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Ph.D. degree in Ecology

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Major professor

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STRUCTURE AND DYNAMICS IN THE COLORADO FOREST OF THE LUQUILLO MOUNTAINS OF PUERTO RICO

by

Peter L. Weaver

A DISSERTATION

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

DOCTOR OF PHILOSOPHY

Department of Botany and Plant Pathology

1987

ABSTRACT

STRUCTURE AND DYNAMICS IN THE COLORADO FOREST OF THE LUQUILLO MOUNTAINS OF PUERTO RICO

By

Peter L. Weaver

The influence of past hurricanes and environmental gradients on forest structure, species composition, regeneration and productivity, was investigated in the colorado forest (subtropical lower montane wet and rain forests, sensu Holdridge) of the Luquillo Mountains of Puerto Rico. Forest recovery after the passage of hurricane San Cipriano in 1932 was assessed on 2.8 ha of permanent plots located in natural forest. During the 35-year period of measurement from 1946 to 1981, secondary tree species declined in abundance whereas shade tolerant climax species, the size of residual trees, and the mean specific gravity of the overall wood biomass, increased. Species richness was greater on lower elevation valley plots than on higher elevation slope plots, and declined over time on the most diverse plots and increased on the least diverse plots. Aboveground woody biomass increased from 121 to 145 t/ha with an average accrual of 0.67 t/ha/yr. In comparison, the increase in stem numbers and biomass on a 0.4 ha thinned plot in the same forest was greater than the mean for the natural forest plots. The regeneration of Cyrilla racemiflora, the largest and oldest tree species within the forest, appeared related to past hurricanes.

Forest structure and soil characteristics were studied on 75 temporary 500 m^2 plots, stratified by elevation, life zone (wet and rain), and topography (ridge, slope, and valley), throughout the colorado

forest. Stem density increased with elevation in the rain forest but not in the wet forest whereas tree height declined with elevation in both life zones. Species richness showed no relationships with any of the environmental factors. Basal area, wood volume, and wood biomass varied with topography and elevation in the rain forest, but not in the wet forest, and bulk density, percent organic matter, and soil organic matter content, varied with elevation in the wet forest, but not in the rain forest.

Reciprocal averaging and polar ordinations of species and plot data from the temporary plots provided evidence of species' preferences in a complex, montane habitat, including trends by topography, aspect and elevation. Of the 39 species used in ordinations, five were largely confined to valleys, eight were found in valleys from 30 to 65 percent of the time, and the remainder were tallied on ridges or slopes more than 75 percent of the time.

The regeneration of 20 canopy tree species was studied using centrally located subplots on each of the temporary plots. Data on seedling regeneration, understory stems, seed size and wood density were used to classify canopy species as shade intolerant pioneers, gap or late secondary species, and shade tolerant species with different gap requirements for maturity.

The net primary production of 7.83 t/ha/yr for two 0.4 ha permanent colorado forest plots was determined by summing biomass accrual (0.82 t/ha/yr), litterfall (6.80 t/ha/yr), and herbivory (0.21 t/ha/yr). To elucidate spatial and temporal trends in hurricane disturbance and recovery, as well as primary production and related measures in the Luquillo Mountains, the results of this study were compared with

information for the forests above and below the colorado forest. Overall, the structural and dynamic parameters for the colorado forest were intermediate between those of the lower and higher elevation forests in the Luquillo Mountains.

This dissertation is dedicated to Alba Iris

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Assistance in field work was provided by many of the Institute's forestry technicians. Most notable for his contribution was Carlos Rivera who helped tally trees on many of the permanent and temporary plots. Others who assisted at one time or another were: Carlos Dominguez, Hector

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GENERAL INTRODUCTION

Purpose and Organization of the Study

Forest vegetation types develop mainly in response to climate and exhibit intrinsic variation in structure and species composition according to environmental conditions. On the islands of the Caribbean, the major spatial variables within montane forests are elevation, aspect and topography, all of which comprise gradients that influence microclimate. The major stochastic climatic event is the hurricane. The four major hurricanes that traversed the Luquillo Mountains during the past two centuries had an impact on the vegetation.

For most tropical forests, historical and environmental information is extremely limited. This, in part, has contributed to the view that tropical forests are homeostatic ecosystems with a complex, randomly distributed, species component. Only recently has there emerged a more dynamic concept of tropical forests. The availability of structural data for the colorado forest a few years after the passage hurricane San Cipriano, as well as adequate taxonomic information on its component tree species, provided a rare opportunity to demonstrate the effects of both historical and environmental influences on forest structure and composition.

Because forest structure, species composition, and dynamics are all related, this study of the colorado forest was divided into three parts. The purpose of the first part was to determine temporal changes in forest

structure and species composition wrought by hurricane San Cipriano of 1932. Eight permanent 0.40 ha plots established in the mid-1940's and re-measured in 1981 were used to assess these changes. The plots were located between 650 and 900 m in elevation on windward and leeward aspects. In essence, this section provides a chronology of the colorado forest between 1946 and 1981, and characterizes typical changes in species composition and structure associated with the recovery of the colorado forest from a major hurricane.

The second part of the study concerned the current condition of closed canopy forest, including regeneration, and elucidated spatial patterns in species composition relative to environmental gradients. Canopy vegetation was sampled in 1981 on 75 temporary, 500 m^2 plots, stratified by elevation, topography and aspect, and regeneration was tallied on 20 subplots of 1 m^2 located in the center of each plot. Soil organic matter in the top 50 cm was also determined. Species distributions were investigated using direct gradient analyses (summarizing distributions by elevation and topography), and indirect gradient analyses including reciprocal averaging and polar ordinations. Structural parameters were investigated using covariance analysis.

The third part of the study was to determine forest productivity and to assess the influence of elevation on forest structure and dynamics by comparing the results of the colorado forest study with those available for the forest types above and below it.

The Study Site

The Luquillo Experimental Forest is located in northeastern Puerto Rico at 18°N latitude and 66°W longitude (Fig. 1) and encompasses

Figure 1. The Luquillo Experimental Forest. The colorado forest is divided into wet forest (oblique lines) and rain forest (cross-hatched) life zones (Holdridge 1967; Ewel and Whitmore 1973). Dark circles represent temporary plots used in species-site ordinations. Dark triangles represent the permanent plots used in growth and stand dynamics studies.

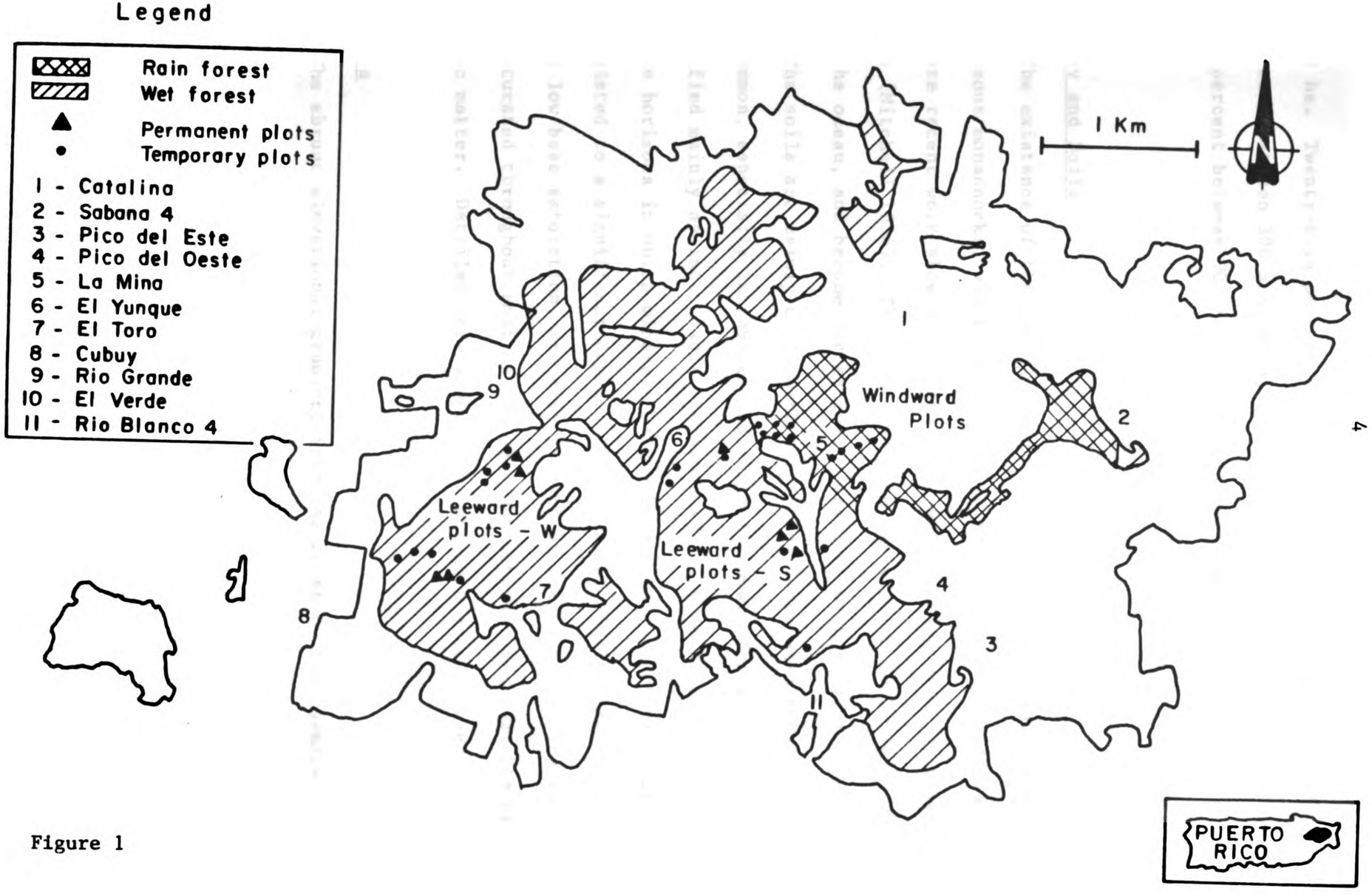

Legend
Rain forest
Wet forest
Permanent plots
Temporary plots
1 - Catalina
2 - Sabana 4
3 - Pico del Este
4 - Pico del Oeste
5 - La Mina
6 - El Yunque
7 - El Toro
8 - Cubuy
9 - Rio Grande
10 - El Verde
11 - Rio Blanco 4
1 Km
N
Windward Plots
Leeward plots - W
Leeward plots - S
PUERTO RICO

Figure 1

11,200 ha. Twenty-five percent lies between 120 and 300 m in elevation, 47 percent between 300 and 600 m, 25 percent between 600 and 900 m, and three percent between 900 and 1075 m (Wadsworth 1951).

Site Characteristics

Geology and Soils

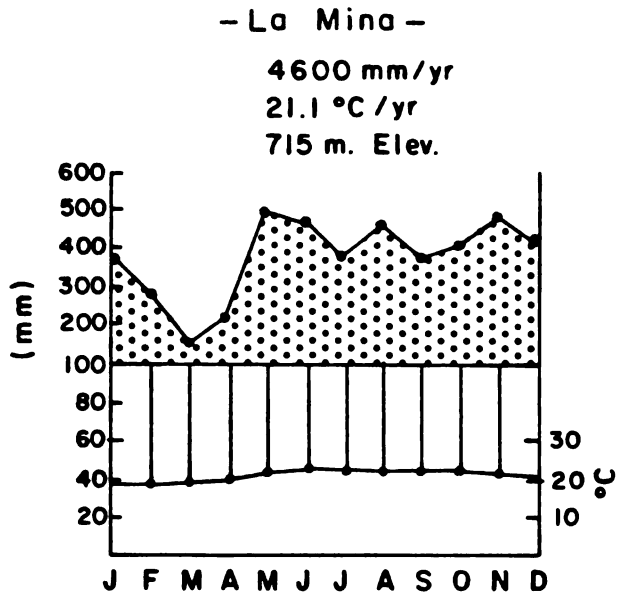
The existence of the Luquillo Mountains, an isolated range of upper Cretaceous monadnocks, was first attributed to folding (Meyerhoff 1933), but more recent work showed that uparching and faulting were the probable causes (Mitchell 1954). The mountains rise abruptly to 1075 m only 8 km from the ocean, and become increasingly dissected with elevation.

The soils are mainly clays with silty clay loams also present. Rocks are common, especially in ravines and large streams. The soils are classified mainly as inceptisols (Beinroth 1971), mineral soils having one or more horizons in which minerals have been altered or removed, but not accumulated to a significant degree. Ultisols, or highly leached soils with a low base saturation, are also present on small areas. The soils are saturated throughout most of the year and contain large amounts of organic matter. Detailed soil mapping has not been accomplished.

Climate

The abrupt elevational gradient from the coast to the summits profoundly influences the climate of the mountains. Rainfall increases from 2300 mm/yr at 200 m near the northern forest boundary (Crow and Weaver 1977) to 4600 mm/yr at La Mina near 715 m elevation (Fig. 2), and averages 4450 mm/yr on Pico del Este at 1050 m. The mean annual temperatures vary from 23°C to 19°C over the same gradient. Because

Figure 2. Climate diagrams (Walter 1975) for La Mina based on data collected from 1935 to 1943 (Wadsworth 1948) and for Pico del Este from 1969 to 1982 (U.S. Department of Commerce 1970-82). Striped areas indicate periods of water surplus and stippled areas indicate rainfall greater than 100 mm/month.


-La Mina-
4600 mm/yr
21.1 °C /yr
715 m. Elev.
600
500
400
300
200
100
80
60
40
20
(mm)
30
20
10
°C
J F M A M J J A S O N D

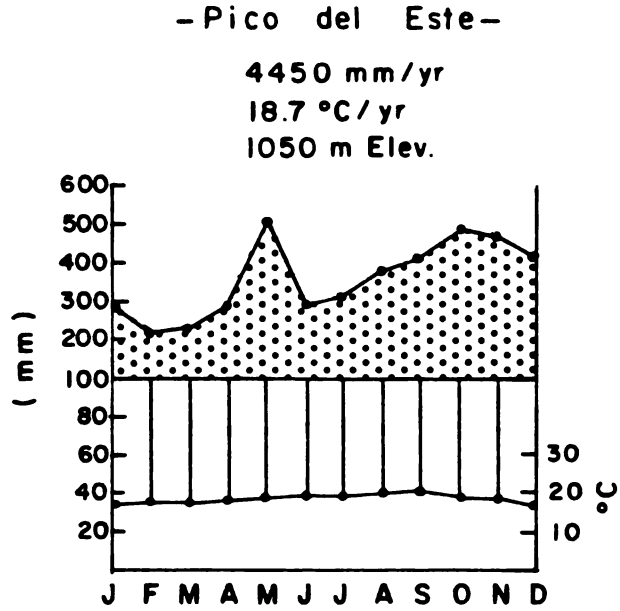

-Pico del Este-
4450 mm/yr
18.7 °C/ yr
1050 m Elev.
600
500
400
300
200
100
80
60
40
20
(mm)
30
20
10
°C
J F M A M J J A S O N D

Figure 2

these measurements were not concurrent, only general trends can be surmized.

The upper ridges and summits of the mountains are frequently enveloped in clouds, reducing solar insolation on El Yunque peak to just 60 percent of that in coastal areas (Briscoe 1966), and increasing the annual moisture available on the exposed summits by about 10 percent (Baynton 1968; Weaver 1972). Transpiration and evapotranspiration decrease with altitude; relative humidity and wind velocity increase (Briscoe 1966; Weaver et al. 1973).

The destructive force of hurricanes can impose long-term changes in the natural forest (Crow 1980). September is the month of most frequent occurrence followed by August and July (Fig. 3; Salivia 1972). Over 70 storms have occurred in Puerto Rico since the early 1700's, many of which probably caused localized damage to vegetation in the Luquillo Mountains. Of these, 13 were A storms (vortex of hurricane passed directly over the island with hurricane force winds) and 10 were B storms (vortex of hurricane may or may not have passed over the island, but only part of the island experienced hurricane force winds), for an average of one storm over at least part of the island every 12 years (Fig. 4). Of the A storms, four had trajectories directly over the Luquillo Mountains (Figs. 4 and 5). The last of these was San Cipriano in 1932.

Vegetation

Because certain audiences are better acquainted with particular forest classification schemes (i.e., local names (Table 1) in Puerto Rico, Beard's (1944, 1949) terminology in the Caribbean, and Holdridge's (1967) life zone system in continental Central and South America, and on larger

Figure 3. Monthly occurrence of 102 hurricanes in Puerto Rico, 1508-1970 (Salivia 1972). Oblique lines indicate hurricanes for which only the month was recorded. These were arbitrarily assigned to the middle of the month.

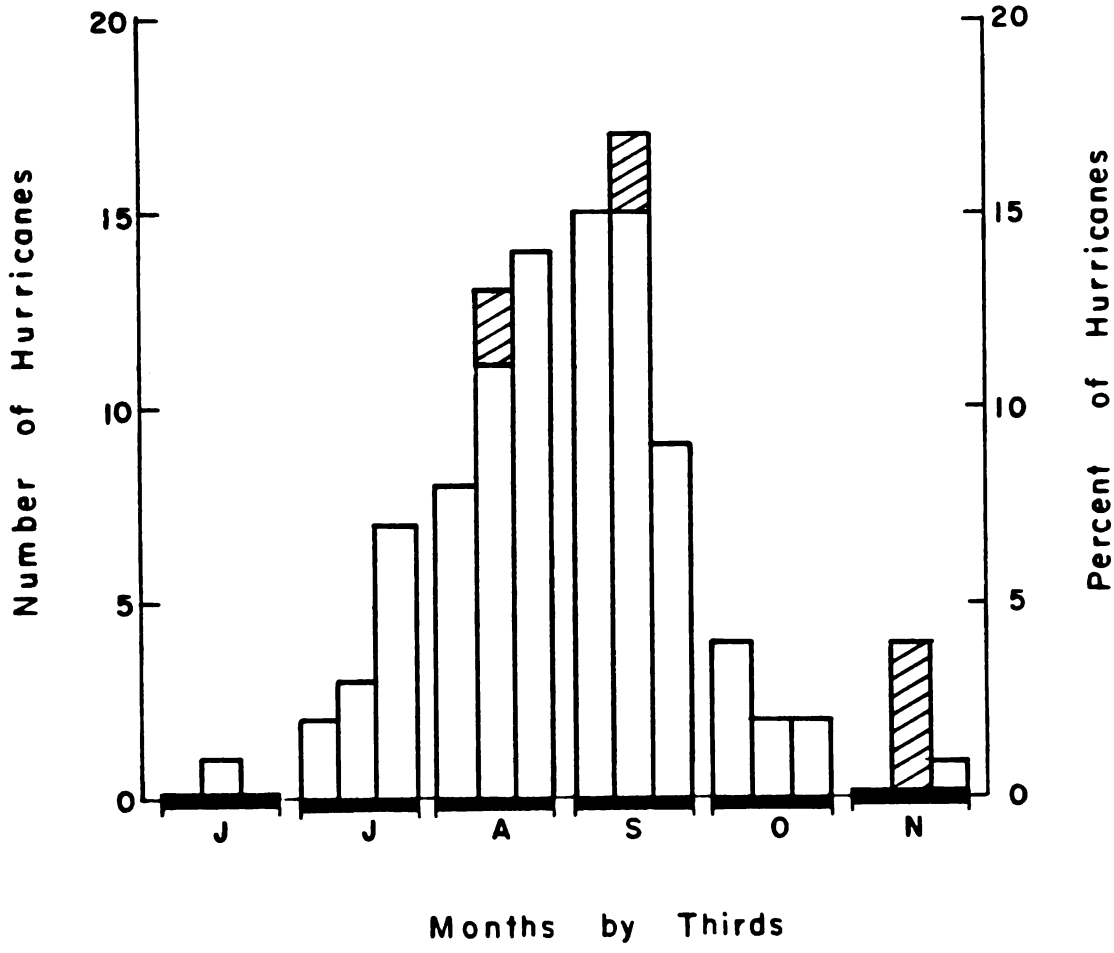

20
15
10
5
0
Number of Hurricanes
20
15
10
5
0
Percent of Hurricanes
J
J
A
S
O
N
Months by Thirds

Figure 3

Figure 4. Hurricane record for Puerto Rico from 1700 to 1970 (Salivia 1972). Long vertical I bar - type A storm (vortex of hurricane passes directly over the island with hurricane force winds); intermediate vertical I bar - type B storm (vortex of hurricane may or may not have passed over the island, but only part of the island experienced hurricane force winds); short vertical I bar - type C storm (vortex passed at some distance from the island, which experienced high winds (not hurricane force) and heavy rains); double I bar - two storms in the same year with intensity of second storm indicated by position of second I bar within the first; horizontal line from 1946 to 1981 - years of measurement of tree growth in the Luquillo Forest; black circle - type A storms that passed directly over the Luquillo Forest.

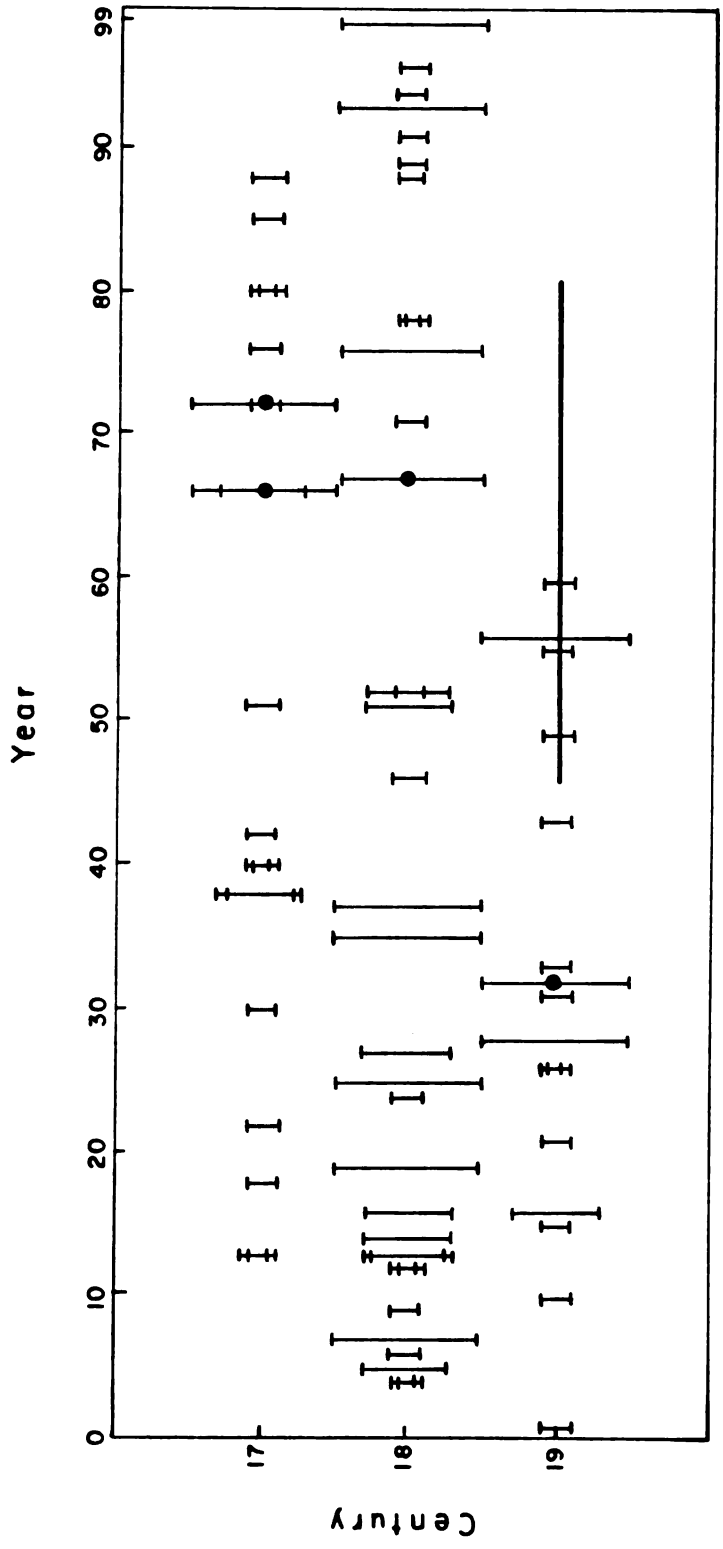


Figure 4

Figure 5. Path of type A hurricanes with trajectories directly over Puerto Rico from 1700 to 1970. Solid lines are known trajectories and dashed lines are assumed trajectories based on descriptions (adapted from Salivia 1972).

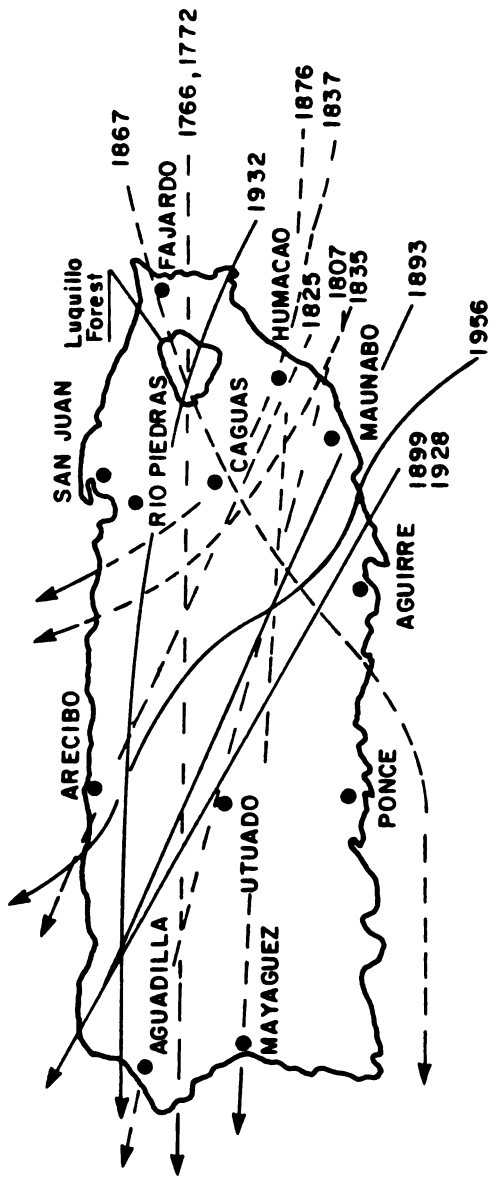

1867
1766, 1772
1932
1876
1837
Luquillo Forest
FAJARDO
HUMACAO
1825
1807
1835
1893
1956
SAN JUAN
RIO PIEDRAS
CAGUAS
MAUNABO
1899
1928
AGUIRRE
ARECIBO
UTUADO
PONCE
AGUADILLA
MAYAGUEZ

Figure 5

Table 1. Comparison of stand structure in four forests of the Luquillo Mountains[1]

Factor	Forests			
	Tabonuco	Colorado	Palm	Dwarf
Stems/ha	1800	1900	1750	3800
Canopy height (m)	20-30	8-20	8-15	3-8
Basal area (m^2/ha)	40-45	40-45	30	40-55
Volume (m^3/ha)	300-350	175-225	150-200	75-150
Leaf area index (m^2/m^2)	6-7	3-5	3.3	3-3.5

1 Estimates drawn from several stands (Institute of Tropical Forestry, unpublished files; Benedict 1976; Weaver 1983).

Caribbean islands), approximate equivalents are indicated here. Local names are given first. Tabonuco forest is Beard's lower montane rain forest, and Holdridge's subtropical wet or rain forest, depending upon rainfall. Colorado forest is Beard's montane rain forest, and Holdridge's lower montane wet or rain forest, again dependent upon rainfall. Palm forest is Beard's palm brake and an edaphic association in each of the aforementioned life zones of Holdridge. Finally, dwarf forest is also called dwarf by Beard and is an atmospheric association in either the lower montane wet or rain forests of Holdridge. Local forest names will be used hereafter to avoid confusion in text. Appropriate terminology from the life zone system will be indicated when there is a need to differentiate.

Ascending the Luquillo Mountains from a northeasterly direction, four forest types are encountered. The tabonuco forest, which extends from the forest border through about 600 m, is dominated by Dacryodes excelsa, Sloanea berteriana, and Manilkara bidentata in the overstory. The colorado forest, ranging generally from 600 through 900 m, contains Cyrilla racemiflora, Micropholis chrysophylloides, and M. garciniaefolia in the canopy. The palm forest, dominated by Prestoea montana, is found on steep slopes and arroyos above 500 m. Finally, the dwarf forest, a gnarled, epiphyte laden, and dense forest type with few tree species including Tabebuia rigida and Ocotea spathulata, is located on the exposed slopes and ridges above 900 m.

The colorado forest has two strata, evergreen foliage, and an abundance of superficial roots (Wadsworth 1949). A representative sample of trees greater than 10 cm in diameter on 4 ha contained 60 species averaging 830 stems/ha, 95 percent of which were less than 45 cm in

diameter (Wadsworth 1951). Forests similar in physiognomy to the colorado forest, according to the Holdridge system, occupy about 100,000 km^2 and constitute a little over two percent of the Caribbean and Central and South American region (Table 2). In addition, several islands of the Lesser Antilles not yet classified by the life zone system contain a relatively small area of "montane rain forest," which is Beard's terminology for the same or a very similar forest type (Beard 1944, 1949).

The most recent classification of the vegetation of the Luquillo Mountains (Ewel and Whitmore 1973) uses the life zone system (Holdridge 1967), and provides a basis for comparison among tropical forests in other areas. Along the same transect mentioned above, the following life zones are encountered: subtropical wet and rain forests at lower and intermediate elevations to the windward, respectively, lower montane rain forest on the summits, and descending to the leeward, lower montane wet forest, subtropical wet forest again, and finally, subtropical moist forest. Other classifications of the vegetation of the Luquillo Mountains are also available (Gleason and Cook 1927; Stehle 1945; Wadsworth 1951; Dansereau 1966).

A brief description of the vegetation according to the life zone system follows:

The subtropical wet forest life zone - This life zone is located at low to intermediate elevations and occupies 4150 ha or about 37 percent of the Luquillo Forest. Mean rainfall ranges from 2300 to 3800 mm/yr. The vegetation tends to form a closed canopy at 20 m and is generally rich in tree species, epiphytic ferns and bromeliads. Orchids are common.

The subtropical rain forest life zone - This life zone is found at intermediate elevations to the windward where it occupies 1420 ha or 13

Table 2: An approximation of the areal extent of colorado forest elsewhere in Latin America[1/].

Geographic Area Country (reference)	Area (km^2)	Percent of total area
Caribbean		
Haiti (OAS 1972)	1,820	6.3
Dominican Republic (Tasaico 1967)	3,215	6.7
Puerto Rico (Ewel and Whitmore 1973)	110	1.2
Jamaica (Gray and Symes 1969)[2/]	1,360	11.9
Subtotal	6,505	6.5
Central America		
Guatemala (Holdridge 1959a)	3,150	2.9
Honduras (Holdridge 1962a)	2,430	2.1
El Salvador (Holdridge 1959b)	340	1.6
Nicaragua (Holdridge 1962b)	-----	---
Costa Rica (Tosi 1969)	4,100	7.8
Panama (FAO 1971)	-----	---
Subtotal	10,020	1.9
South America		
Venezuela (Ewel et al. 1968)	8,800	0.9
Colombia (Espinal et al. 1963)	45,220	4.0
Ecuador (Vivanco de la Torre et al., no date)	6,490	2.4
Peru (Tosi 1960)	22,430	1.7
Subtotal	82,940	2.2
Grand Total	99,460	2.3

[1/] Areas determined as Lower montane wet forest according to Holdridge (1967) life zone classification.

[2/] Information based on climatic and topographic data only.

percent of the forest. Mean rainfalls exceed 3800 mm/yr. The vegetation forms a closed canopy at 20 m. Palms and epiphytes are more abundant than in the previous type.

The lower montane wet forest life zone - This life zone is located mainly to the leeward of the summit areas and occupies 4300 ha or 38 percent of the forest. Mean rainfall ranges between 2900 and 3800 mm/yr. The vegetation varies from 12 to 15 m in height and is characterized by reddish-brown, corriaceous leaves. Palms and epiphytes are abundant.

The lower montane rain forest life zone - This life zone is concentrated on the windward ridges and summits of the Luquillo Mountains and occupies 1180 ha or about 10 percent of the forest. Mean rainfall exceeds 4300 mm/yr. The vegetation is similar to that of the above life zone but has more epiphytes. The dwarf cloud forest association, principally situated on the exposed peaks, has few tree species.

The subtropical moist forest life zone - This life zone is found in a disjunct section of the forest southwest of the main portion and occupies 150 ha or about one percent of the forest. Mean rainfall is slightly under 2000 mm/yr. Scattered remnants of the zonal vegetation are characterized by trees to 20 m in height, many of them deciduous during the dry season. Species diversity is high.

In the Luquillo Mountains, the number of trees and basal area per hectare tend to increase, whereas mean height of the dominant trees, mean and maximum tree diameter, and the number of tree species all tend to decrease with an increase in elevation (White 1963). Comparative structural information for the montane forests of the Luquillo Mountains is shown in Table 1. Of the 225 tree species native to the forests of the Luquillo Mountains, 41 percent are also found on the continents (South

America, Central America, Mexico and Florida), 28 percent are found in the West Indies but not on the continents, and 31 percent are endemic to Puerto Rico (Little and Woodbury 1976).

Past Research in the Luquillo Forest

The forests of the Luquillo Mountains rank among the best studied tropical forests in the world with numerous publications on the flora, fauna, and related topics. A complete bibliography on research does not exist but citation of a few major works will point out the extent of the investigations.

From 1968 through 1977, beginning with an article introducing the research (Howard 1968), some 17 studies appeared in the Journal of the Arnold Arboretum concerning the dwarf forest in the vicinity of Pico del Oeste. Wadsworth (1970) cited 118 references on geography, climatology, geology, flora, fauna, ecology, archeology, agriculture and forestry for the Luquillo Mountains. Odum and Pigeon (1970) presented a large compendium of information on plant and animal life and the effects of radiation, mainly in the tabonuco forest. A more recent history of research and opportunities for additional investigation (Brown et al. 1983) listed many of the previous works as well as studies completed since their publication.

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PART I

CHANGES IN FOREST STRUCTURE AND GROWTH AFTER HURRICANE DISTURBANCE

INTRODUCTION

Cyclones and hurricanes accompanied by heavy rains occur commonly in the Caribbean and have an impact on forest ecosystems and local economies (Howard 1962; Salivia 1972; Tomblin 1981). When the trajectories of 761 cyclones since 1886 with windspeeds between 40 and 120 km/hr are plotted on a basin-wide map of the Caribbean, all of the islands are obscured by black ink (Neumann et al. 1978). About 100 hurricanes passed over or very close to Puerto Rico between 1508 and 1970 (Salivia 1972); those occurring in 1766, 1772, 1867 and 1932 passed directly over the Luquillo Mountains.

Defoliation, breakage and windthrow are common effects of hurricanes in forests (Lugo et al. 1983; Wilkinson et al. 1978). The severity of disturbance is related to storm intensity (Sauer 1962), forest structure (Wadsworth and Englerth 1959), and soil conditions (Cremer et al. 1977; Wilson 1976; Wood 1970). Understanding the response of ecosystems to random events such as hurricanes requires aedequate sampling on permanent plots (Bormann and Likens 1979; Callahan 1984). Such monitoring in the tropics today is limited to Venezuela (Veillon 1983) and Puerto Rico (Lugo and Brown 1981; Weaver 1979, 1983), where records are available for 30 and 40 year periods, respectively. Partial analysis of the Puerto Rican data has provided limited information on growth and changes in forest structure and species composition over time (Crow 1980; Weaver 1983). However, this study is the first to provide a detailed analysis of all data sets for a specific forest.

In 1928, San Felipe passed over Puerto Rico southwest of the Luquillo Mountains, and in 1931, San Nicolas passed just north of the island. The only precise data available on recovery after San Felipe indicated the elapsed time before certain tree species refoliated in the Luquillo district (Bates 1929). Both presumably caused localized damage within the forest but no description of this damage exists. San Cipriano of 1932 passed directly over the Luquillo Forest with winds of 200 km/hr and rainfalls in excess of 40 cm (Crow 1980). Again, no direct observations of damage in the forest are available.

Cyrilla racemiflora is long-lived and reaches large diameters in the colorado forest. The recent loss of several large trees suggested that its regeneration might be associated with past disturbances, particularly destructive hurricanes. Because it survives for long periods, its diameter class distribution might be compared with hurricanes during the past three centuries. Eight permanent plots, established in the colorado forest in 1946-47, were used to test the hypothesis that recovery from substantial damage would cause changes in forest structure and species composition. In addition, growth data for Cyrilla were used to estimate the relationship between its diameter and age.

The colorado forest type is widely distributed in the Caribbean Basin and in Central and South America (Table 2). A knowledge of its reaction to disastrous hurricanes is important not only to ecologists as they refashion their thinking on the function of disturbance and succession in natural ecosystems (Cairns 1980; Ewel 1980; Pickett and White 1985), but also to foresters whose management policies and silvicultural practices may be modified by these catastrophic events.

METHODS

The eight permanent 0.4 ha plots used in this study were established in the mid-1940's to determine diameter growth. Three plots, located on lower slope and valley topography ranging from 650 to 750 m in elevation, occasionally flooded in riparian areas. Four plots, located on slope topography ranging from 700 to 900 m in elevation, had better drained soils. The remaining plot, on slope topography at 670 m in elevation, was thinned at the beginning of the study. Its basal area was reduced from about 40 to 20 m^2/ha providing a balance between large and small individuals for sustained yield. Canopy trees were allowed at least 2 m of crown freedom on all sides (Wadsworth 1957). Hereafter, the term natural forest will be used to indicate a plot where no silviculture was practiced -- that is, no thinning or stand improvement. The thinned stand will be referred to as thinned. All stands were subjected to natural disturbances such as high winds, heavy rains and hurricanes.

All trees $\geq$4.1 cm at breast height (dbh, or 1.4 m above the ground) were measured to the nearest 0.1 inch (0.25 cm). Height was estimated visually to the nearest 0.5 m and checked occasionally by abney level on all natural forest plots. Height was not estimated on the thinned plot. Crown classes were recorded as dominant, codominant, intermediate or suppressed (Baker 1950). Dominant trees rise above the general level of the canopy and receive light from above and to some extent laterally. Codominant trees reach the level of the canopy and receive light from

above. Intermediate trees are below the general level of the canopy but receive some direct light through gaps. Suppressed trees are overtopped and receive no direct light. Some of the plots were visited again in 1951, 1956 and 1976, but neither tree nor stand measurements were complete. Species were tallied, but height was not recorded and ingrowth (recruitment, or trees that grew into the minimum diameter class) was partially recorded but trees were never tagged.

Detailed tree measurements on all plots were made again in 1981. Diameter was measured to the nearest 0.1 cm and height was determined by rangefinder to the nearest 0.1 m. Untagged trees were assessed by their diameter and position as either old trees that had lost their tags or ingrowth that had not yet been tagged. Missing trees were recorded as mortality.

Basal area, volume and biomass were determined for each plot. Heights for use in volume and biomass estimates on the thinned plot at the time of establishment, and for the determinaton of volume and biomass of dead stems from mortality which occurred in the years 1951, 1956 and 1976, were estimated by a height vs. diameter curve based on data for dicot species from other plots where diameters had been measured and heights estimated simultaneously. Trees that died between measurements were assumed to continue diameter growth at the rate of the mean tree in the stand for half of the interim between the last live measurement and the time when the tree was recorded as dead. With palms, mean height growth was used in the same manner.

Statistical testing for differences in mean annual diameter increment (MAI) by crown class was analyzed with Duncan's multiple range test (Steel and Torrie 1960). Dicot tree volumes, including branches $\geq$2.5 cm in

diameter, were determined using an existing equation derived in English units for the construction of volume tables in the colorado forest (Wadsworth 1949). This equation would likely be useful for volume estimates in similar forests in the Caribbean region. The equation converted to metric units is:

$$\text{Volume } (m^3) = (0.000074931\ D^{1.8748}\ H^{0.9165}.$$

The r^2 for the original equation is not available, but the relationship was derived from 302 trees of 35 species and had a mean deviation of 14.83 percent and an aggregate difference of 1.07 percent (Wadsworth 1949). These are mensurational measures (Chapman and Meyer 1949) and are defined thus: mean deviation, the average of the differences or deviations of single observations from the means of these observations, without consideration of the sign of the differences (equal to approximately 80 percent of the standard deviation); and aggregate difference, 100 times (the sum of actual tree volumes minus the sum of estimated tree volumes) divided by the sum of actual tree volumes. It indicates goodness of fit of sample data to the developed volume table charts. Aboveground woody biomass estimates were then derived by multiplying individual tree volumes by their respective specific gravities (Jordan and Farnworth 1982). The latter were obtained from published sources (Little and Wadsworth 1964, Little et al. 1974) or from the Forest Products Laboratory in Madison, Wisconsin. A few small, rare or endangered species, were arbitrarily assigned a value of 0.6 g/cm^3, the weighted average specific gravity for the forest. Palm volumes were determined by multiplying cross sectional area by height, then adjusted for biomass by multiplying with specific gravity.

Tree diameters were grouped into 5 or 10 cm classes (except for the smallest and largest classes), tree heights into 3 m classes, and specific gravity into decimal classes, in both 1946 and 1981, to observe trends in forest recovery and growth. Changes in crown classes were also observed.

Age of Cyrilla racemiflora trees was estimated as follows (Osmaston 1956):

(1) Six 10 cm diameter classes were selected between 20 and 80 cm. The seventh and largest diameter class, >80 cm, was chosen so that its midpoint was equal to the mean diameter of the measured trees within it;

(2) For diameter classes ≥20 cm, MAI was determined for all trees within the respective classes. Those trees not attaining a growth rate at least 50 percent of the class mean were eliminated (Webb 1964) under the assumption that they would not grow into the next diameter class;

(3) MAI of the ingrowth on the thinned plot was used for the diameter class 0 to 19.9 cm. All trees were assumed to have regenerated at the time of thinning, or to be of maximum possible age, that is, 34 years old. MAI was calculated for all trees. Again, those trees with diameter increment ≥50 percent of the diameter class mean were used to calculate a new mean for the diameter class under the assumption that those individuals were the oldest on the plot and most likely to survive into the next diameter class. The new mean was used as the growth rate for trees from 0 to 19.9 cm dbh;

(4) The MAI's for diameter classes ≥20 cm were then plotted vs. the midpoint (i.e., the calculated mean for all stems) of each diameter class. A least squares linear regression was fitted to the data points ≥20 cm;

(5) Adjusted or fitted MAI's were read from the curve at the midpoint of each diameter class $\geq$20 cm and divided into the width of the class to yield the time in years required for the mean tree to move through the class;

(6) The cumulative time for the mean trees to move through the respective diameter classes was then determined;

(7) Finally, an age curve was generated by plotting the upper endpoints of the diameter classes on the ordinate axis vs. the cumulative ages on the abscissa. Graphing in this manner facilitates comparison of colorado growth with diameter/age relationships of other species.

The age curve was then compared with the diameter class distribution of Cyrilla to determine if its regeneration pattern was correlated with past hurricane disturbance in the colorado forest.

Percent importance values based on the relative density, relative frequency and relative basal area of each species (Kershaw 1973; Brown and Curtis 1952) were determined for 1946 and 1981 to elucidate species trends. Percent similarity, the summation of the lowest percentages (percentage = the number of individuals per species/total number of individuals per plot) by species within each pair of stands being compared (Brower and Zar 1977) was used to estimate community similarity among plots. The Shannon-Wiener Index (Krebs 1972), which is a function of both the number of species (variety) and their relative abundances (equitability), was used to determine species diversity on natural forest plots. A species count was also used.

Trends in species composition were studied by following the survival and changes in stem numbers and basal area of 'indicator' species which represented a spectrum of ecological roles in the colorado forest

community. The species selected (Little and Wadsworth 1964; Little et al. 1974) were: Hedyosmum arborescens and Psychotria berteriana, small, short-lived, understory trees maturing at 10 cm in diameter and 6 m tall, found mainly in small openings in the forest; Cecropia peltata and Didymopanax morototoni, common, intermediate to large-sized pioneer trees, found in secondary forests and in gaps in primary forests in the American tropics, growing to 30 to 50 cm in diameter and 15 to 20 m tall; Miconia laevigata, a small to intermediate-sized tree, reaching 15 cm in diameter and 8 m tall, widely scattered in the lower part of the colorado forest mainly in small openings; Cyrilla racemiflora, a long-lived, large, canopy tree, occasionally attaining sizes of 100 cm or more in diameter and 15 m tall, whose regeneration is tied to gaps in the mature forest; Cordia borinquensis, a common, shade tolerant, understory tree, to 15 cm in diameter and 7 m tall, capable of regenerating and growing under a canopy; Prestoea montana, a shade tolerant canopy palm reaching 15 m tall, most common on steep, unstable soils and along drainages throughout the colorado forest; and Micropholis crysophylloides and M. garciniaefolia, both shade tolerant, canopy trees reaching 50 to 60 cm in diameter and 15 m tall. Rare and endangered species were tallied separately by topography and elevation to elucidate their distributions within the forest.

Species nomenclature used was that of "Common trees of Puerto Rico and the Virgin Islands" (Little and Wadsworth 1964; Little et al. 1974).

RESULTS

Stand Changes

Ingrowth, mortality and number of stems

The number of stems at the beginning and end of the study for all natural forest plots combined was virtually the same. The means and standard errors of stem numbers/ha were 1860 ± 73 in 1946 and 1858 ± 89 in 1981 (Table 3). Ingrowth averaged 20.0 ± 2.2 stems/ha/yr and mortality averaged 20.0 ± 0.8 stems/ha/yr. Annual flux for ingrowth and mortality averaged 1.1 percent of the original stem density.

