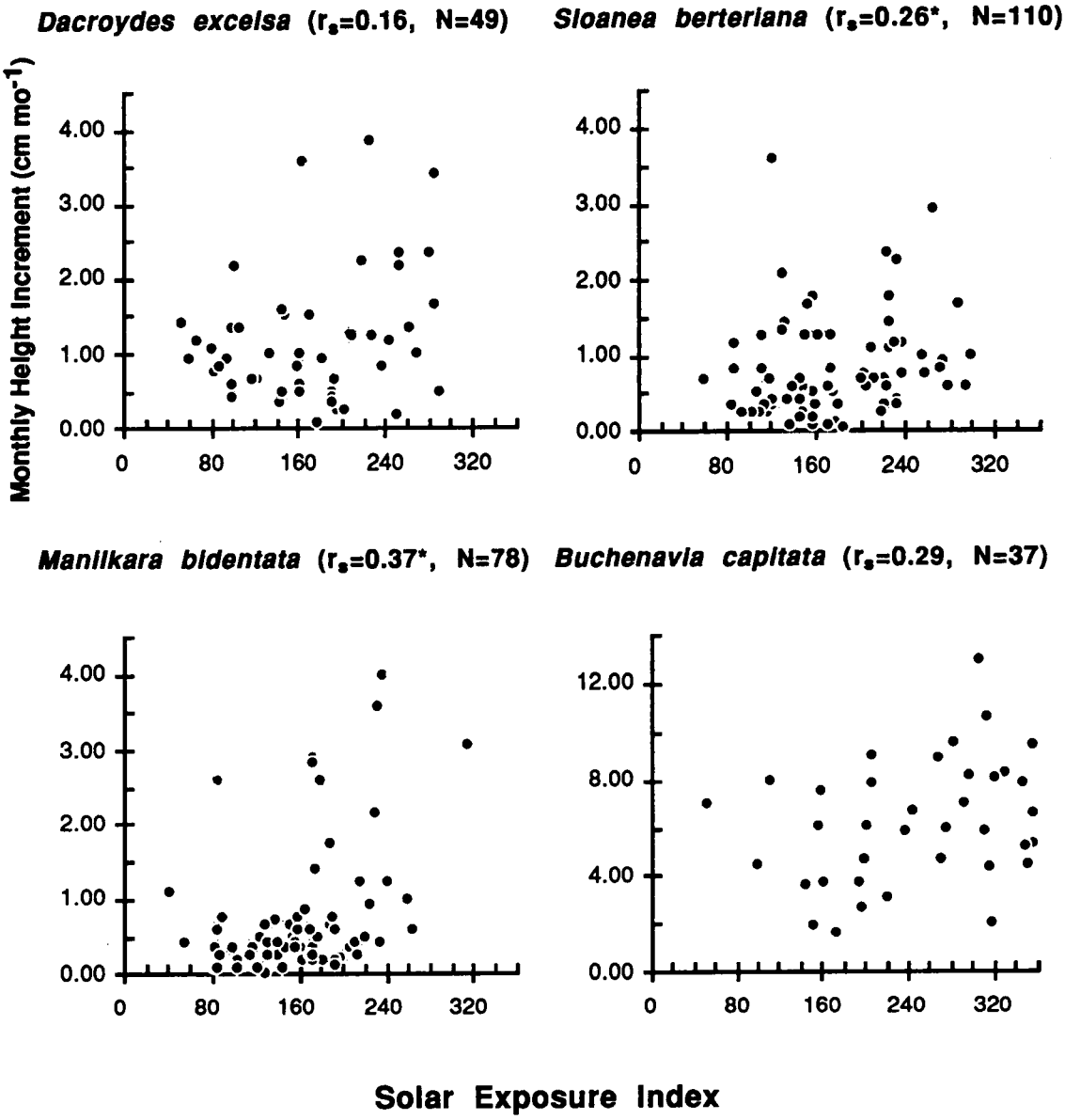


FIGURE 9. Seedling growth under varying levels of solar exposure for all seedlings. Note change in the Y-axis scale for *Buchenavia capitata*. Asterisk (*) indicates significance at P<0.05.

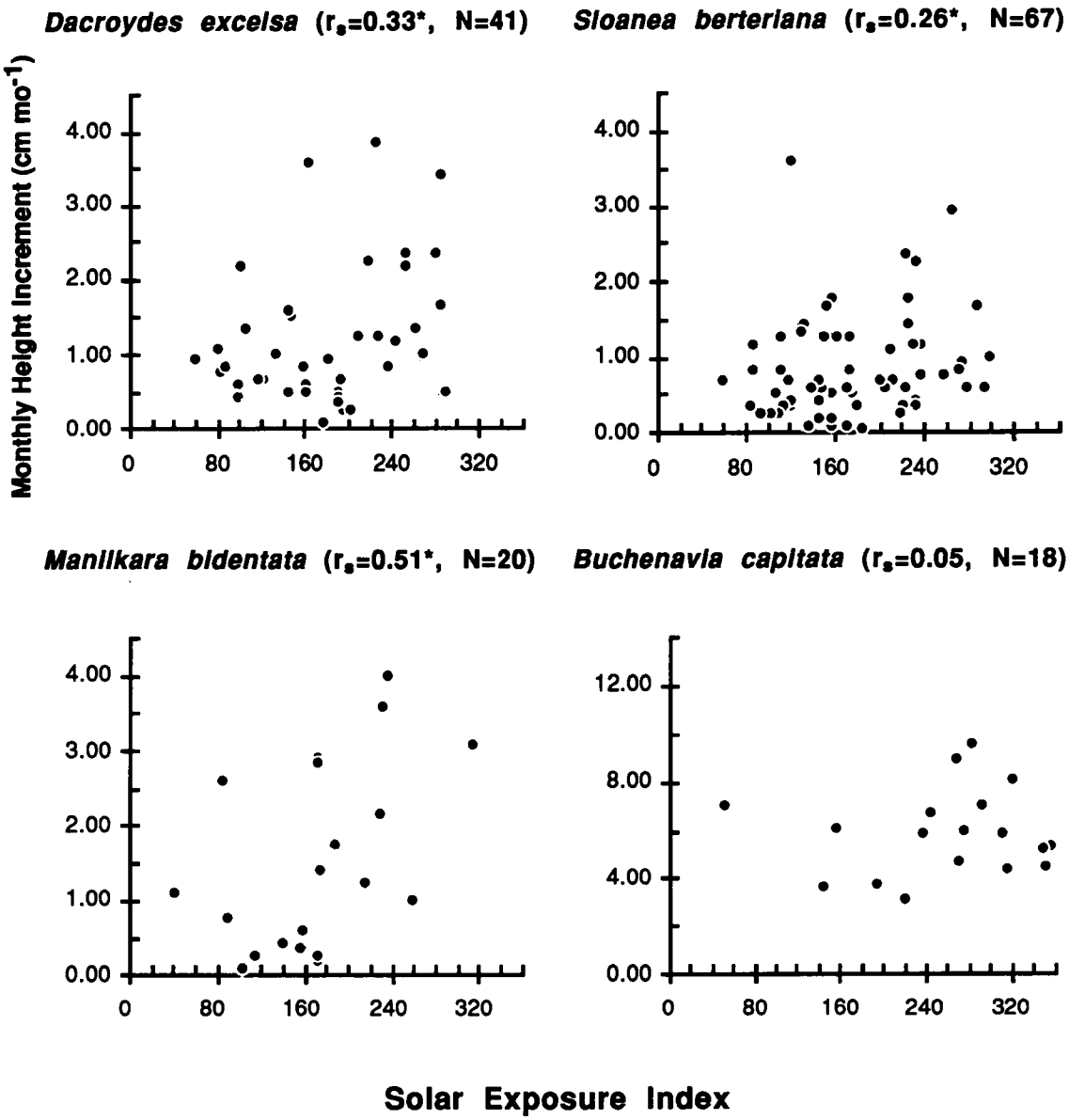


FIGURE 10. Large seedling growth under varying levels of solar exposure. Note change in the Y-axis scale for *Buchenavia capitata*. Asterisk (*) indicates significance at P<0.05.