When stem density on plots is considered by topography, the four slope plots declined by 6 percent while the two valley plots increased by 9 percent from 1946 to 1981. The plot with mixed slope and valley topography also increased in stem density by 2 percent.

In contrast, the previously thinned plot had three times more ingrowth than mortality. Survival of stems measured in 1946 was highest on the thinned plot with over 70 percent while it varied between 50 to 70 percent on the natural forest plots.

Diameter class distribution

The smallest diameter class on the natural forest plots showed a 15 percent decline from nearly 1060 stems/ha to about 900 stems/ha (Fig. 6). In contrast, the 10.0 to 14.9 cm diameter class increased by 33 percent or 100 trees/ha. The remaining classes between 15.0 and 49.9 cm, with the

Table 3. Original stem densities, survival, ingrowth, mortality, and final stem densities for the Colorado forest plots from 1946 to 1981.

Plot[1]	Stem densities (stems/ha)				Survival[2]	Mortality		Ingrowth	
	1946	Mortality	Ingrowth	1981	%	Stems/ha/yr	%/yr[3]	Stems/ha/yr[3]	%/yr[4]
A	2191	647	442	1986	70.5	18.5	0.84	12.6	0.58
B	1788	618	467	1637	65.5	17.6	0.99	13.3	0.75
C	1670	815	748	1603	51.2	23.3	1.39	21.4	1.28
D	1808	635	640	1813	64.9	18.1	1.00	18.3	1.01
Mean	1864	679	574	1760	63.6	19.4	1.00	16.4	0.88
E	1635	684	724	1675	58.2	19.5	1.19	20.7	1.27
G	1939	721	904	2122	62.8	20.6	1.06	25.8	1.33
H	1988	788	968	2168	60.4	22.5	1.13	27.7	1.39
Mean	1964	754	936	2145	61.6	21.5	1.10	26.7	1.36
Mean[5]	1860±73	701±29	699±76	1858±86	62.3	20.0±0.8	1.09	20.0±2.2	1.09
I	1961	558	1803	3206	71.5	15.9	0.81	51.5	2.63

[1]Plots A through D are slopes; plot E is slope and valley; plots G and H are valleys; plot I was thinned.

[2]Survival % = (1946 density - mortality)/1946 density.

[3]Mortality % = (Mortality/1946 density)/35 years.

[4]Ingrowth % = (Ingrowth/1946 density)/35 years.

[5]Mean for all natural forest plots combined.

Figure 6. Diameter class distributions for seven natural forest permanent plots and one thinned permanent plot in the colorado forest in 1946 and 1981.

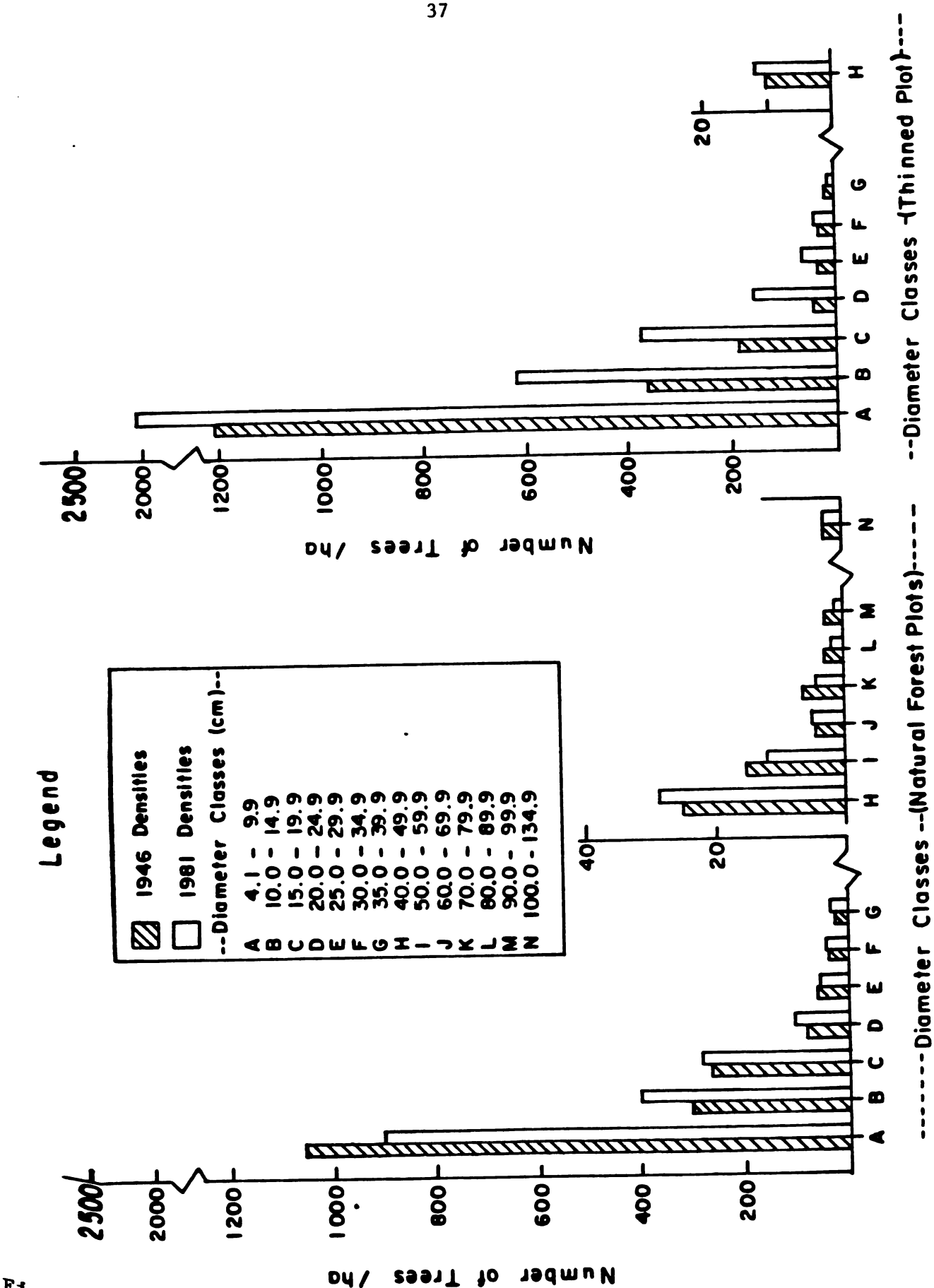
Legend
1946 Densities
1981 Densities
--Diameter Classes (cm)--
A 4.1 - 9.9
B 10.0 - 14.9
C 15.0 - 19.9
D 20.0 - 24.9
E 25.0 - 29.9
F 30.0 - 34.9
G 35.0 - 39.9
H 40.0 - 49.9
I 50.0 - 59.9
J 60.0 - 69.9
K 70.0 - 79.9
L 80.0 - 89.9
M 90.0 - 99.9
N 100.0 - 134.9
Number of Trees /ha
2500
2000
1200
1000
800
600
400
200
40
20
A B C D E F G H I J K L M N
------Diameter Classes --(Natural Forest Plots)-----
Number of Trees /ha
2500
2000
1200
1000
800
600
400
200
20
A B C D E F G H
--Diameter Classes -(Thinned Plot)---

Figure 6

exception of the 25.0 to 29.9 cm class, also showed an increase in stem numbers ranging from 4 to 18 trees/ha. The diameter classes ≥50 cm showed either a slight decline in the number of stems, or remained about equal.

All of the plots, regardless of topography, showed a decrease in the smallest diameter class ranging from 11 percent in the valleys through 13 percent on the slopes to 23 percent on the mixed plot (Fig. 7). Moreover, all showed an increase in the 10.0 to 14.9 cm diameter class varying from 13 percent on the slopes through 61 percent in the valleys to 66 percent on the mixed plot. The valley plots showed an increase in all diameter classes from 1 .0 to 49.9 cm whereas the mixed plot remained about equal or increased in these classes. The slope plots showed more variability, but the trend was toward an increase. Diameter classes ≥50 cm for all groupings of plots fluctuated slightly between measurements but demonstrated a general decline with mortality of larger stems.

In contrast, the thinned plot showed an increase of stems in all diameter classes except for a slight decline in the 35.0 to 39.9 cm class.

Height class distribution

The trend in height class distribution on the natural forest plots parallels that of the diameters. The smallest class, 0 to 2.9 m, decreased between 10 and 84 percent, with the smallest decline on the mixed plot (Fig. 8). The next size class, from 3.0 to 5.9 m also showed a decline, ranging from 35 to 81 percent. All remining size classes increased in numbers of stems, some of them considerably. The most notable gains were in the 9.0 to 11.9 m and 12.0 to 14.9 m classes in the valley plots.

Figure 7. Diameter class distributions by topography for natural forest permanent plots in the colorado forest in 1946 and 1981.

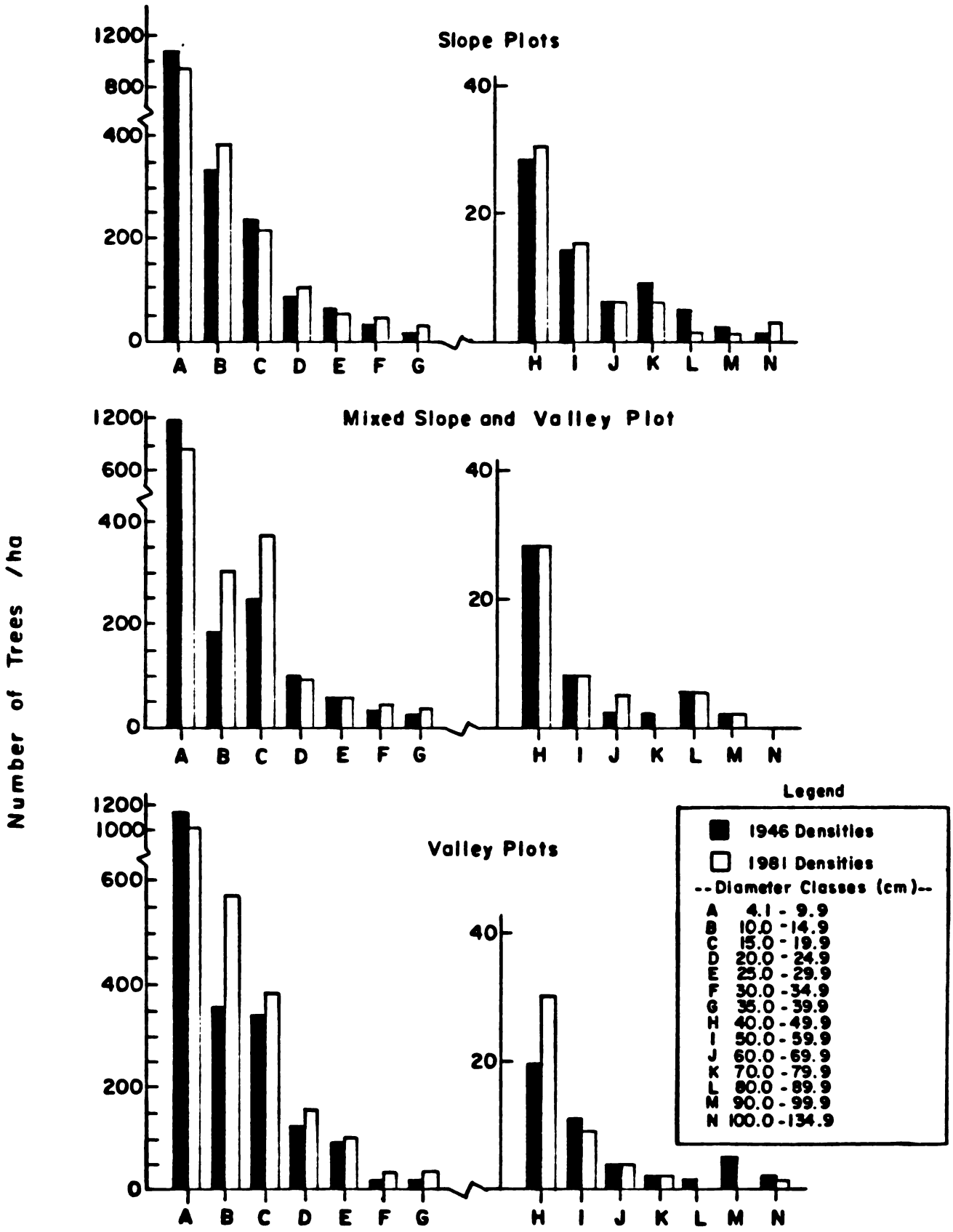
Slope Plots
Mixed Slope and Valley Plot
Valley Plots
Number of Trees /ha
1200
800
400
200
0
1200
600
400
200
0
1200
1000
600
400
200
0
40
20
A B C D E F G H I J K L M N
Legend
1946 Densities
1981 Densities
--Diameter Classes (cm)--
A 4.1 - 9.9
B 10.0 - 14.9
C 15.0 - 19.9
D 20.0 - 24.9
E 25.0 - 29.9
F 30.0 - 34.9
G 35.0 - 39.9
H 40.0 - 49.9
I 50.0 - 59.9
J 60.0 - 69.9
K 70.0 - 79.9
L 80.0 - 89.9
M 90.0 - 99.9
N 100.0 - 134.9
Diameter Classes

Figure 7

Figure 8. Height class distribution by topography for natural forest permanent plots in the colorado forest 1946 and 1981.

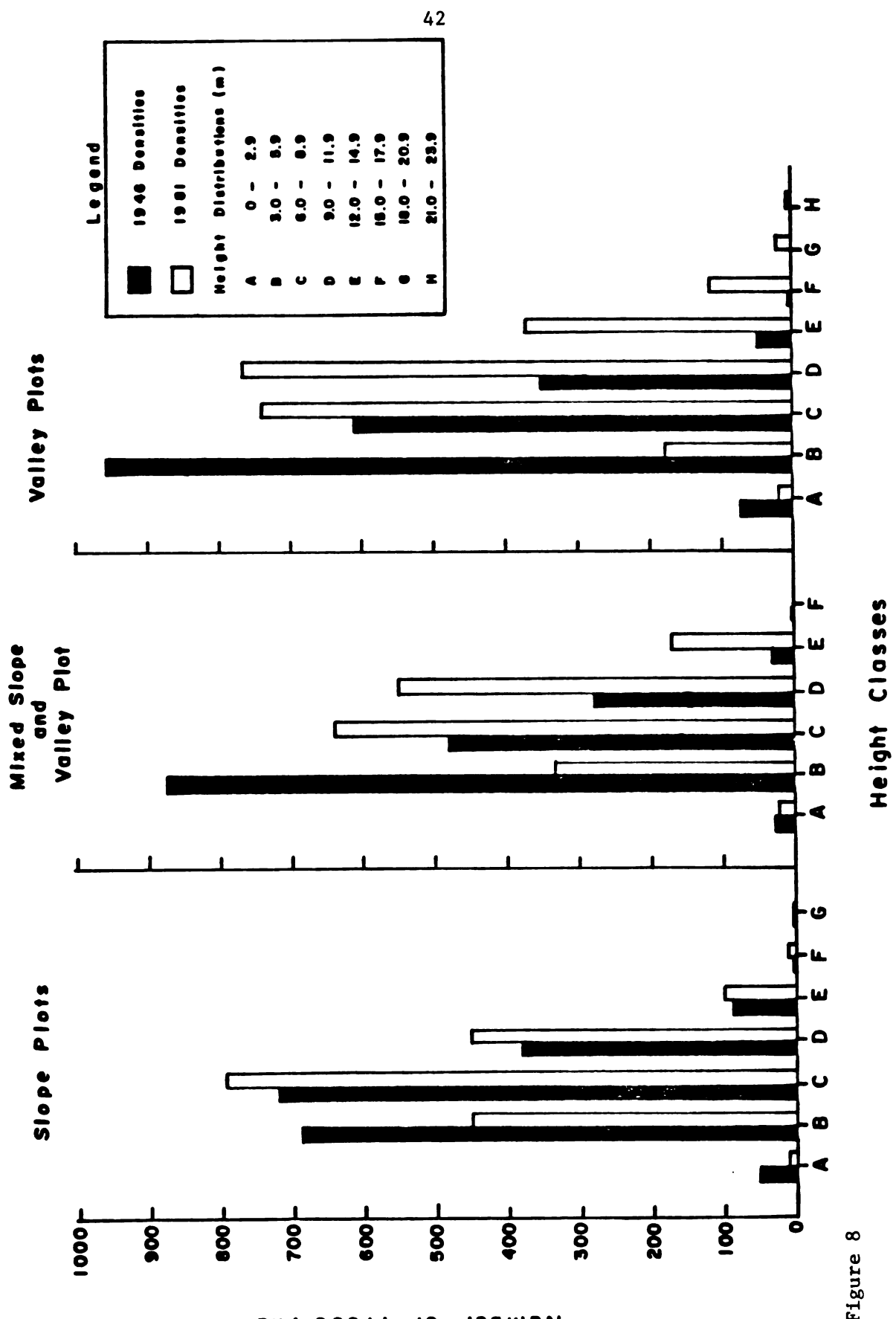
Legend
1948 Densities
1981 Densities
Height Distributions (m)
A 0 - 2.9
B 3.0 - 5.9
C 6.0 - 8.9
D 9.0 - 11.9
E 12.0 - 14.9
F 15.0 - 17.9
G 18.0 - 20.9
H 21.0 - 23.9
Slope Plots
Mixed Slope and Valley Plot
Valley Plots
Number of Trees /ha
0
100
200
300
400
500
600
700
800
900
1000
A B C D E F G
A B C D E F
A B C D E F G H
Height Classes

Figure 8

Because heights were not measured on the thinned plot in 1946, changes of height classes during the period of measurement could not be determined.

Crown class distribution

The dominant and intermediate crown classes on all the natural forest plots decreased by about 70 stems/ha, or 3 percent, from 1946 to 1981, while the suppressed crown class increased by about 175 stems/ha, or 6 percent (Fig. 9). The codominant crown class remained virtually unaltered. Despite these changes, the pattern of crown class distribution in both years is similar; 45 to 50 percent in the suppressed class, 25 to 30 percent in the intermediate class, and 10 to 12 percent apiece in the dominant and codominant classes.

In contrast, the previously thinned plot had 60 percent of the stems in the intermediate crown class in 1946 but only about 10 percent in 1981. The suppressed class increased from about 10 percent to over 50 percent in the same period of time. The percentage of stems in both the dominant and codominant crown class approximately doubled.

Specific gravity distributions

About 35 percent of the stems on the natural forest plots in 1946 and 1981 were found in the specific gravity class from 0.60 to 0.69 g/cm^3 with another 30 percent between 0.70 and 0.79 g/cm^3 (Fig. 10). When basal area or volume was substituted for number of stems, however, 40 to 43 percent were found in the 0.50 to 0.59 g/cm^3 class in 1946 and about 30 percent in the same grouping in 1981. The 0.60 to 0.69 g/cm^3 class had about 28 percent in 1946 and about 35 percent in 1981.

Figure 9. Crown class distribution for the natural forest and thinned permanent plots 1946 and 1981.

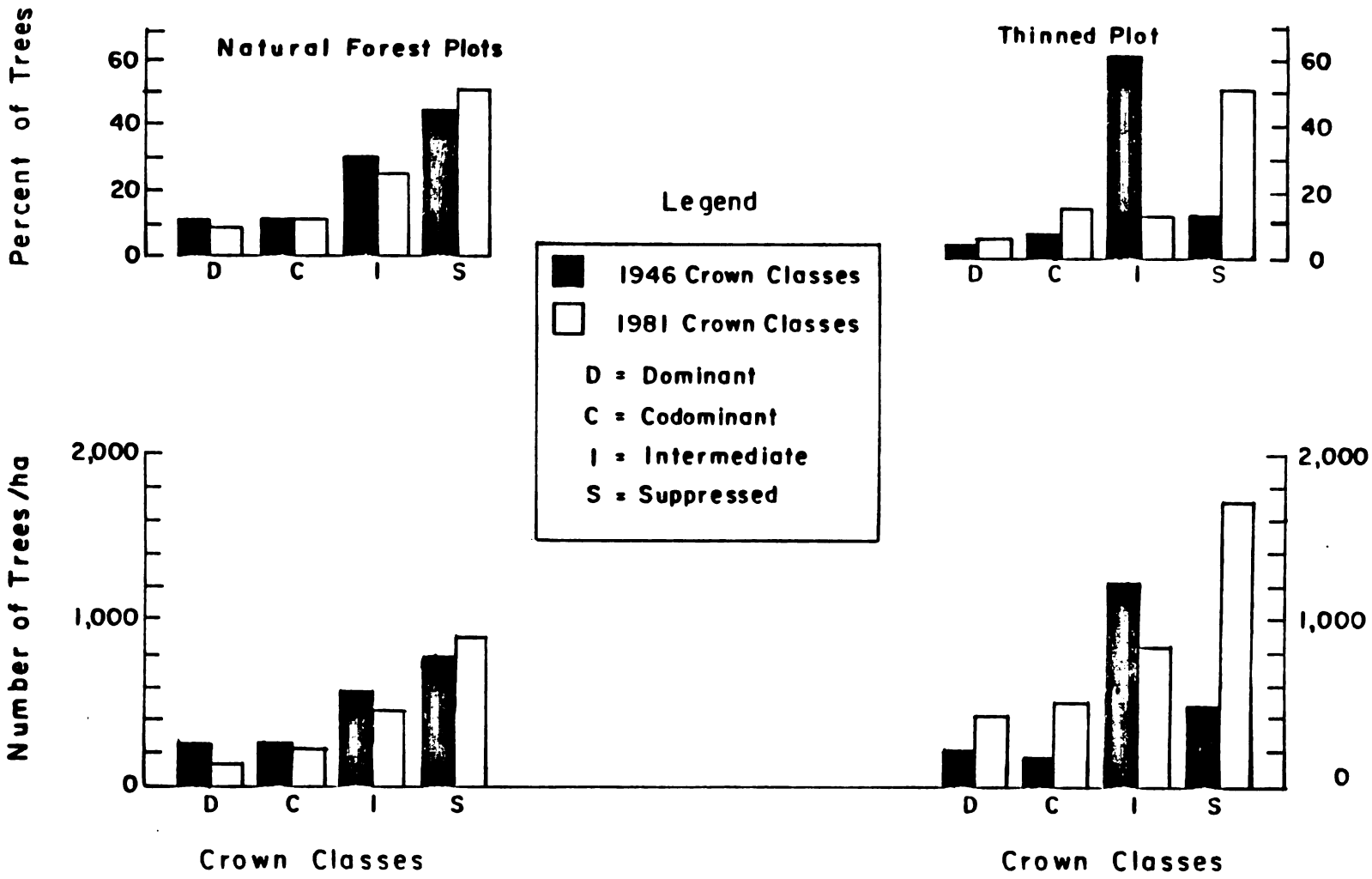
Percent of Trees
Natural Forest Plots
Thinned Plot
60
40
20
0
D
C
I
S
Legend
1946 Crown Classes
1981 Crown Classes
D = Dominant
C = Codominant
I = Intermediate
S = Suppressed
Number of Trees/ha
2,000
1,000
0
Crown Classes

Figure 9

Figure 10. Specific gravity by groupings (0.25 = 0.2 to 0.29, etc.) for number of stems, basal area, and volume in 1946 (shaded) and 1981 (unshaded) on the natural forest and thinned permanent colorado plots.

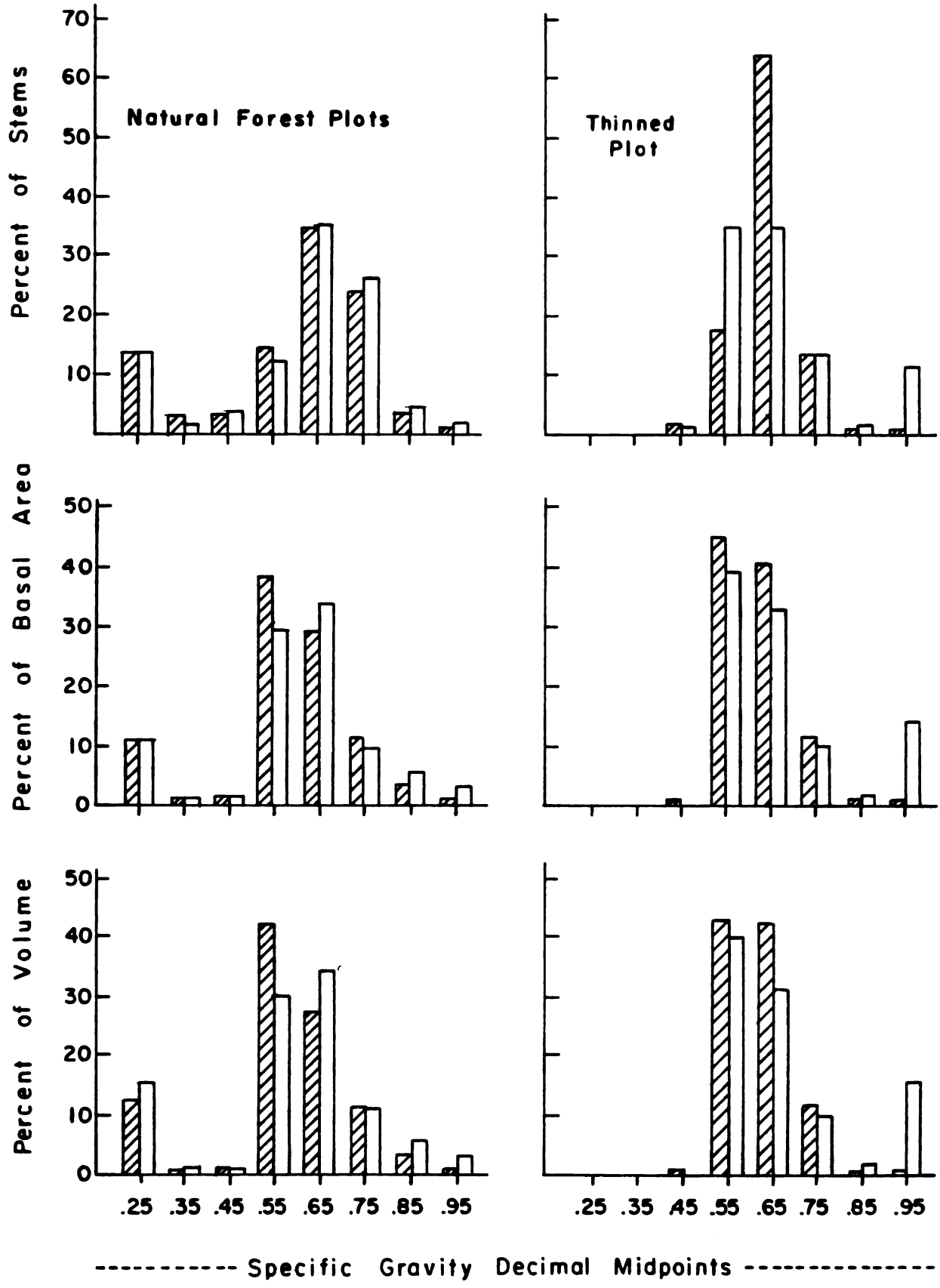
Natural Forest Plots
Thinned Plot
Percent of Stems
Percent of Basal Area
Percent of Volume
70
60
50
40
30
20
10
0
.25 .35 .45 .55 .65 .75 .85 .95
---------- Specific Gravity Decimal Midpoints ----------

Figure 10

The weighted mean specific gravity for all trees, based on their respective volumes, showed a 1.9 percent increase from 0.563 to 0.574 g/cm^3 between 1946 and 1981 for the entire forest. This estimate includes palms which have a low specific gravity. When palms are excluded from the sample, mean specific gravity for all dicots, based on their respective volumes, showed a 3.9 percent increase from 0.608 to 0.632 g/cm^3.

The thinned plot had fewer specific gravity classes than the natural forest plots mainly because of the selective removal of species. The increase in the percent of stems in both the 0.50 to 0.59 and 0.90 to 0.99 g/cm^3 classes reflected the massive influx of Cyrilla racemiflora and Clusia krugiana, respectively. The decline in the 0.60 to 0.69 class was due mainly to the mortality of Micropholis garciniaefolia. When considered on the basis of basal area and volume, the pattern in the 0.50 to 0.59 class was reversed because much of the Cyrilla ingrowth was of small diameter, and was offset by the mortality of larger stems in the same specific gravity class. The mean specific gravity for all stems showed an increase from 0.60 to 0.66 g/cm^3. The change in mean specific gravity was greater than that on the natural forest plots because of the influx of Clusia and the abscence of palms.

Changes in Species Composition

Survival of indicator species

Nearly all of the Hedyosmum arborescens and all of the Psychotria berteriana stems originally found on the natural forest plots in 1946 had disappeared by 1981 (Fig. 11). When ingrowth was added to survival, however, the 1981 populations of these species amounted to 10 and 19

Figure 11. Percent survival of indicator species in the colorado forest from 1946 to 1981. Lines indicate survival of original trees. Dot is 1981 population of trees (survival of residual trees and ingrowth). Bars indicate basal area: shaded bars, 1946 basal area; unshaded bars, 1981 basal area survivor and growth on survivors; and obliquely-lined bars, 1981 total basal area, growth of residual basal area and ingrowth. Number of trees/ha are indicated for slope (S), slope and valley (M), and valley (V) plots.

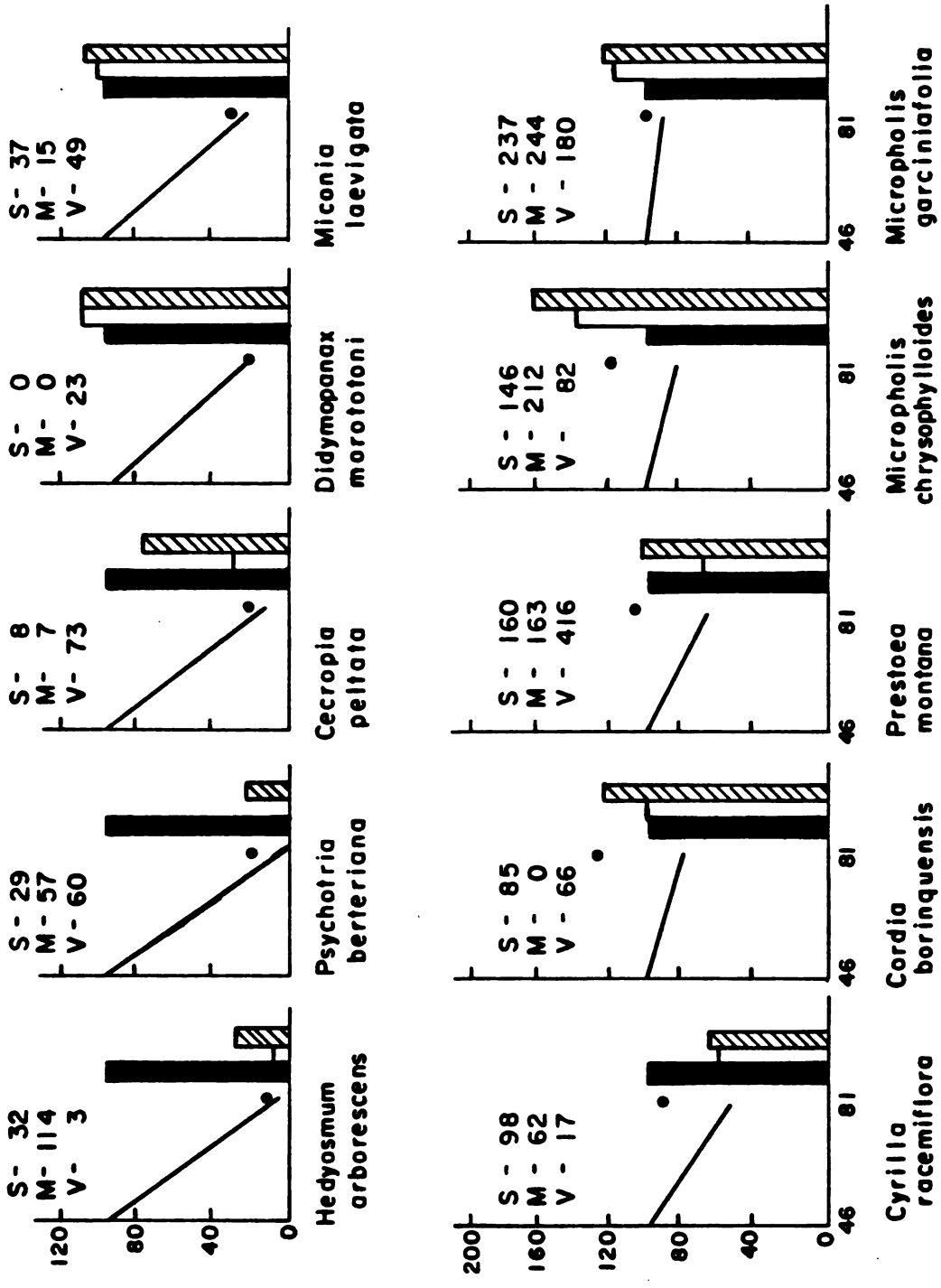
Percent Survival (trees and basal area)
S- 32
M- 114
V- 3
Hedyosmum arborescens
S- 29
M- 57
V- 60
Psychotria berteriana
S- 8
M- 7
V- 73
Cecropia peltata
S- 0
M- 0
V- 23
Didymopanax morototoni
S- 37
M- 15
V- 49
Miconia laevigata
S - 98
M - 62
V - 17
Cyrilla racemiflora
S - 85
M - 0
V - 66
Cordia borinquensis
S - 160
M - 163
V - 416
Prestoea montana
S - 146
M - 212
V - 82
Micropholis chrysophylloides
S - 237
M - 244
V - 180
Micropholis garciniafolia
0
40
80
120
160
200
46
81

Figure 11

percent, respectively, of the 1946 populations. Moreover, the percent importance of Hedyosmum and Psychotria had declined from 1.4 to 0.5 and from 1.5 to 0.7, respectively (Table 4). The 1981 total basal area (growth on residual trees + ingrowth) was 30 percent of the 1946 value for Hedyosmum and 23 percent for Psychotria.

Cecropia peltata, Didymopanax morototoni, and Miconia laevigata also declined to 20 percent or less of their 1946 densities. Their percent importance values decreased from 1.2 to 0.7, 0.4 to 0.3, and from 1.5 to 0.9, respectively. Regeneration of these species between measurements ranged from 0 to 10 percent of their 1946 populations. The 1981 total basal areas, however, were higher than for the previous species, and ranged from 80 to 110 percent of the 1946 basal areas. This was due mainly to the larger size and longer survival of these species.

Cyrilla racemiflora lost 45 percent of the stems present in 1946. Regeneration of new stems, however, left the total population of trees only slightly lower in 1981. Total basal area in 1981 was only 65 percent of that in 1946. Since many of the stems that perished were large in diameter, the percent importance declined considerably from 11.9 to 7.5.

Cordia borinquensis showed a survival rate of 80 percent for its 1946 population. With regeneration, this species increased to 130 percent of its original population. Total basal area in 1981 was nearly 130 percent of that in 1946 due to ingrowth and increment on residual stems. Its percent importance also increased from 2.2 to 2.6.

In contrast, Prestoea montana, Micropholis garciniaefolia, and M. chrysophylloides showed survivals ranging from 65 to 90 percent of their 1946 populations. When ingrowth was added to the original stem numbers, the final populations of these climax species ranged from 100 to 120

Table 4. Relative density,[1] relative frequency[2] and relative basal area[3] and percent importance[4] for major tree species on all natural forest plots in the colorado forest in 1946 and 1981. Species are arranged from highest to lowest percent importance based on the 1946 values for the 25 most important species.

Species	Measurement - 1946				Measurement - 1981			
	- - - Relative values - - -			Percent importance	- - - Relative values - - -			Percent importance
	Density	Frequency	Basal area		Density	Frequency	Basal area	
Cyrilla racemiflora	0.036	0.023	0.297	11.9	0.034	0.024	0.167	7.5
Micropholis garciniafolia	0.116	0.023	0.176	10.5	0.113	0.024	0.217	11.8
Calycogonium squamulosum	0.157	0.023	0.113	9.8	0.161	0.024	0.094	9.3
Prestoea montana	0.122	0.023	0.105	8.3	0.128	0.024	0.109	8.7
Micropholis chrysophylloides	0.072	0.020	0.049	4.7	0.089	0.020	0.082	6.4
Croton poecilanthus	0.084	0.023	0.031	4.6	0.091	0.020	0.057	5.6
Ocotea spathulata	0.052	0.023	0.031	3.5	0.029	0.024	0.013	2.2
Magnolia splendens	0.026	0.023	0.046	3.2	0.017	0.024	0.043	2.8
Haenianthus salicifolius	0.028	0.023	0.028	2.7	0.039	0.024	0.043	3.5
Cordia borinquensis	0.035	0.020	0.010	2.2	0.046	0.020	0.013	2.6
Daphnopsis philippiana	0.033	0.023	0.004	2.0	0.040	0.024	0.005	2.3
Tabebuia rigida	0.013	0.023	0.011	1.6	0.017	0.024	0.014	1.8
Miconia laevigata	0.019	0.023	0.004	1.5	0.005	0.017	0.004	0.9
Psychotria berteriana	0.022	0.020	0.002	1.5	0.004	0.017	0.000	0.7

Table 4 (continued).

Ditta myricoides	0.016	0.023	0.003	1.4	0.019	0.024	0.005	1.6
Hedyosmum arborescens	0.019	0.020	0.002	1.4	0.002	0.014	0.001	0.5
Cecropia peltata	0.014	0.017	0.006	1.2	0.003	0.014	0.005	0.7
Sloanea berteriana	0.007	0.017	0.010	1.1	0.007	0.017	0.014	1.3
Byrsonima wadsworthii	0.007	0.023	0.004	1.1	0.008	0.024	0.005	1.2
Dacryodes excelsa	0.005	0.013	0.015	1.1	0.006	0.017	0.017	1.3
Eugenia borinquensis	0.008	0.020	0.004	1.1	0.007	0.020	0.003	1.0
Ilex sideroxyloides	0.005	0.023	0.002	1.0	0.005	0.024	0.001	1.0
Clusia krugiana	0.006	0.017	0.007	1.0	0.011	0.020	0.029	2.0
Miconia tetrandra	0.004	0.017	0.001	0.7	0.022	0.024	0.010	1.9
Myrcia fallax	0.006	0.013	0.002	0.7	0.007	0.020	0.003	1.0
Subtotal	0.919	0.516	0.963	79.8	0.910	0.528	0.954	79.6
Remaining species [5]	0.081	0.484	0.037	20.2	0.090	0.472	0.046	20.4
Total	1.000	1.000	1.000	100.0	1.000	1.000	1.000	100.0

[1] The number of individuals of a particular species as a proportion of the total number of individuals of all species.

[2] Frequency is the chance of finding a given species within a sample. Relative frequency is the frequency of a given species as a proportion of the sum of frequencies for all species.

[3] The basal area of individuals of a particular species as a proportion of the total basal area of all species.

[4] The sum of relative density, relative frequency and relative dominance divided by 3.

[5] Eighty-eight species were tallied in 1946 and 83 in 1981.

Figure 12. Diameter class distributions for indicator species on 2.8 hectares of natural forest permanent plots in 1946 and 1981. Class A = 4.1 to 9.9 cm; class B = 10.0 to 14.9 cm; subsequent classes are in 5 cm increments through class Y = 130.0 to 134.9 cm. The species indicated by asterisk are also canopy species.