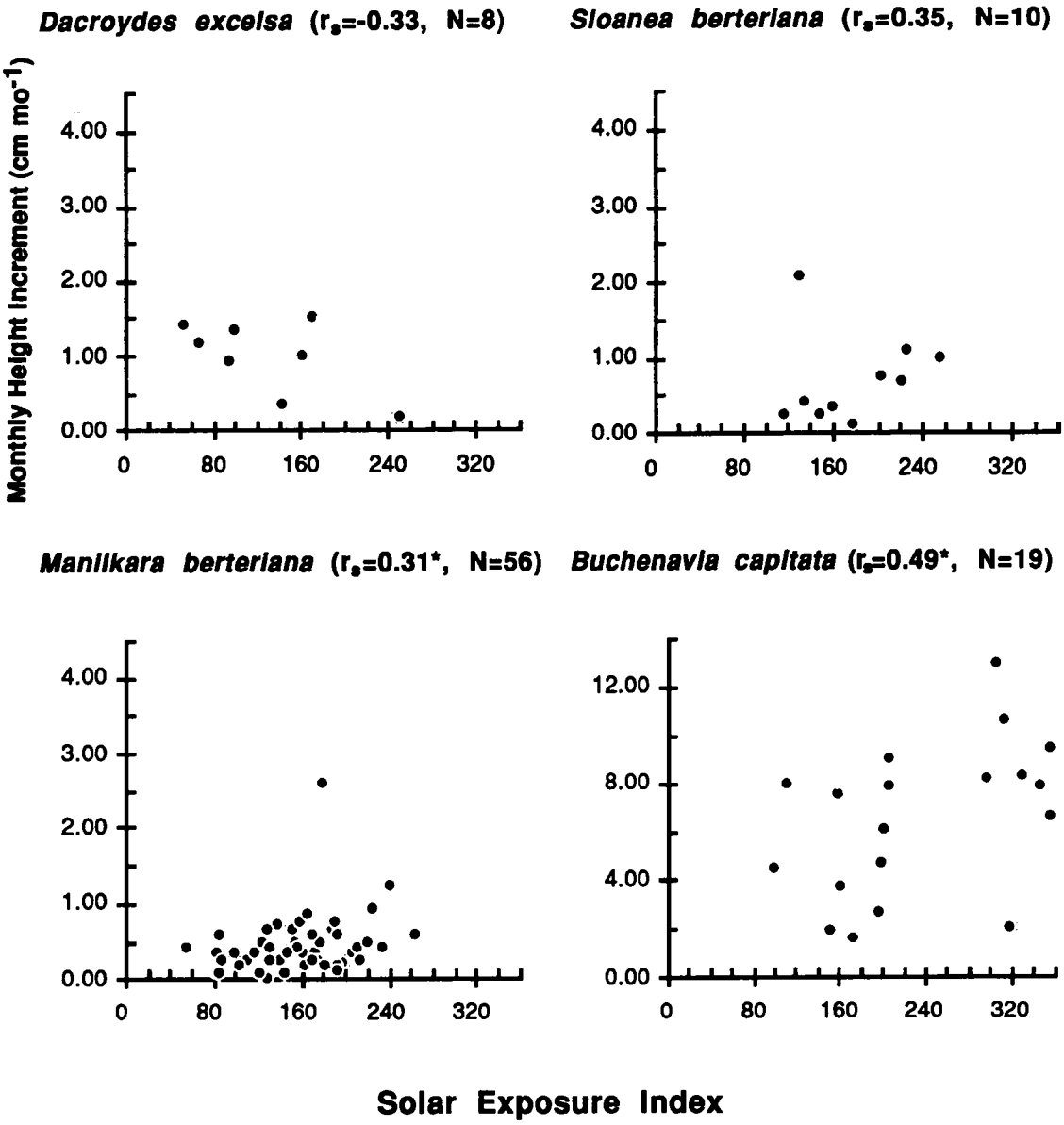


FIGURE 11. Small seedling growth under varying levels of solar exposure. Note change in the Y-axis scale for *Buchenavia capitata*. Asterisk (*) indicates significance at P<0.05.

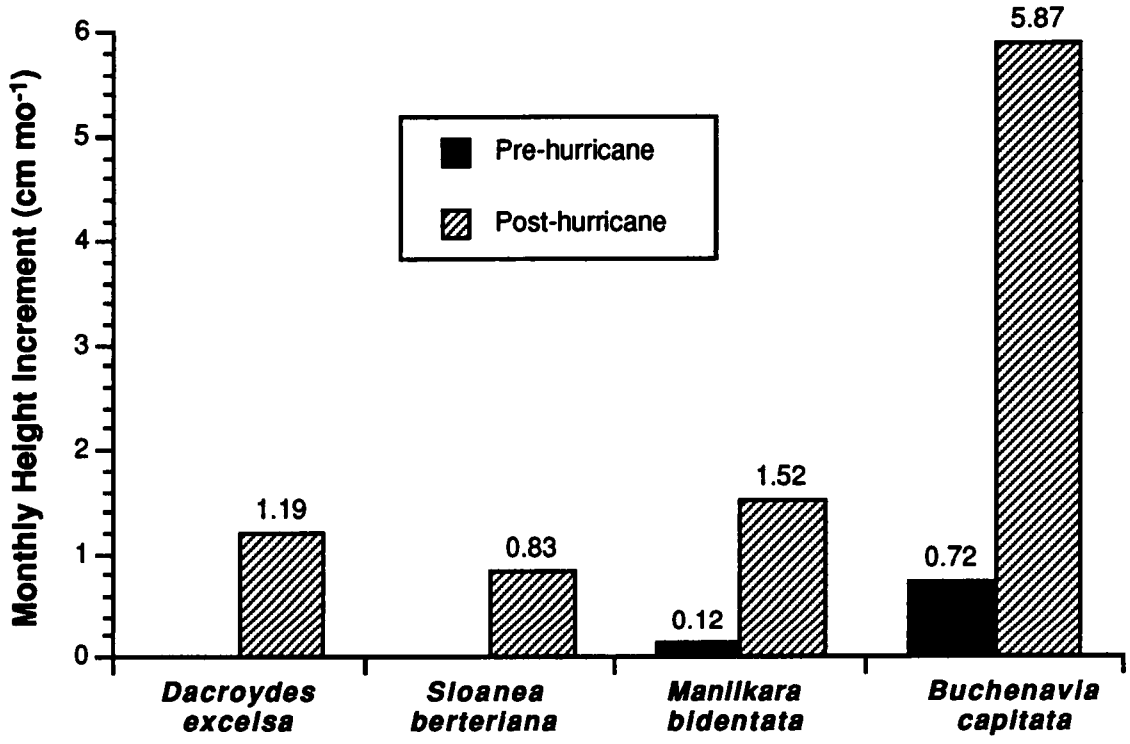


FIGURE 12. Large seedling growth rates for each species under pre- and post-hurricane conditions, where available. Average post-hurricane PPFD equaled 5.53 mol m^{-2} d^{-1}. Pre-hurricane data for *Manilkara bidentata* from You and Petty (1991). Pre-hurricane data for *Buchenavia capitata* from Sastre-DeJesus (1979).

seedlings which had high SEI but relatively low growth rate. Second, variation at high light levels may reflect inaccuracies in measurement of the true light environment for each seedling. This inaccuracy is due to the inability of the method to assess variation in openness above 2 meters. At lower light levels, this variation would be masked by pioneer species overgrowing individuals of shade-tolerant species. This effect was also evident in the correlation between predicted PPFD from hemispherical photographs and SEI (Fig. 3).

Over the course of the study, it was possible to determine changes in seedling growth rates from the first half of the study (H+3-9 mo. = 12/89 - 7/90) to the second half of the study (H+9-15 mo. = 7/90 - 1/91) (Table 7). Average growth rates for all small and large seedlings of each species decreased from H+3-9 to H+9-15. This decrease in growth rate corresponds to a simultaneous decrease in average SEI measured at the time of the three censuses. With the exception of *Dacroydes*, large seedlings consistently had lower initial SEI's than small seedlings, indicating that some of the seedlings in that size class had recently been released from growth suppression by a pre-hurricane canopy opening allowing for the simultaneous growth of other, more rapidly growing species as well. Final SEI values measured H+15 months were not significantly different within size classes between species (Table 7).