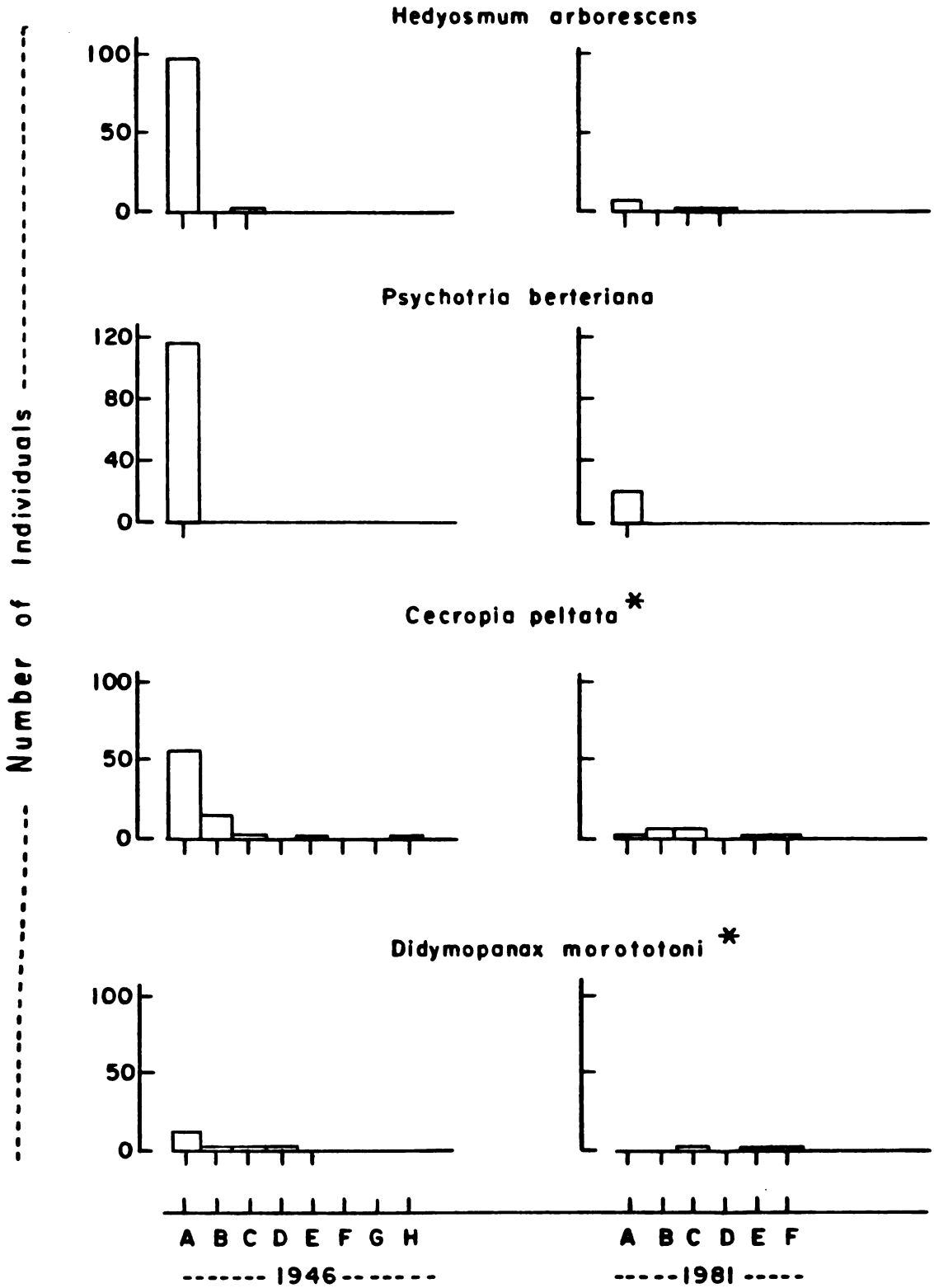
Hedyosmum arborescens
100
50
0
Psychotria berteriana
120
80
40
0
Cecropia peltata *
100
50
0
Didymopanax morototoni *
100
50
0
Number of Individuals
A B C D E F G H
1946
A B C D E F
1981
Diameter Class Distributions

Figure 12

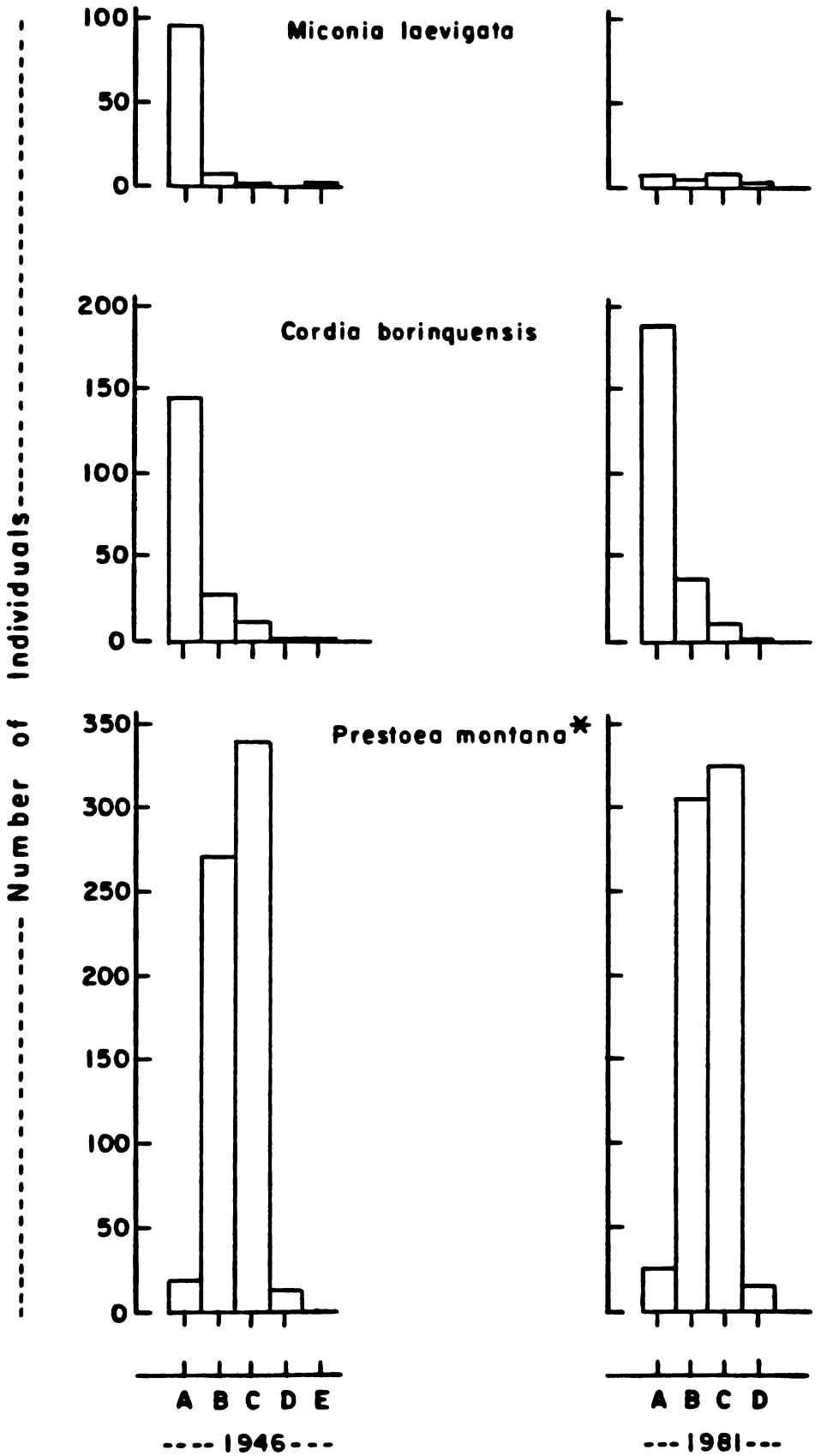
Miconia laevigata
100
50
0
Cordia borinquensis
200
150
100
50
0
Prestoea montana*
350
300
250
200
150
100
50
0
Number of Individuals
A B C D E
---1946---
A B C D
---1981---
Diameter Class Distributions

Figure 12

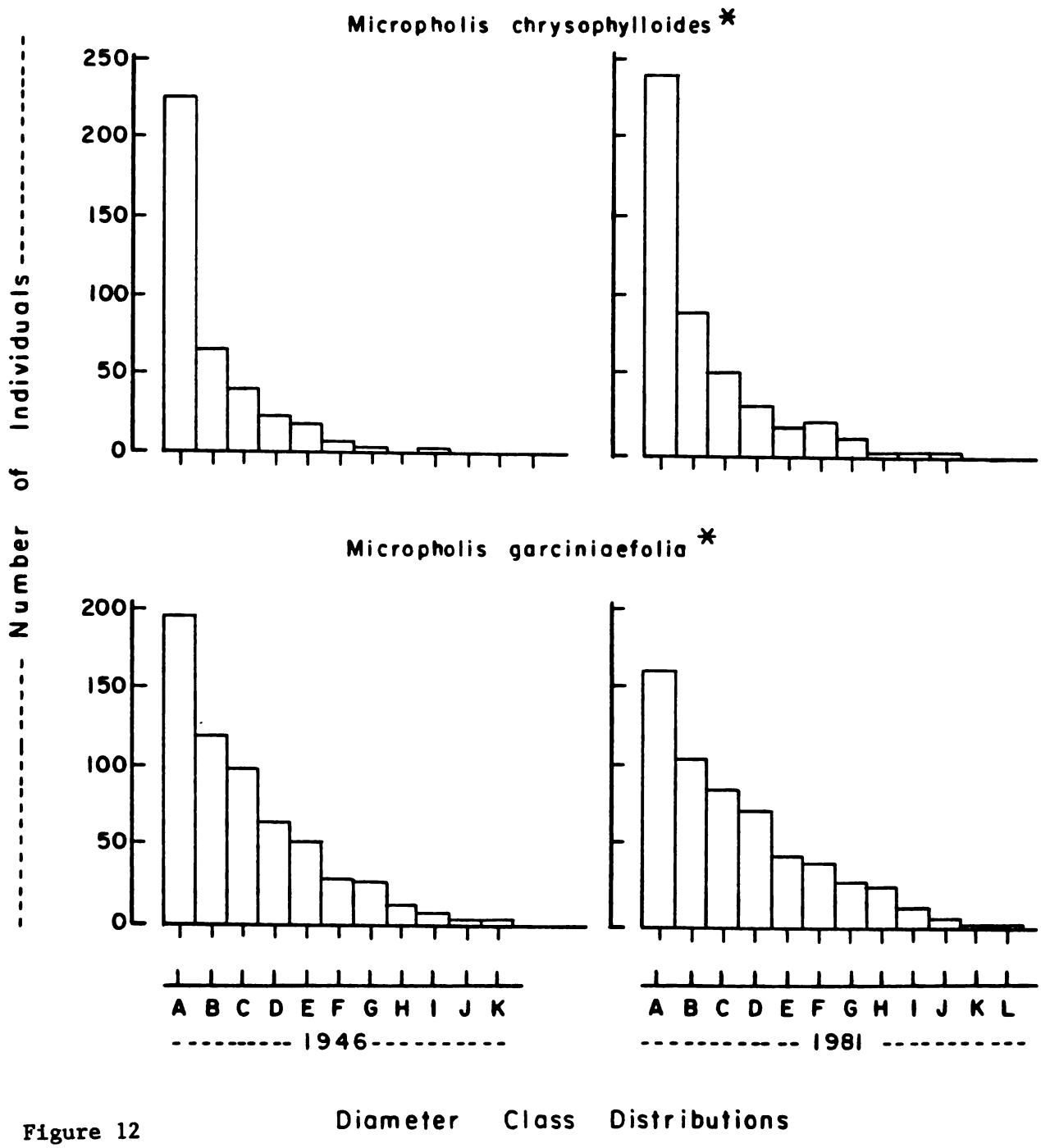
Micropholis chrysophylloides *
250
200
150
100
50
0
Micropholis garciniaefolia *
200
150
100
50
0
---------- Number of Individuals ----------
A B C D E F G H I J K
1946
A B C D E F G H I J K L
1981
Diameter Class Distributions

Figure 12

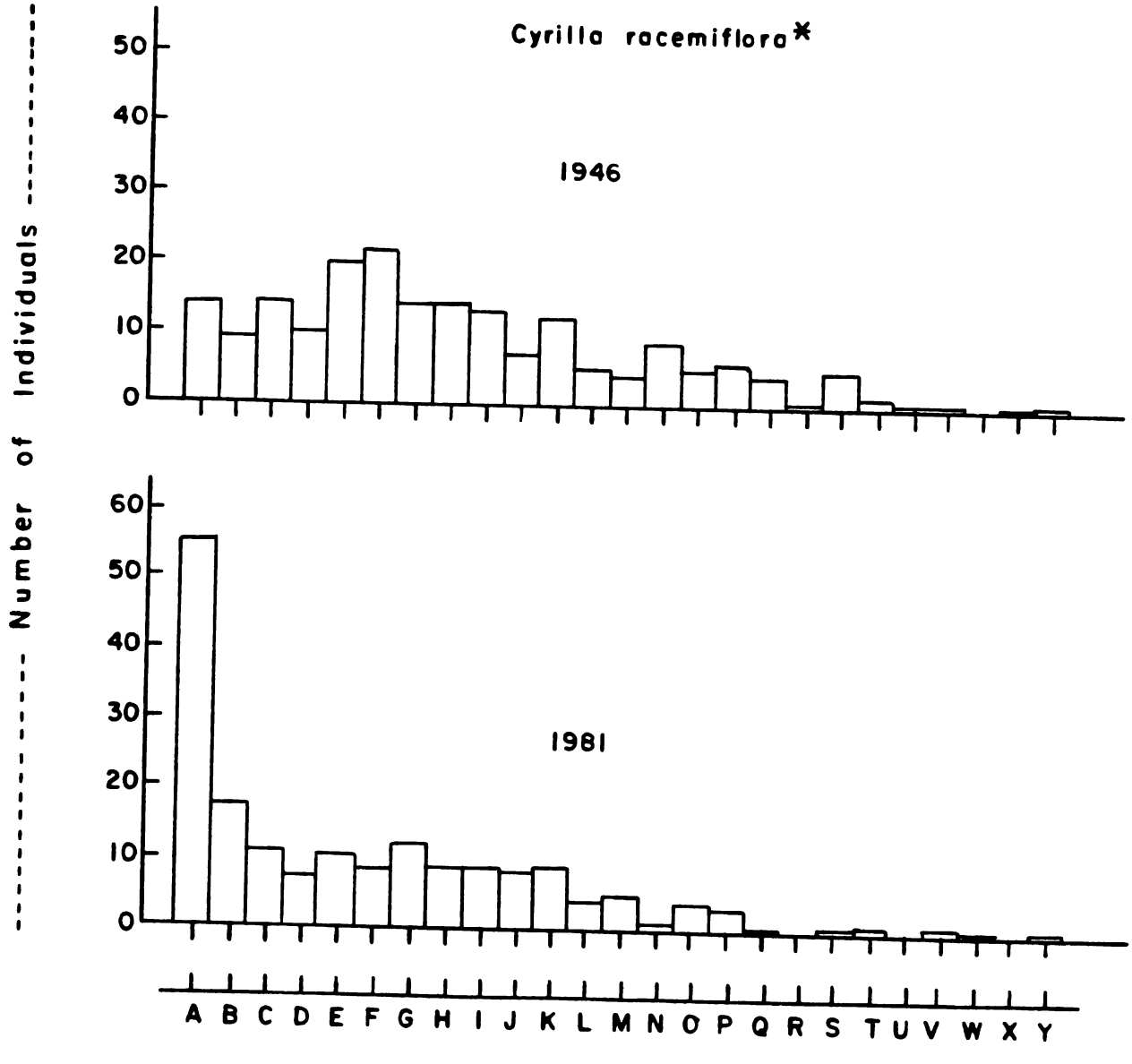
Cyrilla racemiflora*
1946
1981
Number of Individuals
0
10
20
30
40
50
60
A B C D E F G H I J K L M N O P Q R S T U V W X Y
Diameter Class Distributions

Figure 12

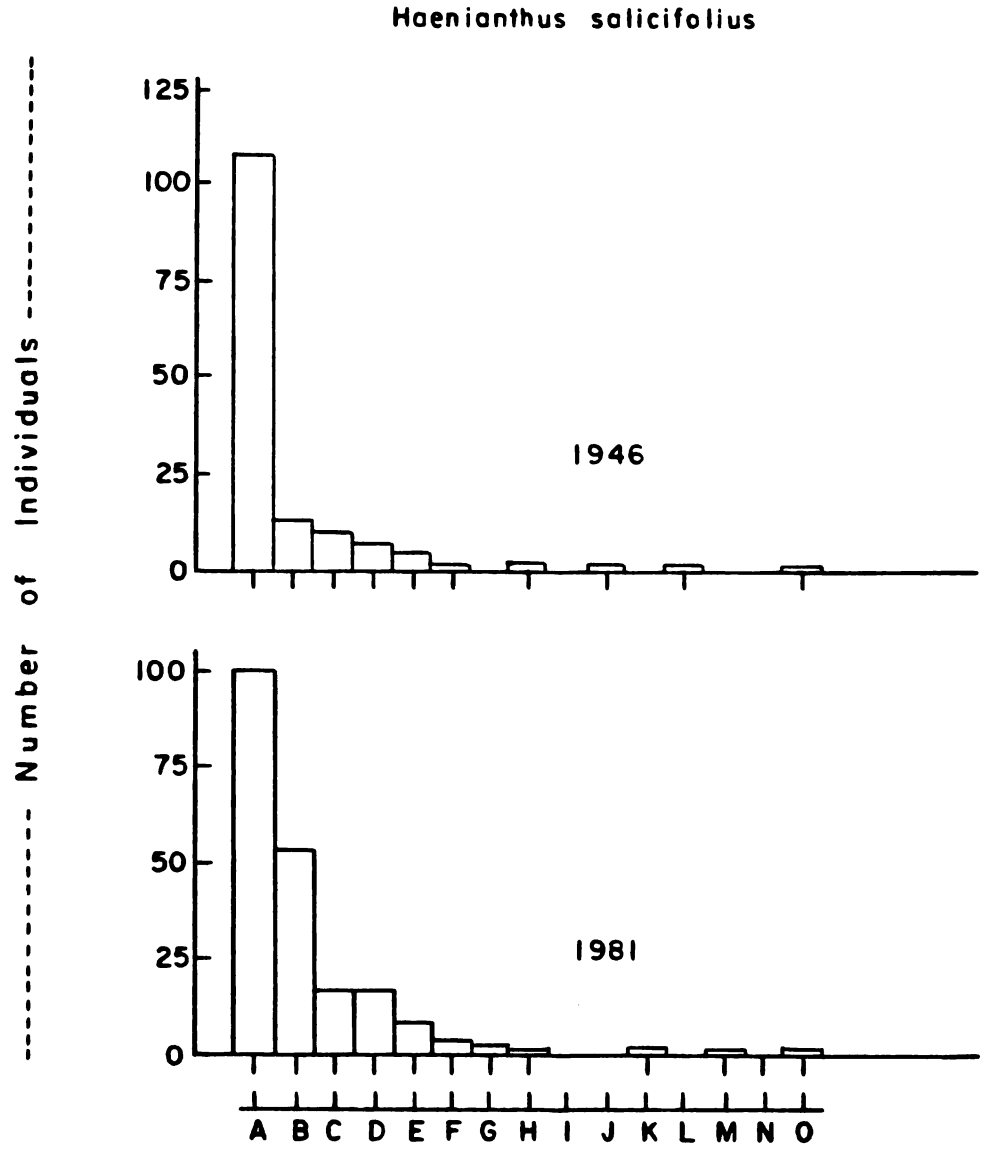
Haenianthus salicifolius
---------- Number of Individuals ----------
125
100
75
50
25
0
1946
100
75
50
25
0
1981
A B C D E F G H I J K L M N O
Diameter Class Distributions

Figure 12

percent of the 1946 populations. The 1981 total basal areas were also greater than in 1946, ranging from 125 to over 160 percent of the 1946 values for both species of Micropholis. Prestoea only increased to 105 percent of the 1946 value because it lacks diameter increment. Percent importance values also increased for each of these species, ranging from 0.4 percent for Prestoea to about 1.5 percent apiece for both species of Micropholis.

The abundance of species by topography is also shown in Fig. 11. Hedysomum, Cyrilla and both species of Micropholis are more common on slope plots whereas Cecropia, Didymopanax, and Prestoea are found mainly on valley plots. The remaining species, Psychotria, Miconia, and Cordia are well represented on both topographic positions.

The 1946 and 1981 diameter class distributions of these same species are shown in Fig. 12. Hedyosmum and Psychotria stems were largely confined to the smallest diameter class in both years. Cecropia and Miconia showed considerable regeneration in the smallest class in 1946 but the pattern was altered with the loss of stems by 1981. Didymopanax showed only a few stems in either year, with none in the smallest diameter class in 1981.

The diameter class distribution of Cyrilla showed an influx into the smallest class in 1981, and a decline in the larger diameter classes. Cordia showed the typical negative exponential pattern of shade tolerant species in both years, but it was more pronounced in 1981. The same general pattern was also apparent for both species of Micropholis. The diameter class distribution for Prestoea approached that of a normal curve in both years.

Diameter class distributions of canopy species

Diameter distributions for 11 of the remaining species that reach canopy size in some part of the colorado forest are given in Fig. 13. Eugenia stahlii and Ocotea moschata have been omitted because each had fewer than 10 stems in 1946 and 1981. Magnolia splendens, Eugenia borinquensis, Clusia krugiana, Matayba dominguensis and Sapium laurocerasus showed comparatively even distributions for all but the smallest diameter classes in both years. Haenianthus salicifolius and Tabebuia rigida showed relatively even distributions in 1946, except for the smallest diameter class, but approached a reverse J-shaped curve in 1981. The remaining species, Calycogonium squamulosum, Croton poecilanthus, Ocotea spathulata, Brysonima wadsworthii and Myrcia fallax, showed reversed J-shaped distributions in both years. These results will be discussed in conjuntion with species classifications in Part II.

Species survival on thinned plot

The thinned plot in 1981 had about five times the stem density of Micropholis garciniaefolia and Tabebuia rigida and about twice the density of Cyrilla racemiflora as the average for the natural forest plots (Fig. 14). Regeneration after thinning increased the stem density of Clusia krugiana from 10 to 360 stems/ha, Cyrilla racemiflora from 84 to 780 stems/ha, and Miconia tetrandra from 0 to 190 stems/ha during the 35-year period of measurement. Haenianthus salicifolius increased from 17 to 54 stems/ha and Tabebuia from 215 to 311 during the same period, and Micropholis garciniaefolia declined in numbers.

Figure 13. Diameter class distributions for canopy species on 2.8 hectares of natural forest permanent plots in 1946 and 1981. Class A = 4.1 to 9.9 cm; class B = 10.0 to 14.9 cm; subsequent classes are in 5 cm increment through class 0 = 75.0-79.9 cm. Indicator species not included.

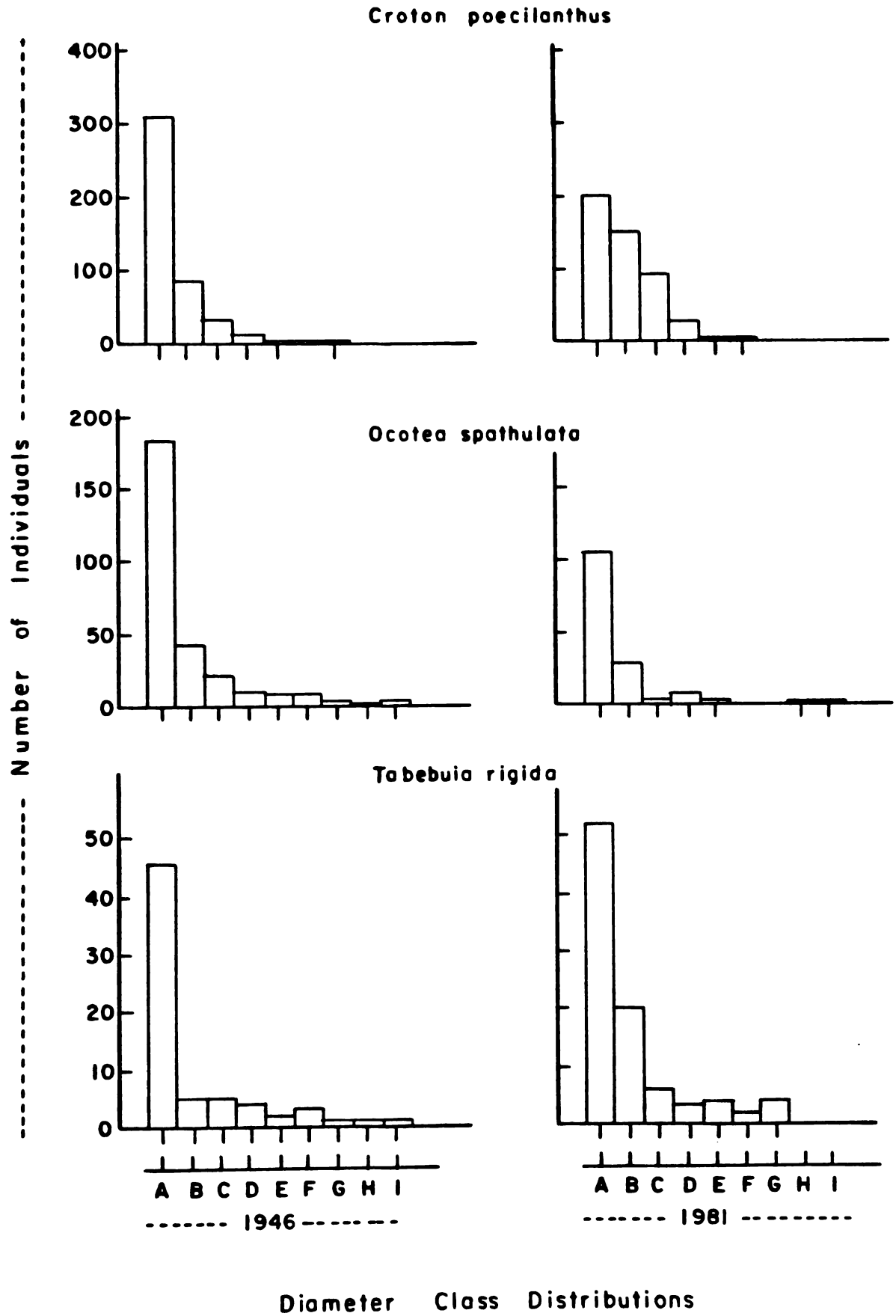
Croton poecilanthus
Ocotea spathulata
Tabebuia rigida
Number of Individuals
400
300
200
100
0
200
150
100
50
0
50
40
30
20
10
0
A B C D E F G H I
1946
A B C D E F G H I
1981
Diameter Class Distributions

Figure 13

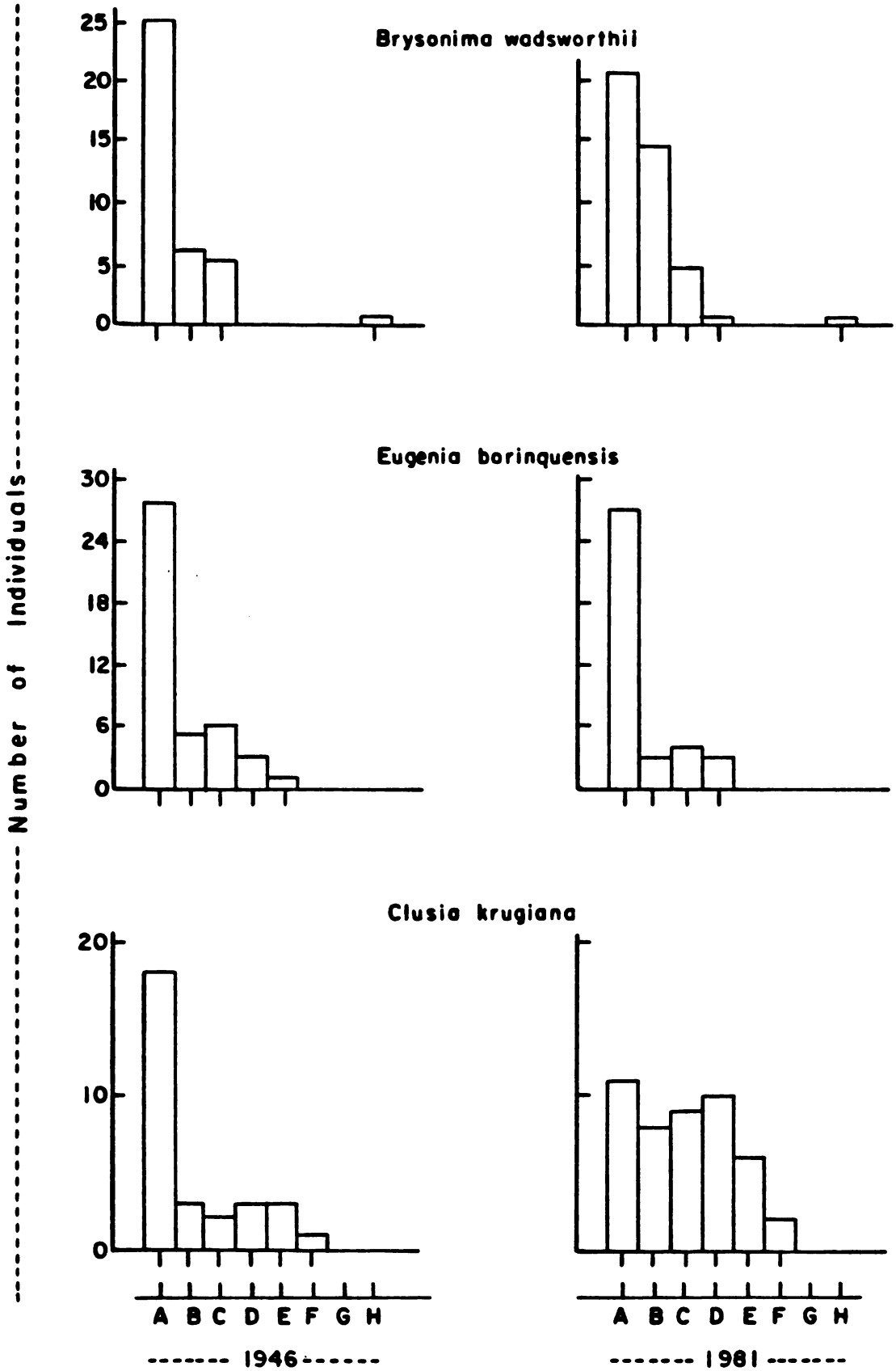
Brysonima wadsworthii
Eugenia borinquensis
Clusia krugiana
Number of Individuals
25
20
15
10
5
0
30
24
18
12
6
0
20
10
0
A B C D E F G H
1946
1981
Diameter Class Distributions

Figure 13

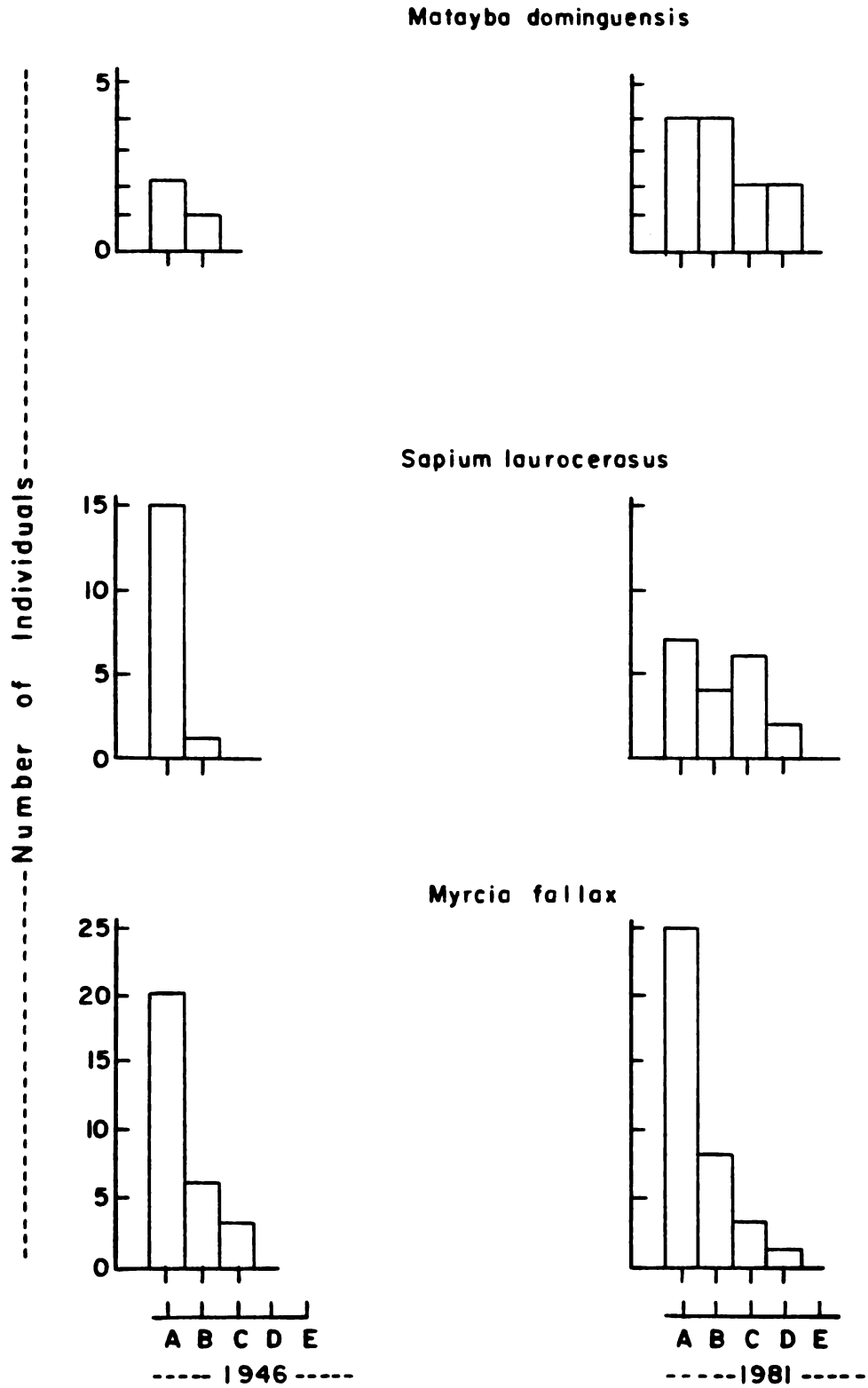
Matayba dominguensis
Sapium laurocerasus
Myrcia fallax
Number of Individuals
5
0
15
10
5
0
25
20
15
10
5
0
A B C D E
1946
A B C D E
1981
Diameter Class Distributions

Figure 13

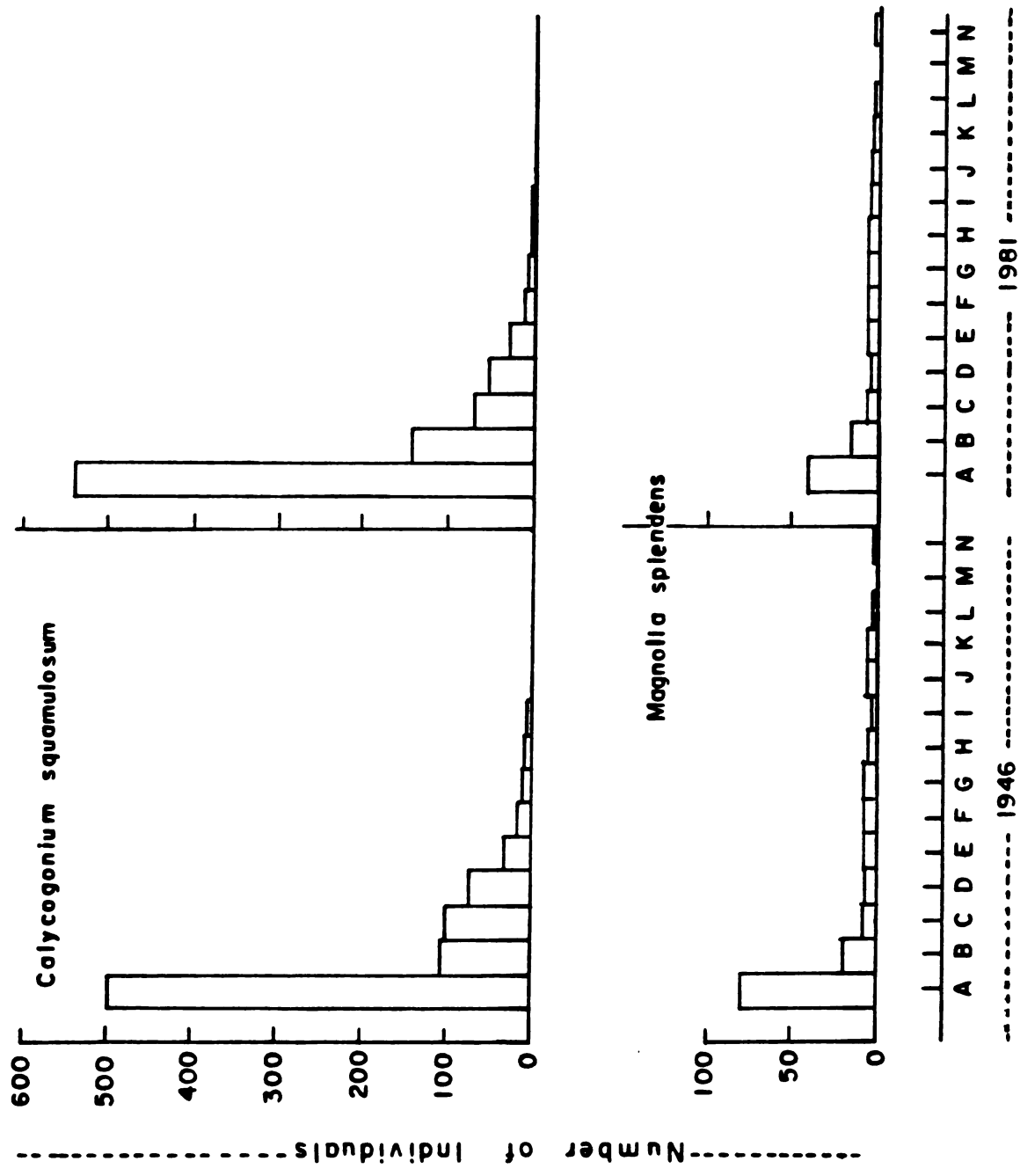
Calycogonium squamulosum
Magnolia splendens
Number of individuals
600
500
400
300
200
100
0
100
50
0
A B C D E F G H I J K L M N
A B C D E F G H I J K L M N
1946
1981
Diameter Class Distributions

Figure 13

Figure 14. Change in number of stems/ha by species on the thinned colorado plot vs. all natural forest colorado plots. In each case, the thinned plot is the first pair of entries by species.

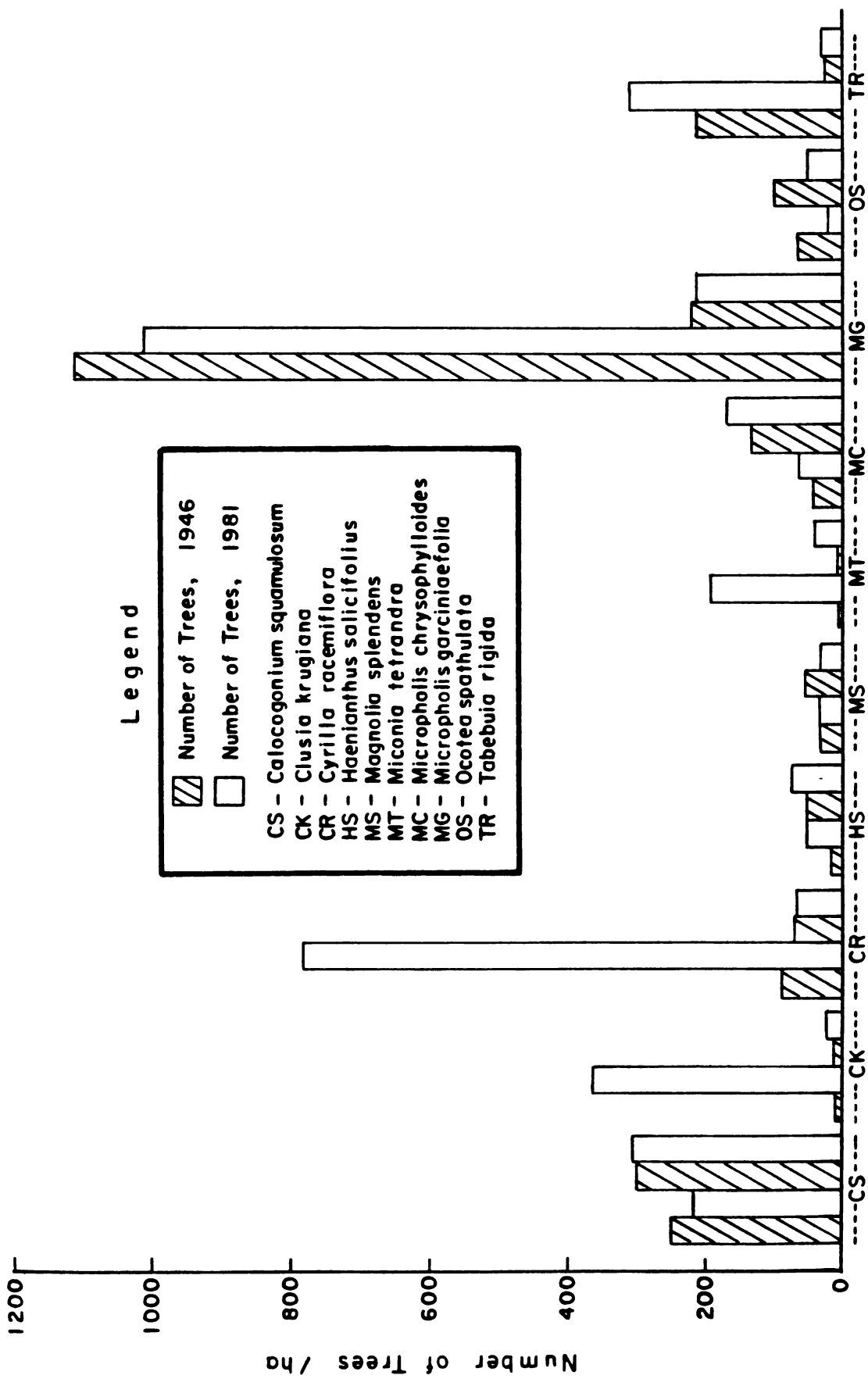
Legend
Number of Trees, 1946
Number of Trees, 1981
CS - Calocoganium squamulosum
CK - Clusia krugiana
CR - Cyrilla racemiflora
HS - Haenianthus salicifolius
MS - Magnolia splendens
MT - Miconia tetrandra
MC - Micropholis chrysophylloides
MG - Micropholis garciniaefolia
OS - Ocotea spathulata
TR - Tabebuia rigida
Number of Trees /ha
0
200
400
600
800
1000
1200
CS
CK
CR
HS
MS
MT
MC
MG
OS
TR
Species

Figure 14

Species richness

The total number of tree species found on the natural forest plots declined from 88 in 1946 to 83 in 1981 (Fig. 15). Three notable observations may be made. First, the variability of species numbers for plots of the same size is considerable. Second, species numbers tend to converge through time. In 1946, species numbers ranged from 33 through 58 but by 1981 the range decreased to 36 through 49. Third, there is a considerable difference in species numbers according to topography. The slope plots A through D ranged from 33 to 46 in 1946 and from 37 to 43 species in 1981. The mixed plot E remained unchanged at 36 species in both years. The valley plots G and H ranged from 48 to 58 species in 1946 and from 45 to 49 species in 1981.

Five fewer species between 1946 and 1981 represents a flux in which 12 species were lost and seven species gained. Of the 12 lost, Cupania americana, Guarea guidonia, Laplacea portoricensis, Nectandra antillana, N. sintenisii, and Rheedia portoricensis are more common to the tabonuco forest, and Hibiscus tiliaceous to the coastal lowlands. Cyathea arborea, a tree fern, is more common in the dwarf forest although it occurs in openings at lower elevations. The remaining species, Heterotrichum cymosum and Coccoloba swartzii are uncommon in the colorado forest, and two unknowns are assumed to be uncommon colorado forest species. Of the seven species gained, Beilschimiedia pendula and Manilkara bidentata are more common in the tabonuco forest, and Grammadenia sintenisii in the dwarf forest. The remaining species are components of the colorado forest including Mecraneum amygdalinum, Miconia pachyphylla, and Miconia mirabilis which are uncommon, and Ouratea striata which is rare.

Figure 15. Change in number of species by plot and for the entire forest from 1946 to 1981.

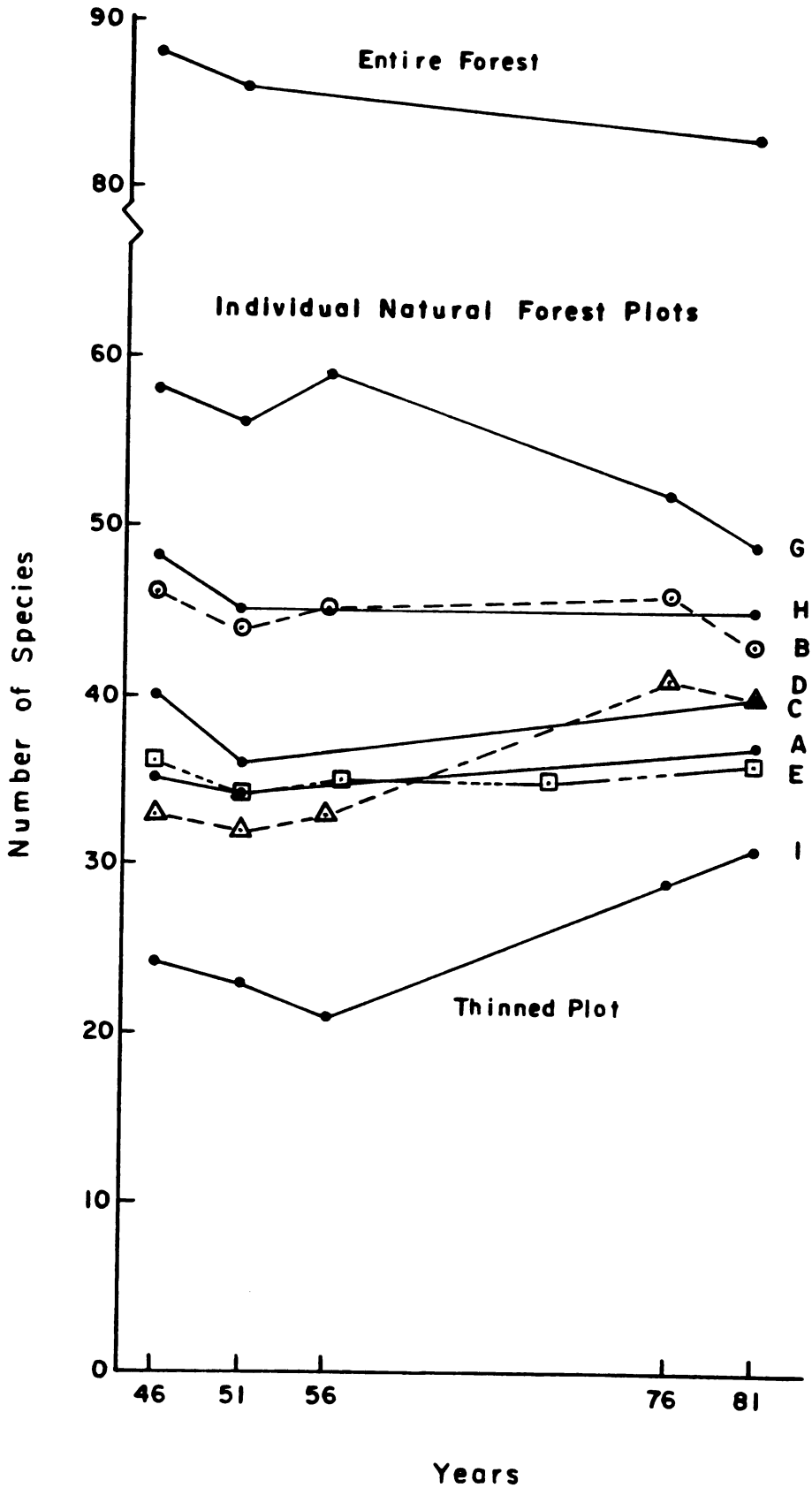
90
80
60
50
40
30
20
10
0
Entire Forest
Individual Natural Forest Plots
Thinned Plot
G
H
B
D
C
A
E
I
Number of Species
46
51
56
76
81
Years

Figure 15

On the thinned plot, there were only 24 species in 1946. After a slight decline, species numbers increased to 31 in 1981. Shannon-Wiener indices for all natural forest plots combined showed a decline from 4.81 to 4.33 during the period of measurement (Table 5). For individual plots, indices declined or remained the same in all but one instance. On the thinned plot, the index increased from 2.37 to 2.90 from 1946 to 1981.

Rare and endangered species

Tree species tentatively classified as rare or endangered in the mid-1970's (Soil Conservation Service and Department of Natural Resources 1973) decreased from 339 to 305 individuals on all 3.2 ha of natural forest and thinned plots during the period of measurement (Table 6). Most of this decline occurred with Magnolia splendens and Ternstroemia luquillensis. No species disappeared and two new species, Ardisia luquillensis and Ouratea striata reached minimum dbh and were recorded on two of the plots.

For convenience, information on rare species found during the ordination study (Part II) is reported here. When partitioned by topography, Ardisia luquillensis, Byrsonima wadsworthii, Magnolia splendens, Marliera sintensii, and Xylosma schwanekeanum were more common on ridges and slopes while Ditta myricoides was more abundant on slopes and valleys (Table 7). When stratified by life zone, Ardisia, Magnolia, and Marleira occurred more frequently in the rain forest than wet forest. When partitioned by elevation, Ditta and Xylosma appeared more commonly above 800 m while Brysonima was encountered more frequently below 800 m.

Table 5: Shannon-Wiener indices (Krebs 1972) in 1946 and 1981 on the permanent colorado forest plots.

Plot[1]	Years	
	1946	1981
A	3.88	3.77
B	4.23	4.23
C	4.07	3.95
D	3.51	3.63
E	4.03	3.78
G	4.20	4.08
H	4.13	3.93
I	2.37	2.90
A-H[2]	4.81	4.33

[1]Plot sizes in all instances are 0.40 ha. Plots A through H are undisturbed and plot I was thinned.

[2]Sum of seven 0.40 ha plots or total of 2.8 ha.

Table 6. Rare and endangered tree species of Puerto Rico found on the colorado forest permanent plots.

Classification Species	Permanent plots (1946-1981)[1] A	B	C	D	E	G	H	Total
Rare and endemic								
Ardisia luquillensis			0-1		0-1			0-2
Ilex sintinisii		1-1			0-1			1-2
Rare and non-endemic								
Ditta myricoides	21-21	7-17	8-4	17-21	12-15	9-12	9-11	83-101
Laetia procera				1-0				1-0
Endangered and endemic								
Brysonima wadsworthii	14-11	6-7	2-3	8-7	1-6	3-3	4-4	38-41
Eugenia eggersii					3-9			3-9
Mangnolia splendens	13-10	11-8	33-21	25-18	34-28	11-4	11-1	138-90
Marliera sintinisii	7-8						0-1	7-9
Maytenus elongata						1-1	0-1	1-2
Styrax portoricensis						0-1		0-1
Ternstroemia leptosepala	15-14	1-1		2-3				18-18
Ternstroemia luquillensis	4-2	2-3	19-3		4-2			29-10
Ternstroemia subsessilus	0-1							0-1
Xylosma schwaneckanum					1-5			1-5
Endangered and non-endemic								
Cleyera albopuctata		1-1						1-1
Ouratea striata			0-2					0-2
Total	74-67	29-38	62-34	53-49	55-67	24-21	24-18	321-294

[1] First number is the number of stems found in 1946; the second in 1981. All plots are 0.40 ha in size.