Gas Exchange

Photosynthetic rates measured under high light conditions (>1000 $\mu mol\ m^{-2}\ s^{-1}$) on single large seedlings of each species were comparable (Table 8). *Dacroydes* and *Sloanea* had higher average rates of net photosynthesis

TABLE 7. Changes in average seedling growth rates and solar exposure index over one year, starting three months after Hurricane Hugo (9/89).

Species	Height Increment (cm mo^{-1})		Solar Exposure Index		
	H+3-9[1]	H+9-15	H+3	H+9	H+15
Dacroydes excelsa					
SSE[2](8)[3]	1.20	0.75	143	130	117
LSE(41)	1.62	0.76	217	174	150
Sloanea berteriana					
SSE(10)	1.12	0.28	238	173	121
LSE(67)	1.02	0.64	220	157	141
SAP(33)	1.51	1.33	303	267	206
Manilkara bidentata					
SSE(56)	0.66	0.25	232	130	107
LSE(20)	2.31	1.19	213	164	138
SAP(2)	3.82	4.10	302	267	254
Buchenavia capitata					
SSE(6)	6.28	3.06	310	188	170
LSE(5)	9.53	0.60	274	267	133

[1]H+n=number of months since Hurricane Hugo (September 1989).
[2]SSE=small seedling, LSE=large seedling, SAP=sapling.
[3](N)=number of individuals in size class. Only those individuals surviving entire period are included.

TABLE 8. Photosynthesis, dark respiration, and P/R ratio for individual large seedlings of each species.

Species	Photosynthesis[1] (μmol m^{-2} s^{-1})	Respiration (μmol m^{-2} s^{-1})	P/R ratio[2]
Dacroydes excelsa	**8.93**	**0.81**	**11.08**
St. dev.[3]	0.18	0.09	
N[4]	2	2	
Sloanea berteriana	**5.60**	**1.50**	**3.73**
St. dev.	2.21	0.32	
N	4	3	
Manilkara bidentata	**4.35**	**0.17**	**25.46**
St. dev.	1.17	0.08	
N	4	4	
Buchenavia capitata	**5.03**	**0.26**	**19.30**
St. dev.	0.76	0.07	
N	4	4	

[1]Photosynthesis measurements were made under high light conditions (>1000 μmol m^{-2} s^{-1}).
[2]P/R ratio = Photosynthesis/Respiration ratio.
[3]St. dev. = Standard deviation.
[4]N = number of samples from a single individual. Each sample consisted of three 30-second observations.

(8.93 and 5.60 μmol m^{-2} s^{-1}, respectively) than *Manilkara* and *Buchenavia* (4.35 and 5.03 μmol m^{-2} s^{-1}, respectively). For dark respiration the pattern was the same (Table 8). Due to low rates of dark respiration for *Manilkara* and *Buchenavia*, their P/R ratios were much higher than P/R ratios for *Dacroydes* and *Sloanea*. Since it is the balance between photosynthesis and respiration that is important in determining growth, these results are consistent with large seedling growth rates of the four species under post-hurricane conditions (Table 6). For these species the rate of dark respiration, rather than photosynthesis, appears to be the more important determinant of growth rate in the post-hurricane environment.

Mortality

Overall seedling mortality varied significantly between species and was consistently lower with increased size class (Table 9). *Dacroydes* and *Buchenavia* suffered the highest mortality (expressed as fraction of initial population dying) and *Sloanea* and *Manilkara*, the lowest. When mortality is expressed as absolute number of stems dying per hectare per month, *Buchenavia*, considering its small population size, suffered the lowest mortality. Over the course of the study, small seedling mortality rate increased for *Sloanea*, *Manilkara*, and *Buchenavia* and decreased for *Dacroydes* (Table 10). Large seedling mortality increased for *Dacroydes* and *Buchenavia* but decreased by one half for *Sloanea* and *Manilkara*. Sapling mortality did not change during the study. *Manilkara* mortality at the less damaged El Verde site was higher for small seedlings but lower for large seedlings (Table 10). Pre-hurricane mortality rate at El Verde was even higher

TABLE 9. Small and large seedling and sapling mortality for each species from 3-15 months after Hurricane Hugo. Size class mortality is expressed as fraction of initial population. SSE=small seedling, LSE=large seedling, SAP=sapling.

Species	Size Class[1]			OVERALL	
	SSE	LSE	SAP	(proportion)	(stems$ha^{-1}m\sigma^{1}$)
Dacroydes excelsa	**0.81a**[2]	**0.72a**	–[3]	**0.74a**	**196.6**
N[4]	55	200		255	
Sloanea berteriana	**0.23b**	**0.15b**	**0.06**	**0.13b**	**22.6**
N	16	99	52	167	
Manilkara bidentata	**0.24b**	**0.13b**	**0.0**	**0.21b**	**25.4**
N	85	27	4	116	
Buchenavia capitata	**0.65a**	**0.38a**	–	**0.56a**	**14.6**
N	17	8		25	

[1]SSE=small seedling, LSE=large seedling, SAP=sapling.
[2]Means with the same letter are not significantly different between species ($P<0.05$). There were no significant differences within species.
[3]No individuals in this size class occurred within the study area at the beginning of the study.
[4]N=Number of individuals in each size class at the beginning of study.

TABLE 10. Changes in seedling and sapling mortality from 3-9 months (H+3-9) to 9-15 months (H+9-15) after Hurricane Hugo.

	Mortality Rate (stems ha^{-1} mo^{-1})			
Species	H+3-9 (Bisley)	H+9-15 (Bisley)	H+3-9 (El Verde)	Pre-hurricane (El Verde)
Dacroydes excelsa				
SSE[1]	56.0	37.3		
LSE	144.6	155.9		
Sloanea berteriana				
SSE	2.6	5.1		
LSE	20.9	10.4		
SAP	3.09	3.09		
Manilkara bidentata[2]				
SSE	12.5	32.5	36	101
LSE	5.0	2.5	1	0.4
SAP	0.0	0.0		
Buchenavia capitata				
SSE	4.2	18.8		
LSE	0.0	6.3		

[1]SSE=small seedling, LSE=large seedling, SAP = sapling.
[2]*Manilkara* data from the less damaged, post-hurricane El Verde site and pre-hurricane El Verde site are from You and Petty (1991).

for small seedlings and lower still for large seedlings, indicating that mortality for *Manilkara* seedlings is returning to pre-hurricane conditions.

Recruitment

Assessing relative species performance by comparing growth and mortality rates is difficult since the number of recruits into larger size classes is a function of not only mortality but growth and initial population size as well. One way of estimating the significance of seedling mortality for a species is to look at how many seedlings die for every one that grows or is recruited into the next size class. This "recruitment cost" has the advantage of being a function of growth as well as mortality. To incorporate the influence of initial population size, the "recruitment ratio" for a size class can be calculated by dividing the number of stems recruited into a larger size class by the initial number of stems in the smaller size class. Recruitment cost and recruitment ratio for the four study species had a wide range of values (Table 11). *Dacroydes* large seedlings had the highest recruitment cost and the lowest recruitment ratio, and *Sloanea* small seedlings had the lowest recruitment cost and highest recruitment ratio. Recruitment ratio showed a significant ($P<0.05$) negative relationship with initial population size (Fig. 13), suggesting that some density dependent factor is in operation.

TABLE 11. Summary of initial population size, growth, mortality, and recruitment for small and large seedlings of each species.

Species	Pop. size (stems ha^{-1})	Mortality (proportion)	Growth (cm mo^{-1})	Recruits[1] (stems ha^{-1})	R. cost[2]	R. ratio[3]	R. ratio[4] (Pre-Hugo)
Dacroydes excelsa							
SSE	500	0.81	0.98	131	3.10	0.26	----[5]
LSE	1825	0.72	1.19	125	10.5	0.07	----
Sloanea berteriana							
SSE	188	0.23	0.70	150	0.29	0.80	----
LSE	1225	0.15	0.83	225	0.82	0.18	----
Manilkara bidentata							
SSE	925	0.24	0.45	325	0.68	0.35	<0.01
LSE	300	0.13	1.52	75	0.52	0.25	0.12
Buchenavia capitata							
SSE	213	0.65	4.67	75	1.85	0.35	0.14
LSE	100	0.37	5.07	63	0.59	0.63	0.41

[1]Recruits = number of stems growing into next larger size class per year over the course of the study.
[2]R. cost = Recruitment cost = number of individuals dying per successful recruit into next larger size class.
[3]R. ratio = Recruitment ratio = number of stems in a size class recruited into the next larger size class per total number of stems in the smaller size class.
[4]R. ratio (Pre-Hugo) = Pre-hurricane data from You and Petty (1991) (*Manilkara bidentata*), and Sastre-De Jesus (1979) (*Buchenavia capitata*).
[5]No data available.

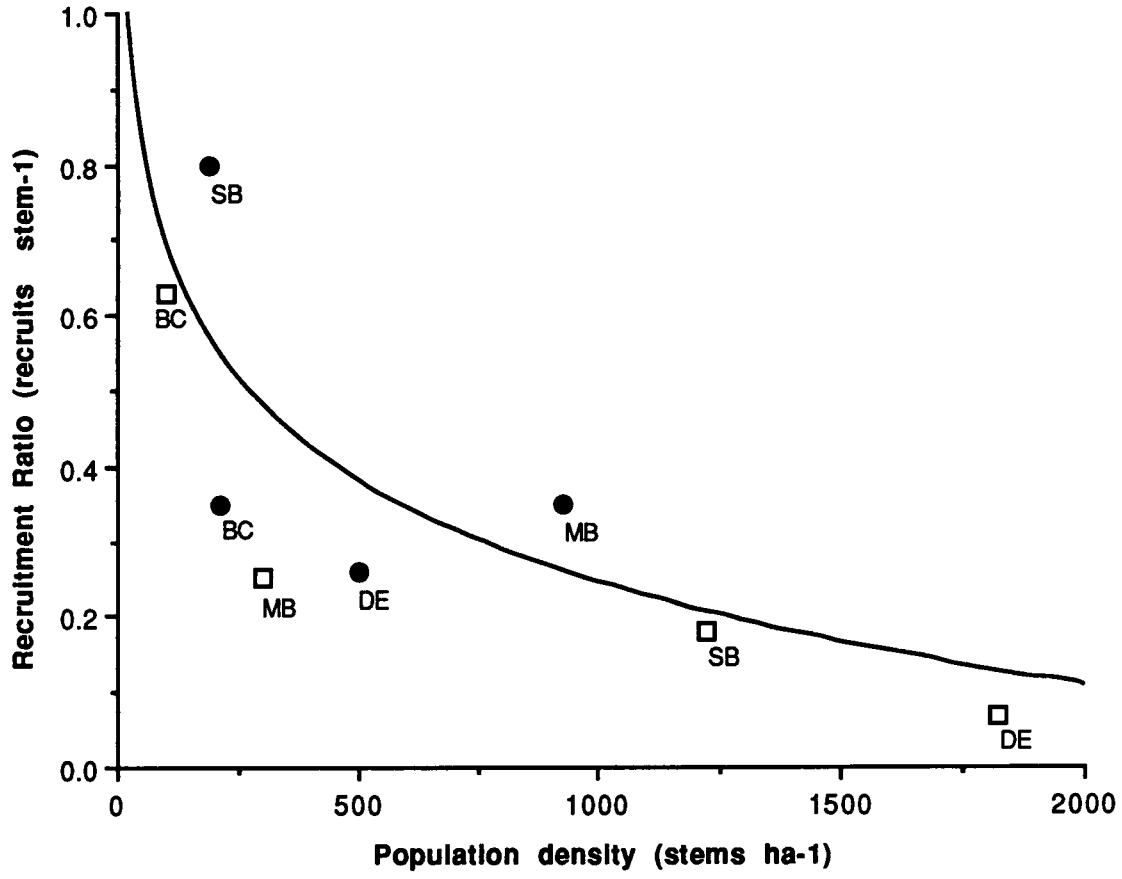


FIGURE 13. Population size vs. recruitment ratio for small and large seedlings. DE = *Dacroydes excelsa*, SB = *Sloanea berteriana*, MB = *Manilkara bidentata*, BC = *Buchenavia capitata*. Recruitment ratio for small seedlings (black dot, ●) is calculated as the number of small seedlings recruited into the large seedling size class divided by the initial number of small seedlings. Recruitment ratio for large seedlings (white square, □) is calculated as the number of large seedlings recruited into the sapling size class divided by the initial number of large seedlings. Linear regression model ($Y=-0.186\log X+1.49$, $R^2=0.61$) was statistically significant at $P<0.05$, ($P=0.021$)and is shown here for visual inspection. With data from additional species this model might prove to be even more significant. Note that log model is plotted on linear scale.

CHAPTER IV

DISCUSSION

A. Advanced Regeneration of Shade-Tolerant Species

Disturbance caused by Hurricane Hugo drastically increased solar irradiance reaching the forest floor. Increased solar radiation increased air and soil temperature, and increased the vapor pressure deficit above that of the closed canopy understory. The magnitude of these microenvironment changes in the post-hurricane environment varied considerably on a small spatial scale. Post-hurricane microenvironment conditions were comparable to conditions reported elsewhere for 200-400m^2 gaps (reviewed in Denslow 1980). Comparisons of percent PPFD in the open with other researchers show that those of this study (5-47%) ranged from those of a 200m^2 gap to those slightly more than a 400m^2 gap (Table 5). Chazdon's measurement of median PPFD at the center of a 400m^2 gap in Costa Rica was 5.79 mol m^{-2} d^{-1} (Chazdon 1986), almost identical to the average PPFD measured in this study of 5.53 mol m^{-2} d^{-1} (Table 3). Maximum vapor pressure deficit measured at H + 4 months (1.1 kPa) was below that found at the edge of clearings (Fetcher 1979, Lebron 1977) and lower than that found to significantly alter transpiration rates elsewhere (Langenheim *et al.* 1984). In spite of a decrease in precipitation, soil moisture remained high in the post-hurricane environment (Steudler *et al.* 1991). High soil moisture in treefall gaps due to decreased transpiration has been reported in Puerto Rico (Lebron 1977) as well as in other forests (Becker *et al.* 1988, Kapos 1989). Maximum air temperature was less than the maximum air temperature found in a large gap in Surinam (Shultz 1960 in Denslow 1980) or near the ground in a 6-acre abandoned field in Indiana in

August (Petty 1966), both 36.1° C. From these results it is clear that Hurricane Hugo did not create a "supergap" with environmental extremes greater than those typical of large gaps reported elsewhere (hypothesis 1 is rejected). It is important to note, however, that damage to valleys and riparian habitats between slopes in the Bisley Watersheds suffered more damage than did slopes and ridges (Basnet *et al.* 1992).

Seedling banks of shade-tolerant canopy species were able to survive in, acclimate to, and capitalize on microenvironment changes created by Hurricane Hugo. One month after Hurricane Hugo, leaves of many seedlings showed burn damage due to increase solar irradiance (pers. observation). This damage only appeared on older leaves and not on newly emerged apparently sun-tolerant leaves. At later censuses no seedlings showed evidence of sunburn on new or old leaves.

None of the study species were eliminated from any transect, although all species experienced a significant reduction in the small seedling size class. This reduction was due to three factors: 1) cessation of seedling recruitment from seeds, 2) high mortality of small seedlings, and 3) recruitment of small seedlings into the large seedling size class. Germination of seeds of shade-tolerant species characteristically is promoted by rainfall (Ausburger 1979, Garwood 1983, Sork 1985, and Foster and Janson 1985) and inhibited by high light (Quarterman 1970). Since shade-tolerant species tend to have little seed dormancy (Ng 1978), *seedling* banks rather than seed banks are the life-cycle stage which respond to development of canopy gaps. This factor, combined with high levels of solar irradiance and lack of normal rainfall, explains reduced densities of seedling populations.

Seedling growth rates were higher than those reported in Malaysia (Turner 1990) and more comparable to those reported by Langenhiem *et al.* (1984) in Brazil and Australia. Growth rates of large *Manilkara* and *Buchenavia* seedlings increased dramatically from pre-hurricane rates (Fig. 12). All species showed positive correlations between growth and increased solar exposure index (Fig. 9-11). *Manilkara* large seedlings had the strongest correlation (r_s=0.51, P<0.05) suggesting that large seedlings of this species are more responsive to changes in solar irradiance at these light levels. *Buchenavia* large seedlings had the smallest correlation (r_s=0.05, P>>0.05) between growth and light. Possible explanations for this poor correlation (and low correlations in general) between growth and light level include: 1) light is no longer limiting growth and other resources such as water and nutrients are, 2) seedlings reach saturated photosynthesis at low levels of PPFD and do not substantially increase beyond this level, or, 3) inaccuracies in SEI measurement of the true seedling light environment contributes to the scatter of the data, especially at high SEI.