Table 7. Rare and endangered tree species (stems/ha) found on the colorado forest temporary plots.

Species	Topography			Life zone		Elevation (m)[1]	
	Ridge	Slope	Valley	Wet	Rain	Low	High
Ardisia luquillensis	4.0	4.8	0.8	1.8	5.3	3.5	2.8
Ditta myricoides	8.0	21.6	23.2	16.4	19.3	14.8	22.1
Brysonima wadsworthii	32.0	16.0	5.6	19.6	15.3	22.2	10.3
Cleyera albopuntata	0.8	---	---	---	0.7	---	0.7
Eugenia eggersii	0.8	---	2.4	1.3	0.7	1.7	---
Grammadenia sintenisii	---	1.6	---	---	1.4	0.7	0.7
Magnolia splendens	22.4	26.4	8.0	14.2	26.0	18.7	19.3
Marliera sintenisii	8.0	9.6	---	2.2	11.3	5.6	6.2
Xylosma schwaneckeanum	4.0	0.8	0.8	2.2	1.3	0.9	3.4

[1] Elevation: low from 615-790 m; high, from 800-970 m.

Similarity of the plots

Similarity comparisons between pairs of plots in 1946 and 1981 are shown in Table 8. Of the 21 comparisons between natural forest plots, 14 showed greater similarity in 1981 than in 1946 and six showed less similarity. One comparison was the same. In general, the loss of secondary and late secondary indicator species (Fig. 11, top row and Cyrilla) contributed to greater dissimilarity in 14 comparisons whereas the gain in climax indicator species (Fig. 11, bottom row except Cyrilla) contributed to greater similarity in 16 comparisons. The six comparisons that showed increases in dissimilarity had either large negative trends among declining secondary species, or negative trends among both secondary and climax species.

The slope plots A through D when compared among themselves showed similarities ranging from 51 to 69 percent regardless of the year; whereas, when compared with valley plots G and H, they showed similarities ranging from 37 to 57 percent. The valley plots and showed similarities ranging from 69 to 72 percent when compared among themselves in both years. The mixed plot E showed similarites ranging from 51 to 71 percent when compared with the slope plots, and from 48 to 58 percent when compared with the valley plots, regardless of the year.

Of the seven comparisons of natural forest plots with the thinned plot, six showed a decrease in similarity from 1946 to 1981 and one showed an increase. Indices ranged from 26 to 45 percent similarity.

Table 8: Percent similarity[1] indices for the colorado forest permanent plots in 1946 and 1981

Plot	A	B	C	D	E	G	H	I
A	---	62-69	52-59	65-65	61-62	53-56	43-46	42-34
B	---	---	57-54	51-49	66-71	42-43	47-57	32-30
C	---	---	---	64-57	63-56	37-39	44-48	40-34
D	---	---	---	---	64-51	41-38	45-47	45-33
E	---	---	---	---	---	53-58	48-54	40-38
G	---	---	---	---	---	---	69-72	30-29
H	---	---	---	---	---	---	---	26-30
I	---	---	---	---	---	---	---	---

[1] Percent similarity of two sample plots is the sum of the lowest percentages within the respective samples of species shared by both plots: Percent similarity = $\sum$ (lowest percentage for each species).

Growth and Production

Diameter growth of select species by crown class

The greatest MAI attained by canopy species with adequate numbers of trees for analysis was 0.30 cm/yr by dominant specimens of Tabebuia rigida (Table 9). Dominant specimens of Ocotea spathulata, Haenianthus salicifolius, and Micropholis chrysophylloides as well as codominant specimens of Croton poecilanthus averaged $\geq$0.20 cm/yr. For all species, trees in the dominant or the codominant crown classes were the fastest growing, and trees in the suppressed crown class were the slowest growing.

Different 35-year MAI patterns were evident when species were stratified by crown class. One that emerged for Calycogonium squamulosum and Magnolia splendens was generally slow growth in which the dominant, codominant, and intermediate trees did not grow at significantly different rates from each other, but were significantly faster growing than suppressed trees. A more common pattern shown by Haenianthus salicifolius, Micropholis garciniaefolia, M. chrysophylloides, Ocotea spathulata, and Tabebuia rigida was a gradual decline in diameter growth from dominant through suppressed trees. For all species combined, when stratified by crown class, the growth of dominants, codominants and intermediates averaged 3.2, 2.6, and 1.8 times, respectively, the growth rates of suppressed stems. Ratios, however, varied among species.

When all survivors, regardless of species, were compared by crown class, a significant decline in MAI was observed between 1946-51 and 1976-81 in the intermediate and suppressed crown classes (Table 10). The dominant crown class also declined in growth, but the difference was not

Table 9. Mean annual diameter increment (MAI) of 35-year survivors of select species by crown class on the natural forest permanent plots.

Species	MAI (cm/yr) ± SE[1] by Crown class (n)[2]			
	Dominant (D)	Co-dominant (C)	Intermediate (I)	Suppressed (S)
Calycogonium squamulosum	0.12 ± 0.027 (9)[a]	0.11 ± 0.008 (56)[a]	0.10 ± 0.004 (170)[a]	0.06 ± 0.002 (278)[b]
Croton poecilanthus	0.12 ± 0.040 (2)[ab]	0.26 ± 0.022 (41)[b]	0.18 ± 0.009 (131)[b]	0.08 ± 0.006 (113)[a]
Cyrilla racemiflora	0.12 ± 0.019 (54)[a]	0.14 ± 0.020 (25)[a]	0.09 ± 0.023 (21)[a]	0.12 ± 0.039 (4)[a]
Haenianthus salicifolius	0.26 ± 0.026 (28)[a]	0.19 ± 0.017 (32)[b]	0.16 ± 0.023 (29)[b]	0.08 ± 0.111 (23)[c]
Magnolia splendens	0.11 ± 0.019 (26)[a]	0.06 ± 0.016 (9)[a]	0.07 ± 0.010 (17)[a]	0.04 ± 0.009 (24)[b]
Micropholis chrysophylloides	0.20 ± 0.021 (33)[a]	0.18 ± 0.013 (56)[a]	0.12 ± 0.006 (130)[b]	0.05 ± 0.005 (108)[c]
Micropholis garciniafolia	0.14 ± 0.013 (58)[a]	0.11 ± 0.007 (135)[b]	0.07 ± 0.004 (178)[c]	0.04 ± 0.003 (173)[d]
Ocotea spathulata	0.28 ± 0 (1)[a]	0.09 ± 0.019 (11)[b]	0.05 ± 0.010 (31)[c]	0.02 ± 0.003 (66)[d]
Tabebuia rigida	0.30 ± 0.087 (4)[a]	0.20 ± 0.035 (8)[ab]	0.16 ± 0.027 (17)[b]	0.05 ± 0.009 (20)[c]
Remaining species	0.14 ± 0.015 (170)[a]	0.13 ± 0.014 (164)[a]	0.06 ± 0.004 (307)[b]	0.04 ± 0.002 (517)[c]
All species combined	0.16 ± 0.008 (385)[a]	0.13 ± 0.006 (537)[b]	0.09 ± 0.001 (1032)[c]	0.05 ± 0.001 (1326)[d]

[1]SE = Standard error.

[2]n = number of individuals

[3]Means not indicated with the same superscript are significantly different at the 95% level according to the Duncan's multiple range test.

Table 10. Comparison of mean annual diameter increment (MAI) of surviving dicot trees by crown class between 1946-51 and 1976-81 on four natural forest permanent plots.

Crown class[2]	MAI (cm/yr ± SE (n))[1]	
	1946-51	1976-81
Dominant	0.15 ± 0.011 (219)	0.12 ± 0.012 (141)
Codominant	0.14 ± 0.009 (256)	0.16 ± 0.010 (309)*
Intermediate	0.14 ± 0.006 (550)	0.09 ± 0.004 (674)*
Suppressed	0.12 ± 0.005 (620)	0.05 ± 0.004 (521)*
Total	0.14 ± 0.004 (1645)	0.09 ± 0.004 (1645)*

[1] SE= Standard error; n= number of trees. Significant differences at the 95% level are indicated by an asterisk.

[2] Palms excluded from the calculations.

significant. In contrast, codominant trees showed a significant increase in diameter growth.

Basal area changes

The mean decrease in basal area for all natural forest plots was 0.01 m^2/ha/yr (Fig. 16). Two slope plots decreased slightly averaging 0.04 m^2/ha/yr, another declined 0.26 m^2/ha/yr, and the last remained virtually the same. The two valley plots and the mixed topography plot increased from 0.05 through 0.14 m^2/ha/yr. In contrast, the thinned plot increased 0.42 m^2/ha/yr during the period of measurement.

When mortality was added to ingrowth (in this case, ingrowth was equal to recruitment and growth on residual stems) to determine basal area growth, it ranged from 0.32 to 0.58 m^2/ha/yr with a mean of 0.43 m^2/ha/yr on the natural forest plots (Fig. 16). The thinned plot grew most rapidly at 0.67 m^2/ha/yr.

Volume changes

The mean increase in aboveground volume for all natural forest plots was 1.06 m^3/ha/yr during the period of measurement. Individual plots ranged from 0.17 to 2.56 m^3/ha/yr with the exception of plot D which declined 0.82 m^3/ha/yr (Fig. 17). The four slope plots averaged only 0.18 m^3/ha/yr while the two valley plots and mixed topography plot averaged 2.24 m^3/ha/yr. The 2.38 m^3/ha/yr increase on the thinned plot was also considerable.

Again, when mortality was added to ingrowth to determine volume growth, it averaged 3.37 m^3/ha/yr for all natural forest plots, ranging between 2.00 and 5.66 m^3/ha/yr on individual plots. In this instance,

Figure 16. Basal area changes for all permanent plots from 1946 to 1981. Mean is for all natural forest plots combined. Ingrowth includes recruitment and growth of residual stems. Mean annual basal area growth (in m^2/ha) is shown above the bars. The top value is for ingrowth alone. The bottom value sums both ingrowth and mortality as growth.

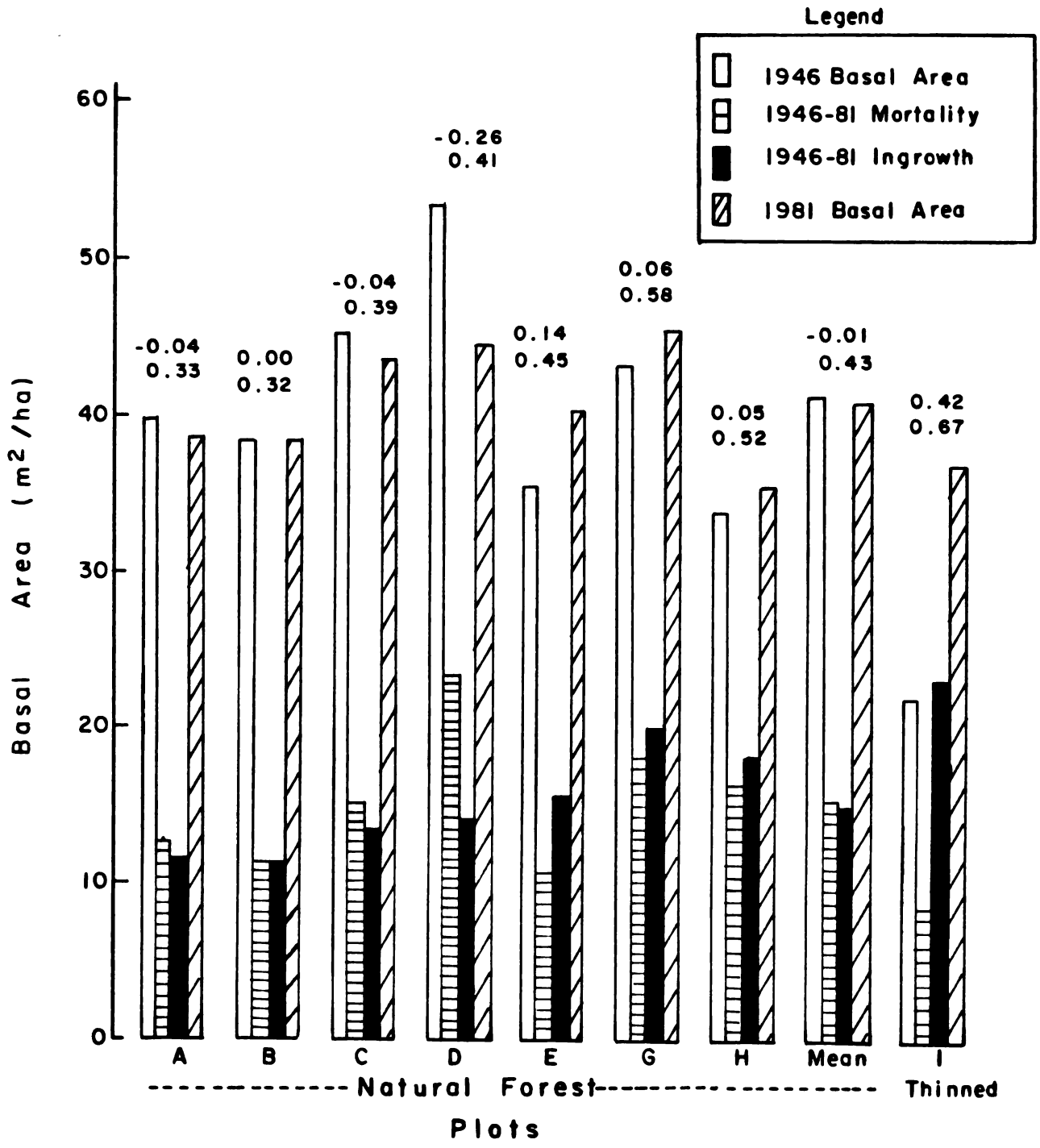
Legend
1946 Basal Area
1946-81 Mortality
1946-81 Ingrowth
1981 Basal Area
Basal Area (m²/ha)
60
50
40
30
20
10
0
-0.04
0.33
0.00
0.32
-0.04
0.39
-0.26
0.41
0.14
0.45
0.06
0.58
0.05
0.52
-0.01
0.43
0.42
0.67
A
B
C
D
E
G
H
Mean
I
Natural Forest
Thinned
Plots

Figure 16

Figure 17. Volume changes for all permanent plots from 1946 to 1981. Mean is for all natural forest plots combined. Ingrowth includes recruitment and growth on residual stems. Mean annual volume growth (in m^3/ha) is shown above the bars. The top value is for ingrowth alone. The bottom value sums both ingrowth and mortality as growth.

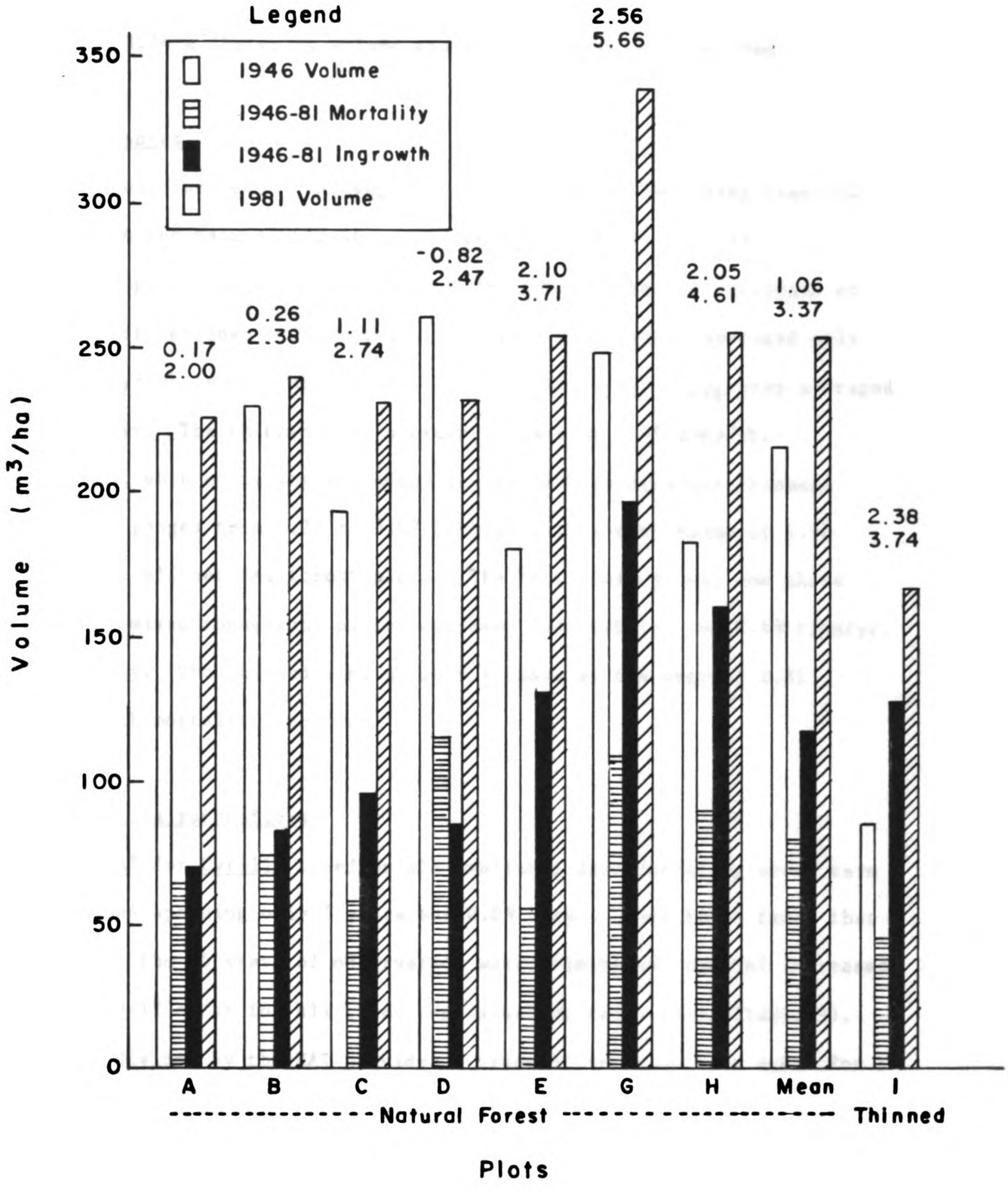
Legend
1946 Volume
1946-81 Mortality
1946-81 Ingrowth
1981 Volume
Volume (m3/ha)
350
300
250
200
150
100
50
0
0.17
2.00
0.26
2.38
1.11
2.74
-0.82
2.47
2.10
3.71
2.56
5.66
2.05
4.61
1.06
3.37
2.38
3.74
A
B
C
D
E
G
H
Mean
I
Natural Forest
Thinned
Plots

Figure 17

the four slope plots averaged 2.40 m^3/ha/yr while the two valley and mixed topography plots averaged 4.66 m^3/ha/yr. The thinned plot increased 3.74 m^3/ha/yr in volume growth with mortality included.

Biomass changes

The mean increase in aboveground woody biomass, including branches ≥2.5 cm, on the natural forest plots was 0.67 t/ha/yr (Fig. 18). Individual plots ranged from 0.24 to 1.58 t/ha/yr with the exception of plot D which declined 0.36 t/ha/yr. The four slope plots averaged only 0.22 t/ha/yr while the three plots on valley and mixed topography averaged 1.27 t/ha/yr. The thinned plot accrued biomass at 1.71 t/ha/yr.

Again, when mortality was added to ingrowth to determine biomass growth, it ranged from 1.33 to 3.07 t/ha/yr with a mean value of 1.90 t/ha/yr for all natural forest plots. The four slope plots, and three valley and mixed topography plots, averaged 1.45 t/ha/yr and 2.49 t/ha/yr, respectively. The thinned plot accrued biomass at the rate of 2.51 t/ha/yr with mortality included.

Age of Cyrilla racemiflora

The MAI for Cyrilla based on all available data including short term observations spanning only 5 years was 0.09 cm/yr. When those trees that died during the 35 years of observation were eliminated, the MAI increased to nearly 0.12 cm/yr for all trees regardless of crown class (Table 9). Tree size divided by the MAI provides a crude estimate of tree age. For a Cyrilla 1 m in diameter, an MAI of 0.09 cm/yr yielded an estimate slightly more than 1100 years. An MAI of nearly 0.12 cm/yr yielded an estimate of nearly 850 years old.

Figure 18. Aboveground woody biomass changes for all natural forest permanent plots from 1946 to 1981. Mean is for all natural forest plots combined. Ingrowth includes recruitment and growth on residual stems. Mean annual biomass growth (in t/ha) is shown above the bars. The top value is for ingrowth alone. The bottom value sums both ingrowth and mortality as growth.

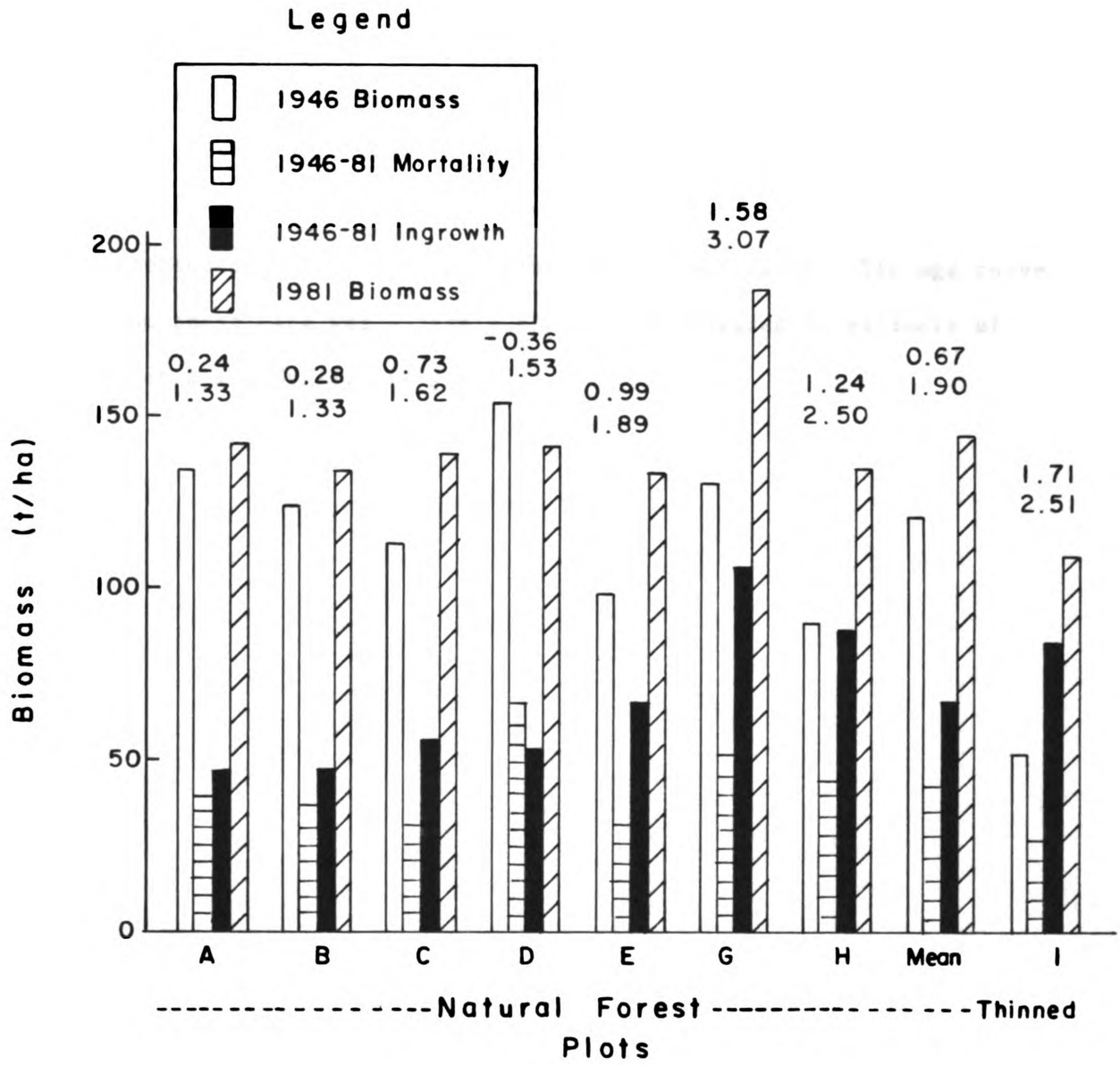
Legend
1946 Biomass
1946-81 Mortality
1946-81 Ingrowth
1981 Biomass
Biomass (t/ha)
200
150
100
50
0
0.24
1.33
0.28
1.33
0.73
1.62
-0.36
1.53
0.99
1.89
1.58
3.07
1.24
2.50
0.67
1.90
1.71
2.51
A
B
C
D
E
G
H
Mean
I
Natural Forest
Thinned
Plots

Figure 18

The mean MAI for the largest ingrowth ≤20 cm in diameter on the thinned plot averaged 0.36 cm/yr after slower growing stems were removed (Fig. 19; Methods). Elimination of the slowest growing trees in each diameter class ≥20 cm yielded a smaller data set (Fig. 19, circled points) from which means and standard errors were calculated for each class. These showed a decline in diameter increment with larger diameter classes. The linear regression of these MAI vs. the midpoint of the diameter class for trees ≥20 cm in diameter was highly significant although the scatter of individual points was considerable. The age curve derived from these data was slightly convex and provided an estimate of 660 years for a 1 m *Cyrilla* (Fig. 20).

Figure 19. Scatter of points for diameter growth by diameter classes for Cyrilla racemiflora. Circled points were those used in the weighted least squares regression. Points with standard error bars represent the means and standard errors for the circled points within the respective diameter classes. The mean and standard error at 10 cm is for the ingrowth on the thinned plot. Solid dots indicate growth rates that were discarded in the calculations of tree age.

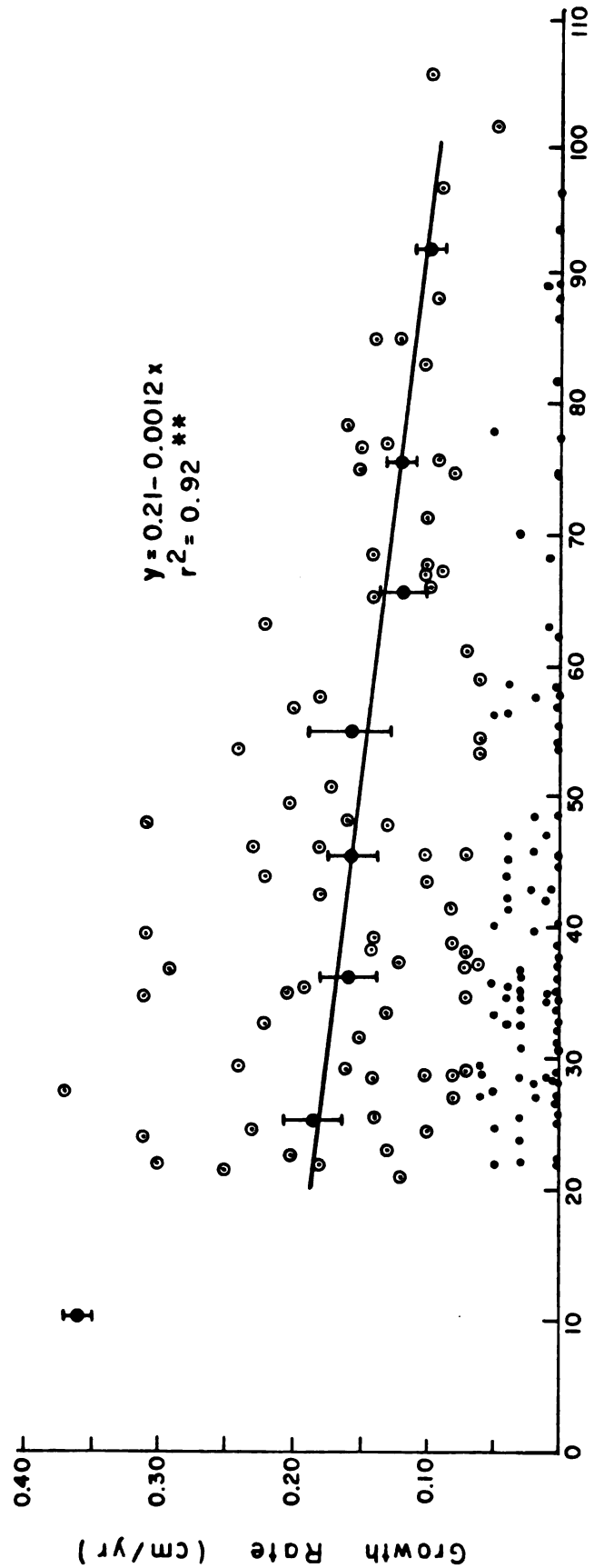
y = 0.21 - 0.0012x
r² = 0.92 **
Growth Rate (cm/yr)
0.40
0.30
0.20
0.10
0
10
20
30
40
50
60
70
80
90
100
110
Diameter Classes (cm)

Figure 19

Figure 20. Curve of age related to diameter for Cyrilla racemiflora. The circles represent the upper endpoints of the diameter classes on the ordinate vs. the cumulative ages on the abscissa.

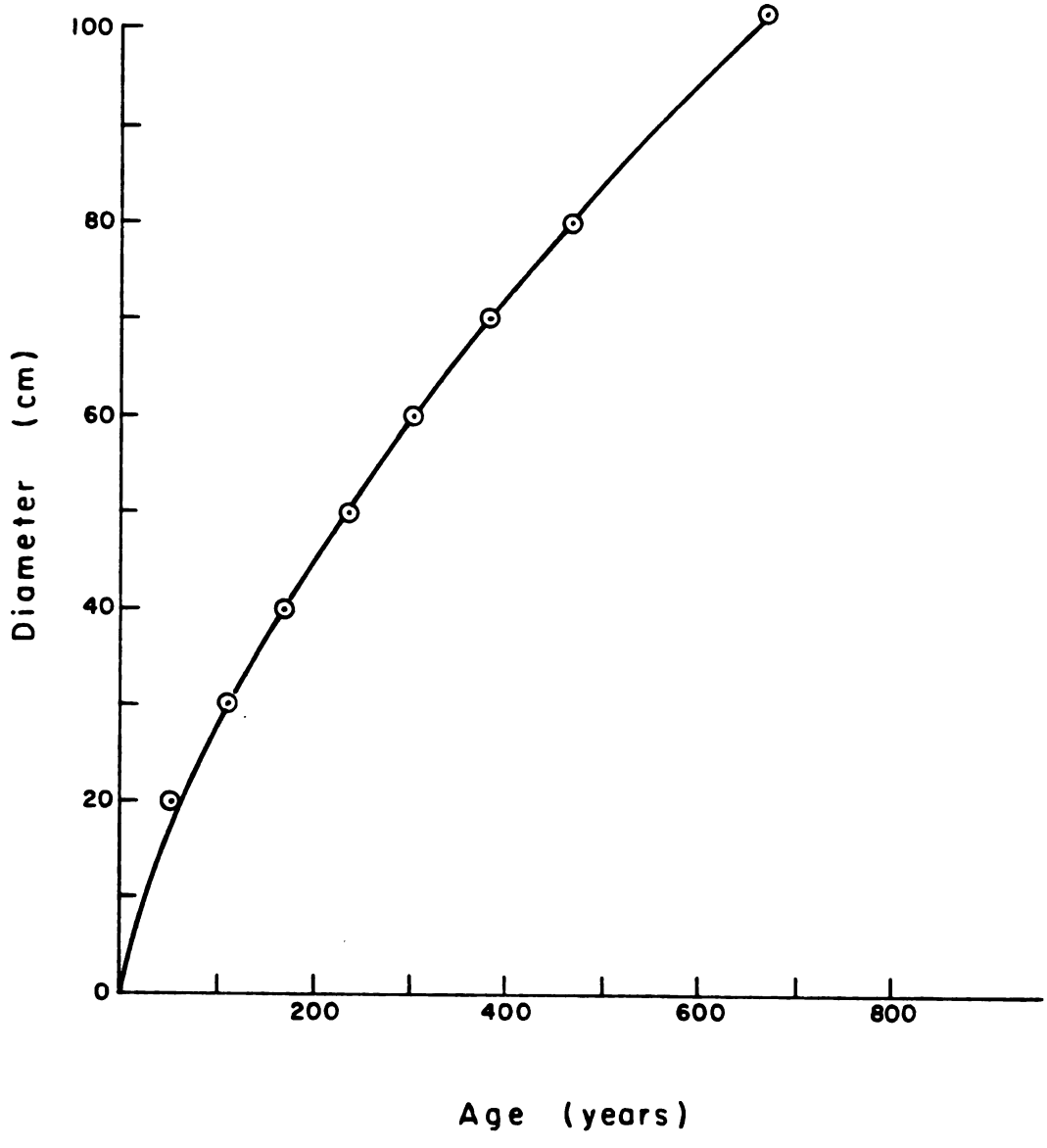

Figure 20

DISCUSSION

The Natural Forest Plots

Hurricane-induced changes in forest structure and composition

The observed trends in forest structure, species composition and forest growth during the 35-year measurement period, can be correlated with hurricane disturbance between 1928 and 1932, and subsequent forest recovery. Hurricane San Felipe, with maximum winds of 240 km/hr and 36 hours duration, passed southwest of the Luquillo Forest in 1928, and San Nicolas, with 140 km/hr winds and 40 hours duration, paralleled the north coast of the island in 1931 (Salivias 1972). These storms probably had some impact on the Luquillo Forest. San Cipriano of 1932, however, with 200 km/hr winds, more than 43 cm rainfall and 18 hours duration, had a trajectory directly over the Luquillo Mountains (Crow 1980; Fig. 5). This storm caused considerable defoliation, windfall, stem breakage, and mortality. A later hurricane, Santa Clara of 1956, traversed the island southwest of the Luquillo Mountains and caused only slight, localized damage within the Luquillo Forest (Wadsworth and Englerth 1959).

Forest recovery begins as a mosaic of patches of different ages and gaps of different sizes, followed by colonization and growth, building, and maturity, to be renewed again by treefalls (Whitmore 1975; Brokaw 1985). In the colorado forest, most treefalls, or major forest damage, are concentrated into a short period of time during and after recurrent hurricanes. Immediately after the hurricanes, fallen debris including

leaves, branches and entire trees adds a considerable organic load to the ground surface (Lugo et al. 1983) and simultaneously allows light to reach the forest floor. Increased solar insolation, reduced transpiration, and direct contact of the biotic components of the soil and litter with fallen debris, creates an environment favorable for increasing the rate of decomposition of the debris and increasing nutrient availability (Bormann and Likens 1979; Master and Trappe 1984; Canham and Marks 1985).

In response to improved environmental conditions, secondary species increase in prominence (White 1979) by means of a regeneration niche (Grubb 1977; Fox 1977) and help to conserve nutrients that otherwise might be exported due to heavy rains. Elsewhere, the abnormal production of seeds after storms (Bates 1929; King 1945; Webb 1958), regeneration in gaps of various sizes (Whitmore 1974), and the growth of secondary forest in patchy arrangements (Browne 1949) have been suggested as adaptive features that enhance the survival of pioneer and secondary species within the natural forest. Although this second phase of forest recovery, early colonization and growth (Brokaw 1985) including the response of residual stems to altered forest conditions, was not assessed directly, evidence of this phenomenon is available from the first plot measurements of 1946. In that year, 55 percent of the total stems were found in the smallest diameter class (Fig. 6). Moreover several short-lived pioneer and early secondary tree species such as Hedyosmum arborescens, Psychotria berteriana, Cecropia peltata, Didymopanax morototoni, and Miconia laevigata were numerically more abundant at that time than in 1981 (Table 4 and Fig. 11).

The third stage of recovery, that of building, is characterized by a gradual decline in the number of secondary species coupled with the

ingrowth and continued development of longer-lived, shade tolerant understory and canopy species like Cordia borinquensis, Prestoea montana, Calycogonium squamulosum, and both species of Micropholis (Fig. 11). The observed shifts in the distributions of diameter, height, crown and specific gravity classes are all consistent with the steady trend of forest recovery (Figs. 6, 7, 8 and 9). The decline of stems in the smallest diameter and height classes is due in part to growth and competition among survivors, as well as the mortality of short-lived secondary species. Intermediate size trees, usually very vigorous, increase in numbers because of additions from smaller diameter classes as well as the continued survival of trees within the class. The general decline in the largest diameter classes is due to senescence and mortality of large trees that survived the hurricane. The increased number of suppressed stems in 1981 as compared with 1946 indicates that the forest is being gradually dominated by larger stems, or is 'closing'. The trend toward higher specific gravity for the entire forest reflects the gradual decline of light weight pioneer and early secondary species as well as the increased dominance of larger, heavier, shade tolerant, climax species. This occurs despite an influx of palms, which have a low specific gravity.

The stem density for the entire forest remained approximately equal although the increases on the mixed plot and valley plots balanced the overall decline on the slope plots (Table 3). A priori, one would expect a decline in stem numbers immediately after the hurricane, followed by a maximum 15 to 20 years later in the second phase of recovery, as was observed in the tabonuco forest (Crow 1980). Subsequently, during the building phase, stem numbers should decline due to increasing competition among survivors. This trend is apparent on the slope plots to different

degrees, although one of the four plots remained essentially stable in numbers.

The forest-wide equilibrium in ingrowth and mortality during the period of measurement is due to the offsetting trends on slope and valley plots as well as the fact that the colorado forest is a dense formation characterized by small-size, slow-growing trees (Wadsworth 1951; Weaver 1983). Change during recovery within this forest is not as rapid as in the tabonuco forest where an 18 percent decline in stem numbers was observed between 1951 and 1976 as the forest approached steady-state (Crow 1980). Regardless, an increase in stem numbers on the valley plots during the building phase merits attention. Two phenomena may account for the differences between slopes and valleys. The first is that the valleys support larger trees, particularly in height (Fig. 8). When these die, they create large openings, or growing space for saplings. Six trees with dbh's >90 cm died during 35 years on valley plots but none that size were lost on the mixed or slope plots (Fig. 7). Moreover, the ingrowth of palms on the mixed plot and valley plots averaged 150 trees/ha compared with only 50 trees/ha on the slope plots during the period of measurement. The average number of palms in 1981 on the mixed plot and valley plots was 380/ha whereas on the slope plots it was only 140/ha. Palms are not only shade tolerant, slow growing and persist for long periods (Bannister 1970), but also require less space to mature than the larger dicot species, commonly growing to maturity in their shade.

The six percent decline in the number of tree species for the entire forest is also a trend evident during the building phase (Fig. 15). Individual natural forest plots, however, show increases, decreases, and stable numbers of species, yielding ambiguous trends if considered alone.

Species diversity is a topic that has received considerable review in the literature with several authors postulating greater diversity in mature forest (Budowski 1965; Margalef 1968; Odum 1969). Others have suggested that recurrent disturbance should provide more niches (Sloan Denslow 1985) and subsequently greater species diversity, and that species richness will be the highest in communities subject to intermediate levels of disturbance (Connell 1978; Pickett and White 1985) or in regimes where disturbance is more frequent than the time required to competitively exclude certain species (Huston 1979).

The most notable decreases in species' numbers are on both valley plots located near the transition between tabonuco and colorado forest at 650 m in elevation. The disturbance of this area during and after the hurricane led to colonization from both forest types giving these plots a higher species richness about 15 years after the storm. It has been suggested that a landscape under a stable disturbance regime should develop a dynamically stable mosaic of patches of different ages (Sprugel 1985), and to this could be added a dynamically changing number of species at any particular locale. Perhaps the most interesting trend in the colorado forest is the apparent convergence of species' numbers on individual plots during the period of measurement. This suggests that after disturbance, localized species richness may vary considerably because of the status of the patch before disturbance, the amount of disturbance, the particular locale, and the availability of seed, among other factors, and that during recovery, species numbers tend to converge as the stands mature. For all natural forest plots combined, the floristic richness appears greatest a few years after disturbance during the phase of colonization and growth, when both primary and secondary

species are components of the stand. During the building phase, the gradual dominance of shade tolerant species leads to decreases in abundances of secondary species and may locally exclude some of the uncommon species.

The increase in similarity among two-thirds of the natural forest plots (Table 8) reflects the increase of indicator primary species as well as many additional changes in similarity among the most common species. In general, the decline of secondary and late secondary species led to greater dissimilarity between plots.

Similarity changes $\geq$2 percentage points occurred for 20 species including the first 17 species and Clusia krugiana and Miconia tetrandra in Table 4, and Guettarda valenzuela, a species not listed. The species which provided the most frequent and largest percent changes, in descending order, were Prestoea montana, Calycogonium squamulosum, Micropholis chrysophylloides, Cyrilla racemiflora, and Croton poecilanthus.

Except for Magnolia splendens, which may attain sizes of 1 m in diameter and 20 m in height, the remaining 11 species tentatively classified as rare or endangered in 1973 (Table 6 and 7) are small, usually not exceeding 15 cm in diameter and 10 m in height. Ditta myricoides is found locally between 600 and 750 m elevation in the Luquillo Mountains, frequently in valley topography. Maytenus elongata, Eugenia eggersii, and Xylosma schwaneckeanum are found from about 300 m to the summits. The remaining species are most common in the dwarf forest on the exposed summits of the Luquillo Mountains and largely survive on ridges and upper slopes within the colorado forest.

Growth

Mean annual diameter growth for all stems in the colorado forest (Table 9) is slower than in the tabonuco forest of Puerto Rico (Wadsworth 1951, 1952; Tropical Forest Experiment Station in 1953; Crow and Weaver 1977; Weaver 1979); only the subtropical dry forest in the southwest (Weaver 1979) and the dwarf forest on mountain summits (Weaver 1983) have slower mean diameter growth rates. In the dry forest, growth is clearly limited by a lack of moisture (Lugo et al. 1978) and in the dwarf forest by the adverse growing conditions of summit areas (this study, Part III). Elsewhere in the humid tropics, including 13 sites ranging from 20 to 2100 m in elevation with annual rainfalls between 1960 and 7500 mm (Leigh and Smythe 1978), diameter growth for the trees measured exceeded that of the colorado forest. Many temperate forest trees with limited growing seasons have more rapid annual diameter growth (USDA Forest Service 1965) than colorado forest trees.

The pattern of similar diameter growth by crown class, except for suppressed stems, of some species, suggests that once light is available, rapid growth is possible. Another pattern with a decreasing trend in growth from dominants through suppressed trees suggests that maximum diameter growth is attained by larger trees with good exposure to light. The second pattern is particularly interesting because it substantiates the utility of simple crown class designations as indicators of growth potential for a period as long as 35 years.

The 35 percent decline of diameter growth on the trees that survived the 35-year period of measurement (Table 10) probably indicates that the forest building phase is ending and the mature phase is beginning.

Similar declines in the rates of biomass and nutrient accumulation have been observed in both natural forests and plantations following the phase of most rapid growth (Vitousek 1985).

Growth in basal area, volume, and biomass may be estimated from differences in the standing crop of trees in 1946 and 1981, providing an estimate of net change, or by summing net change and mortality over the same period. The second method yields a better estimate of actual stand production because it includes all trees that exploited growing space within the stand. Mortality is not estimated in most studies because they are of short duration and little mortality is evident, or because it is not considered important. Omission of mortality underestimates actual forest production, and is analogous to excluding intermediate thinnings in studies of plantation production.

Mean basal area changed little on all natural forest plots. This indicates a long-term dynamic balance between the loss of secondary species and mortality of large stems that survived the passage of the hurricane, and ingrowth and increment on numerous residual stems in the small and intermediate diameter classes. Because measurements such as diameter and basal area do not reflect height changes, they are of limited use as indicators of forest production unless correlated with them.

The mean net volume growth was 1.06 m^3/ha/yr during 35 years, and was positive on six of the seven natural forest plots suggesting recovery from past forest disturbance. In steady-state conditions, individual plots might show minor increases or decreases in standing volume, but mean net volume change would approach zero. The notable variability in growth rates between slope and valley topography may be partly attributable to better site conditions and partly to different species' compositions.

Valley plots in colorado forest, especially at lower elevation, contain Dacryodes excelsa, Manilkara bidentata, Buchenavia capitata, Matayba dominguensis and Miconia laevigata from the tabonuco forest, all of which attain larger size than most colorado forest species, and tend to grow at faster rates.

Several other estimates of net volume growth in previously disturbed tropical moist and wet forests are in the range between 1 to 5 m^3/ha/yr. Virgin tabonuco forest in Puerto Rico recovering from disturbance by San Cipriano had a net volume growth of 2.5 m^3/ha/yr (Wadsworth 1957). Partially cut, or disturbed rain forest in Malaysia, yielded 1 to 3 m^3/ha/yr, rain forest in Nigeria 2, and dipterocarp forest in the Philippines from 2.9 to 4.3 m^3/ha/yr (Johnson 1976). Tropical high forest in Uganda appeared incapable of yielding >1.4 m^3/ha/yr under any management system involving multiple cutting, nor >4.2 m^3/ha/yr under a single harvest system (Dawkins 1959). Although these data are not directly comparable because of differences in forest composition and structure as well as the nature of past disturbance and forest measurement, they do demonstrate the generally low volume accumulations in previously disturbed natural forests.

Net aboveground woody biomass accumulation was also positive on six of the seven natural forest plots, with a mean rate of 0.67 t/ha/yr. Again, the valley plots G and H exceeded the slope plots, averaging 1.41 t/ha/yr. These plots are located only 2 km horizontally and 200 m vertically from a 0.72 ha tabonuco plot that was monitored for 33 years after the same disturbance. Net aboveground woody biomass accumulation on the tabonuco plot was estimated at 1.50 t/ha/yr (Crow 1980).