In a study of the shade-tolerant shrub *Palicourea riparia* in Puerto Rico, Lebron (1977) demonstrated that this species can carry out photosynthesis at light levels as low as 20 μmol m^{-2} s^{-1}. *Palicouria* can also acclimate to light levels of 2000 μmol m^{-2} s^{-1} with a net increase in CO_2 fixation of 25% after 21 days. Similarly, in Costa Rica, Fetcher *et al.* (1983) found that seedlings of *Dipteryx* were able to acclimate to both full sun (27.6 mol^{-2} d^{-1}) and full shade (0.38 mol^{-2} d^{-1}) light conditions. Seedlings grown in full sun for one month and then placed in full shade for two months were able to acclimate to the lower light levels. Seedlings grown in full shade were able to acclimate to full sun but did not show greater increases in height than they did in partial shade

(7.05 mol^{-2} d^{-1}, 25% full sun)(Fetcher *et al.* 1983). Canham (1988) found that in a temperate deciduous forest saplings of *Fagus grandifolia* and *Acer saccharum* increased growth rates in small (<75m^2) gaps but did not experience any further increase in growth rates in larger gaps. Results from these studies support the idea that while seedlings of shade-tolerant species do not benefit from light levels above those experienced in small gaps, they are not harmed by them either. You (1991) found that small *Manilkara bidentata* seedlings transplanted from closed canopy to small (50 m^2, 15% full sun) and very large (2,500 m^2, 58% full sun) gaps increased growth rates 3 and 20 fold, respectively. Thus, he showed that *Manilkara* seedlings are quite capable of acclimating to not only small gap conditions, but very large gap conditions as well, with continued increases in growth rate. Significant positive correlations between growth and SEI for both *Manilkara* seedling size classes (Fig. 9-11) support this conclusion.

Photosynthesis and respiration rates compare favorably with measurements made on other shade-tolerant species under high light conditions (Lugo 1970, Lebron 1977, Langenheim *et al.* 1984, Walters and Field 1987). Photosynthesis of shade-tolerant shrubs (*Piper arieanum, P. urostachyum*) grown at gap centers in Costa Rica equaled 4.9 and 4.1 mol m^{-2} s^{-1} at 400-500 μmol m^{-2} s^{-1} (satuated net photosynthesis)(Walters and Field 1987). Thompson *et al.* (1988) found that photosynthesis rates of seedlings of the shade-tolerant species *Flindersia brayleyana* were maximum when grown under solar irradiance of 5.6 mol m^{-2} d^{-1}, very close to the average measured in this study (5.53 mol m^{-2} d^{-1}). *Manilkara* and *Buchenavia* respiration rates were lower than those of *Dacroydes* and *Sloanea*, resulting in a much higher

P/R ratio (Table 8). This indicates that *Manilkara* and *Buchenavia* have an even greater ability to acclimate to high levels of solar irradiance.

In spite of initial differences in size class distributions, all species increased densities of sapling size classes by 100-125 stems ha^{-1} during the first 16 months following the hurricane (Fig. 7). Since sapling mortality caused directly by Hurricane Hugo is not known for Bisley, it is not certain that these post-hurricane increases raised sapling densities above those of the pre-hurricane forest. In order to estimate this mortality the El Verde site can be used for a conservative comparison.

Manilkara mortality caused directly by Hurricane Hugo at El Verde occurred among 4% of the mature trees, close to 0% of the saplings, 30% of the large seedlings, and 61% of the small seedlings (You and Petty 1991). High seedling mortality was caused mainly by litter burial. In contrast, saplings (50-200cm) are less susceptible to litter burial than seedlings (Clark and Clark 1991) and are less vulnerable to direct wind damage than are canopy trees. At Bisley, hurricane-caused mortality among mature trees was not significantly greater than at El Verde, although defoliation and branch damage was significantly greater (Walker *et al.* 1992). This difference was attributed to the fact that Bisley was closer to the eye of the hurricane than El Verde. Increased branch damage at Bisley likely resulted in greater sapling mortality, although post-hurricane increases in the sapling densities may have made up for this decrease. For example, if sapling mortality at Bisley were as high as 14%, then all four species would still have increased sapling densities to above pre-hurricane levels. Low post-hurricane sapling mortality will result in these gains being reflected in future population structure. This 'hurricane imprint' has been demonstrated in the age-class structure of *Manilkara* (You 1991) .

Recruitment ratios of *Manilkara* and *Buchenavia* did increase above pre-hurricane values (Table 11). For shade-tolerant species on Barro Colorado Island, Brokaw (1985) found that individuals ≥ 1m tall increased in density during the first three years after formation of gaps up to at least 532m^2 in size. Density, however, did not increase with increased gap size, *i.e.* recruitment remained constant between gaps of different size.

Results of this study show that these four shade-tolerant species are able to survive and perform quite well in large gaps created by Hurricane Hugo (hypothesis 2 is supported). Recovery of surviving canopy trees quickly ameliorates what would otherwise be more severe microenvironment conditions (Denslow 1980). Advanced regeneration by seedlings of shade-tolerant species after the hurricane is very important for the future canopy composition of these species. It is important to emphasize that species which have been characterized as small-gap specialists will not necessarily do poorly when confronted with large gaps.

B. Performance Differences Among Shade-Tolerant Species

Significant differences in growth and mortality were found between species (Table 6 and Table 9) (hypothesis 3 is supported). However, differences did not exist between all pairs of comparisons. Species with slower growth rates did not consistently exhibit higher or lower rates of mortality. Additionally, the average Solar Exposure Index of surviving large seedlings at the end of the study (H+15) was very similar for all species, ranging from 133 to 150 SEI (Table 7). Thus, in spite of significant differences between species, they do not appear to partition light. The lack of evidence for resource

partitioning, however, does not support the idea that species coexist by means of chance and history alone.

The most important measure of success for seedlings of these species is their ability to be recruited into low-mortality size classes. The first of these "stable" size classes is characteristically the sapling size class (Turner 1990, You and Petty 1991, Clark and Clark 1992). In a lowland Malaysian rain forest, Turner (1990) found 0% mortality in the 60-99.9 cm height class over a 16-month period. In the post-hurricane environment there was no significant difference in the number of sapling recruits among the four study species, although each species exhibits a different "strategy" for maintaining itself in the forest. The number of recruits into a larger size class is a function of initial population size, growth rate and mortality. A brief summary of species performances in the post-hurricane environment is as follows:

Dacroydes excelsa. Mortality among the four study species was highest for *Dacroydes* seedlings, contributing to its relatively low recruitment ratios (Table 11). High densities of initial large seedling populations was critical for increases in the sapling size class. *Dacroydes* growth rates were near average for small and large seedlings.

Sloanea berteriana. Mortality of *Sloanea* small seedlings was the lowest of all four species. Large-seedling mortality was second lowest. Growth rates for non-sprouting *Sloanea* small and large seedlings were second slowest and slowest, respectively. Sprouting by large seedlings, however, appears to be an important survival strategy, compensating for relatively slow growth rates.

Manilkara bidentata. With the highest initial small seedling density combined with low mortality, *Manilkara* had an abundant source of small

seedlings for recruitment into the large seedling size class. Large seedlings of this species had the lowest mortality and the second highest large seedling growth rate. *Manilkara* had significant increases in its recruitment ratios from pre-hurricane levels (Table 11).

Buchenavia capitata. In spite of small initial seedling density and high mortality, *Buchenavia* sapling density increased from near zero to 100 stems ha^{-1} due to very high growth rates (Table 11) (37 of the small seedlings which were recruited into the large seedling size class continued to grow into the sapling size class). Post-hurricane recruitment ratios were greater than those under pre-hurricane conditions.

Three different survival strategies emerge from these seedling population dynamics under post-hurricane conditions: 1) Conservative strategy: Species which have slow growth rates "compensate" with low mortality (*Sloanea*), 2) Maximal performance strategy: Species with high mortality "compensate" with either high initial seedling densities (*Dacroydes*) or high growth rates (*Buchenavia*), 3) Moderate strategy: Other species (*Manilkara*) have intermediate growth and initial seedling density combined with moderate mortality.

Because all species survived in the post-hurricane environment, had similar increases in sapling density, and survived under near identical light regimes, resource partitioning of light is not evident among these species. The lack of resource partitioning, however, does not negate the importance of different species strategies as discussed above. Distinction between small-gap and large-gap species is not very clear and this concept should be used with caution.

For the last 290 years, hurricanes of Hugo's magnitude have passed over the LEF once every 50-60 years. While it is clear that the forest is capable of fast recovery, hypotheses about species adaptations to a ~60 year hurricane cycle are spurious given that hurricane frequency is unlikely to have been constant on a larger time scale. Hurricanes occur when the area of sea surface temperature (SST) at 26.8°C is above 8.5×10^6 km^2. Due to cooler sea surface temperatures during glacial periods, hurricane frequency as recently as 18,000 B.P. is estimated to have been zero, or insignificant (Wendland 1977). During these periods (90% of the Quaternary), treefalls and landslides would exert greater influence on forest structure. For the current interglacial, especially with predicted increases in mean annual temperature due to global warming, the effect of hurricanes on forest structure is hypothesized to be dominant. You (1991) demonstrated that the age structure of *Manilkara* shows a 'hurricane imprint,' as evidenced by peaks in tree densities in the 70-80 year age class and the 130-140 year age class. These individuals would have been seedlings at the time of the 1932 (59 years ago) and 1867 (124 years ago) hurricanes, respectively. So, while species adaptations to a hurricane cycle may be unlikely, population age structure of canopy species and, thus, overall forest structure is affected.

C. Post-hurricane Trends in Species Performance

Occurrence of Hurricane Hugo created a relatively brief but dramatic change in the structure and microclimate of the forest. Surviving canopy trees and saplings responded to these changes by sprouting and refoliating remaining branches (Walker 1991). Pioneer species germinated within six

months and began growing very rapidly (Gruzman-Grajales and Walker 1991).

As the canopy began to close and pioneer species started to overtop slower growing species, SEI decreased for seedling size classes of the four study species (Table 7). Growth rates also decreased for all seedling size classes (Table 7). In spite of decreases in solar exposure and reduced growth, growth rates are still eight and two and a half times greater than pre-hurricane levels for *Manilkara* small and large seedlings, respectively (You and Petty 1991). Mortality increased from time H+3-9 to H+9-15 for small seedlings except for *Dacroydes* (Table 10). In contrast, large seedling mortality decreased for *Sloanea* and *Manilkara* and increased for *Dacroydes* and *Buchenavia* populations.

Initial closure of the canopy was due mainly to the refoliation of canopy branches which survived the hurricane. With decreasing canopy openness and overgrowth of pioneer species, seedlings will likely experience further reductions in solar irradiance. Gaps formed by larger branch and treefalls take considerably longer to recovery (Fig. 4). At this time, rate of canopy closure appears to be slowing (Fig. 5). Populations of pioneer species (predominantly *Cecropia peltata*) are expected to experience high mortality with increased time since the hurricane (Silander 1979, Brokaw 1985). This mortality will result in a continued level of solar irradiance above that of the closed mature canopy. Under microenvironment conditions 16 months after Hurricane Hugo, there is considerable potential for further increases in sapling size classes of the four shade-tolerant tree species studied. Based on recruitment ratios of large seedlings to saplings, *Manilkara* sapling density will soon be above that of *Dacroydes*, due to the fact that large seedling

mortality is increasing for *Dacroydes* and is decreasing for *Manilkara* (Table 10). At present recruitment ratios (Table 11) species populations may experience increased sapling densities over the next 12 months as follows: *Dacroydes*, 25 stems ha^{-1}, *Sloanea*, 175 stems ha^{-1}, *Manilkara* 90 stems ha^{-1}, and *Buchenavia*, 24 stems ha^{-1}.

Continued monitoring of seedling and sapling growth rates will be important in predicting future forest canopy composition. At this time none of the populations of the four study species appears to be experiencing negative impacts from the hurricane. In fact, they all are thriving in the post-hurricane environment. Results concur with those of Yih *et al.* (1991) after Hurricane Joan, and Spurr (1956) after the 1938 northeastern United States hurricane. Direct regeneration of shade-tolerant canopy species contributes significantly to forest recovery.

CHAPTER V

CONCLUSIONS

A. Summary

1. The post-Hurricane Hugo microenvironment on slopes in and near the Bisley Watersheds had a range of conditions, equivalent to micro-environments of gaps ranging from <200 m^2 to 400m^2 gaps, but far below microenvironmental extremes of large clearings (Hypothesis 1 is rejected).

   a. Light conditions ranged from 5 to 47% of full sun.

   b. VPD was consistently below that which adversely effects photosynthesis.

   c. Air temperature was below the extremes characteristic of large clearings.

   d. Soil temperatures were above those of the understory but below those characteristic of clearings and old fields reported elsewhere.

2. Established seedlings of each shade-tolerant canopy species (*Dacroydes excelsa, Sloanea berteriana, Manilkara bidentata, Buchenavia capitata*) were able to thrive in the post-hurricane forest environment (Hypothesis 2 is supported). Advanced regeneration from seedling pools plays an important role in forest recovery and survival of the species studied.

   a. All species increased sapling densities within the first year following the hurricane due to recruitment from smaller size classes.

   b. Post-hurricane species size class distributions were greatly influenced by pre-hurricane size class densities. Historical effects on initial population size-class densities were evident.

3. Significant differences in growth and mortality occurred among species (Hypothesis 3 is supported). Species differences, however, did not show any consistent pattern with regard to mortality and growth rate.

   a. Recruitment ratios were inversely proportional to initial size-class population density, suggesting a possible density-dependent factor influencing recruitment.
   b. Large seedling populations of all species occurred under near identical light conditions at the end of the study period. Therefore, resource partitioning with respect to light is not evident.

4. Hurricane disturbance accelerates recruitment of seedlings of shade-tolerant species into larger size classes (Hypothesis 4 is supported). This recruitment leads to advanced regeneration of the forest directly from surviving populations of shade-tolerant species.

5. The four shade-tolerant species exhibited three distinct recruitment strategies that can be summarized as follows:

   a. Conservative strategy: Species which have slow growth rates compensate by having low mortality (*Sloanea berteriana*)
   b. Maximal performance strategy: Species with high mortality compensate by having either high initial seedling densities (*Dacroydes excelsa*) or high growth rates (*Buchenavia capitata*)
   c. Moderate strategy: Other species (*Manilkara bidentata*) have intermediate growth and initial seedling density combined with moderate mortality.

6. Results of this study indicate that there were no significant differences between impacts of Hurricane Hugo on slopes and large treefall gaps, measured in terms of microenvironment conditions and population performance of seedlings of four shade-tolerant tree species.

Results presented here provide valuable baseline data on the microenvironment conditions, growth and mortality of seedlings of four shade-tolerant tree species immediately after a hurricane. Post-hurricane data on species specific population performance are important for predicting overall future forest structure under various disturbance regimes.

B. Recommendations

Species distributions and abundances in the wet tropics have been explained by numerous life-history characteristics, including: mode of dispersal (You 1991), seedling type (Hladik and Miquel 1990), photosynthetic capacity (Chazdon 1988, Field 1988), staggered germination (Ng 1978), and herbivory/pathogen susceptibility (Ausburger and Kelly 1984, Ausburger 1990). The validity of each of these factors for various species under different conditions underscores the value of autecological life-history studies. Autecological studies need to be conducted on *Dacroydes excelsa* and *Sloanea berteriana* so that information about their reproduction, dispersal and age structure can be incorporated into population and forest structure models.

Future studies should include a similar analysis of sapling size classes. While data are not conclusive, gas exchange measurements made here suggest that respiration rate rather than photosynthetic rate has a larger influence on the post-hurricane rate of growth for seedlings of these shade-

tolerant species. Understory gas exchange values for all species are needed in order to further understand the determinants of seedling performance.

Using hemispherical photographs directly in order to combine the effect of understory and canopy obstructions is recommended. Due to the time required for analysis, fewer individuals would be able to be sampled; however, the information gained would likely show stronger relationships between study variables.

LITERATURE CITED

LITERATURE CITED

ANDERSON, M. C. 1964. Studies of the woodland light climate. II. Seasonal variation in the light climate. Journal of Ecology 52:643-663.