Net aboveground woody biomass accumulation rates for secondary and mature natural forests elsewhere in the American tropics are presented along with those determined in this study in Fig. 21. Site details are presented in Appendix Table 1. All net woody biomass accumulation values for mature forest plots are clustered in the range of 0.5 to 3.5 t/ha/yr. Secondary net woody biomass accumulations are more variable, but except for the youngest stands, exceed those in the mature forest, ranging up to 12 t/ha/yr in tropical moist forest. Because all of the secondary forest sites were cleared before establishment of the growth plots, their biomass accumulation rates should approach the maximum for the colonization and growth, and early building phases of natural forests after disturbance.

The Thinned Plot

Changes in forest structure and composition induced by thinning

Thinning in 1947 eliminated diameter classes $\geq$50 cm (Fig. 6), reduced the number of species to about 60 percent of the average for the natural forest (Fig. 15), removed seed sources from the plot area, and provided growing space for the residual trees. The 50 percent reduction of basal area, which included canopy and understory stems, probably simulated the most destructive effects that could be inflicted on forest structure and composition by a hurricane. The combined effects of the 1766 and 1772 type A hurricanes that passed directly over the Luquillo Mountains may have caused similar destruction in certain localities.

Records of recovery on the thinned plot begin after two disturbances, one by hurricanes, and the second by silvicultural treatment. Because the increment of residual stems was slow and growing space remained available (Weaver 1983), a massive influx of new stems increased stem density on the

Figure 21. Net biomass growth rates (aboveground woody biomass) for secondary and mature natural forests in the American tropics: (1) tropical moist forest (Salas 1978; Folster, Salas and Khanna 1976); (2) tropical moist forest (Ewel 1971); (3) subtropical moist forest (Snedaker 1970); (4) tropical wet forest (Golley et al. 1976); (5) tropical moist forest (Uhl 1980); (6) subtropical wet forest (Crow 1980); (7) lower montane wet forest (Tanner 1980); and (8) lower montane wet forest -- colorado forest (this study). Forest formations are Holdridge (1967) life zones.

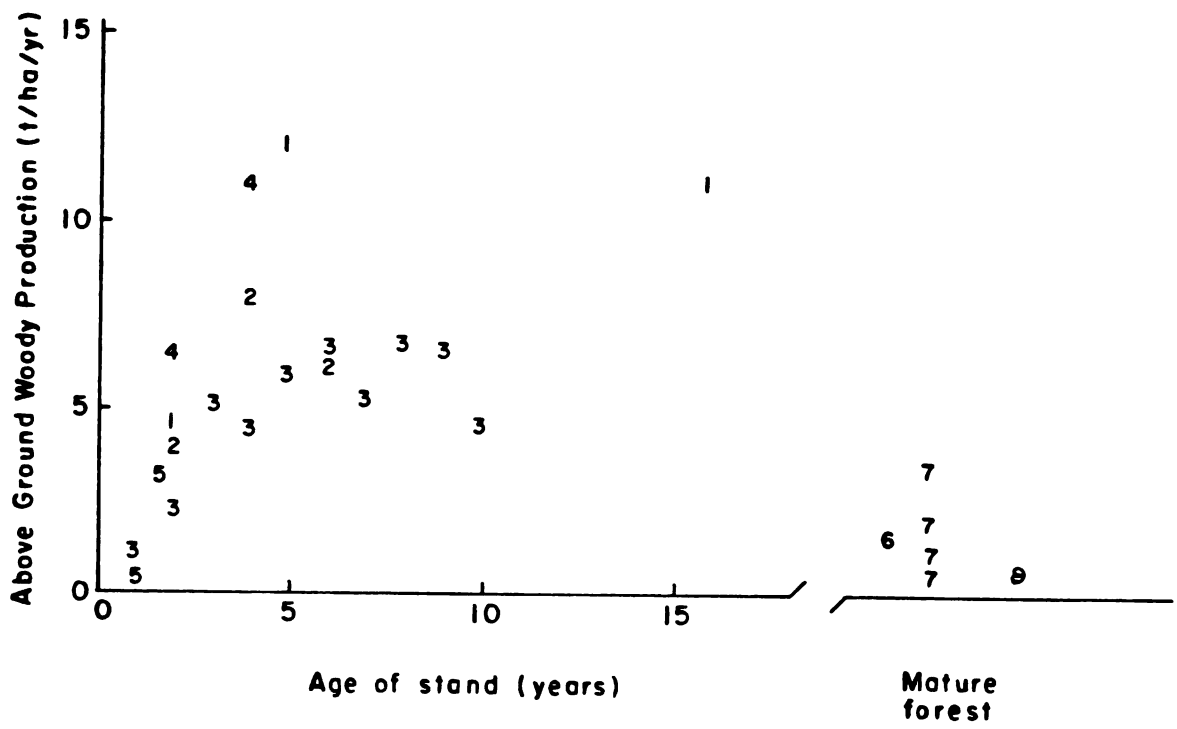
Above Ground Woody Production (t/ha/yr)
15
10
5
0
0
5
10
15
Age of stand (years)
Mature forest

Figure 21

plot by nearly 40 percent (Table 3; Fig. 6). The five species that increased considerably in numbers (Fig. 14) were not considered secondary or late secondary indicator species (Fig. 11, top row of species and Cyrilla), except for Cyrilla. The increases in abundance of Tabebuia rigida and Cyrilla racemiflora can be attributed to the proximity of seed sources. Both of these species along with Haenianthus salicifolius, Clusia krugiana, and Miconia tetrandra appear capable of exploiting small gaps within the colorado canopy. Moreover, of the seven new species recorded on the thinned plot during the period of measurement, Cecropia peltata, Alchornia latifolia, and Psychotria berteriana are pioneer or secondary species that had largely disappeared on the natural forest plots, and Ficus trigonata and Marliera sintenisii are uncommon within the colorado forest.

The general decline in similarity between the natural forest plots and the thinned plot during recovery (Table 8) is related to the thinning itself and its subsequent effect on the regeneration of several species (Fig. 14). The greatest declines in similarity were caused by Calycogonium squamulosum and Ocotea spathulata, both of which increased on the thinned plot, but not in proportion to the influx of new stems (Fig. 14). The largest increases in similarity between the thinned plot and valley plot H, the only natural forest plot which became more similar to the thinned plot, were for Cyrilla racemiflora, Miconia tetranda, and Tabebuia rigida. Valley plot H was the only natural forest plot on which Cyrilla regenerated well.

Growth

The initial basal area, volume and aboveground woody biomass on the thinned plot were only 54, 40, and 43 percent, respectively, of the means for the natural forest plots at first measurement. Net growth of all three parameters was positive and higher than on any individual natural forest plot, with the exception of volume on valley plot G. This comparatively rapid and sustained development is partly attributable to more ingrowth (Weaver 1983) during the colonization phase, and a prolonged building phase due to the initial thinning. The apparent anomaly with greater biomass but less volume growth than on plot G is caused by the differences of the specific gravities of the species common on each of the plots. Palm, with a specific gravity of 0.26 g/cm^3, is common on plot G whereas Clusia krugiana and Micropholis garciniaefolia with specific gravities of 0.90 and 0.64 g/cm^3 are abundant on the thinned plot.

Mean annual diameter growth for all surviving stems averaged 0.10 cm/yr on the thinned plot (Weaver 1983), a value which is not significantly different from the mean annual increment for all species combined, regardless of crown class, on the natural forest plots (Table 9).

Age and Dynamics of Cyrilla racemiflora

Regeneration of Cyrilla is stimulated by openings within the forest. Seedling regeneration on the natural forest plots is low (Fig. 38, Part II) showing that it does not regenerate as well in shaded conditions as do known climax species. This evidence is corroborated by the paucity of

suppressed trees which were found on the natural forest plots in 1946 (Table 9).

The distribution of Cyrilla trees by diameter class on the natural forest plots in 1946 (Fig. 12; see also Appendix Fig. A-1) strongly suggests that regeneration was concentrated in relatively short intervals at some time in the past, possibly after major disturbances (Jones 1945; Knight 1975; Lorimer 1980). In contrast, the 1981 distribution for Cyrilla shows a disproportionate number of stems in the smallest diameter class (Fig. 12). Most of the change in distribution was caused by the ingrowth of Cyrilla into smaller diameter classes after the 1932 hurricane, but there was a slight decline of stems in the larger diameter classes as well. The most valuable information derived from the availability of two diameter class distributions in different years is that conclusions regarding regeneration strategies based on a single observation may be erroneous if past disturbance of the forest is not considered.

The abundant regeneration of Cyrilla on the previously thinned plot supports the hypothesis that Cyrilla requires a gap to regenerate. Whereas the natural forest plots showed a general decline of Cyrilla stems during the measurement period (Fig. 11), the previously thinned plot had nearly a 10-fold increase (Fig. 14). Initial growth of the stems was rapid compared to the residual stand, with many narrow-crowned trees exploiting small openings in the canopy.

The convex pattern of diameter growth shown by Cyrilla (Fig. 20) is not characteristic of shade tolerant climax trees. For shade tolerant species, there is considerable variability of diameter increment in the seedling and sapling stages (Brown and Matthews 1914, Brown 1919, Richards

1952). In closed forest, diameter increment of these species commonly increases with tree size, yielding a sigmoid growth curve during the life cycle of the tree. An initial slow phase of seedling growth is followed by rapid increment approaching linearity during youth and early maturity, gradually slowing, and finally ceasing altogether in senescence (Whitmore 1975). The rapid growth of Cyrilla in the juvenile stage assures its early establishment in the canopy and is followed by slower growth in mature stages. This pattern is similar to that suggested for Didymopanax morototoni, a known secondary species (Crow and Weaver 1977).

Because Cyrilla attains large size within montane areas of the Antilles where tree diameter growth averages about 0.10 cm/yr (Wadsworth 1951; Weaver 1982, 1983), the age of the largest trees may approach 1000 years. Using the synthesis technique, a tree 1 m in diameter was estimated to be 660 years old. Critics of the technique, however, point out that validation is difficult, and that confirmation of the age of any particular tree is impossible. Although this is true for the individual tree, records of hurricanes that passed directly over Puerto Rico from the 1500's to 1970 (Salivia 1972) allows comparison with the diameter class distribution of Cyrilla and its estimated diameter growth rate.

According to the record, no hurricanes passed near Puerto Rico from 1673 to 1713 (Salivia 1972), and none passed directly over the island from 1713 to 1737 (Fig. 4). In 1738, two storms, either type A or B, passed over the south coast where damage was reported. When a temporal scale derived from the age curve (Fig. 20) is superimposed over the 1946 Cyrilla diameter class distribution (Appendix Figure A-1), the dates of major hurricanes known to have passed directly over the Luquillo Mountains coincide with observed concentrations of stems. In 1766, San Jenaro and

San Marcos, and in 1772, San Agustin, all type A or B storms, passed over the mountains. These storms probably did considerable damage to the forests which resulted in the notable increase in the 30 to 40 cm diameter class (Fig. 12). The fact that the storms were concentrated in a brief period of only six years, and that many trees in the forest may have been senescent after nearly a century without disturbance, probably accentuated their effect.

Although its trajectory was not directly over the Luquillo Forest, Santa Ana of 1825 may rank as the greatest of recorded hurricanes. It caused considerable damage to the central and eastern end of the island, and probably disturbed the forest. San Narciso of 1867 was another very damaging storm whose effect may be detectable in the 20 to 30 cm diameter classes.

The effects of the most recent hurricane that traversed the Luquillo Mountains, San Cipriano of 1932, are not noticeable in the lowest 1946 diameter class distribution. This may be in part due to the limited amount of time for regeneration and growth to 4.1 cm, the lower limit of the smallest diameter class. A recent study of stand dynamics in the subtropical wet forest of the Luquillo Mountains during the period between 1943 and 1976 (Crow 1980) implicated this hurricane in species composition changes over time including the presence of secondary tree species a few years after the storm followed by a gradual increase in dominance of climax species with stand recovery.

It should be pointed out that information on trajectories, intensity and duration of past hurricanes, in particular those before the 20th century, is vague. At least the hurricane record does not detract from

the hypothesis that regeneration of Cyrilla is tied to recurrent climatic events and stand disturbance.

The loss of Cyrilla in the larger diameter classes and the current lack of seedling regeneration are probably attributable to a 54-year hiatus in hurricane disturbance. This decline in Cyrilla is a major concern of wildlife biologists working to save the rare and endangered Puerto Rican parrot. Once found throughout the island, the parrots are now confined to the colorado forest of the Luquillo Mountains where they use hollow Cyrilla trees for nesting sites. One possible method to increase Cyrilla tree density in the Luquillo Mountains evident from this study is selective thinning favoring Cyrilla trees in the residual stand to serve as a seed source.

Additional field observations of Cyrilla throughout the Luquillo Mountains have shown that trees are capable of growing to large size within 1 m of each other. The largest trees are found at low elevations in the colorado forest, or at high elevations in the the tabonuco forest. Extremely large trees, in excess of 2.5 m, have been seen only twice. These trees have an oblong shape and a major bifurcation two or three meters above the ground. Moreover, the intervening diameter classes between those reported in this study (Fig. 13) and the largest specimens, that is, between 1.3 and 2.5 m, have not been seen in the field. These observations lead to the conclusion that large Cyrilla trees found in Puerto Rico, and presumably elsewhere in the Antilles, are the result of growth and development on favorable, protected sites at the lower limits of their elevational range. Furthermore, extremely large Cyrilla trees probably result from the coalescence of proximate trees. If this is true, it is doubtful that the largest trees live much beyond 1,000 years.

On occasion, fallen Cyrilla trees have developed new crowns from already exisiting branches thus 'walking' to a new microsite (Bodley and Benson 1980) and surviving into a new generation! Moreover, trees with damaged crowns have been observed to sprout from the base. These characteristics are combined with the capability to regenerate and grow into small openings in the canopy, and persist for what appears to be about 1000 years for the largest individuals.

Hurricane Damage and Recovery in the Luquillo Mountains

Hurricane damage is a function of numerous factors among which storm characteristics (wind velocity, total rainfall, and duration), storm recurrence, vegetation features (tree size, stem density, crown growth patterns, and tree specific gravities) and soils and topography all play a role. Sufficient information is available from this and other studies to propose a comprehensive hypothesis regarding hurricane damage and recovery in the forests of the Luquillo Mountains. The principal storm event, in this instance, San Cipriano, was already described. The soils in the Luquillo Mountains are mainly clays. The vegetation, for the most part, lacks an emergent story which has been attributed to recurrent hurricanes (Odum 1970).

With ascent in the mountains, the soils become wetter, notably so above the rather abrupt transition between tabonuco and colorado forest (Wadsworth and Bonnet 1951). Tree size declines along the same elevational gradient (Wadsworth 1951), and at any particular elevation in both the colorado and dwarf forests, trees are tallest in the valleys and smallest on ridges, with greatest stem densities on ridges. In contrast,

the tabonuco forest has some of its tallest trees on upper slopes and ridges (Wadsworth 1953; Crow and Grigal 1980).

In tabonuco forest, windfall is most prevalent in valleys where the soils are wet and the trees have large crowns, whereas on ridges, breakage prevails (Wadsworth and Englerth 1959). The small, dense vegetation on upper slopes and ridges in both colorado and dwarf forest is characterized by woods with high specific gravities, which should reduce both uprooting and breakage (Lawton 1984; Putz et al. 1983), resulting in damage mainly by defoliation. Indeed, this forest type was designated as "hurricane hardwood" long ago (Murphy 1916). The lower slopes and valleys in the upper forests probably suffer more windthrow because trees are larger and the soils wetter on that topographic position. In summary, the gaps created by storm damage should not only diminish in size with an increase in elevation, but also should decrease in size from valley through slopes to ridges at any particular elevation. The greater occurrence of Cecropia peltata, a known pioneer, in valley topography of colorado forest (Fig. 33, Part II), lends support to this idea. Moreover, the greater net aboveground biomass increment on valley plots as compared with slope plots (Fig. 18) may partially reflect greater windthrow in valleys.

Recovery after hurricanes in the tabonuco forest is by colonization of large pioneer trees such as Cecropia peltata, Didymopanax morototoni, Alchornea latifolia, and Alchorneopsis portoricensis along with smaller trees in the Rubiaceae and Melastomataceae. The number of stems peaks after 15 to 20 years (Crow 1980) and then declines due to competition among the survivors. In the colorado forest, Cecropia and Didymopanax also colonize but the trees are smaller and grow slower. The number of stems fluctuates widely several years after disturbance, generally

declining on slopes and increasing in valleys, the latter because of palm growth. No direct observations of hurricane damage are available for the dwarf forest. However, recovery on two sites, one that had been clearcut and the second which had been cleared by a plane wreck, showed a dense growth of grass and ferns with some sprouting after six years (Byer and Weaver 1977), a condition that has prevailed for 17 years. Vegetative reproduction was observed elsewhere in the same forest (Nevling 1971). It may be surmised, then, that major windthrow would be detectable many decades after a hurricane. Indeed, the formation of "alpine meadows" in isolated areas within the dwarf and upper colorado forest may be related to landslides and windthrow caused by hurricanes. Once formed, their recovery may span centuries. The fact that they are rare, and that secondary tree species are largely absent (Byer and Weaver 1977), indicates that uprooting of trees and the creation of large gaps in the dwarf forest are uncommon.

The building phase in the tabonuco and colorado forest is characterized by a shift in the number of stems to larger diameter and height classes, as well as a shift from intermediate to suppressed crown classes. Because growth is more rapid in tabonuco forest, the changes occur more rapidly. In the dwarf forest, localized damage could result in a greater number of stems due to sprouting, but stem number changes should be minimal.

Species richness in the tabonuco and colorado forests varies from one locale to another with disturbed areas containing greater relative abundances of secondary species. As these forests recover from hurricane damage, secondary species decline in number and primary species increase in dominance. In the dwarf forest, damage is not as extensive, secondary

species are largely absent, and tree species richness remains unaltered during recovery.

Biomass increment in the tabonuco forest is initially rapid and later declines producing a convex recovery pattern (Crow 1980). In colorado forest where damage is not as extensive, and secondary species are fewer and slower-growing, the recovery pattern is probably linear. The dwarf forest recovery pattern is surmised to be linear as well, but slower than in colorado forest.

In the event of another hurricane in the near future, damage and recovery of the forest should be similar to that described for San Cipriano. Storm attributes and the interval between storms would influence the amount of forest damage and recovery processes. If the Luquillo Forest continues to mature for many more years, however, senescence, mortality, and individual tree falls during periods of unusually heavy rainfall and high winds should play a prominent role in creating gaps and initiating recovery on a smaller scale.

SUMMARY

Periodic damage and recovery from hurricanes constitute an integral phase of forest growth and development in the Caribbean. Recovery of the colorado forest on seven natural forest permanent plots in the Luquillo Mountains of Puerto Rico from 15 to 50 years after the passage of San Cipriano is characterized by:

(1) ingrowth and mortality rates of about 20 stems/ha/yr, or 1.1 percent/yr of the number of stems at first measurement;

(2) shifts to larger diameter and height classes. This includes a decline in the smallest diameter class, and the 2 smallest height classes, accompanied by increases in intermediate diameter classes, and all remaining height classes. The largest diameter classes showed minor declines caused by the loss of larger trees, mainly Cyrilla racemiflora;

(3) a 5 percent decline of stems in the intermediate crown class accompanied by a 7 percent increase in the number of suppressed stems. Dominant stems also declined slightly while the codominant stems remained nearly equal;

(4) an increase from 0.563 to 0.574 g/cm^3 in the average specific gravity of the forest including palms. Dicots alone increased from 0.608 to 0.632 g/cm^3;

(5) a change in species composition with the loss of pioneers and secondary species and increasing dominance of climax species;

(6) a decline in species numbers from 88 to 83 on all plots, or 2.8 ha combined, with a convergence of species numbers to about 35 to 45 on most individual 0.4 ha plots. The Shannon-Wiener diversity index also declined from 4.81 to 4.33 for all plots combined, and decreased on all but one of the individual plots;

(7) mean diameter increment on all surviving stems of 0.16 $\pm$ 0.08 cm/yr for dominants (D), 0.13 $\pm$ 0.01 for codominants (C), 0.09 $\pm$ 0.09 for intermediates (I), 0.05 $\pm$ 0.00 cm/yr for suppressed (S) stems. Two basic growth patterns were shown, namely, D = C = I > S, and a gradual decline in annual diameter increment from D through S, with at least three significant differences;

(8) a decline in diameter increment between 1946-51 and 1976-81 on surviving dominant, intermediate and suppressed stems, and an increase in diameter increment on surviving codominant stems;

(9) little change in basal area, with a mean and standard error of 41.2 $\pm$ 1.4 m^2/ha for all plots combined in 1946 and 1981. Slope plots remained equal or declined while valley plots increased slightly in basal area; and

(10) an increase in standing volume from 216.7 $\pm$ 12.1 to 253.8 $\pm$ 14.7 m^3/ha and standing biomass from 121.5 $\pm$ 8.2 to 145.0 $\pm$ 7.2 t/ha for all plots combined, yielding net growth rates of 1.06 m^3/ha/yr and 0.67 t/ha/yr for volume and biomass, respectively. Again, growth on the valley plots exceeded that on the slope plots.

A thinned plot that had not only been disturbed by the hurricanes but also had been reduced in basal area by 50 percent at the time of first measurement showed the following differences when compared with the natural forest plots during the same period of measurement:

(1) 20 percent less mortality and 260 percent more ingrowth of stems than on the natural forest plots;

(2) an increase in the number of species from 24 to 31 and an increase in the Shannon-Wiener diversity index from 2.31 to 2.90;

(3) a greater increase in numbers of Clusia krugiana, Miconia tetrandra, and Cyrilla racemiflora than on the natural forest plots;

(4) greater changes in crown class distribution than on the natural forest plots with a 47 percent decline in intermediate stems and a 40 percent increase in suppressed stems; and

(5) a positive net basal area increment averaging 0.42 m^2/ha/yr with net volume and net biomass increments also positive, averaging 2.38 m^3/ha/yr and 1.71 t/ha/yr, respectively.

Moreover, data from both of the above groupings of plots disclosed that:

(1) 12 tree species tentatively classified as rare and endangered for Puerto Rico in 1973 were found in the colorado forest, the majority of these on ridges and upper slopes at higher elevations; and

(2) the age of a 1 m Cyrilla racemiflora, the largest and most prominent tree species within the forest, is about 660 years old. Also, the diameter class distribution of Cyrilla was tentatively correlated with previous hurricanes whose trajectories passed directly over the Luquillo Mountains around 1770.

Hurricane damage within the Luquillo Mountains appears to vary considerably by forest type, topography, and elevation. Windthrow is more common in humid valleys particularly at lower elevations where trees are larger. Breakage, in turn, is more common on upper slopes and ridges where trees are better anchored, in particular, in colorado and dwarf

forests, where these topographic positions are occupied by densely-packed, small and heavy-wooded species.

Recovery patterns in the forests after hurricanes are also distinct. In the tabonuco forest, fast-growing pioneers and secondary species rapidly invade gaps in the tabonuco forest resulting in a convex recovery curve for biomass accumulation. In the colorado forest where gaps are smaller and the secondary species slower growing, biomass recovery appears linear for several years. In the dwarf forest at the summits, breakage creates small openings that are filled by vegetative reproduction or sprouting of climax species rather than regeneration of secondary species. In instances where damage is severe, recovery may take more than a century.

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APPENDIX TABLES

Appendix Table 1. Biomass accumulation rates for secondary and mature natural forests in the American Tropics.

Code No.[1]	Life zone[2]	Age (yrs)	Growth rate: Biomass (t/ha/yr)	Source
1	T-mf	2	4.89	Salas 1978; Folster, Salas and Khanna 1976
		5	12.02	
		16	11.05	
2	T-mf	2	3.93	Ewel 1971
		4	8.00	
		6	6.07	
3	ST-mf	1	1.30	Snedaker 1970
		2	2.33	
		3	5.12	
		4	4.67	
		5	5.80	
		6	6.15	
		7	5.12	
		8	6.71	
		9	6.54	
		10	4.67	
4	T-wf	2	6.62	Golley et al. 1976
		4	11.11	
5	T-mf	0.8	0.18	Uhl 1980
		1.8	3.47	
6	ST-wf	M[3]	1.67	Crow 1980
7	LM-wf	M[3]	0.5	Tanner 1980
			1.0	
			2.0	
			3.5	
8	LM-wf	M[3]	0.67	this study

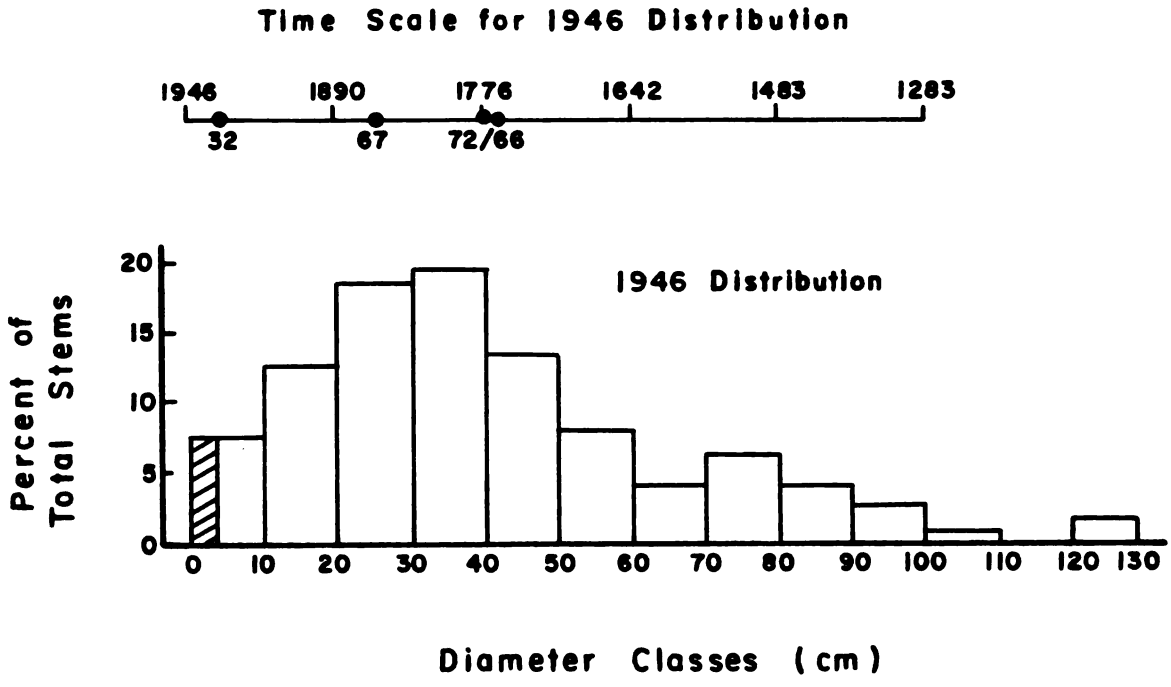
[1]Data coded to Fig. 21.

[2]Life zones (Holdridge 1967): T-wf, Tropical wet forest; T-mf, Tropical moist forest; ST-mf, Subtropical moist forest; ST-wf, Subtropical wet forest; LM-wf, Lower montane wet forest.

[3]M = mature forest

APPENDIX FIGURES

Appendix Figure A-1. Diameter class distribution of Cyrilla racemiflora on the natural forest plots within the colorado forest in 1946. The time scale indicates the years to which the diameter class corresponds as well as the years that type A storms passed directly over the Luquillo Mountains, according to the synthesized age curve. The shaded portion of smallest diameter class, that is, < 4.1 cm in diameter, was not tallied in the field.



Appendix Figure A-1

PART II

STRUCTURE AND COMPOSITION OF CLOSED CANOPY COLORADO FOREST RELATIVE TO ENVIRONMENTAL GRADIENTS

INTRODUCTION

Relationships between vegetation and environmental gradients are difficult to demonstrate in tropical forests because structural complexity and species richness compound the tasks of sampling and interpretation (Hall and Swaine 1976). Moreover, the gradients themselves are often complex, and in montane habitats include elevation, aspect, topography, and associated moisture differences, among others. The existing forest classification schemes for the Caribbean Islands (Beard 1944, 1949) including Puerto Rico (Wadsworth 1951; Little and Wadsworth 1964; Ewel and Whitmore 1973) emphasize forest physiognomy and common tree species but contain little information on variation in species composition within the recognized forest types.

Gradient analysis is the interpretation of vegetational response to spatial variation in environmental factors. The advancement of numerical analysis beginning with the ordination of rain forest in Borneo (Ashton 1964a, 1964b) and the classification of rain forest in Australia (Webb et al. 1967a, 1967b) provided an impetus to the study of gradient analysis in several tropical forests (Table 11). These studies disclosed numerous relationships including forest composition with topography (Ashton 1964a; Austin and Greig-Smith 1968; Ashton 1976), vegetation structure with altitudinal gradients (Webb et al. 1970), forest composition with reproductive biology (Wong and Whitmore 1970), gibbon behavior with forest types and structure (Whitten 1982), and the influence of animals on forest

Table 11. Summary of studies using numerical analyses in tropical forests

Region Locale	Forest type	Authors and dates
Asia and East Indies		
Borneo	rain forest	Ashton 1964a, 1964b; Austin et al. 1972
Sabah	rain forest	Austin and Greig-Smith 1968
Solomon Islands	rain forest	Greig-Smith et al. 1967
Mentawi, Sumatra	lowland rain forest	Whitten 1982
Pasoh Reserve, Malaya	rain forest	Wong and Whitmore 1970; Ashton 1976
Sarawak	lowland rain forest	Newbery and Proctor 1984
Australia		
N. Australia	rain forest	Webb et al. 1967a, 1967b
W. coast, Australia	rain forest	Webb et al. 1970
Africa		
Rwanda, Central Africa	savanna	Bouxin 1976
Ghana	evergreen seasonal and semi-deciduous	Hall and Swaine 1976
Nigeria	high forest	Hall 1977
Nigeria	savanna	Ramsey and de Leeuw 1965
Nigeria	savanna woodland	Onyekwelu and Okafor 1979
Neotropics		
Barro Colorado, Panama	rain forest	Knight 1975
Puerto Rico	lower montane rain forest	Crow and Grigal 1980
Puerto Rico	montane rain forest	this study

composition (Ashton 1976). The effects of soil on species composition within a particular forest, however, were less conclusive (Ashton 1964a, 1976; Austin et al. 1972; Knight 1975; Newbery and Proctor 1984).

In the Luquillo Mountains, two attempts were to made to discern the effects of environmental gradients on species distributions. One was a numerical analysis in tabonuco forest which disclosed eight major forest types that were strongly correlated with past land use and topography (Crow and Grigal 1980). The other was a transect with a fixed aspect on ridge topography, mainly in colorado forest, which indicated variation in tree species abundances according to elevation (White 1963). Additional relationships remained unknown because of the complex nature of the environmental gradients pointing out the need for further work in the forest.

In addition to the lack of information on tree species distributions, little was known about the regeneration patterns and seral stages of canopy trees in the colorado forest. Tree species reflect a gamut of characteristics that comprise their life history strategies to assure survival in a complex, montane environment. These include morphological differences in seed size and wood specific gravity as well as ecological differences in the capacity to regenerate and grow into canopy openings or through a shaded understory. Analysis of these characteristics would provide a basis for the tentative classification of tree species according to seral stage.

The development of management alternatives for timber, wildlife, and rare plant species, and other forest resources, is dependent on a knowledge of forest structure and species distribution patterns. Likewise,

regeneration patterns and seral stages of the component species must be known (Dawkins 1958; Whitmore 1984).

METHODS

Existing trails were used to locate 25 groups of three plots each on different topography scattered between 620 and 970 m elevation within the colorado forest. Groups of plots (i.e., ridge, slope, and valley) were spaced at about 50 m increments in elevation. They contained closed-canopy vegetation, and had varying aspects, slopes, and exposures within the groups (Fig. 1). The definition for topography in this section differed from that in Part I. The slope, valley and mixed designations used in Part I referred to the predominant topography of the plot. In this section, ridge plots were located entirely on convex topography, valley plots were entirely on concave or level topography, and slope plots were located on nearly uniform slopes without concave or convex features.

After preliminary observations, a 50 x 10 m plot size and a minimum stem diameter of 4.1 cm were selected for sampling. The plot size was a tradeoff between a unit large enough to include a representative sample of the most common tree species and small enough to remain entirely on the topographic feature. The short stature of the forest and the inclusion of small trees in the samples were important factors facilitating the use of small plots. On each plot, all trees $\geq$4.1 cm in diameter at breast height (dbh, or 1.4 m above the ground) and rooted within the plot were measured to the nearest 0.1 cm using a diameter tape. Height was measured to the nearest 0.1 m using an optical rangefinder. Crown classes were recorded as dominant, codominant, intermediate or suppressed (Baker 1950). Tree

volumes, including branches $\geq$2.5 cm in diameter, and above ground woody biomass, were derived in the same manner as outlined in the Methods section of Part I.

On each plot, percent forest cover was estimated by taking four densiometer readings at each of two stations spaced about 20 m apart, to substantiate that the canopy of the vegetation was closed. Moreover, at each station, two soils samples to 50 cm depth were collected using a standard soil probe. Soil contents were combined by station and placed in standard collecting bags.

Bulk density was calculated from the dry weights of the samples and the volume of the soil probe. The samples were then ground with a mechanical pulverizer and passed through a 2-mm sieve. Organic matter concentrations were determined using the Walkly-Black method (Black 1967).

An unbalanced two-way analysis of variance (ANOVA) including topography (ridge, slope or valley) and life zone (wet or rain), with a continuous elevation covariate, was used to explore variance in forest parameters. The parameters tested for each plot were: the number of trees, the number of species, the mean height of dominant and codominant stems, basal area (m^2/ha), volume (m^3/ha), aboveground woody biomass (t/ha), soil bulk density (g/cm^3), percent organic matter, and soil organic matter content (kg/m^2).

In the data analysis, the main effects of life zone, topography, and elevation were considered along with interaction. Initially, for each parameter (Y), the complete model was:

Y = life zone + topography + elevation + (life zone x topography interaction) + (life zone x elevation interaction) + (topography x elevation interaction) + (life zone x topography x elevation interaction) + e.

The null hypothesis of the complete covariance model was that the interaction terms involving elevation were not significant, or specifically, that the difference between (topography x elevation) = (life zone x elevation) = (topography x life zone x elevation) = zero. If the F value for any of the parameters under consideration was significant, then it followed that elevation could not be used as a covariate. In all instances where F values for interaction were not significant in the complete covariance model, these terms were eliminated and a reduced model was developed.

Within each plot, a centrally located strip of 20 subplots 1 m^2 in size was used to sample seedling regeneration of tree species that reached canopy size. All seedlings between 15 cm and 1.5 m tall were recorded by species. Seedlings of tree species characteristic of mid-elevations in the tabonuco forest (Wadsworth 1951) were eliminated from consideration because they were not major components of the colorado forest whereas seedlings of tree species most abundant in the transition zone at about 600 m were included. Seedlings of tree species common to the dwarf forest were also included because exposed slopes and summits where they occur may be found within the elevational limits of the colorado forest.

Aspects of the life history strategies of the 20 canopy species were assessed by comparing the abundance of seedlings and understory trees to canopy trees, and by determining seed sizes and tree specific gravities (Smith 1970). These four indices, which reflect the capacity of individual

species to develop under closed canopy, were used to differentiate between primary and secondary tree species. The capacity of canopy trees to produce seedlings, and their capacity to grow into the understory (defined as stems between 4.1 and 7.5 cm dbh and in the suppressed crown class), were termed success. The following definitions were used:

(1) Seedling success of canopy trees: relative density of seedlings of each canopy species under forest shade divided by the relative density of canopy-size trees of the same species. Relative density ratios based on all 20 canopy species were used to reflect success with regard to all species, and not just per species.

(2) Understory success of canopy trees: relative density of understory trees of each species divided by the relative density of canopy-size trees of the same species.

(3) Seed size: one half the length plus the width of the disseminule.

(4) Specific gravity: the ratio of weights of a given volume of oven-dried wood to that of an equal volume of water.

Each species was ranked from one (most secondary) to 20 (most primary) for each of the four factors. Higher ratios in both seedling and understory success indicated the capacity to survive in shade whereas lower ratios indicated intolerance to shade. Large seeds, dispersed mainly by gravity or animals, characterize primary species whereas small, usually wind-dispersed seeds, are typically borne by secondary species (Budowski 1965; Gomez-Pompa and Vazquez-Yanes 1974). Wood specific gravity is also an index to life history strategy in that primary species grow slower and have denser wood than secondary species (Budowski 1965; Smith 1970). Conversely, secondary species require more rapid growth to avoid shade and their wood densities tend to be less than those of shade tolerant species (Lawton 1984).

After ranking each tree species according to each factor, a composite species score was derived by the following relationship: Species score = ((2 x understory ranking) + seedling ranking + seed ranking + wood density ranking)/5. Greater emphasis was given to understory success as compared to other components of the composite score because it showed the capacity of the seedlings to survive and grow in shaded environment. These scores, in turn, were ranked from 1 to 20.

Other complementary information was also compared with the above to aid in the classification of species:

(1) Population structure: Reversed J-shaped diameter class distributions are indicative of those species capable of reproducing and growing in the shade, and those with greater proportions of stems in intermediate size classes, or equal distribution of size classes, are indicative of species that reproduce in openings or gaps created by recurrent disturbance of the forest (Knight 1975).

(2) Differential survival after disturbance: Rapid increase in basal area and numbers a few years after disturbance followed by decline is characteristic of pioneer species. A gradual accumulation of basal area, and possibly stem numbers, several years after disturbance, characterizes primary species. Gap species may give varied trends depending on their growth rates and longevity.

Reciprocal averaging and polar ordination techniques outlined in Ordiflex (Gauch 1977) were selected to determine the similarity of species compositions on plots from the dozen or so multivariate techniques available (Gauch 1982). Reciprocal averaging accommodates a wide range of community variation and simultaneously provides species and sample configurations. Polar ordination, in turn, provides several options for

data analysis (Gauch 1973) making it a versatile technique (Cottam et al. 1973). Ordination was favored over classification because relationships between species and the environment were being explored.

Stem densities were used as basic input data for reciprocal averaging. For polar ordination, stem densities in the form of percent similarity were employed along with a double standardization option and both program and user selected endpoints. Species with fewer than 30 occurrences were eliminated from each data set. This break-off point eliminated about 55 percent of the total species. However, each of these eliminated species constituted less than 0.4 percent of the total number of stems, or less than an average of 0.4 stems per plot. Elimination of rare species is supported in the literature because they contain little ecological information and their incidence is a matter of chance (Gauch 1977). Use of canopy species alone was sufficient for a classification of tropical and subtropical forests in Australia (Webb et al. 1967b) and less than 25 percent percent of the species were adequate for a gradient analysis on the Solomon Islands (Austin and Grieg-Smith 1968).

Different combinations of input data were run in the ordinations and different endpoints were tested with polar ordination. Included were: forest-wide tree species and sample plot ordinations; composite sample plot ordinations (that is, combined ridge, slope, and valley plots at the same elevation within the same life zone) for the entire data set; ordinations of sample plots by life zone; and ordinations of species by topography (ridge, slope or valley) without regard to life zone. The last two ordinations limited the sample plot data sets to those plots located on an elevational transect over a ridge between El Yunque and El Toro peaks (Fig. 1, Part I).

Rain forest was located to the windward and wet forest to the leeward on the transect.

Finally, stem densities of 20 common colorado forest trees grouped in topographic composites (ridge, slope, and valley plots), were plotted by elevation and aspect on a transect over the ridge between El Yunque and El Toro peaks. The number of stems per species were also plotted by topography without regard to elevation or aspect.

All species were identified using the taxonomic descriptions and keys for the trees of Puerto Rico (Little and Wadsworth 1964; Little et al. 1974). These references also provided information on seed sizes and tree specific gravities.

RESULTS AND DISCUSSION

Forest Cover

Canopy closure for the plots sampled ranged from 81 to 97 percent with a mean and standard error for all 75 composite readings of 90.8 $\pm$ 0.5 percent (Table 12). No statistical differences were observed by life zone, elevation or topography. Cover percentages in this range of values indicate closed canopy with occasional small openings among the branches of trees.

Species Richness

The increase in number of species according to topographic position was most pronounced for cumulative areas $\leq$5000 m^2 (Fig. 22). Thereafter, additional plots increased the total number of species at a slower rate.

Tree species averaged 15/plot and did not demonstrate significant relationships with components of the covariance model (Table 13). However, certain trends were apparent. The greatest mean number of species was found on ridge topography and the least on valley topography, with species numbers in the wet forest greater than those in the rain forest for comparable topographic positions. With an increase in elevation, the average number of species/plot declined (Fig. 23).

The topographic variation in species' occurrence with the greatest numbers on ridges may be related to the lower forest canopy and better drainage conditions on these sites. Many small, rare tree species survive on ridges in the colorado forest (Table 7, Part I). In contrast, fewer

Table 12: Summary of percent cover in closed canopy stands in the colorado forest

Factor	Percent cover Mean ± SE (n)[1/]
Topography	
Ridge	91.9 ± 0.9 (25)
Slope	90.8 ± 0.8 (25)
Valley	89.6 ± 0.9 (25)
Life Zone	
Rain	90.1 ± 0.8 (30)
Wet	91.4 ± 0.6 (45)
Elevation	
615 to 790 m	90.9 ± 0.7 (37)
800 to 970 m	90.6 ± 0.8 (38)
Mean	90.8 ± 0.5 (75)

1/ SE = standard error and n = number of observations.

Figure 22. Tree species-area relationships for 25 valley, 25 slope, and 25 ridge plots 500 m^2 in size in the colorado forest. All stems were $\geq$ 4.1 cm dbh.

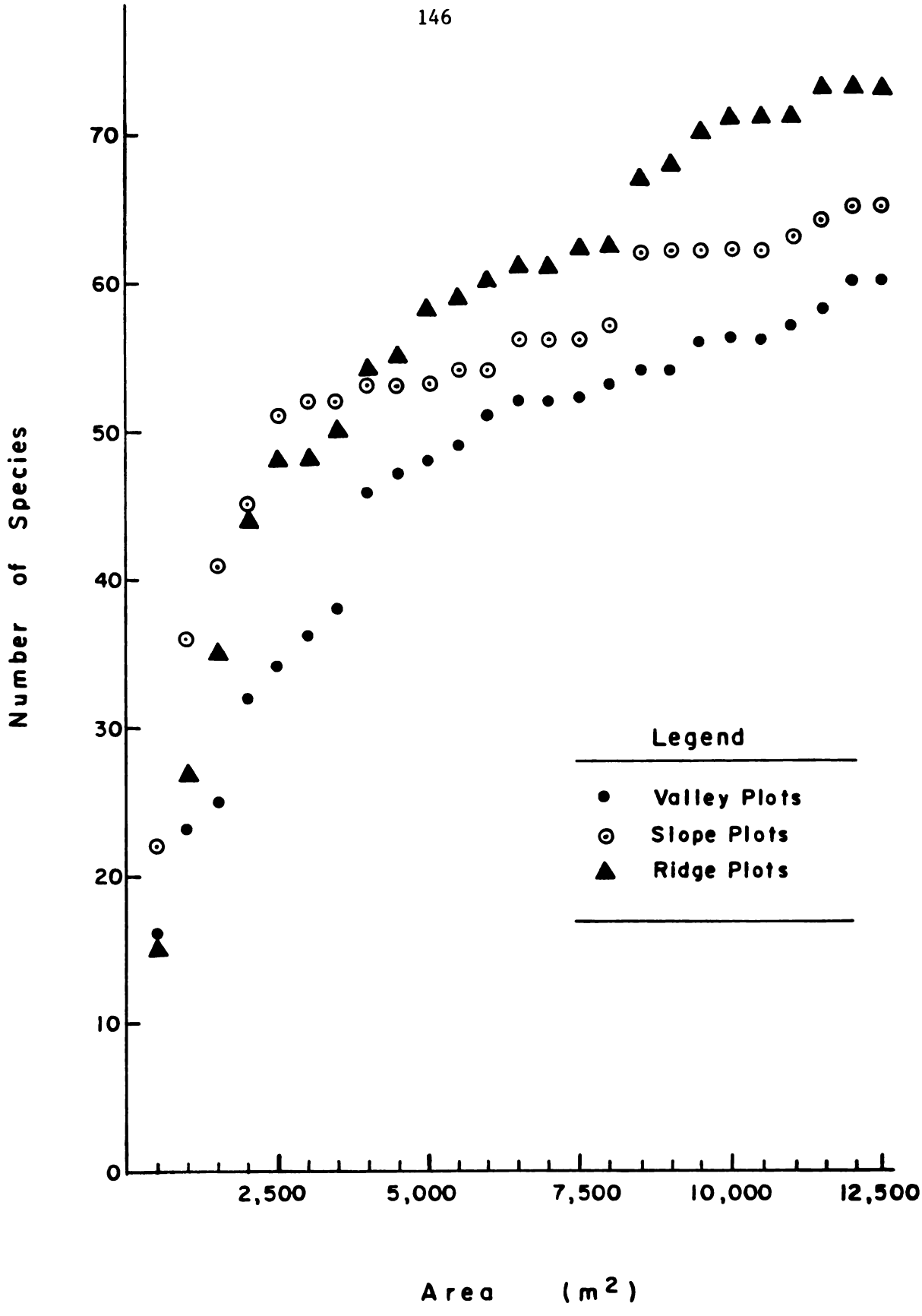

Number of Species
0
10
20
30
40
50
60
70
2,500
5,000
7,500
10,000
12,500
Area (m²)
Legend
Valley Plots
Slope Plots
Ridge Plots

Figure 23

Table 13. Values of forest parameters by life zone and topography [1/]

Forest parameter / Topography	Life Zone: Wet forest		Life Zone: Rain forest		Combined Mean
	Mean ± Standard Error		Mean ± Standard Error		
Tree species (No.) [2/]					
Ridge	19.1	(1.1)	15.1	(1.2)	17.1
Slope	18.1	(1.5)	13.4	(1.3)	15.8
Valley	14.1	(1.2)	11.4	(0.7)	12.8
Total	17.1	-----	13.3	-----	15.2
Tree density (No./ha) [3/]					
Ridge	2500	(130.9)	2468	(302.2)	2484
Slope	2272	(99.2)	2360	(308.7)	2316
Valley	1808	(132.7)	1636	(167.3)	1722
Total	2193	------	2155	------	2174
Tree height (m) [3/]					
Ridge	12.2	(0.5)	11.7	(0.9)	12.0
Slope	12.3	(0.6)	11.9	(0.8)	12.1
Valley	14.1	(0.5)	13.8	(0.8)	14.0
Total	12.9	-----	12.5	-----	12.7
Basal area (m^2/ha) [4/]					
Ridge	52.3	(3.2)	57.9	(5.1)	55.1
Slope	47.5	(2.3)	45.6	(3.0)	46.5
Valley	37.7	(5.0)	31.7	(1.7)	34.7
Total	45.8	-----	45.1	-----	45.4
Volume (m^3/ha) [5/]					
Ridge	294.4	(24.5)	318.4	(48.7)	306.4
Slope	270.8	(17.9)	236.9	(19.7)	253.8
Valley	219.3	(28.2)	177.9	(11.0)	198.6
Total	261.5	------	244.4	------	252.9

Table 13. (continued)

Biomass (t/ha) 5/					
Ridge	185.7	(14.8)	203.4	(30.9)	194.5
Slope	167.6	(11.8)	143.3	(9.9)	155.4
Valley	108.1	(17.3)	81.1	(5.2)	94.6
Total	153.8	------	142.6	-----	148.2
Bulk density (g/cm^3) 6/					
Ridge	0.99	(0.05)	0.94	(0.06)	0.96
Slope	0.94	(0.05)	0.86	(0.06)	0.90
Valley	0.89	(0.05)	0.91	(0.06)	0.90
Total	0.94	------	0.90	------	0.92
Organic matter (%) 6/					
Ridge	7.6	(1.39)	8.8	(1.56)	8.2
Slope	8.6	(1.09)	13.9	(1.53)	11.2
Valley	8.4	(1.66)	10.2	(1.32)	9.3
Total	8.2	------	11.0	------	9.6
Organic matter (kg/m^2) 6/					
Ridge	29.2	(3.16)	31.9	(5.18)	30.5
Slope	33.4	(2.58)	46.6	(1.77)	40.0
Valley	27.5	(3.48)	34.6	(3.94)	31.0
Total	30.0	------	37.7	------	33.8

1/ The wet life zone had 15 samples for each topographic position and the rain life zone had 10 samples. All models reported below use the following notation: Y = forest parameter, LZ = life zone, T = topography, and E = elevation. Interactions between factors are shown with an x and significance for factors or interactions at the 95 percent level is indicated by an asterisk. Standard errors are for the cells indicated and not the model.