AUSBURGER, C. K. 1979. Irregular rain cues and the germination and seedling survival of a Panamanian shrub (*Hybanthus prunifolius*). Oecologia 44:53-59.

AUSBURGER, C. K. 1990. The potential impact of fungal pathogens on tropical plant reproductive biology. *In* Bawa, K. S. and M. Hadley (Eds.). Reproductive Ecology of Tropical Plants, pp. 237-245. The Parthenon Publishing Group, Paris.

AUSBURGER, C. K. AND C. K. KELLY. 1984. Pathogen mortality of tropical seedlings: experimental studies of dispersal distance, seedling density, and light conditions. Oecologia 61:211-217.

BASNET, K. 1992. The effect of topography on the pattern of trees in Tabonuco (*Dacroydes excelsa*) dominated rain forest of Puerto Rico. Biotropica 24: 31-42.

BASNET, K., G. E. LIKENS, F. N. SCATENA, AND A. E. LUGO. 1992. Hurricane Hugo: damage to a tropical rain forest in Puerto Rico. Journal of Tropical Ecology 8:47-55.

BAZZAZ, F. A. 1979. The physiological ecology of plant succession. Annual Review of Ecology and Systematics 10:351-371.

BECKER, P., D. W. ERHART, AND A. P. SMITH. 1989. Analysis of forest light environments Part 1. Computerized estimation of solar radiation from hemispherical canopy photographs. Agricultural and Forest Meteorology 44:217-232.

BECKER, P., P. E. RABENHOLD, J. R. IDOL, AND A. P. SMITH. 1988. Water potential gradients for gaps and slopes in a Panamanian tropical moist forest's dry season. Journal of Tropical Ecology 4:173-184.

BROKAW, N. V. L. 1985. Gap-phase regeneration in a tropical forest. Ecology 66:682-687.

BROKAW, N. V. L. 1987. Gap-phase regeneration of three pioneer tree species in a tropical forest. Journal of Ecology 75:9-19.

BROWN, S., A. E. LUGO, S. SILANDER, AND L. LIEGEL. 1983. Research history and opportunities in the Luquillo Experimental Forest. U. S. For. Serv. Gen. Tech. Rep. SO-44. Southern Forest Experiment Station, New Orleans, Louisiana.

CANHAM, C. D. 1988. Growth and canopy architecture of shade-tolerant trees: response to canopy gaps. Ecology 69:786-795.

CANHAM, C. D., J. S. DENSLOW, W. J. PLATT, J. R. RUNKLE, T. A. SPIES, AND P. S. WHITE. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. Canadian Journal of Forest Research 20:620-631.

CHABOT, B. F., T. W. JURIK, AND J. F. CHABOT. 1979. Influence of instantaneous and integrated light-flux density on leaf anatomy and photosynthesis. American Journal of Botany 66:940-945.

CHAZDON, R. L. 1986. Light variation and carbon gain in rain forest understory palms. Journal of Ecology 74:995-1012.

CHAZDON, R. L. 1988. Sunflecks and their importance to forest understory plants. *In* Advances in Ecological Research Vol. 18. Academic Press, Inc., London.

CHAZDON, R. L. AND N. FETCHER. 1984. Photosynthetic light environments in a lowland tropical rain forest in Costa Rica. Journal of Ecology 72:553-564.

CHAZDON, R. L. AND C. B. FIELD. 1987a. Determinants of photosynthetic capacity in six rain forest *Piper* species. Oecologia 73:222-230.

CHAZDON, R. L. AND C. B. FIELD. 1987b. Photographic estimation of photosynthetically active radiation: evaluation of a computerized technique. Oecologia 73:525-532.

CLARK, D. A. AND D. B. CLARK. 1992. Life history of canopy and emergent trees in a neotropical rain forest. Ecological Monographs 62:315-344.

CLARK, D. B. AND D. A. CLARK. 1991. The impact of physical damage on canopy tree regeneration in tropical rain forest. Journal of Ecology 79:447-457.

CROW, T. R. 1980. A rain forest chronicle: A 30-year record of change in structure and composition at El Verde, Puerto Rico. Biotropica 12: 42-55.

CROW, T. R. AND P. L. WEAVER. 1977. Tree growth in a moist tropical forest of Puerto Rico. Research Paper ITF-22, Forest Service, U. S. Department of Agriculture.

DENSLOW, J. S. 1980. Gap partitioning among tropical rain forest trees. Biotropica 12:47-55.

DENSLOW, J. S. 1987. Tropical rain forest gaps and tree species diversity. Annual Review of Ecology and Systematics 18:431-451.

DENSLOW, J. S., J. C. SCHULTZ, P. M. VITOUSEK, AND B. R. STRAIN. 1990. Growth responses of tropical shrubs to treefall gap environments. Ecology 71:165-179.

DUKE, J. A. 1970. Keys for the identification of seedlings of some prominent woody species in eight forest types in Puerto Rico. *In* Odum, H. T. and R. F. Pigeon (Eds.). A Tropical Rain Forest, pp. B-239-274. United States Atomic Energy Commission. TID-24270.

FERNANDEZ, D. S., AND N. FETCHER. 1991. Changes in light availability following Hurricane Hugo in a subtropical montane forest in Puerto Rico. Biotropica 23:393-399.

FETCHER, N., B. R. STRAIN, AND S. F. OBERBAUER. 1983. Effects of light regime on the growth, leaf morphology, and water relations of seedlings of two species of tropical trees. Oecologia 58:314-319.

FETCHER, N. 1979. Water relations of five tropical tree species on Barro Colorado Island, Panama. Oecologia 40:229-233.

FIELD, C. B. 1988. On the role of photosynthetic responses in constraining the habitat distribution of rain forest plants. Australian Journal of Plant Physiology 15:343-58.

FOSTER, S. A. AND JANSON, C. H. 1985. The relationship between seed size and estimated conditions on tropical woody plant. Ecology 66:773-80.

GARWOOD, N. C. 1983. Seed germination in a seasonal tropical forest in Panama: A community study. Ecological Monographs 53:159-81.

GRUBB, P. J. 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. Biological Reviews 52:107-145.

GUZMAN-GRAJALES, S. M. AND L. R. WALKER. 1991. Differential seedling response to litter after Hurricane Hugo in the Luquillo Experimental Forest, Puerto Rico. Biotropica 23:407-413.

HLADIK, A. AND S. MIQUEL. 1990. Seedling types and plant establishment in an African rain forest. *In* Bawa, K. S. and M. Hadley (Eds.). Reproductive Ecology of Tropical Plants, pp. 261-282. The Parthenon Publishing Group, Paris.

HOLDRIDGE, L. R. 1967. Life zone ecology. Tropical Science Center, San Jose, Costa Rica.

HUBBELL, S. P. AND R. B. FOSTER. 1986. Biology, chance, and history and the structure of tropical rain forest tree communities. *In* Diamond, J. and T. J. Case (Eds.). Community Ecology. Harper and Row, Publishers, New York.

JORDAN, C. F. 1970. Vegetative sprouting following irradiation of a tropical rain forest. *In* Odum, H. T. and R. F. Pigeon (Eds.). A Tropical Rain Forest, pp. D-305-308. United States Atomic Energy Commission. TID-24270.

KAPOS, V. 1989. Effects of isolation on the water status of forest patches in the Brazilian Amazon. Journal of Tropical Ecology 5:173-185

LANGENHEIM, J. H., C. B. OSMUND, A. BROOKS, AND P. J. FERRAR. 1984. Photosynthetic responses to light in seedlings of selected Amazonian and Australian rain forest tree species. Oecologia 63:215-224.

LASKO, A. N. 1980. Correlations of fisheye photography to canopy structure, light climate, and biological responses to light in apple trees. Journal of the American Society of Horticultural Science 105:43-46.

LEBRON, M. L. 1977. An autecological study of *Palecouria riparia* Bentham (Rubiacea): An ecologically important species in the recovery of a disturbed tropical rain forest in Puerto Riço. Ph.D. dissertation, University of North Carolina, Chapel Hill.

LITTLE, E. L. JR. AND F. H. WADSWORTH. 1964. Common Trees of Puerto Rico and the Virgin Islands. U. S. Dept. of Agriculture Handbook, No. 249, Washington, D. C.