2/ No interaction with E in complete model was significant. Therefore, Y = T + LZ + (TxLZ) + E.

Table 13. (continued)

3/ (LZxE) was the only significant interaction term in the complete model. Therefore, two separate analyses by LZ: for tree density - Y (wet forest) = E; and Y (rain forest) = E*. For tree height - Y (wet forest) = E*; and Y (rain forest) = E*.

4/ (TxE) and (TxLZxE) were the significant interaction terms in the complete model. Therefore, two separate analyses by LZ: Y (wet forest) = T + E + (TxE); and Y (rain forest) = T* + E + (TxE)*.

5/ (TxE), (LZxE), and (LZxTxE) were significant in complete model. Therefore, two separate analyses by LZ: Y (wet forest) = T + E + (TxE); and Y (rain forest) = T* + E* + (TxE)*.

6/ (LZxE) was significant in complete model. Therefore, two separate analyses by LZ: Y (wet forest) = E; and Y (rain forest) = E*.

Figure 23. Distribution of data points in the covariance model Y = T + LZ + TxLZ + E where Y = the number of species per 500 m^2, T = topography, LZ = life zone, and E = elevation. None of the component terms of the model was significant.

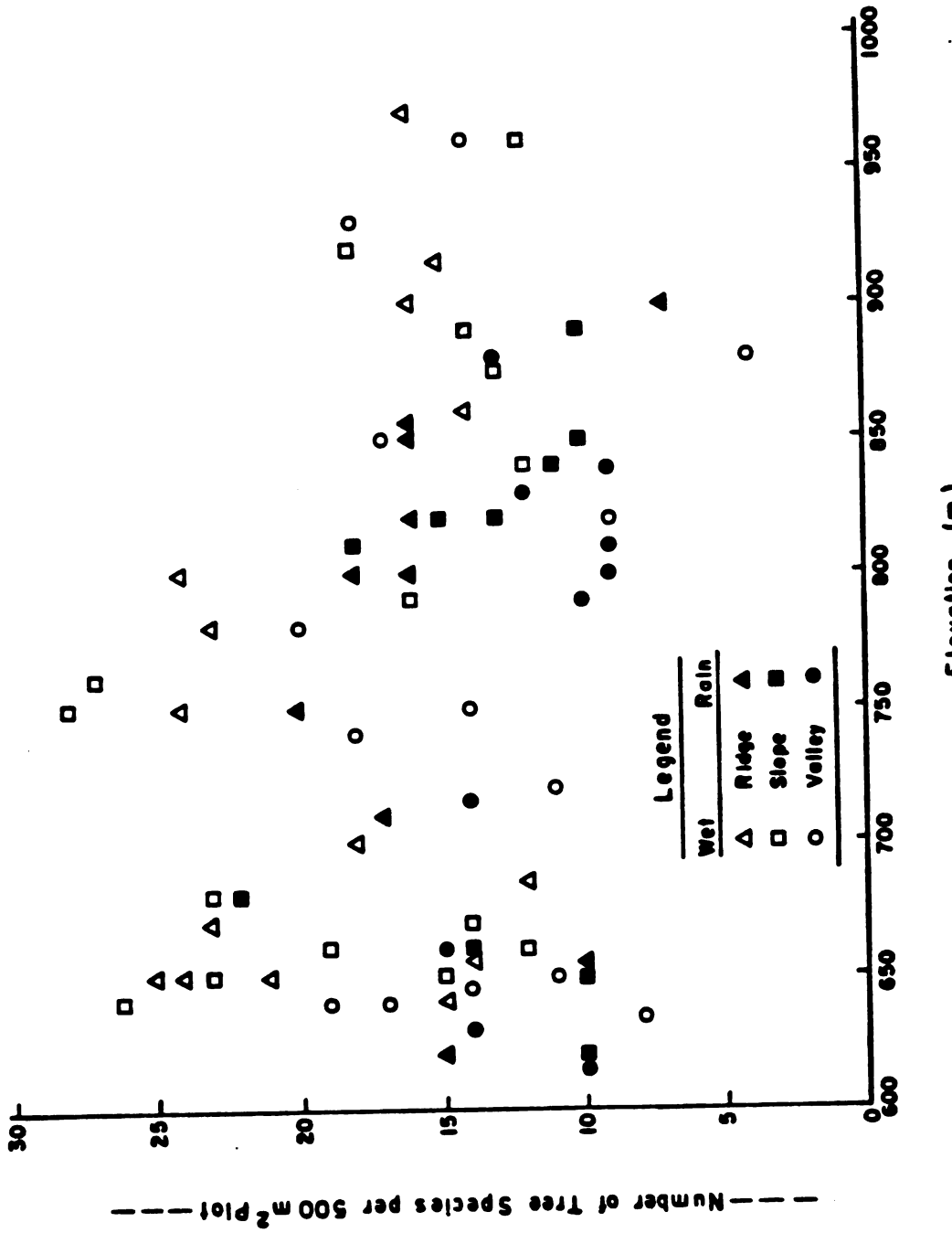

Legend
Wet
Rain
Ridge
Slope
Valley
Elevation (m)
600
650
700
750
800
850
900
950
1000
0
5
10
15
20
25
30
Number of Tree Species per 500 m² Plot

Figure 23

species are adapted to the valley plots where wetter soils and occasional flooding preclude them. In comparison, tree species diversities in the Smokies of the United States were highest on intermediate sites along a moisture gradient (Whittaker 1965). The extremely high rainfalls in the colorado forest would render all topographic positions wet, but the ridges would be the most mesic because of drainage.

The decline in species numbers with an increase in elevation is a common phenomenon in both temperate and tropical plant communities (Beard 1949; Glenn-Lewin 1977; Wadsworth 1951; Whittaker 1956, 1960). With ascent from the tabonuco through the colorado to the dwarf forests of the Luquillo Mountains, 0.4 ha plots average 45 to 55, 35 to 45, and about 15 tree species, respectively.

The lower average number of species in rain forest as compared to wet forest may be due to environmental factors. All rain forest sites are to the windward where the effects of greater rainfall and cloud cover are similar to those of increased elevation in that solar insolation is reduced, soil water content is increased, and organic matter mineralization is slowed down. Tree species common to lower elevations are not as competitive as high elevation species in the rain forest. Consequently, species richness is reduced.

The comparison of numbers of tree species in this study with other research plots in the colorado forest is confounded by sampling technique and plot size. The 500 m^2 plots used in this study varied from four species on a high elevation wet forest valley plot to 28 species on a mid-elevation wet forest slope plot (Fig. 23). For all 75 temporary plots combined, or 3.75 ha in total, 87 species were found (Appendix Table 2). Virtually the same number of species was found on the combined 2.8 ha of the

seven permanent plots (Table 4, Part I). Individually, the permanent 0.40 ha plots ranged from 35 to nearly 60 species for all stems $\geq$4.1 cm in diameter (Fig. 15, Part I; Weaver 1983). The permanent plot with the most species was located near the transition between the colorado and tabonuco forests and contained several species from the lower forest. In earlier work, about 60 species $\geq$10 cm in diameter were reported on 4 ha of contiguous virgin colorado forest (Wadsworth 1951).

Previous estimates of species richness from 0.4 ha plots in the colorado forest, although valid for the plots sampled, only contained 1/3 to 1/2 of the total species of the forest. This is, of course, to be expected. The plot samples estimated alpha diversity, or that found within a community, whereas the forest-wide sample included beta diversity, or the relative extent of differentiation of communities along an elevational gradient (Whittaker 1965). The comprehensive design and larger area used in the sampling of temporary plots included a number of rare species that increase the richness estimate.

Stem Density

The mean stem density for all 75 plots was 2174 trees/ha and was significantly related to elevation in the rain forest but not in the wet forest (Table 13; Fig. 24). Individual plot values ranged from 1060 to 4660 trees/ha. Although there were consistent differences by topographic position with valley plot densities averaging 75 percent and 70 percent of slope and ridge densities, respectively (Table 13), these were not significant because of considerable variation among plots within each life zone. Ultimately, the covariance model was reduced to a simple linear regression of tree density vs. elevation in each life zone.

Figure 24. Distribution of data points in the covariance model Y = E where Y = the number of stems/ha and E = elevation, according to life zone. The elevation component of the model is significant at alpha = 0.05 in the rain forest, but not in the wet forest. Topography of plots is indicated.

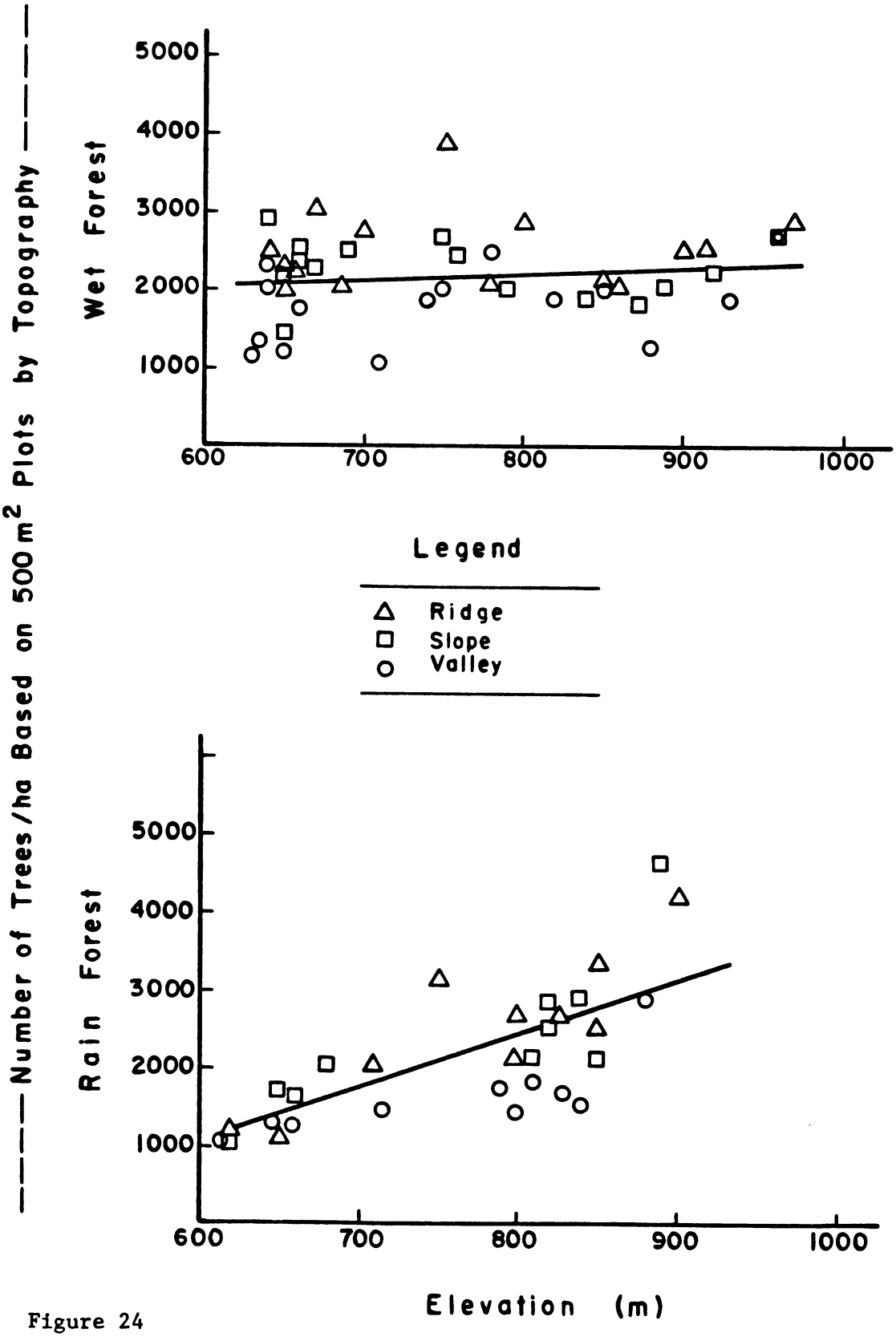

Number of Trees/ha Based on 500 m² Plots by Topography
Wet Forest
5000
4000
3000
2000
1000
600
700
800
900
1000
Legend
Ridge
Slope
Valley
Rain Forest
5000
4000
3000
2000
1000
600
700
800
900
1000
Elevation (m)

Figure 24

The decline in stem density reflected the elevational gradient sampled, varying from fewer stems at lower elevations where trees were larger to greater densities at higher elevations where trees were smaller. Moreover, the topographic variability in stem numbers also reflected a gradient in stem size with the largest trees in valleys and the smallest trees on ridges. The mean tree density for all plots was high reflecting the selection of closed canopy stands for the ordination study. Other work in the same forest using 0.40 ha plots showed mean stem densities ranging from 1635 to about 2190/ha with an average of 1860/ha (Table 3, Part I; Weaver 1983). The 0.40 ha plots contained some gaps created by the loss of canopy stems.

Tree Size Gradient in the Forest

The mean height for all dominant and codominant stems on the 75 plots was 12.5 m and was significantly related to elevation in both life zones (Table 13; Fig. 25). Individual plot mean heights ranged from 8.1 to 17.2 m. Although there were consistent differences among topographic positions within the life zones (Table 13), these differences were not significant because of considerable variation among individual plots. Ultimately, the covariance model was reduced to a simple linear regression of tree size vs. elevation in each life zone.

At low elevations in the colorado forest, some of the tallest trees were found on ridges where *Dacryodes excelsa*, *Manilkara bidentata*, *Ormosia krugii*, and other species from the tabonuco forest, occasionally grow. At higher elevations, ridges are often exposed and develop a "dwarf" vegetation (Beard 1944, 1949; Wadsworth 1951) because of the adverse conditions. At

Figure 25. Distribution of data points in the covariance model Y = E where Y = the mean height of dominant and codominant trees on the 500 m^2 plots and E = elevation, according to life zone. The elevation component of the model is significant at alpha = 0.05 in both the wet and rain forest. Topography of plots is indicated.

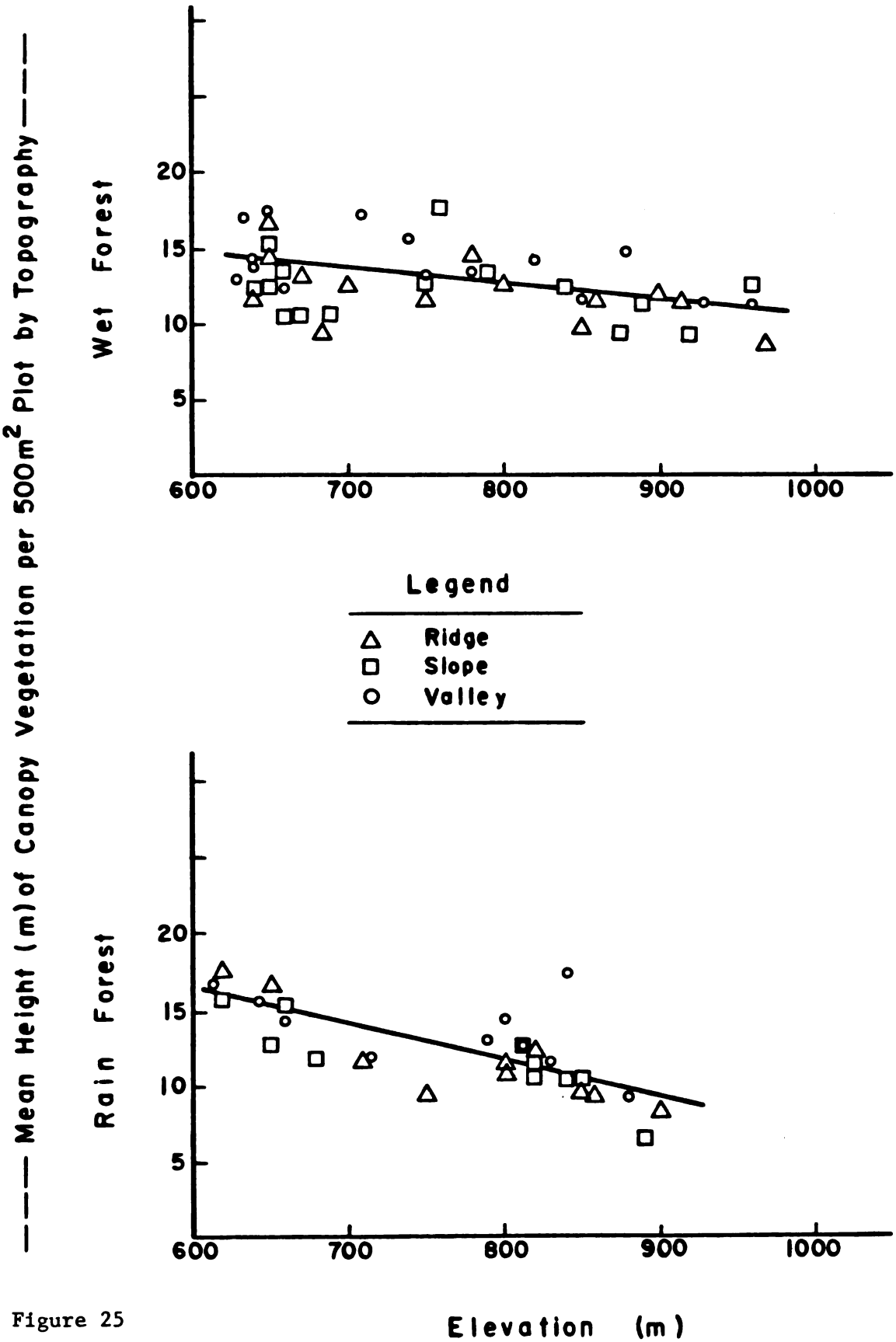

Wet Forest
Rain Forest
20
15
10
5
600
700
800
900
1000
Legend
Ridge
Slope
Valley
——— Mean Height (m) of Canopy Vegetation per 500m² Plot by Topography ———
Elevation (m)

Figure 25

all elevations, trees on the better protected valley plots were among the tallest.

The mean basal area, volume and biomass for all 75 plots combined were 45.4 m^2/ha, 252.9 m^3/ha and 148.2 t/ha, respectively (Table 13). Neither topography nor elevation explained a significant portion of the variance for basal area differences in the wet forest whereas topography and the interaction between topography and elevation did in the rain forest (Fig. 26). Volume and biomass results were similar. Again, in wet forest, no significant trends were apparent. In rain forest, however, topography, elevation and the interaction between both were significant (Figs. 27 and 28).

The comparatively low basal areas and volumes in valleys were partially caused by differences in stem densities (Table 13) and species' compositions. At mid-elevations in particular, valley plots are dominated by palms which averaged about 15 cm in dbh whereas slopes and ridges at the same elevation contain proportionately more hardwood species that occasionally attained much larger diameters. One notable exception was a wet forest valley plot near 800 m elevation which contained a large Cyrilla racemiflora (Fig. 26). In a forest with generally small diameter stems, a few large trees influence plot values considerably.

At higher elevations, the increase in numbers of stems and decrease in mean heights of the canopy trees are more pronounced within the rain forest as compared with the wet forest. Topographic differences in tree size diminish and the forest is more uniform in size, in particular, in the rain forest (Figs. 25-28). Elsewhere in the Caribbean, including the Lesser Antilles (Beard 1944, 1949) and Jamaica (Asprey and Robbins 1953), a similar decline in forest stature over an elevational gradient was observed.

Figure 26. Distribution of data points in the covariance model Y = T + E + TxE where Y = the basal area (m^2/ha) on the 500 m^2 plots and T = topography, E = elevation, and TxE = interaction, according to life zone. The topography and interaction components of the model are significant at alpha = 0.05 in the rain forest, but none of the components are significant in the wet forest.

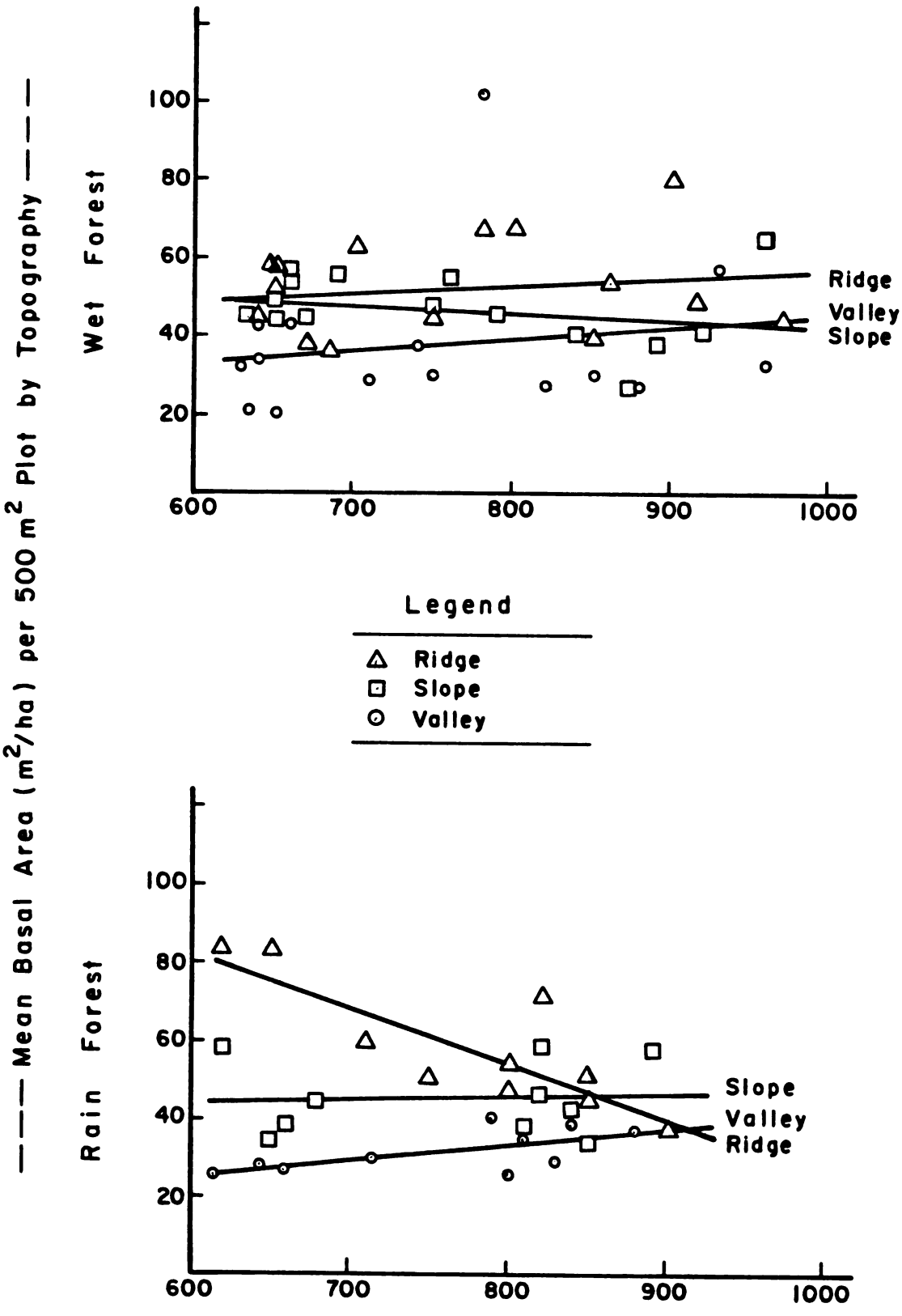

Wet Forest
100
80
60
40
20
600
700
800
900
1000
Ridge
Valley
Slope
Legend
Ridge
Slope
Valley
Rain Forest
100
80
60
40
20
600
700
800
900
1000
Slope
Valley
Ridge
——— Mean Basal Area (m^2/ha) per 500 m^2 Plot by Topography ———
Elevation (m)

Figure 26

Figure 27. Distribution of data points in the covariance model Y = T + E + TxE where Y = aboveground woody volume (m^3/ha) per 500 m^2 plot and T = topography, E = elevation, and TxE = interaction, according to life zone. All components of the model are significant at alpha = 0.05 in the rain forest, but none of the components are significant in the wet forest.

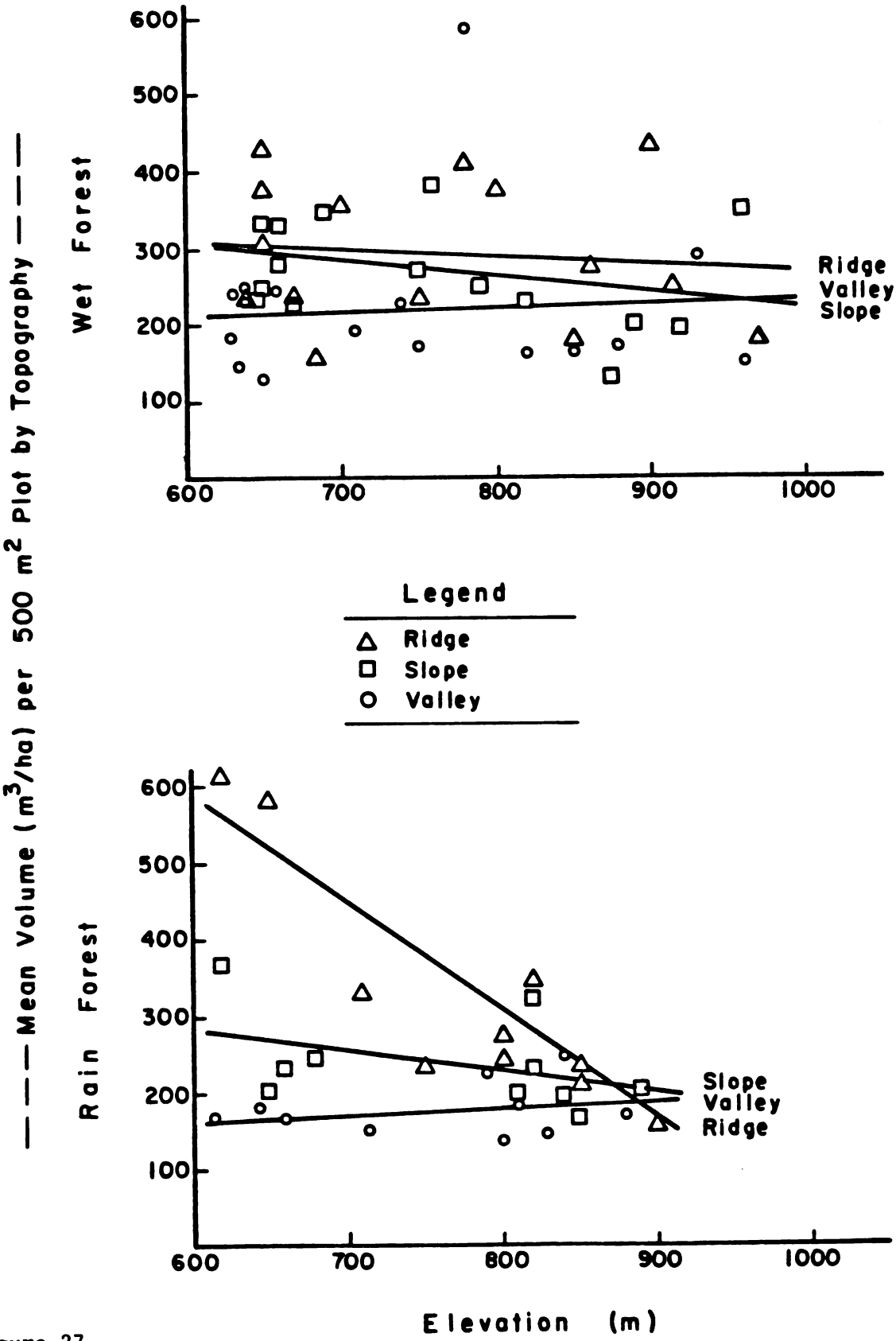

Wet Forest
600
500
400
300
200
100
600
700
800
900
1000
Ridge
Valley
Slope
Legend
Ridge
Slope
Valley
Rain Forest
600
500
400
300
200
100
600
700
800
900
1000
Slope
Valley
Ridge
Elevation (m)
— — — Mean Volume (m^3/ha) per 500 m^2 Plot by Topography — — —

Figure 27

Figure 28. Distribution of data points in the covariance model Y = T + E + TxE where Y = aboveground woody biomass (t/ha) per 500 m^2 plot and T = topography, E = elevation, and TxE = interaction, according to life zone. All components of the model are significant at alpha = 0.05 in the rain forest, but none are significant in the wet forest.

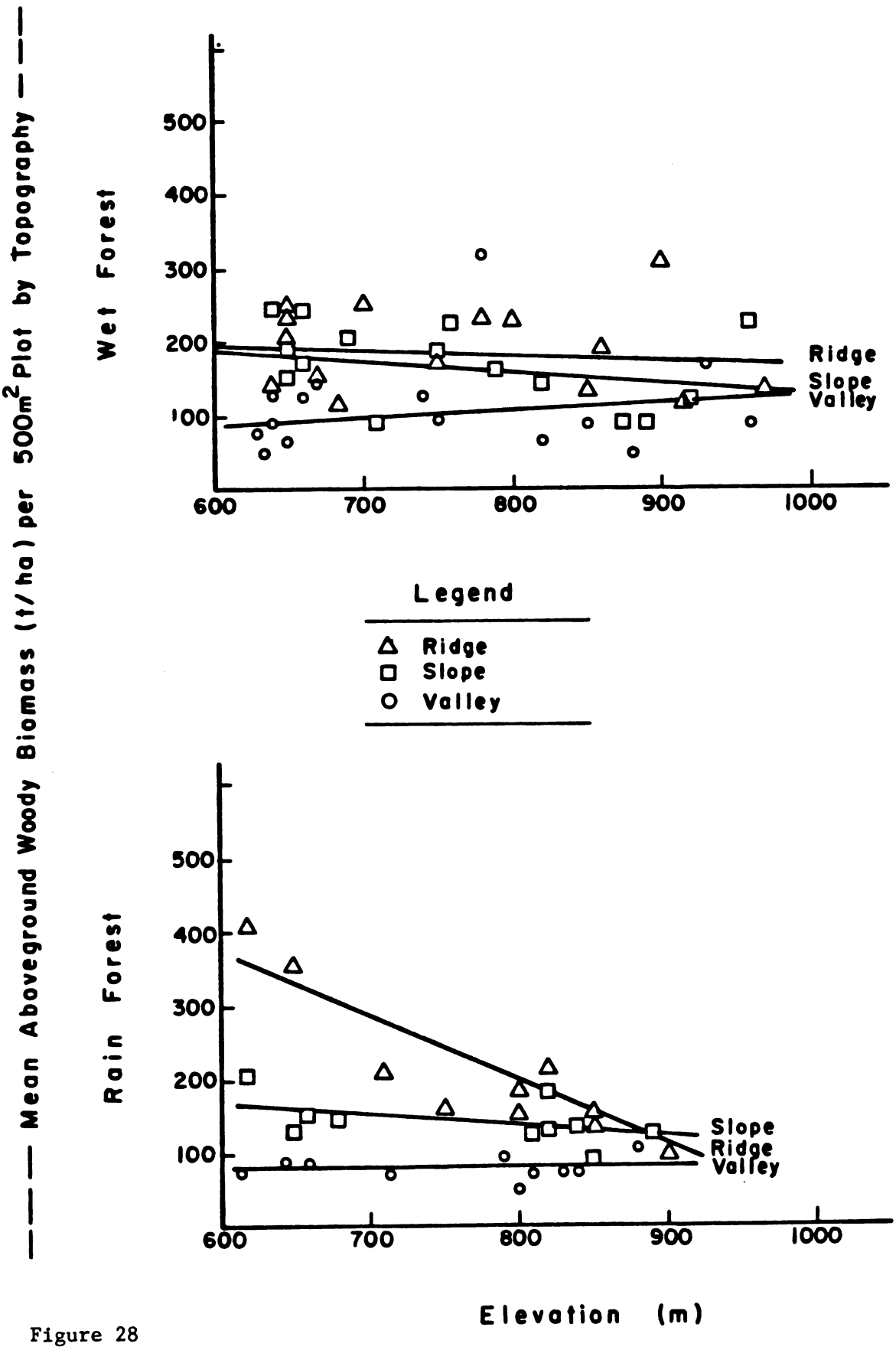

Mean Aboveground Woody Biomass (t/ha) per 500m² Plot by Topography
Wet Forest
500
400
300
200
100
600
700
800
900
1000
Ridge
Slope
Valley
Legend
Ridge
Slope
Valley
Rain Forest
500
400
300
200
100
600
700
800
900
1000
Slope
Ridge
Valley
Elevation (m)

Figure 28

Biomass values in valleys are lower than on slopes and ridges, and the trends are more pronounced than those for basal area and volume. This is because of the lower specific gravities of trees that characterize the canopy species in valleys. Presoea montana, the palm, at 0.26 g/cm^3, the lowest of any tree within the forest, and Cecropia peltata and Sapium laurocerasus, at 0.29 and 0.38 g/cm^3, respectively, are less dense than canopy slope and ridge species which range between 0.50 and 0.70 g/cm^3. Similar topographic differences in specific gravity between tree species in valleys and those on slopes and ridges were observed in the montane forests of Costa Rica (Lawton 1984).

The basal area and volume values for these plots, and consequently the derived biomass values, exceeded previous estimates for the forest (Table 1, Part I; Figs. 16 and 17, Part I; Weaver 1983). This is because plot selection precluded disturbed areas and plot size was small.

Organic Matter of Forest Soils

The mean bulk density, percent organic matter, and organic matter content in the top 50 cm for all 75 plots combined were 0.92 g/cm^3, 9.6 percent and 33.8 kg/m^2, respectively (Table 13). In the rain forest, none of the model components accounted for a significant portion of the variance whereas in the wet forest, only elevation significantly explained the variance for all three soils' parameters (Figs. 29-31).

Mean organic matter percent and mean organic matter content were both greater in the rain forest than in the wet forest (Table 13). Other factors being equal, organic matter of soils in humid forests should increase with a decrease in temperature or an increase in rainfall, or with a decrease in the temperature/rainfall relation (Brown and Lugo 1982). A priori, a

Figure 29. Distribution of data points in the covariance model Y = E where Y = soil bulk density (g/cm^3) and E = elevation, according to life zone. The elevation component of the model is significant at alpha = 0.05 in the wet forest, but not in the rain forest.

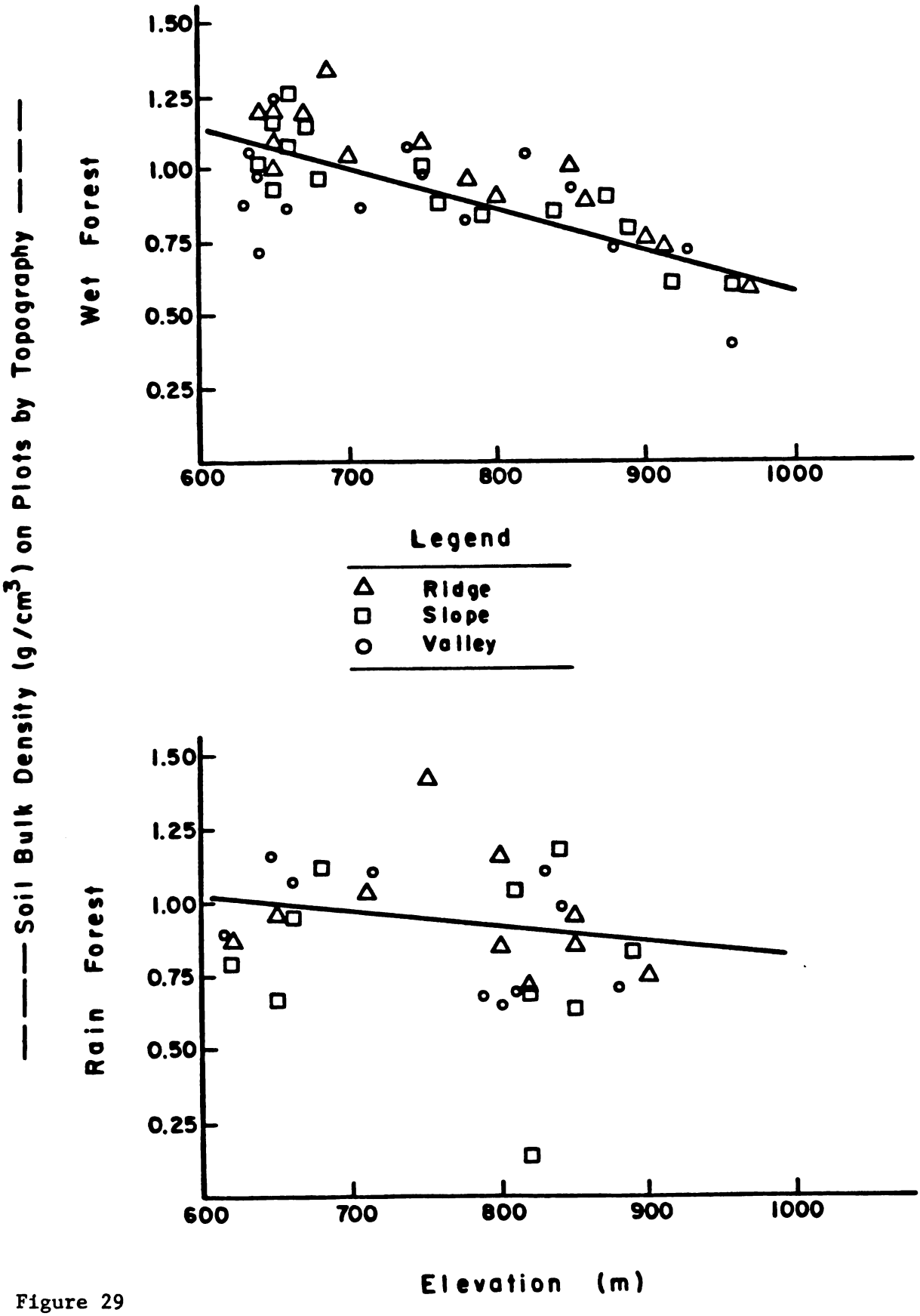

Wet Forest
Rain Forest
1.50
1.25
1.00
0.75
0.50
0.25
600
700
800
900
1000
Legend
Ridge
Slope
Valley
Soil Bulk Density (g/cm³) on Plots by Topography
Elevation (m)

Figure 29

Figure 30. Distribution of data points in the covariance model Y = E where Y = percent organic matter in soil and E = elevation, according to life zone. The elevation component of the model is significant at alpha = 0.05 in the wet forest, but not in the rain forest.

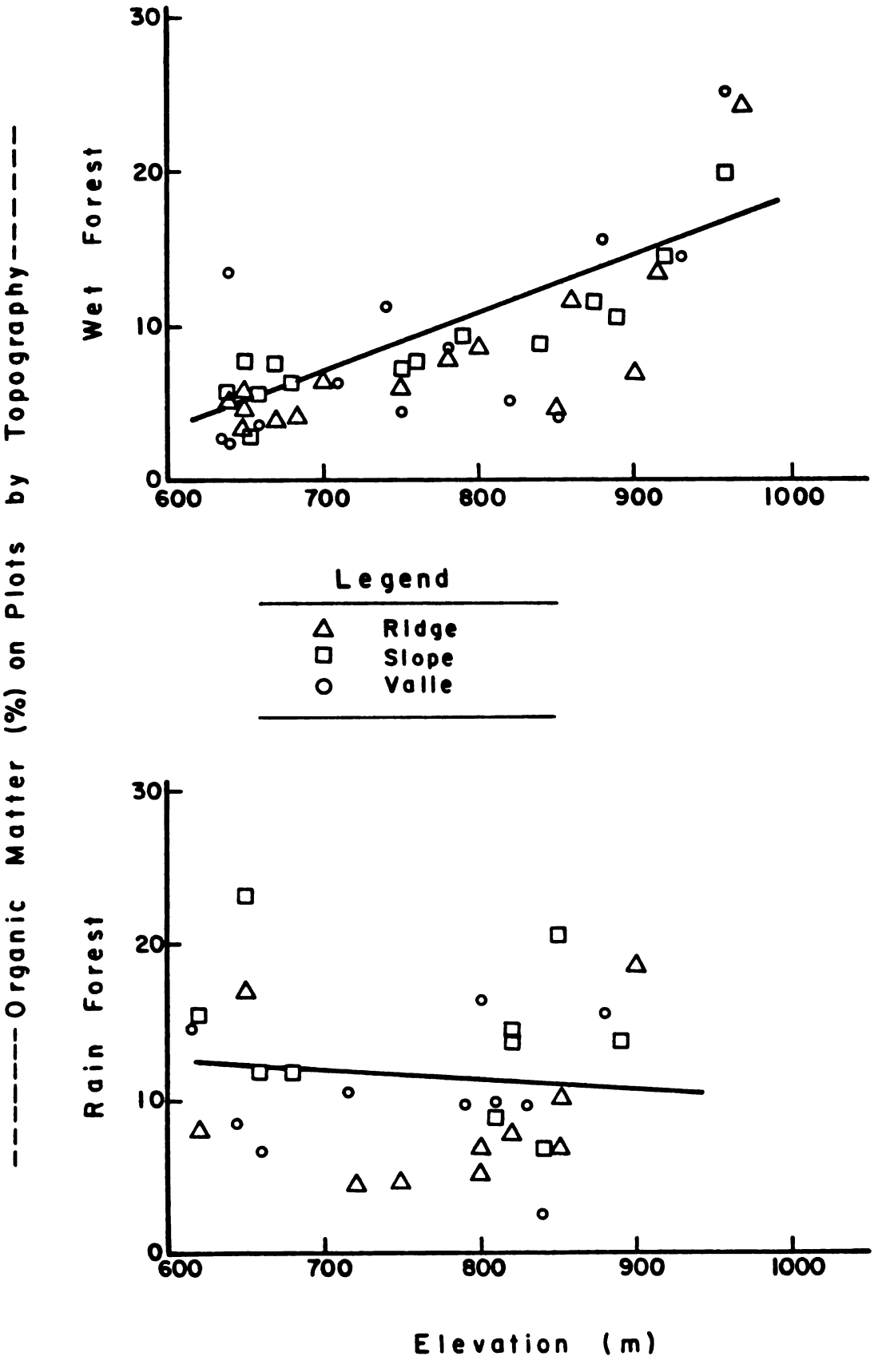

Wet Forest
Rain Forest
Organic Matter (%) on Plots by Topography
Legend
Ridge
Slope
Valle
0
10
20
30
600
700
800
900
1000
Elevation (m)

Figure 30

Figure 31. Distribution of data points in the covariance model Y = E where Y = soil organic matter content (kg/m^2) and E = elevation, according to life zone. The elevation component of the model is significant at alpha = 0.05 in the wet forest, but not in the rain forest.

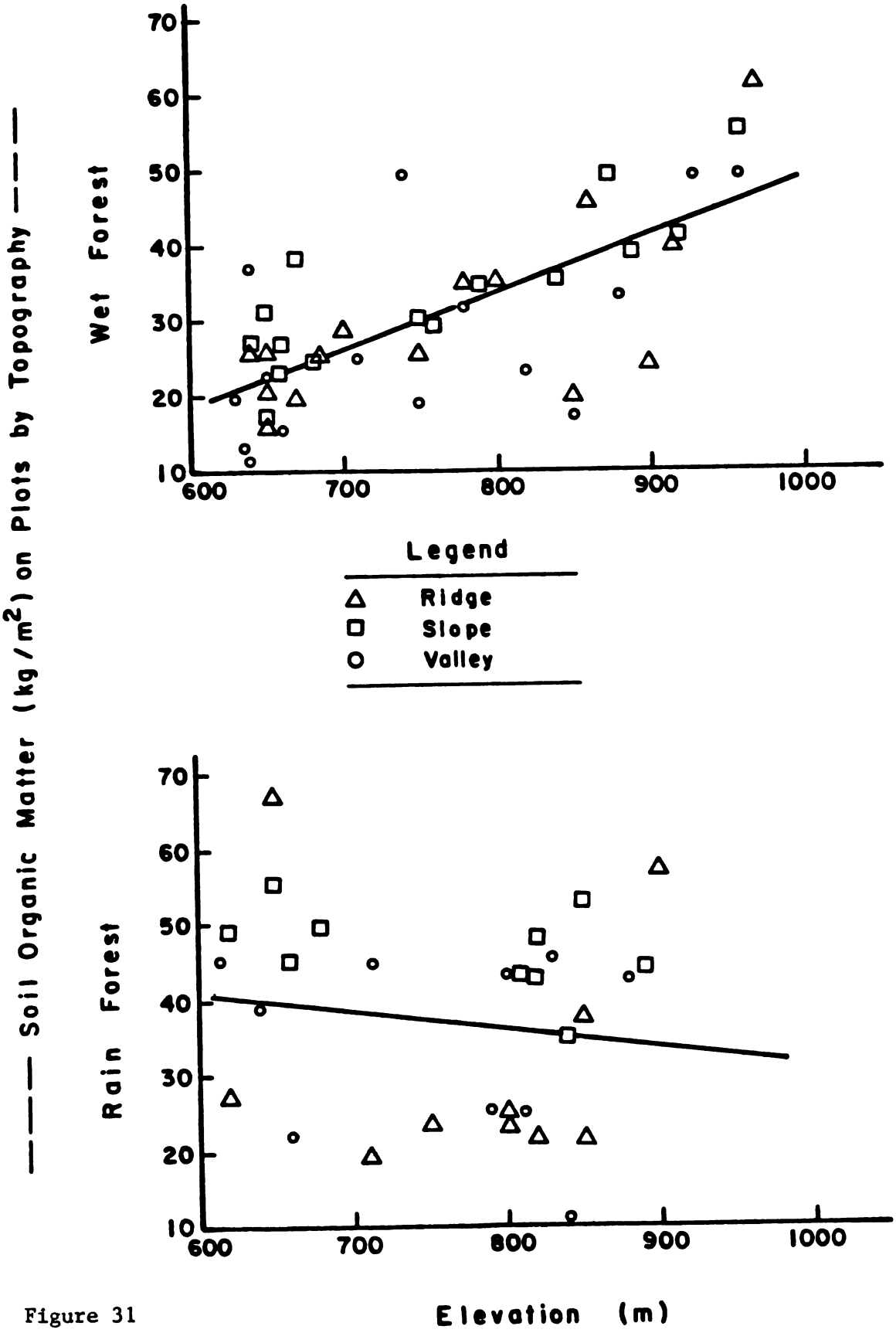

Wet Forest
Rain Forest
Legend
Ridge
Slope
Valley
70
60
50
40
30
20
10
600
700
800
900
1000
Elevation (m)
—— Soil Organic Matter (kg/m²) on Plots by Topography ——

Figure 31

decrease in bulk density, and an increase in organic matter content and percent, would be expected with an increase in elevation in the colorado forest. With an increase in elevation, temperature decreases and both rainfall and cloud cover increase, raising the soil water content and retarding the mineralization of organic matter (Grubb 1971). Increased organic matter, in turn, leads to a decrease in soil bulk density.

The gradients in the wet and rain forests, however, are not the same, and the differences between them may account for the bulk density and organic matter trends observed. First, precipitation is greater in the rain forest which is located largely near the summits and to the windward of the Luquillo Mountains, than in the wet forest which is found mainly to the leeward of the mountain peaks. Moreover, in the rain forest, the distribution of rainfall is more uniform averaging about 4500 mm/yr whereas in the wet forest it ranges from near 4000 mm/yr at high elevation to levels approaching 3300 mm/yr at lower elevation. Second, there may be a difference in temperature gradients between rain and wet forests as well. Cloud build-up is common at 600 m to the windward of the mountain peaks, or in the rain forest life zone. Here, where condensation is occurring, rising air should cool at the moist adiabatic rate. To the leeward, after dissipation of the clouds, warming should occur at the dry adiabatic rate, or roughly twice as fast, yielding a more pronounced temperature gradient. This phenomenon, or rain shadow, is characteristic of areas to the leeward of mountains lying in the path of moisture laden winds from the ocean (Rumney 1968).

Another interesting observation is that the amount of organic matter on slopes exceeded that on ridges or valleys (Table 13). Wind and heavy rainfall in the Luquillo Mountains are probably contributing factors to this

phenomenon. Wind on the more exposed ridges could distribute leaf litter to the leeward of crests as was observed on steep topography in central New York State (Welbourn et al. 1981). Moreover, runoff from the ridges during heavy rains is rapid and should be instrumental in moving organic matter downslope where it may be trapped locally in route or deposited in valleys. In the latter topograhic position, it is washed downstream during peak flows. Recent work adjacent to one of the plots used in this study showed that the downslope export of organic matter ranged from 1 to 4 $g/m^2/day$ (Lugo and Brown 1981).

Ordination of Arborescent Vegetation

Several reciprocal averaging and polar ordinations were computed from various combinations of sample plots and species. The most informative ordinations employed a large complement of species. This was probably because of the variety of habitats studied including plots to the windward (rain forest) and leeward (wet forest), at high and low elevations, and on different topographic positions. In most instances, polar ordination program and user selected endpoints yielded similar patterns.

Ordination 1 - sample plots for the entire forest

The first reciprocal averaging ordination contained all 75 plots and 39 species and yielded a sample, or plot ordination (Fig. 32). The first axis extending from the upper right corner toward the arc of plots in the lower left was topographic and partitioned valley plots from slope and ridge plots, with few exceptions. The second axis was elevational and extended from the lower portion of both valley and combined slope and ridge groupings to the top of the graph. A contour line was used to separate plots above

Figure 32. A reciprocal averaging sample plot ordination comprised of 75 plots based on 39 tree species for the entire colorado forest. Two configurations are separated by the dashed line. Group A contains mainly valley plots ranging from low to high elevation. Group B contains largely slope and ridge plots, again ranging from low to high elevation. The 800 m contour, the midpoint elevation, is indicated.

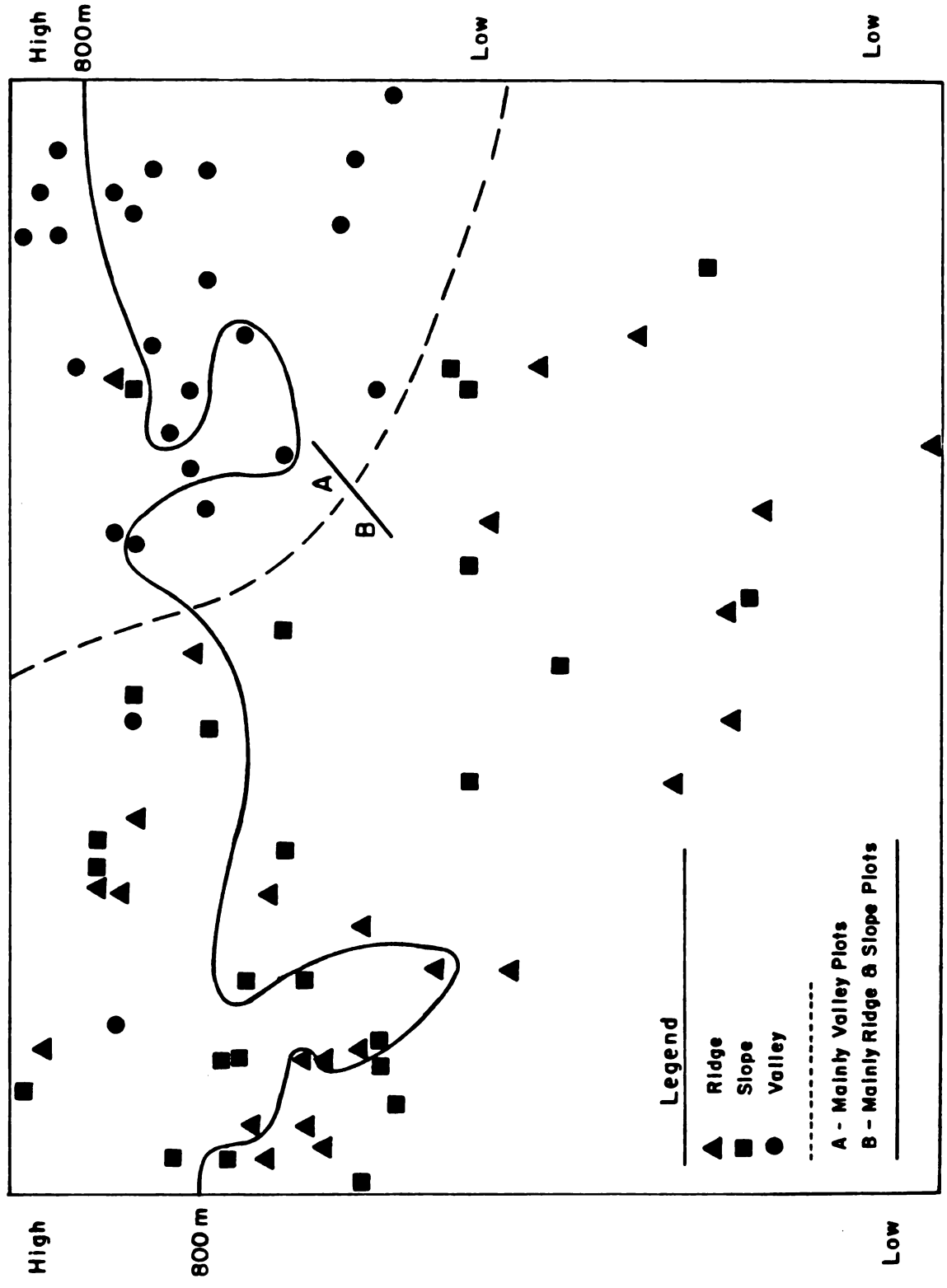


Figure 32 Topographic Gradient from Mixed Ridge and Slope to Valley

and below 800 m. The noticeable dips within both plot configurations were comprised of high elevation leeward plots.

Ordination 2 - species distribution for the entire forest

The second reciprocal averaging ordination produced simultaneously with the first yielded a configuration for the 39 species (Fig. 33). The axes were the same as in the first ordination. For section A in the upper right corner, each of the five species was recorded in valley topography more than 65 percent of the time. The eight species in section B, in contrast, were found in valley topography only from 30 to 60 percent of the time. Indeed, some occurred more frequently on other topographic positions, as indicated. The 26 species in section C were found predominantly on slopes and ridges. In summary, six species occurred predominantly in valleys, five on slopes, 18 on ridges, and 10 species showed distributions without a clear majority of occurrences on any particular topographic feature. In all groupings, species along the bottom of the graph were more common at lower elevations and those at the top at higher elevations.

In ordination 1, the prevalence of Prestoea montana, regardless of elevation, aspect, or forest classification, was the main feature that characterized the valley plots. Other species that were common in valleys included Sapium laurocerasus and Citharexylum caudatum at low and high elevations, respectively, along with Cecropia peltata and Croton poecilanthus. The ridge and slope plots that grouped with the valley plots were both located at high elevation to the windward in an area bordering a palm brake. Conversely, the valley plots that occurred within the slope and ridge configuration of plots were located at high elevations bordering dwarf

Figure 33. A reciprocal averaging species ordination comprised of 39 tree species on 75 plots for the entire colorado forest. Three configurations are separated by solid lines. Group A contains species predominantly found in valleys, from low to high elevation; group B, species with 30 to 65 percent occurrence in valleys, from low to high elevation; and group C, species with combined ridge or slope occurrence greater than 75 percent, from low to high elevation. See legend for more information on topographic occurrence of species.

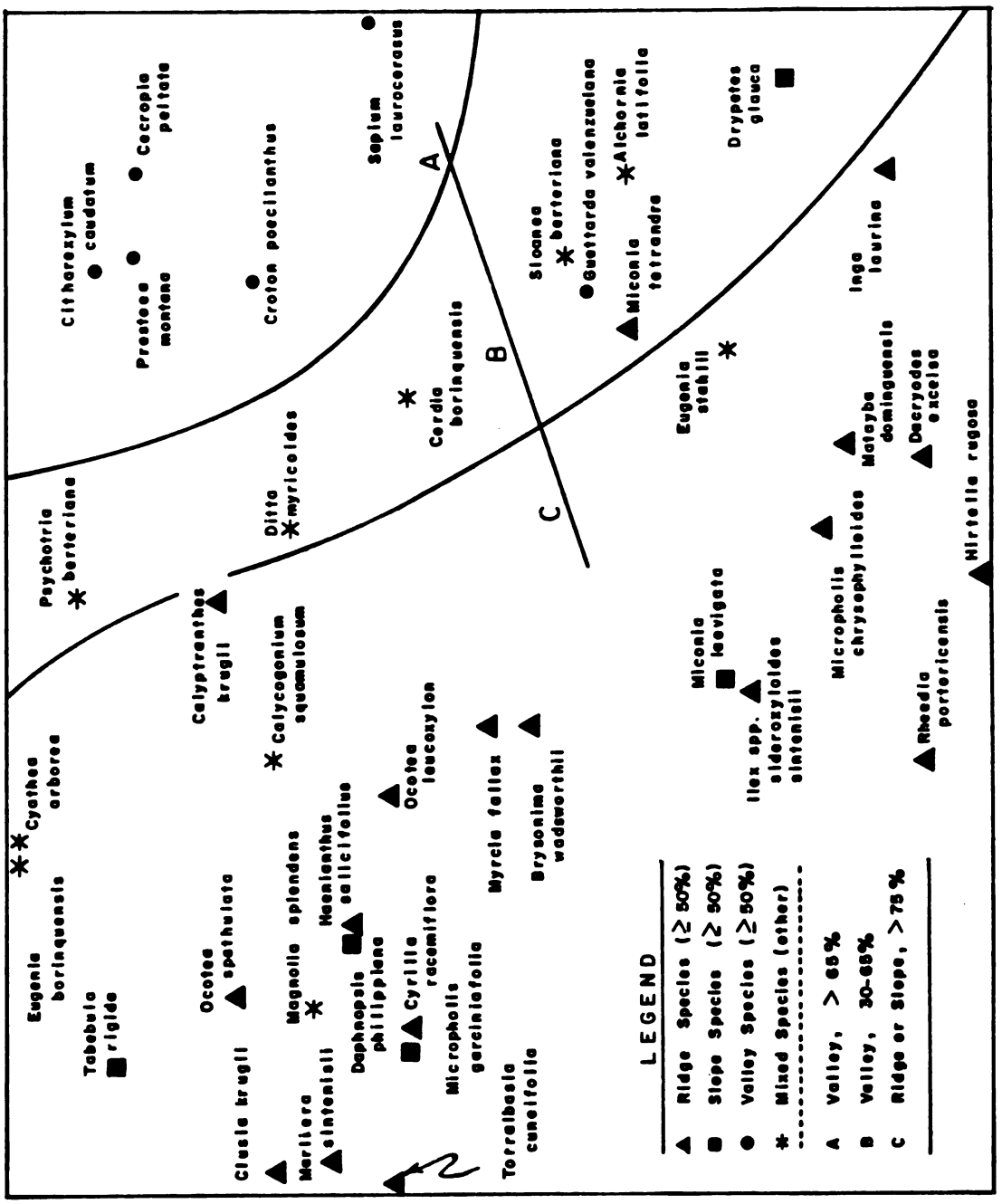


Figure 33 Topographic Gradient from Mixed Ridge and Slope to Valley

forest and were dominated by hardwood species characteristic of that elevation.

In ordination 2, the species along the bottom of the graph were more common to the leeward S and W aspects than to the windward, for the elevations sampled in the study. The species in the middle were common to mid-elevations to the leeward and in lower to mid-elevations on the windward plots. The species at the top of the graph were found in the highest elevation plots regardless of aspect.

Ordination 3 - composite plots

The third reciprocal averaging ordination contained a composite sample of ridge, slope, and valley plots grouped according to elevation, or 25 composite plots and 39 species (Fig. 34). The species and plot data were the same as for the first two ordinations. Four major configurations of plots were observed: leeward wet forest plots to the W at low to mid-elevations, leeward wet forest plots to the S at low elevation, windward rain forest plots at low to mid-elevations, and windward rain forest plots at mid- to high-elevations. In general, the rain forest plots were grouped to the right side of the graph.

In the first grouping, all plots were found to the leeward W and showed a gradual gradient in elevation from the left to right. In the second grouping, all plots were found to the leeward S except #20 which was located at 860 m to the leeward W. Grouping 3 was mainly lower elevation plots to the windward. However, two leeward plots were found. One was located at about 910 m to the W, and the second was located at about 700 m to the W, but considerably farther N in a more humid area of the mountains. Grouping 4 was mainly windward high elevation plots in the rain forest. The

Figure 34. Reciprocal averaging sample plot ordination for 25 composite groupings of ridge, slope and valley topography at the same elevation, based on 39 tree species for the entire colorado forest. Groups 1 through 4 are partitioned on the basis of life zone (coincident with aspect) and elevation, as indicated. Exceptions are explained in text.

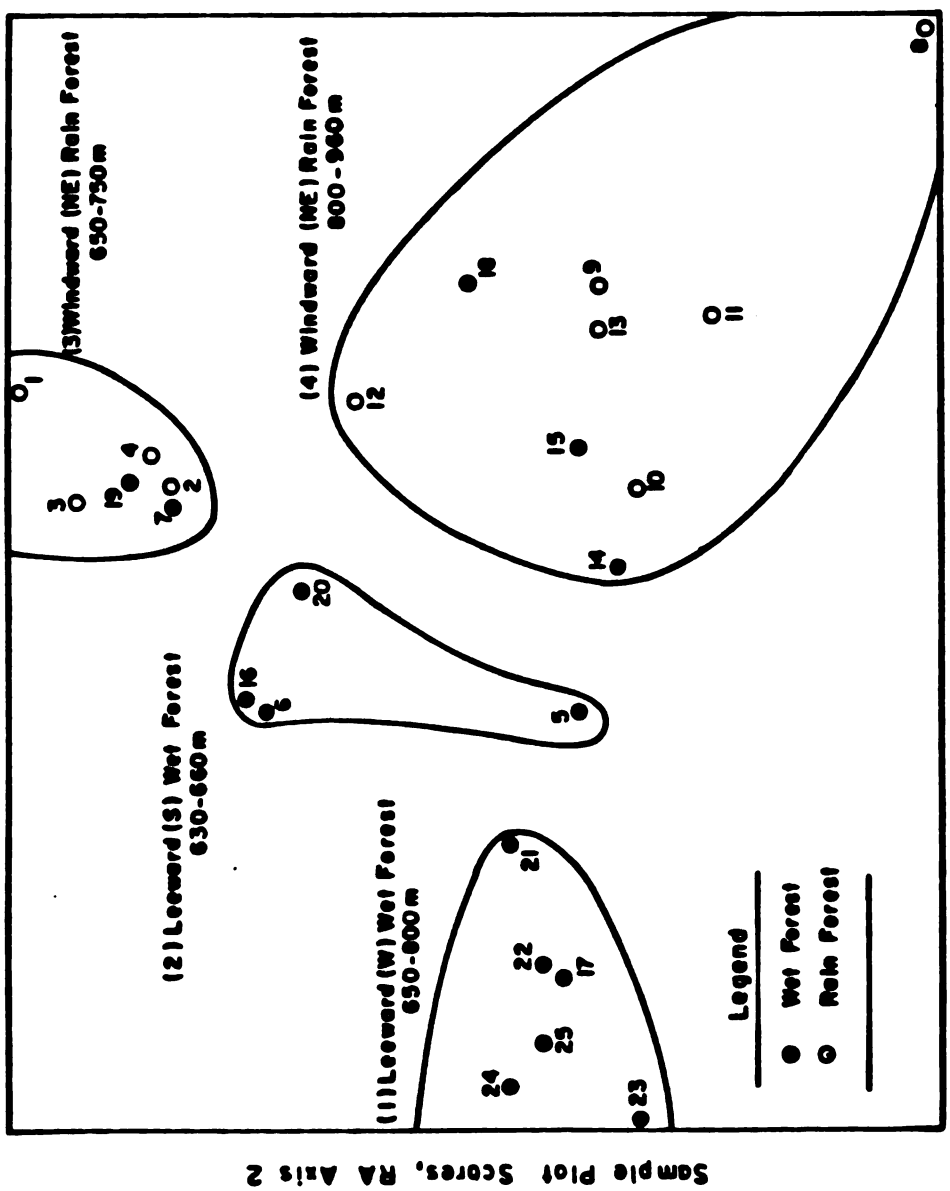

(3) Windward (NE) Rain Forest
650-750m
(4) Windward (NE) Rain Forest
800-960m
(2) Leeward (S) Wet Forest
630-660m
(1) Leeward (W) Wet Forest
650-900m
Legend
Wet Forest
Rain Forest
Sample Plot Scores, RA Axis 1
Sample Plot Scores, RA Axis 2

Figure 34

exceptions were windward wet forest plots 14 and 15, at 900 m and 850 m, respectively, and plot 18 which was located to the leeward W at 960 m. In summary, the plots sorted largely by aspect and elevation with exceptions for high elevation leeward plots.

Ordination 4 - leeward wet forest plots to the west

The fourth ordination was polar with program selected endpoints that contained a subset of 27 plots and 38 species located in wet forest to the leeward (Fig. 35). The subset produced both topographic and elevational groupings. The topographic groupings ranged from valley plots at the top of the diagram through slope plots in the middle to ridge plots at the bottom. The elevation groupings ranged from <740 m on the left, through 750-860 m in the middle, to ≥900 m in elevation at the right of the graph. A similar polar ordination for windward rain forest plots produced a less decisive configuration and is not shown.

Other ordinations

Reciprocal averaging ordinations of species grouped by topography, that is, separate ridge, slope and valley plots, were also conducted. Each ordination included 27 plots to the windward of El Yunque (simultaneously rain forest plots) combined with 30 plots to the leeward (simultaneously wet forest plots). Species ordinations were similar to ordination #2 (Appendix Figures A-2, A-3, and A-4).

Inceptisols and ultisols are found in the colorado forest. Species ordinations using these soil groupings however, produced no trends in species composition by substrate, confirming earlier studies of a similar nature (Wadsworth and Bonnet 1951). In other words, the extent to which

Figure 35. Polar sample plot ordination for 27 individual leeward wet forest plots based on 38 tree species. Solid lines separate different elevational groupings of plots and dashed lines separate different topographic groupings of plots.

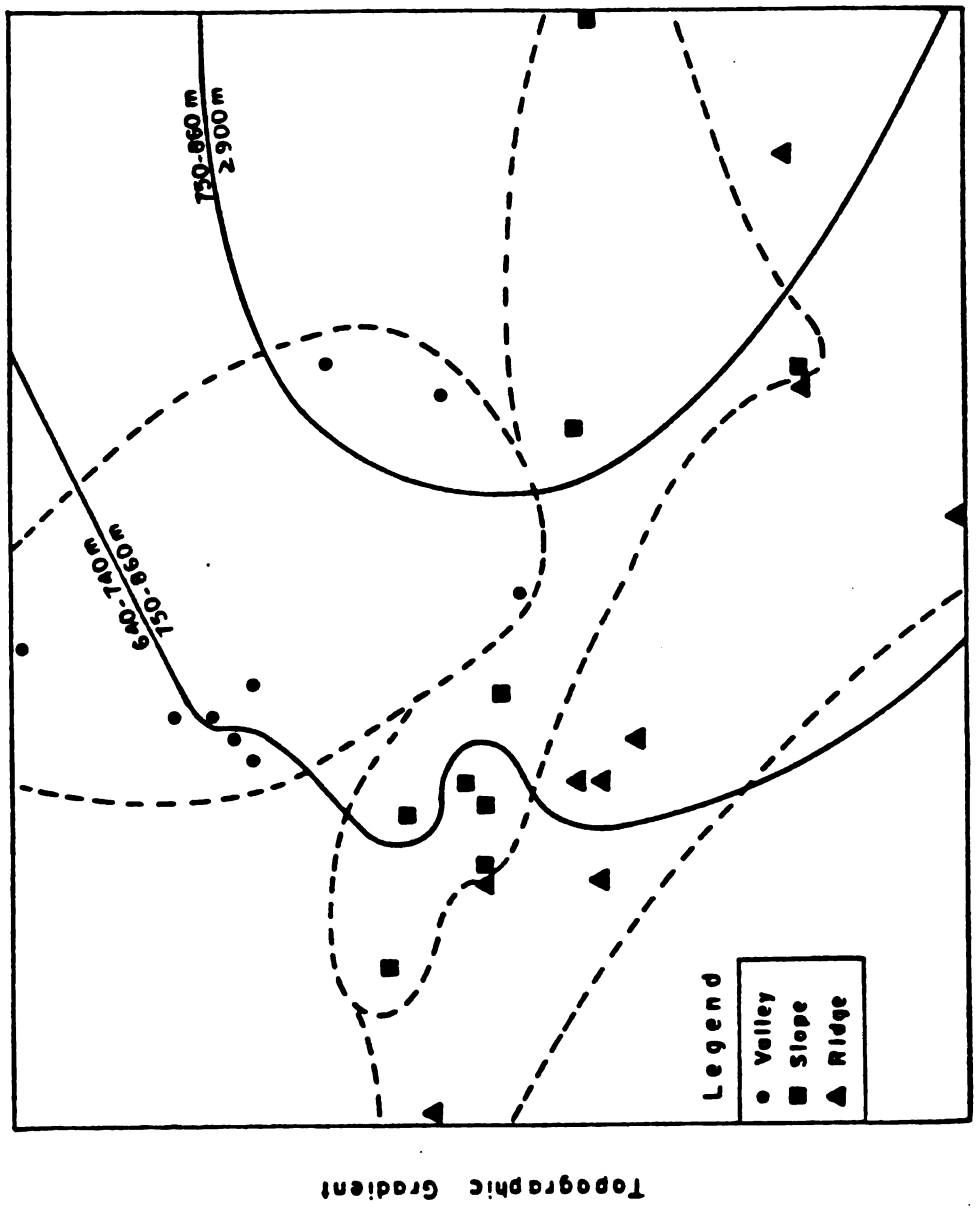

750-860 m
≥900 m
640-740 m
750-860 m
Legend
Valley
Slope
Ridge
Topographic Gradient
Elevational Gradient

Figure 35

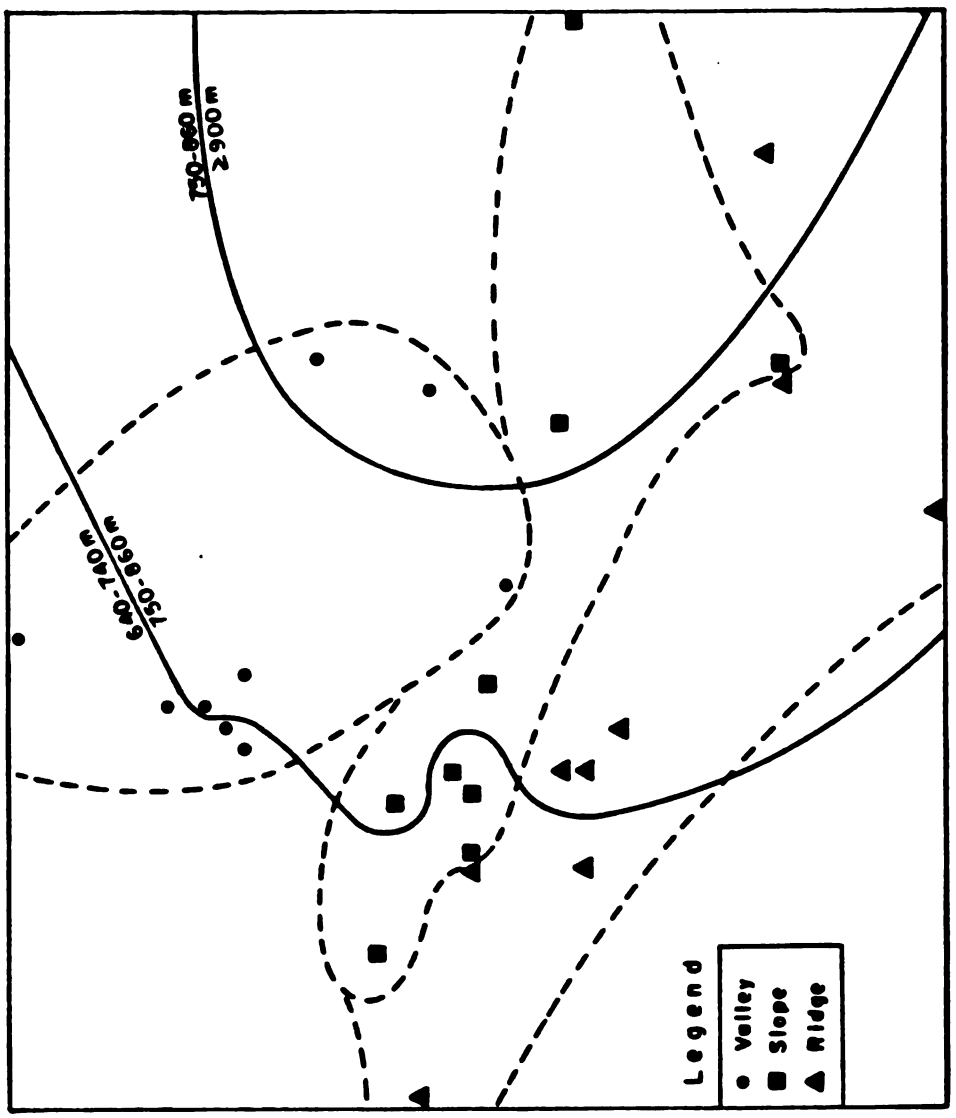

750-860m
≥900m
640-740m
750-860m
Legend
Valley
Slope
Ridge
Topographic Gradient
Elevational Gradient

Figure 35

soil factors can be predicted by species composition data is still not certain (Knight 1975).

Species distributions

The occurrence of major colorado forest tree species is shown by topography in Figure 36. Distribution by elevation, and aspect, which is largely coincident with life zone, is shown in Figure 37.

Prestoea montana, Croton poecilanthus, Cecropia peltata, Citharexylum caudatum, and Sapium laurocerasus are all more common in valleys than in other topographic positions. Prestoea is found in excess of 125 stems/ha throughout the forest but appears more abundant between 800 to 900 m to the windward, and at 750 to 800 m to the leeward. Croton is also found throughout the forest and shows peaks with >100 stems/ha between 700 to 800 m to the windward, and at 750 to 850 m to the leeward. Cecropia fluctuates at low levels averaging about 10 to 20 stems/ha throughout much of the forest. Citharexylum averages about 15 stems/ha, but has greater abundances between 800 to 900 m, whereas Sapium is found at levels below 15 stems/ha, except for one area at 750 m to the leeward.

Ocotea spathulata, Micropholis chrysophyllides, Eugenia borinquensis, Cyrilla racemiflora, Haenianthus salicifolius, Miconia tetrandra, Matayba dominguensis, Myrcia fallax, and Brysonima wadsworthii, all show greater abundance on ridges than other topographic positions. Ocotea is common from 650 m to the windward through 900 m to the leeward where it ranges from 75 to 230 trees/ha. Micropholis has some stems to the windward but is clearly more abundant to the leeward below 800 m where it ranges from 175 to about 300 stems/ha. Eugenia shows a definite peak between 850 m to the windward through 950 m to the leeward where it ranges from 150 to nearly 500

Figure 36. Distribution of the major tree species on 3.75 ha of colorado forest by topographic position (V = valley, S = slope, and R = ridge). The specific gravities given in g/cm^3 are discussed later in text.

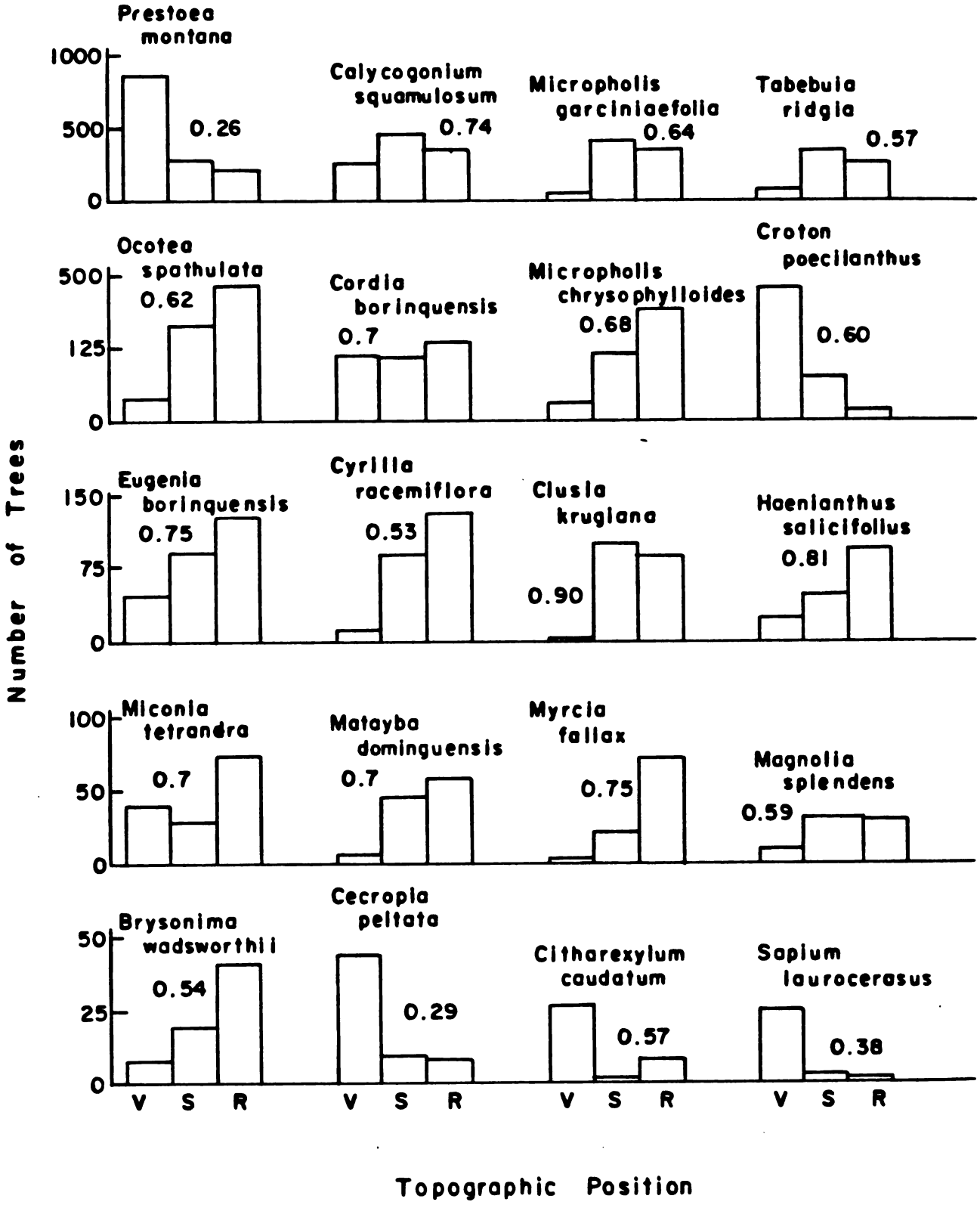

Prestoea montana
1000
500
0
0.26
Calycogonium squamulosum
0.74
Micropholis garciniaefolia
0.64
Tabebuia ridgia
0.57
Ocotea spathulata
500
125
0
0.62
Cordia borinquensis
0.7
Micropholis chrysophylloides
0.68
Croton poecilanthus
0.60
Eugenia borinquensis
150
75
0
0.75
Cyrilla racemiflora
0.53
Clusia krugiana
0.90
Haenianthus salicifolius
0.81
Miconia tetrandra
100
50
0
0.7
Matayba dominguensis
0.7
Myrcia fallax
0.75
Magnolia splendens
0.59
Brysonima wadsworthii
50
25
0
0.54
Cecropia peltata
0.29
Citharexylum caudatum
0.57
Sapium laurocerasus
0.38
V S R
V S R
V S R
V S R
Number of Trees
Topographic Position

Figure 36

Figure 37. Elevational distribution of common colorado forest tree species to the windward and leeward of El Yunque peak. Each point represents the mean value for a ridge, slope, and valley composite plot at a given elevation.

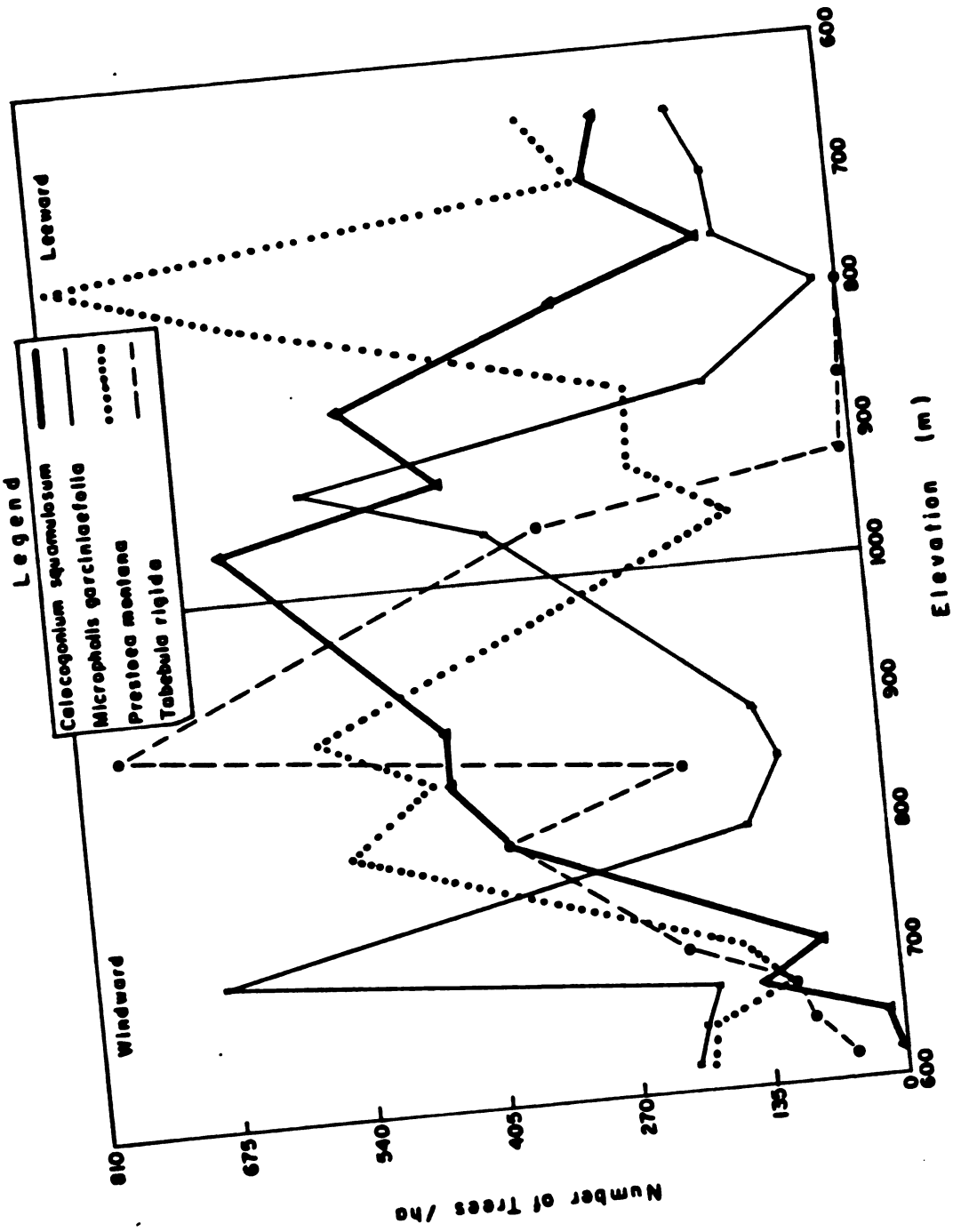

Legend
Calocoponium squamulosum
Microphalis garciniaefolia
Prestoea montana
Tabebuia rigida
Leeward
Windward
Number of Trees /ha
810
675
540
405
270
135
0
600
700
800
900
1000
900
800
700
600
Elevation (m)

Figure 37

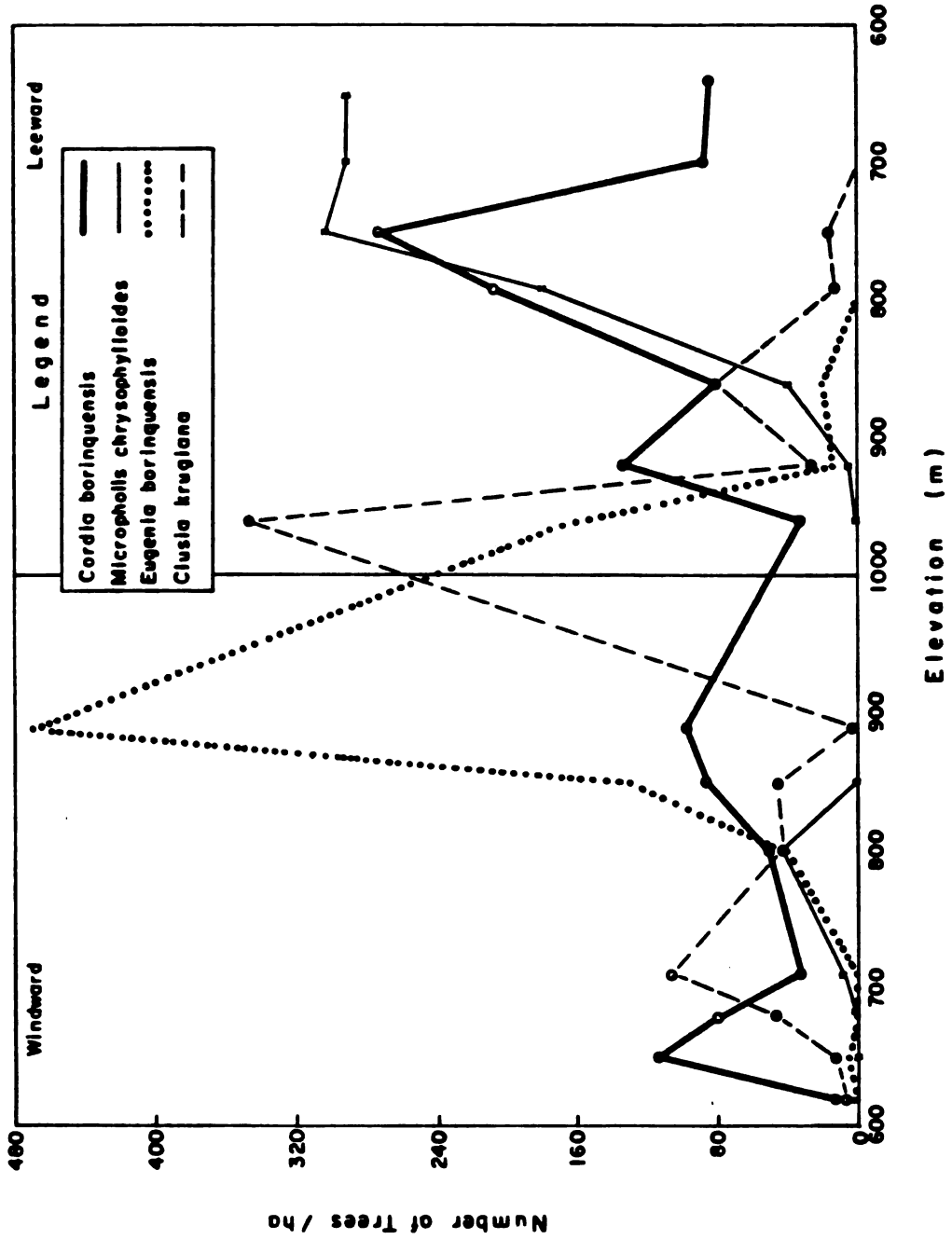

Windward
Leeward
Legend
Cordia borinquensis
Microphollis chrysophylloides
Eugenia borinquensis
Clusia krugiana
Number of Trees /ha
Elevation (m)
0
80
160
240
320
400
480
600
700
800
900
1000
600
700
800
900