LUGO, A. E. 1970. Photosynthetic studies on four species of rain forest seedlings. *In* Odum, H. T. and R. F. Pigeon (Eds.). A Tropical Rain Forest, pp. I-81-101. United States Atomic Energy Commission. TID-24270.

LUGO, A. E. 1986. Water and the ecosystem of the Luquillo Experimental Forest. For. Serv. Gen. Tech. Rep. 50-63. U. S. Department of Agriculture, Forest Service, Southern Experiment Station, New Orleans, LA.

MCARDLE, B. H. 1988. The structural relationship: regression in biology. Canadian Journal of Zoology 66:2329-2339.

MCCORMICK, J. F. In Press. A review of the population dynamics of selected tree species in the Luquillo Experimental Forest, Puerto Rico. *In* Lugo, A. E. and C. Lowe (Eds.). A Century of Tropical Forestry Research: Results from the First Half, Themes for the Second. Elsevier Science Publishers, New York.

MCLAUGHLIN, S. B., C. P. ANDERSEN, N. T. EDWARDS, W. K. ROY, AND P. A. LAYTON. 1990. Seasonal patterns of photosynthesis and respiration of red spruce saplings from two elevations in declining southern Appalachian stands. Canadian Journal of Forest Research 20:485-495.

MURPHY, P. 1970. Tree growth at El Verde and effects of ionizing radiation. *In* Odum, H. T. and R. F. Pigeon (Eds.). A Tropical Rain Forest, pp. D-141-171. United States Atomic Energy Commission. TID-24270.

NG, F. S. P. 1978. Strategies of establishment in Malaysian forest trees. *In* Tomlinson, P. B. and M. H. Zimmerman (Eds.). Tropical Trees as Living Systems, PP. 129-162. Oxford University Press, Oxford.

ODUM, H. T. AND R. F. PIGEON. Editors. 1970. A Tropical Rain Forest. United States Atomic Energy Commission. TID-24270.

ODUM, H. T., G. DREWRY, AND J. R. KLINE. 1970. Climate at El Verde, 1963-1966. *In* Odum, H. T. and R. F. Pigeon (Eds.). A Tropical Rain Forest, pp. B-347-418. United States Atomic Energy Commission. TID-24270.

PEARCY, R. W. AND R. H. ROBICHAUX. 1985. Tropical and subtropical forests. *In* Chabot, B. F. and H. A. Mooney (Eds.). Physiological Ecology of North American Plant Communities, pp. 278-295. Chapman and Hall, New York.

PEREZ, I. E. 1988. Field Guide to the Trees of Bisley Watersheds Luquillo Experimental Forest, Puerto Rico. Institute of Tropical Forestry Publication, USDA Forest Service. Esmaco Printers Corp., Hato Rey, Puerto Rico.

PETTY, R. O. 1966. Rates and pattern of radioisotope release from fresh tree litter at three levels of mesic forest development. Ph.D. dissertation, Purdue University, West Layfayette, Indiana.

PICKETT, S. T. A. 1983. Differential adaptation of tropical species to canopy gaps and its role in community dynamics. Tropical Ecology 24:68-84.

PICKETT, S. T. A. AND P. S. WHITE. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, New York, New York.

PINTO, A. E. 1970. Phenological studies of trees at El Verde. *In* Odum, H. T. and R. F. Pigeon (Eds.). A Tropical Rain Forest, pp. D-237-269. United States Atomic Energy Commission. TID-24270.

QUARTERMAN, E. 1970. Germination of seeds of certain tropical species. *In* Odum, H. T. and R. F. Pigeon (Eds.). A Tropical Rain Forest, pp. D-173-175. United States Atomic Energy Commission. TID-24270.

RICHARDS, P. W. 1952. The Tropical Rain Forest, An Ecological Study. Cambridge University Press, London.

RICKLEFS, R. E. 1977. Environmental heterogeneity and plant species diversity: a hypothesis. American Naturalist 111: 376-381.

RIECHERT, S. E., R. ROELOFFS, AND A. C. ECHTERNACHT. 1986. The ecology of the cooperative spider *Agelena consociata* in equatorial Africa (Araneae, Agelenidae). Journal of Arachnolology 14:175-191.

SASTRE-DE JESUS, I. 1979. Ecological life cycle of *Buchenavia capitata* (Vahl.) Eichl., A late secondary successional species in the rain forest of Puerto Rico. MS thesis, University of Tennessee, Knoxville.

SAS INSTITUTE. 1989. JMP Introductory and user's guide. SAS Institute Inc., Cary, NC, USA.

SCATENA, F. N. 1989. An introduction to the physiography and history of the Bisley Experimental Watersheds in the Luquillo Mountains of Puerto Rico. U. S. Forest Service General Technical Report SO-72.

SILANDER, S. R. 1979. A study of the ecological life history of *Cecropia peltata* L., an early secondary successional species in the rain forest of Puerto Rico. M.S. thesis, University of Tennessee, Knoxville, Tennessee.

SOKAL, R. R. AND F. J. ROHLF. 1981. Biometry, 2nd Ed. W. H. Freeman and Company, New York.

SORK, V. L. 1985. Germination response in a large-seeded neotropical tree species, *Gustavia superba* (Lecythidacea). Biotropica 17:130-36.

SPURR, S. H. 1956. Natural restocking of forests following the 1938 hurricane in central New England. Ecology 37:443-451.

STEUDLER, P. A., J. M. MELILLO, R. D. BOWDEN, M. S. CASTRO AND A. E. LUGO. 1991. The effects of natural and human disturbance on soil nitrogen dynamics and trace gas fluxes in a Puerto Rican wet forest. Biotropica 23:356-363.

TILMAN, D. 1982. Resource Competition and Community Structure. Princeton University Press, Princeton, NJ.

THOMPSON, W. A., G. C. STOCKER, AND P. E. KRIEDEMANN. 1988. Growth and Photosynthetic response to light and nutrients of *Flindersia brayleyana* F. Muell., a rain forest tree with broad tolerance to sun and shade. Australian Journal of Plant Physiology 15:299-316.

TORQUEBIAU, E. F. 1988. Photosynthetically active radiation environment, patch dynamics, and architecture in a tropical rain forest in Sumatra. Australian Journal of Plant Physiology 15:327-342.

TURNER, I. M. 1990. Tree seedling growth and survival in a Malaysian rain forest. Biotropica 22: 146-154.

WADSWORTH, F. H. 1951. Forest management in the Luquillo mountains, I-setting. Caribbean Forestry 12:114-111.

WAIDE, R. B. AND A. E. LUGO. 1988. Long-term ecological research on the Luquillo Experimental Forest. A proposal to the National Science Foundation from the Center for Energy and Environment Research, University of Puerto Rico and Institute of Tropical Forestry, U. S. Department of Agriculture.

WALKER, L. R. 1991. Tree damage and recovery from Hurricane Hugo in Luquillo Experimental Forest, Puerto Rico. Biotropica 23:379-385.

WALKER, L. R., J. VOLTZOW, J. D. ACKERMAN, D. S. FERNANDEZ, and N. FETCHER. 1992. Immediate impact of Hurricane Hugo on a Puerto Rican rain forest. Ecology 73: 691-693.

WALTERS, M. B. AND C. B. FIELD. 1987. Photosynthetic light acclimation in two rain forest *Piper* species with different ecological amplitudes. Oecologia 72:449-456.

WENDLAND, W. M. 1977. Tropical storm frequencies related to sea surface temperature. Journal of Applied Meteorology 16:477-481.

WIELAND, N. K. AND F. A. BAZZAZ. 1975. Physiological ecology of three codominant successional annuals. Ecology 56:681-688.

YIH, K., D. H. BOUCHER, J. H. VANDERMEER, AND N. ZAMORA. 1991. Recovery of the rain forest of southeastern Nicaragua after destruction by Hurricane Joan. Biotropica 23: 106-113.

YOU, C. 1991. Population dynamics of *Manilkara bidentata* (A.DC.) Cher. in the Luquillo Experimental Forest, Puerto Rico. Ph.D. dissertation, University of Tennessee, Knoxville, Tennessee.

YOU, C. and W. H. PETTY. 1991. Effects of Hurricane Hugo on *Manilkara bidentata*, a Primary Tree Species in the Luquillo Experimental Forest of Puerto Rico. Biotropica 23: 400-406.

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