Figure 37

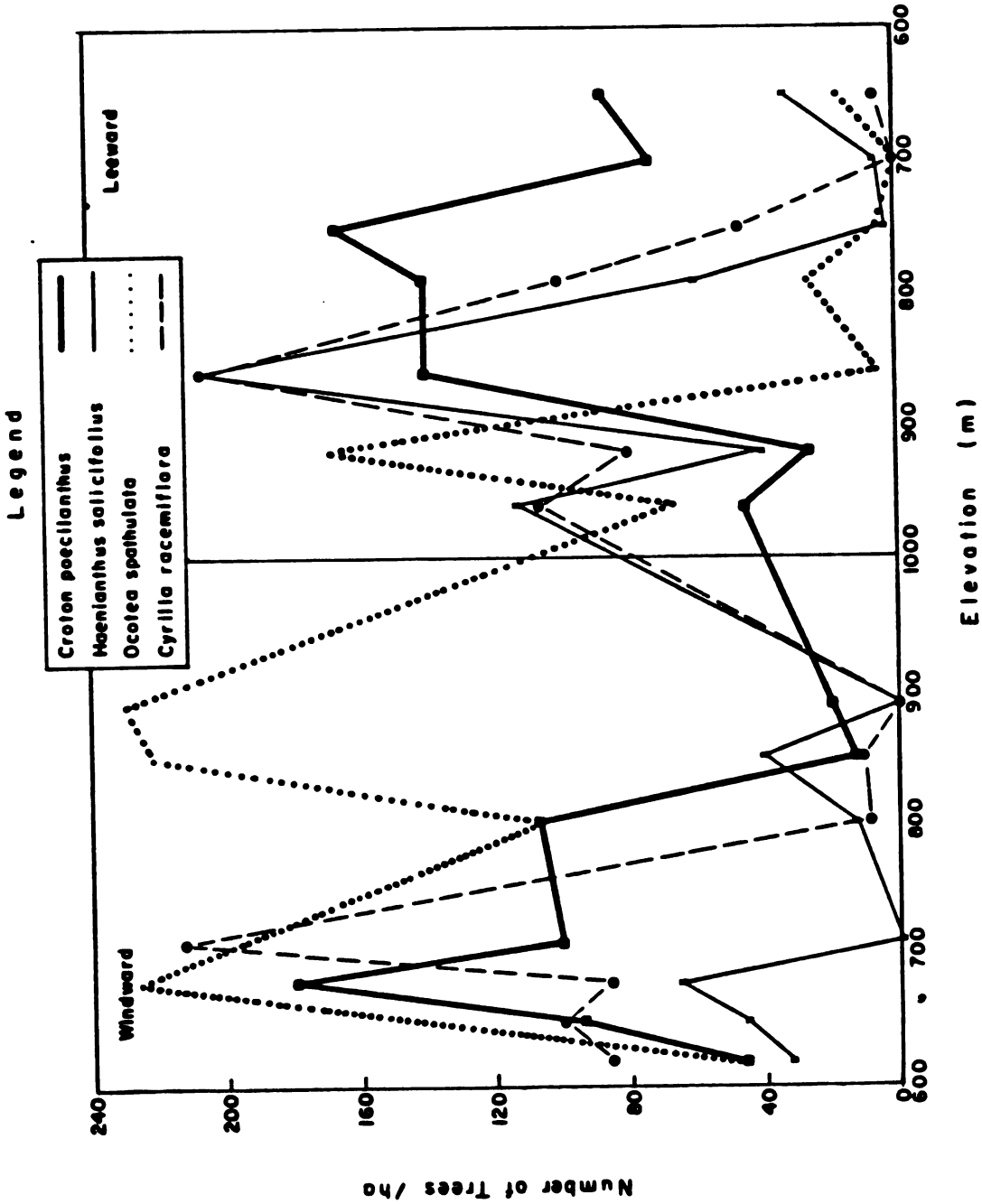

Legend
Croton poecilanthus
Haenianthus salicifolius
Ocotea spathulata
Cyrilla racemiflora
Windward
Leeward
Number of Trees /ha
240
200
160
120
80
40
0
600
700
800
900
1000
900
800
700
600
Elevation (m)

Figure 37

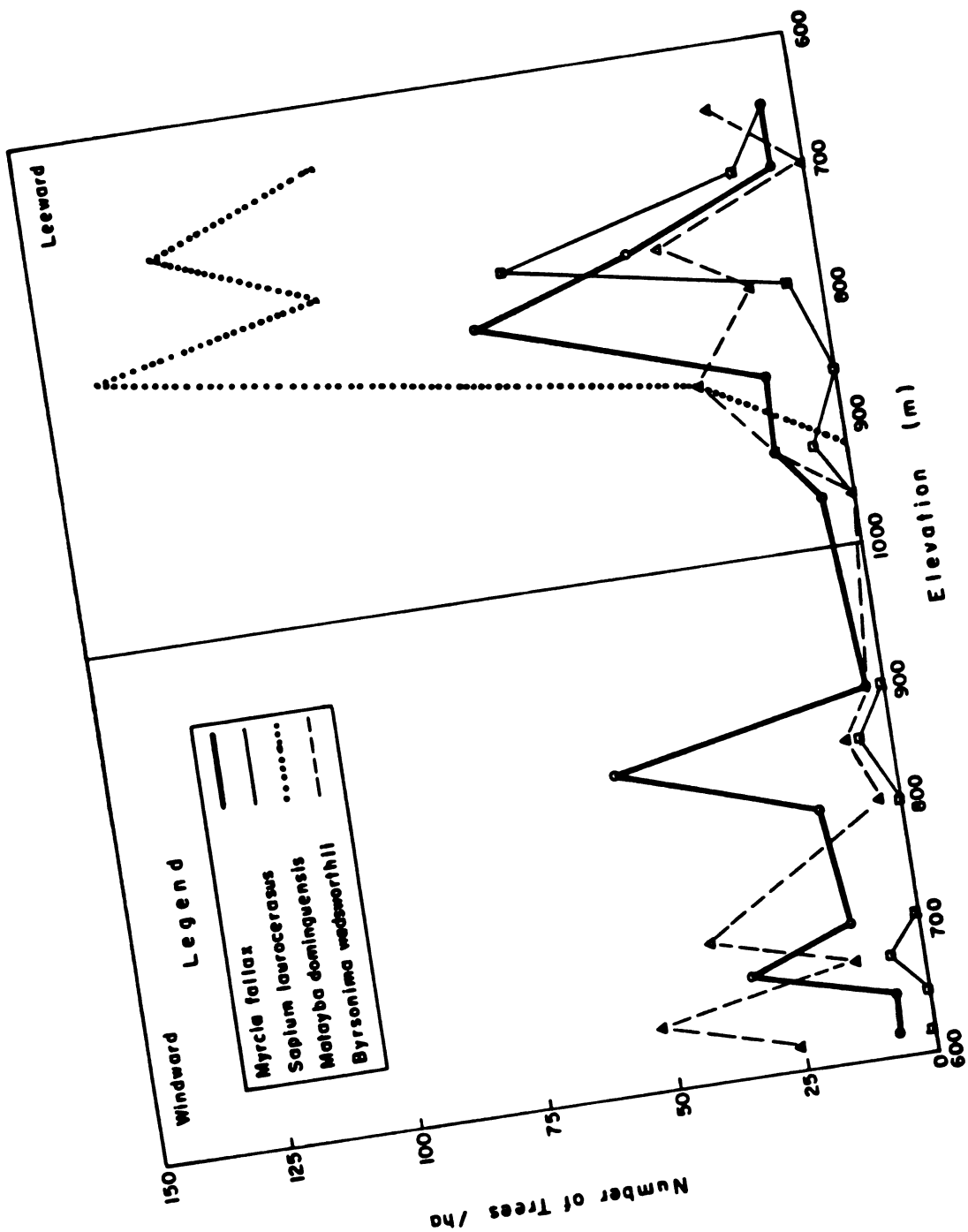

Leeward
Windward
Legend
Myrcia fallax
Sapium laurocerasus
Malaybo dominguensis
Byrsonima wadsworthii
Number of Trees /ha
150
125
100
75
50
25
0
Elevation (m)
600
700
800
900
1000
900
800
700
600

Figure 37

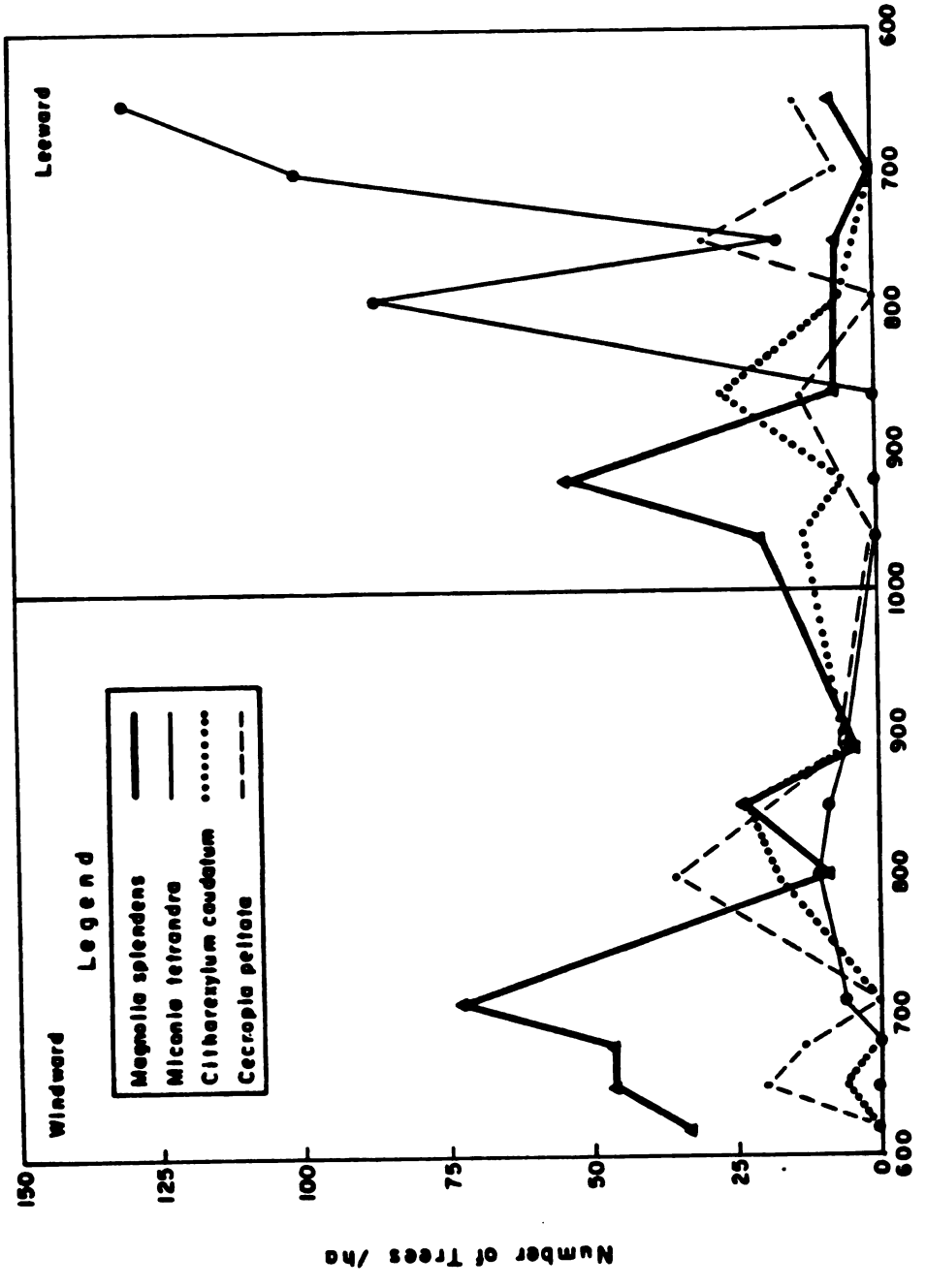

Windward
Leeward
Legend
Magnolia splendens
Miconia tetrandra
Cliftorexylum caudatum
Cecropia peltata
Number of Trees /ha
Elevation (m)
150
125
100
75
50
25
0
600
700
800
900
1000
900
800
700
600

Figure 37

stems/ha. Cyrilla is most common between 600 through 700 m to the windward where it ranges from 80 to over 200 trees/ha, and from 750 to 950 m to the leeward where it varies from 50 to about 200 stems/ha. Haenianthus averages about 20 stems/ha from 600 to 850 m to the windward, and about 100 stems/ha from 800 to 950 m to the leeward. Miconia levels are low to the windward, averaging from 5 to 10 stems/ha between 700 to 900 m. To the leeward, it averages about 75 stems/ha between 650 to 800 m. Matayba is limited to the leeward side where it varies from 25 to 140 stems/ha between 650 to 850 m. Myrcia has a bimodal distribution ranging between 10 to 50 stems/ha to the windward and from 15 to 70 stems/ha between 700 and 950 m to the leeward. Finally, Brysomina shows a bimodal distribution with about 20 stems/ha between 600 through 900 m both the windward and leeward.

Calycogonium squamulosum, Micropholis garciniaefolia, Tabebuia rigida, Clusia krugiana, and Magnolia splendens all show abundant distribution on slopes and ridges with a slightly higher number of stems per hectare on the former. Calycogonium is a very common tree that shows its greatest abundance at highest elevations where it reaches >650 stems/ha. Micropholis appears bimodal, with >135 stems/ha between 600 through 800 m to the windward, and between 850 to 950 m to the leeward. Tabebuia gradually increases from 50 stems/ha at 600 m to the windward to >750 stems/ha at 900 m. To the leeward, it declines rapidly from >300 stems/ha at 950 m to 10 stems/ha at 900 m. Clusia is found from 600 m on the windward to 700 m to the leeward, but shows a definite peak of 350 stems/ha at 950 m to the leeward. Magnolia has a bimodal distribution ranging from 10 to 75 stems/ha between 600 through 850 m to the windward, and from 10 to >50 stems/ha between 750 through 950 m to the leeward.

Cordia borinquensis is unique in that its abundance by topography is essentially equal. It occurs throughout the forest ranging from 15 to 275 stems/ha and shows a peak from 750 to about 900 m to the leeward.

In summary, Calycogonium, Tabebuia, Eugenia, and Clusia show unimodal peaks at higher elevations. Ocotea is more abundant to the windward and at high elevations to the leeward. Prestoea, Micropholis garciniaefolia, Croton, Cyrilla, Myrcia, Brysomina, and Magnolia have biomodal distributions. Prestoea reaches higher elevations to the windward while the remaining species with the exception of Brysomina reach higher elevations to the leeward. Brysonima appears evenly distributed with regard to elevation on both the windward and leeward. Miconia, Micropholis chrysophylloides, Haenianthus, Sapium, and Cordia are found on both aspects, but show greater abundances to the leeward. Mayayba was found only on the leeward, and Citharexylum and Cecropia were found in low numbers throughout the forest.

The differences in plot groupings in ordinations 1, 3, and 4 are related to complex environmental factors. Rainfall at the windward edge of the Luquillo Forest, at about 200 m elevation, averages 2300 mm/yr and increases to 3560 mm/yr at 450 m elevation (Fig. 1; Crow and Weaver 1977). Continuing the windward ascent to the lowest elevations of colorado forest at about 600 m, rainfall averages over 4000 mm/yr, and at La Mina located at 715 m, it averages 4600 mm/yr (Fig. 2, General Introduction; Wadsworth 1948). Pico del Este (Weaver 1972; Brown et al. 1983) and Pico del Oeste (Baynton 1968) located to the southeast of La Mina receive similar annual rainfalls. El Yunque slightly to the west receives about 4000 mm/yr (Briscoe 1966). The latter 3 sites average about 1050 m in elevation. Descending to the west, Rio Grande at 475 m receives 3300 mm/yr (Briscoe 1966) and El Verde at 450 m receives 2920 mm/yr (Smith 1970). Both of these

sites are located at high elevation in tabonuco forest. Descending to the south, Rio Blanco 4 at 550 m, just outside the colorado forest, receives 3870 mm/yr (Brown et al. 1983). The last site, Cubuy, to the southwest of the forest at 450 m elevation, only receives 2000 mm/yr of rainfall (Schmidt and Weaver 1980). The lowest elevation colorado forest at slightly over 600 m elevation to the leeward on the western part of the forest receives about 3500 mm/yr of rainfall. This is considerably less rainfall than received by the windward sites at the same elevation.

Mean annual temperatures measured along with the rainfall also vary with elevation. At the windward edge of the forest, temperature averages about 23°C. This declines to 18 or 19°C at the summits and then increases again to 23°C and the leeward edge of the forest. Two serious problems emerge with the climatic data, however. First, many of the rainfall records are not concurrent and therefore do not provide direct comparisons of the rainfall gradient within the mountains. Second, except for the La Mina site, the weather stations are located in forests above or below the colorado forest.

The characteristic base of trade wind cumulus clouds in the Caribbean ranges between 600 to 750 m (Baynton 1968). In essence, this includes the entire colorado forest of the Luquillo Mountains, and is a major factor defining the border between the tabonuco and colorado forest. The duration of cloud cover increases with elevation, and in summit areas such as Pico del Oeste, the forests are enveloped in cloud cover for more than 60 percent of the daylight hours (Baynton 1968). Incident solar radiation on the mountain summits, for example El Yunque (Briscoe 1966) and Pico del Oeste (Baynton 1968), is reduced by 40 percent of that received on the north coast of the island.

With regard to ordination 3, greater rainfall and cloud cover to the windward may be the critical factors separating low elevation plots to the windward from those of the leeward. Several tree species common to the tabonuco forest are scattered near the transition with the colorado forest. These species appear to occur at higher elevations to the leeward than to the windward (Fig. 33). Indeed, in Beard's (1949) excellent summary of Caribbean forests, the occurrence of dwarf forest at lower elevations to the windward is noted.

The grouping of plots by elevation is a function of the combined effects of rainfall, temperature, and cloud cover gradients within the mountains. The fact that high elevation leeward plots group with windward plots is related to the interaction of these factors near the summit areas. Rainfall on Pico del Este, the eastern-most peak in the Luquillo range, was slightly greater on high elevation leeward slopes than either on the summit or on high elevation windward slopes (Weaver 1972). However, the greater interception of cloud moisture on the windward slopes and summits delivered practically the same amount of moisture to the soil surface on all three sites. These same high elevation leeward slopes are classified as lower montane wet forest (Ewel and Whitmore 1973) yet separate with lower montane rain forest in the ordination. It appears that the small area encompassed by these plots is rain forest and not wet forest. Actual rainfall and cloud moisture interception data for this particular area, El Toro peak, however, are not available.

Ordination 4 reflects elevational and topograhic gradients. Again, the combined effects of rainfall, temperature, and cloud cover appear responsible for the elevational sorting of plots. The topographic sorting may be related to another complex of variables including a moisture gradient

ranging from better drained upper slopes and ridges to more humid lower slopes and valleys. Other important factors related to the topographic gradient include better light conditions and greater exposure to winds on ridges, higher organic matter content on slopes, and recurrent flooding of valley environments. However, while individual plots sorted by topography to the leeward, only valley plots were grouped separately to the windward. This phenomenon may be attributable to the more pronounced effects of topographic differences in slightly drier montane conditions that characterize the leeward plots. The effects of less rainfall and cloud cover combined with greater solar insolation to the leeward allows scattered species from the next lower forest to survive. Their occurrence is helpful in establishing topographic trends.

Regeneration of Canopy Species

Of the 20 species that reach canopy size in some part of the colorado forest, Ocotea spathulata, Tabebuia rigida, Clusia krugiana, and especially Eugenia borinquensis, are more common in the dwarf forest. The remaining 16 species occur either primarily in the colorado forest, or in the transition zone at about 600 m elevation between the colorado and the tabonuco forests.

Prestoea montana, the palm, had the greatest number of seedlings averaging more than 23,000/ha (Table 14). Seven other species had more than 1,000/ha and four species showed no regeneration whatsoever. The number of plots on which regeneration was found generally paralleled seedling abundance.

To partially surmount problems of analyzing seedling data based on a single sampling of subplots, several other factors including seedling success, understory success, seed size, and wood specific gravity of the 20

Table 14. Summary of regeneration characteristics of canopy species in the colorado forest

Species	Seedlings/ha	Frequency of occurrence in plots[1]
Brysonima wadsworthii[2]	47	6
Calycogonium squamulosum	2,487	45
Cecropia peltata	0	0
Clusia krugiana[2]	13	2
Croton poecilanthus	1,240	30
Cyrilla racemiflora	33	2
Didymopanax morototoni	20	2
Eugenia borinquensis[2]	3,413	21
Eugenia stahlii	1,440	18
Haenianthus salicifolius	5,453	40
Magnolia splendens	0	0
Matayba dominguensis	767	20
Micropholis chrysophylloides	3,720	25
Micropholis garciniaefolia	547	29
Myrcia fallax[2]	273	18
Ocotea moschata	0	0
Ocotea spathulata[2]	2,460	44
Prestoea montana	23,147	68
Sapium laurocerasus	0	0
Tabebuia rigida[2]	240	16

[1]Based on 75 plots 20 m x 1 m on which regeneration was found.

[2]Small trees that may reach the canopy locally.

canopy species were assessed (Fig. 38, panels A, B, C, D). The species were arranged from the lowest cumulative scores at the left to the highest scores at the right (see Methods). A priori, one would expect each of the factors to increase from left to right, that is, from species with mainly secondary life history strategies to those with primary life history strategies. With some exceptions, these general trends are apparent.

Seedling and understory success

Eugenia stahlii is uncommon as a mature tree, but it has a comparatively high relative density ratios of seedlings and understory trees to canopy trees. Slow growth may eliminate the species as the forest continues to close after major disturbance. In contrast, Haenianthus salicifolius shows a high ratio for seedling success but a low ratio for understory success. In this instance, the seed is relatively large and germinates in the shade but seedling mortality is high. Its survival may be tied to gaps within the forest. The ratios for both seedling success and understory success for Cecropia peltata are the least for any of the species studied. It regenerates and grows in openings.

A comparison of the seedling and understory relative density ratios provides an insight to the survival strategy of the respective species. Didymopanax morototoni, Matayba dominguensis, Micropholis chrysophylloides, and Haenianthus salicifolius all show ratios of 0.5 or more units greater in the seedling than in the understory classification (Fig. 38). This probably reflects a greater capacity to germinate and grow into seedlings than to compete and survive into later stages of development. Sapium laurocerasus, Ocotea moschata, Tabebuia rigida, Calycogonium squamulosum, and Byrsonima wadsworthii all show ratios 0.5 or more units greater in the understory than

Figure 38. Panel A: The seedling success of canopy tree species based on the seedling relative densities of canopy species divided by the relative density of canopy size plants of the same species; Panel B: The understory success of canopy tree species based on the understory relative densities of canopy species divided by the relative density of canopy size plants of the same species; Panel C: Seed size of canopy tree species, defined as the sum of half the length + the width of the disseminule; and Panel D: Wood specific gravities of canopy tree species. The species are arranged in the same order as they appear in Table 18.

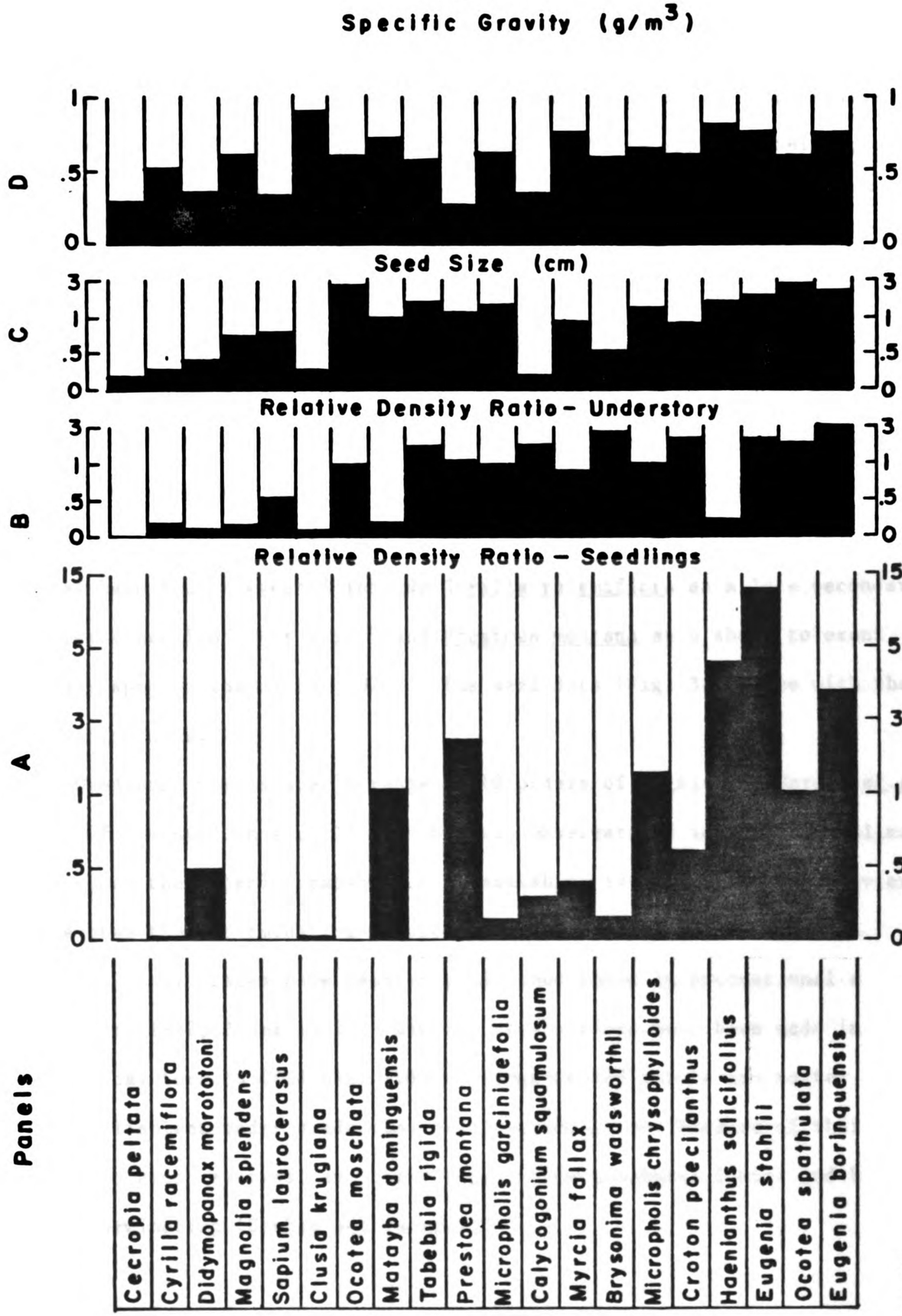

Specific Gravity (g/m3)
D
Seed Size (cm)
C
Relative Density Ratio - Understory
B
Relative Density Ratio - Seedlings
A
Panels
Cecropia peltata
Cyrilla racemiflora
Didymopanax morototoni
Magnolia splendens
Sapium laurocerasus
Clusia krugiana
Ocotea moschata
Matayba dominguensis
Tabebuia rigida
Prestoea montana
Micropholis garciniaefolia
Calycogonium squamulosum
Myrcia fallax
Brysonima wadsworthii
Micropholis chrysophylloides
Croton poecilanthus
Haenianthus salicifolius
Eugenia stahlii
Ocotea spathulata
Eugenia borinquensis
Species

Figure 38

in the seedling classification. This trend may reflect greater capacity to persist in shaded conditions once the seed has germinated. The remaining species have seedling and understory ratios that are approximately equal, or arbitrarily, within 0.4 units of each other.

Seed size of canopy species

Seed sizes ranged from about 2.8 cm for Ocotea spathulata to about 0.15 cm for Cecropia peltata (Fig. 38). Known secondary species such as Cecropia peltata and Didymopanax morototoni have among the smallest seeds recorded, whereas known primary species such as both species of Micropholis range in the upper half of the seed size values. Other species for which seral stages have been suggested include Cyrilla racemiflora as a late secondary species (Part I of this study) and Prestoea montana as a shade tolerant, primary species (Bannister 1970). The seed data (Fig. 38) agree with these classifications.

Seed size varies over a range of 10 orders of magnitude (Harper et al. 1970) if compared on a world-wide basis. Observations in temperate climates have shown that species capable of establishing in the shade have heavier seeds than those germinating in openings, and that species growing in advanced seral stages have heavier seeds than those in successional stages (Salisbury 1942; Baker 1972). Similar observations have been made in neotropical forests (Budowski 1965). Large-seeded plants are better adapted to establishment under shade than small-seeded plants because of their access to seed reserves, and their capacity to penetrate litter and humus after germinating (Canham and Marks 1985).

Specific gravity of canopy species' woods

The specific gravities of dicot canopy species range from a very light 0.29 g/cm^3 for Cecropia peltata to a very dense 0.90 g/cm^3 for Clusia krugiana (Fig. 38). The palm, Prestoea montana, has a specific gravity of 0.26 g/cm^3. Usually, slower-growing, shade tolerant climax trees, have higher specific gravities than faster growing, shade intolerant pioneer and secondary species (Budowski 1965; Smith 1970; Lawton 1984).

Environmental factors have also been implicated in wood density. Species growing on windy sites, such as high elevation ridge species, have denser woods than those on sheltered sites (Fig. 13; Lawton 1984). Prestoea and Cecropia, which are most common in valleys, have specific gravities below 0.30 g/cm^3, and Sapium laurocerasus, Citharexylum caudatum, and Croton poecilanthus, also common in valleys, have specific gravities between 0.38 and 0.60 g/cm^3. In contrast, Ocotea spathulata, Eugenia boringuensis, and Haenianthus salicifolius, all common on ridges at higher elevations (Fig. 13), have specific gravities ranging from 0.62 to 0.81 g/cm^3 (Fig. 13). The mean specific gravity of the five common valley species is 0.42 g/cm^3; for the nine species most commonly found on ridges, 0.68 g/cm^3; and for the remaining six species found predominantly on slopes and ridges, 0.69 g/cm^3. Strength is a function of the amount of material in a given volume (Wangaard 1953; Forest Products Laboratory 1955), and exposed trees should have lower rates of windfall and breakage if denser (Lawton 1984). It is interesting to note that Tabebuia rigida, common on exposed slopes and summits, occasionally blows down and forms new trunks from existing branches. Its specific gravity at 0.57 g/cm^3 is the lowest of all species common to high elevation ridges.

Mortality rates are also correlated with wood density (Lawton 1984). Denser woods on ridges would, other factors being equal, lower the rate of gap formation. Recent investigations in the summit forests of the Luquillo Mountains showed that secondary tree species were notably lacking on cutover areas and the site of an airplane wreck (Byer and Weaver 1977).

Detailed observations of hurricane damage according to forest type and topography in the Luquillo Mountains are lacking. Bates (1929) noted defoliation and broken crowns after San Felipe, but these observations appeared to be confined to accessible sites at lower elevations. A plausible hypothesis for the colorado forest would be that upper slope and ridge forests, mainly composed of more densely packed (Table 11), smaller (Fig. 25), and heavier trees, would be less affected by hurricanes than valley forests.

Tentative Life History Classification of Canopy Trees

Table 15 contains a tentative classification of the life history strategies of colorado forest canopy species. The species are ranked according to the cumulative scores derived from the relative density ratios of seedlings and saplings to canopy trees, seed size, and wood density (Table 15, footnote 1). Ideas regarding life history classifications for forest trees (Budowski 1965; Whitmore 1975; Pickett 1983) and the influence of gap sizes on species which colonize them (Orians 1982; Hartshorn 1978) have been used for the following groupings.

Shade intolerant pioneer species

Cecropia peltata and Didymopanax morototoni are typical pioneer species (Vasquez-Yanes 1980). These species exhibit diameter class distributions in

Table 15. Ranking from most secondary to most primary (top to bottom) of tree species that reach the canopy in the colorado forest.

Species ranking[1]	Diameter class distribution[2]		Relative density ratio		Seed size[3]	Wood density[3]	Number of stems (1946)[4]	Percent Change on Plots[5]		Tentative classification[6]
	1946	1981	Understory[3]	Seedling[3]				stems	basal area	
1 Cecropia peltata	E*	E	1	1	1	2	72	- 78	- 19	P/G/GR
2 Cyrilla racemiflora	N	E*	5	5	3	5	191	- 8	- 44	LS/G/GR
3 Didymopanax morototoni	E	E	2	12	5	3	18	- 94	- 34	P/G-S/GR
4 Magnolia splendens	E*	E*	4	3	7	7	138	- 35	- 8	LS/G/GR
5 Sapium laurocerasus	?	E	8	2	8	4	16	+ 19	+395	LS/G/GR
6 Clusia krugiana	E*	E	3	6	4	20	31	+ 77	+288	LS/G/GR
7 Ocotea moschata	?	?	11	4	19	9	9	- 11	+ 31	LS/G/GB
8 Matayba dominguensis	?	E	6	15	11	14	3	+300	+1300	LS/S/GR
9 Tabebuia rigida	E*	J*	14	7	15	6	68	+ 34	+ 19	C/G-S/GR
10 Prestoea montana	N*	N*	13	17	12	1	641	+ 5	+ 3	C/S/S
11 Micropholis garciniaefolia	J	J	12	8	14	12	611	+ 3	+ 22	C/S/GB
12 Calycogonium squamulosum	J	J	15	10	2	16	829	+ 2	- 18	C/S/GB
13 Myrcia fallax	J	J	9	11	10	18	30	+ 27	+ 55	C/S/GB
14 Brysomina wadsworthii	J*	J	19	9	6	8	38	+ 8	+ 29	C/S/GB
15 Micropholis chrysophylloides	J	J	10	16	13	13	379	+ 24	+ 65	C/S/GR
16 Croton poecilanthus	J	J	17	13	9	10	441	+ 8	+ 79	C/S/GB
17 Haenianthus salicifolius	E*	J	7	19	16	19	150	+ 36	+ 54	C/S/GR
18 Eugenia stahlii	?	?	18	20	17	15	3	- 33	- 33	C/S/GB
19 Ocotea spathulata	J	J	16	14	20	11	272	- 45	- 58	C/S/GR
20 Eugenia borinquensis	E*	E*	20	18	18	17	43	- 14	- 15	C/S/GR

Table 15. (continued).

[1] Species ranking = ((2 x understory ranking) + seedling + seed size + wood density rankings)/5, (see Methods).

[2] E* = approximately even distribution with a disproportionally greater number of stems in the smallest diameter class; E = approximately even distribution; N = approximately normal distribution; N* = normal distribution (palms only); ? = data lacking or insufficient to estimate a diameter class distribution ; J* = distribution approaching a reversed J-shaped curve; and J = distribution in a reversed J-shaped curve (Figs. 12 and 13).

[3] Rankings based on Figure 38.

[4] Data from Table 4, Part I.

[5] Change based on growth information from Part I.

[6] First grouping of letters: P = pioneer, LS = late secondary; C = climax; second grouping: G = gap for regeneration, G-S = gap or shade for regeneration; S = shade for regeneration; third grouping: GR = gap required for maturity; GB = gap benefits growth and development; S = capable of developing in shade.

which the number of stems per class is approximately equal. Seeds are small and easily dispersed by wind. They may germinate in partial shade but are incapable of surviving there. The wood is light in weight, and growth is initially rapid with a decline after reaching the canopy (Crow and Weaver 1978). The trees are usually short to intermediate in longevity. These species are most common after major disturbance although the occasional death of large trees may provide adequate space for their survival in the forest. As the forest recovers from major disturbance, less growing space is available for regeneration of these species, and their numbers gradually decline (Fig. 11 Part I).

Gap or late secondary species

These species may have diameter class distributions that are equal, that contain a greater proportion of stems in intermediate size classes, or that are approximately equal with a disproportionately large representation of stems in the smallest diameter class. Their survival is tied to local disturbance, usually as gaps in mature forest. Seeds are usually small and the wood tends to be intermediate in weight. Volume growth is fairly rapid until the trees are in the canopy, providing that light is adequate. These species are most common several years after disturbance.

Sapium laurocerasus and Clusia krugiana both demonstrate comparatively low relative density ratios of seedlings and understory trees to canopy trees, but show an increase in stem numbers and basal area from 1946 to 1981. Both species are intermediate in size and capable of rapid growth with adequate light. The regeneration of Clusia on the previously thinned plot was considerable (Fig. 14, Part I). Cyrilla racemiflora and Magnolia splendens also show low seedling and understory canopy ratios but decline in

stem numbers and basal area from 1946 to 1981. These are much larger and longer-lived trees than the former. Neither demonstrated particularly rapid increment even when exposed to light (Table 9, Part I). It may be that the disturbance associated with the 1932 hurricane was not sufficient to provide large enough gaps for their regeneration, growth and survival in large numbers. Again, on the thinned plot (Fig. 14, Part I), the growth of Cyrilla in the smallest diameter class is rapid (Fig. 19, Part I). Matayba dominguensis is intermediate in size in the lower part of the colorado forest where its relative density ratios indicate higher seedling than understory success. Its growth is fairly rapid in the upper portions of the tabonuco forest (Crow and Weaver 1977) and its basal area increase in the colorado forest indicates similar growth. Although capable of regenerating in the shade, gaps are required for the species to mature. Fast growth enhances its success.

Shade tolerant species - These species usually have a negative exponential or reversed J-shaped diameter class distributions. The seeds tend to be large and capable of germinating and developing in the shade. The wood is usually heavy or dense, and growth rates slow to intermediate unless the trees are favorably located with regard to light. Trees range from intermediate to long-lived in age. Without major forest disturbance, either human or natural, these trees would tend to increase in basal area and possibly numbers during recovery. Croton poecilanthus, Micropholis chrysophylloides, M. garciniaefolia, Brysonima wadsworthii, Calycogonium squamulosum, Myrcia fallax, and Ocotea spathulata are the best examples of shade tolerant climax species. All have reversed J-shaped diameter class distributions and show intermediate to high seedling and understory to

canopy ratios. Eugenia stahlii and Ocotea moschata may also fit this category but are extremely rare within the forest. Shelterwood plantings of both species showed good survival after several years (Marrero 1948). Six-year-old Ocotea averaged 0.6 cm/yr dbh growth and 0.7 m/yr height growth. Nine-year-old Eugenia, however, only averaged 0.3 cm/yr in diameter at the tree base and 0.1 m/yr in height.

Tabebuia rigida is capable of surviving in the shade as indicated by its high understory to canopy ratio, but has been observed in previously cleared areas at high elevations. Its diameter class distribution is nearly equal in larger classes with a disproportionate number of stems in the smallest class. It is capable of rapid diameter increment when exposed to sunlight (Table 9, Part I).

Prestoea montana demonstrates several characteristics of a shade tolerant climax species. The exceptions are related to the fact that the plant is a monocotyledon: the near-normal diameter class distribution which reflects the range of stem sizes and lack of cambial growth, and the extremely light weight of the wood. The palm's exceptionally low specific gravity distorts its position in the classification scheme (Table 15). Its "slow growth, long survival, apparent shade adaptation, and high moisture requirement suggest that Euterpe [now Prestoea] is adapted to conditions inside the forest and is a normal component of rain forest vegetation, not a successional species as previously assumed" (Bannister 1970). Although particularly common near streams, Prestoea is abundant throughout the colorado forest.

Haenianthus salicifolius is capable of growing in shade but field observations of this species show that it is tied to gaps for survival. Haenianthus has a comparatively low relative density ratio of understory to

canopy plants for a shade tolerant species. Moreover, neither its 1946 or 1981 diameter class distribution is truly reverse J-shaped. Diameter growth is rapid in all crown classes exposed to direct sunlight, and even fairly rapid when shaded (Table 9, Part I).

Eugenia borinquensis is common at higher elevations where its seedlings germinate under shade. It has also been observed in areas previously cleared of trees, growing through thick tangles of grass and ferns.

Of the shade tolerant species, Prestoea is capable of establishing and growing slowly in the understory until gradually reaching the canopy. Eugenia stahlii and Ocotea moschata are difficult to classify because they are rare in the forest. Their growth into mature trees is probably benefited by gaps. Croton, Micropholis garciniaefolia, Calycogonium, Myrcia, and Byrsonima are capable of surviving in the understory for long periods but benefit from gaps to reach the canopy. The remaining species, Tabebuia, Eugenia borinquensis, Ocotea spathulata, Micropholis chrysophylloides, and Haenianthus all appear to require gaps to grow into the canopy. The last two would require larger openings to mature because they are larger trees.

Although this phase of the study emphasized regeneration of canopy trees under closed forest, many of the observations are relevant to the growing body of knowledge regarding the importance of gaps in the success of seedling establishment and penetration of trees through to the forest canopy (Whitmore 1975; Hartshorn 1978; Picket 1980; Pickett and White 1985). Of the 20 tree species that reach canopy size in some part of the colorado forest, two were classified as shade intolerant pioneers, and five were grouped into gap, or late secondary species. The remaining 13 species were classified as shade tolerant, but of these, five benefitted from gaps and

five required them to mature. Two species were difficult to classify, but probably require gaps to mature. Only one species, Prestoea, is capable of routinely growing through closed canopy. In summary, then, at least 70 percent of the species require gaps to either establish seedlings, or grow into mature stems. These results compare favorably with lowland rain forest in Costa Rica where 75 percent of the canopy species required gaps to mature (Hartshorn 1980).

In relatively open forest sampled in the transition between tabonuco and colorado forest, gaps caused mainly by the fall of large Cyrilla racemiflora trees averaged 220 m^2 (Perez Viera 1986). These gaps are intermediate in size between the 90 m^2 average for lowland rain forest in Costa Rica (Hartshorn 1978) and a 600 m^2 gap in Dipterocarp forest of Malesia caused by the fall of adjacent trees (Poore 1968). With an average crown-to-bole ratio of 20:1 in the colorado forest, the fall of a single, large tree, 50 cm in dbh, could create a gap approaching 80 m^2. However, since 95 percent of the stems at mid-elevations in the colorado forest are less than 45 cm in dbh (Wadsworth 1951), most gaps are smaller. Moreover, many gaps are caused by the slow death of a tree, a branch at a time, in which case, the surrounding vegetation occupies a portion of the gap as it is created. In contrast, much larger openings could form as the result of multiple tree falls caused by major disturbances such as hurricanes.

The regeneration and growth of Cyrilla racemiflora and Clusia krugiana trees during 35 years on the thinned colorado plot (Figs. 14, 16, 17, 18, Part I) demonstrate the potential of gap species to exploit available growing space. In other forests, it has been shown that emergents and upper canopy species require forest openings for establishment (Jones 1956; Whitmore 1975).

The presence of gaps and their variation in size are factors that influence subsequent establishment and growth of trees (Whitmore 1978; Denslow 1980; Pickett 1980). At one extreme is closed canopy forest under which tolerant tree species regenerate and remain as seedlings until a gap forms (Whitmore 1978). Without gaps, they may persist for years, but ultimately, most will perish. At the other extreme, large gaps create favorable conditions for large pioneer species which have rapid growth rates. Existing regeneration may respond poorly or die due to the altered environmental conditions. Small gaps, on the other hand, favor the growth of advanced regeneration (Whitmore 1975, 1978).

The classifications assigned to the aforementioned colorado forest species are tentative. As pointed out by Whitmore (1975), each species is unique and many are capable of surviving under different environmental conditions. Variation in elevation, aspect, and topography within the colorado forest, as well as normal gap formation and that caused by major hurricane disturbance, provide a gamut of potential environmental conditions. To these might also be added differences of light penetration through tree canopies varying in foliage density, potential allelopathic reactions about which virtually nothing is known for tropical forest, and physiological capabilities of tree species of different ages and in different developmental stages to survive, or respond to altered conditions.

SUMMARY

The sampling of 75 closed-canopy plots with an average canopy cover of 91 percent throughout the colorado forest of the Luquillo Mountains of Puerto Rico showed that stand structure and species distributions were related to environmental factors. A covariance analysis of forest structure on 500 m^2 plots including the number of species, the number of trees, mean height of dominant and codominant trees, total basal area (m^2/ha), total volume (m^3/ha), and total biomass (t/ha) by two life zones (wet and rain) and three topographic positions (ridge, slope, and valley) with elevation as a covariate showed that:

(1) the number of species averaged 15/plot and was not significantly related to any of the environmental factors;

(2) tree density averaged 2174 stems/ha and was significantly and positively related to elevation in the rain forest, but not in the wet forest;

(3) tree height averaged 12.7 m and was significantly and inversely related to elevation in both the rain forest and the wet forest; and

(4) basal area, volume and biomass averaged 45.4 m^2/ha, 252.9 m^3/ha and 148.2 t/ha, respectively, and were significantly related to topography and elevation in the rain forest, but not in the wet forest.

The same covariance analysis of soils data showed that:

(1) bulk density averaged 0.92 g/cm^3 and was significantly and inversely related to elevation in the wet forest, but not in the rain forest; and

(2) soil organic matter percent and soil organic matter content averaged 9.6 percent and 33.8 kg/m^2, respectively, and were significantly and positively related to elevation in the wet forest but not in the rain forest.

Reciprocal averaging and polar ordinations of sample plots showed that:

(1) the 75 individual plots partitioned into two major groupings which were valley plots, and slope and ridge plots combined. These groupings were based mainly on the relative abundance of Prestoea montana, the palm;

(2) composite plots derived from the grouping of complementary ridge, slope, and valley plots at the same elevation, sorted into four configurations. They were leeward (west) wet forest plots between 650 and 800 m in elevation, leeward (south) wet forest plots between 630 and 660 m, windward (northeast) rain forest plots between 650 and 750 m, and windward (northeast) rainforest plots between 800 and 960 m in elevation; and

(3) the leeward (west) wet forest plots partitioned into groupings which included ridge, slope, and valley plots between 640 and 740 m in elevation, ridge, slope, and valley plots between 750 and 860 m, and ridge, slope, and valley plots greater than 900 m in elevation.

Reciprocal averaging also showed configurations for 39 tree species according to elevation and topography, indicating species preferences in a complex, montane habitat. Five species were largely confined to valleys, eight were observed in valleys from 30-65 percent of the time, and the remainder were tallied on ridges or slopes more than 75 percent of the time.

The occurrence of 20 canopy species with regard to elevation showed four species with unimodal peaks at high elevation, one species with a unimodal peak to the windward, and seven species with bimodal peaks to the windward and leeward. Five species were found on both aspects, but were more common to the leeward. Three species were about evenly represented throughout the forest. Histograms of occurrence for these same species by topography showed that five were found mainly in valleys, nine had greater occurrence on ridges than other topographic positions, and six occurred about equally on both slopes and ridges.

The regeneration of 20 canopy species showed that the palm, Prestoea montana, was the most successful species with an average of nearly 23,150 seedlings/ha. Seven other species had more than 1,000 seedlings/ha and four species had no regeneration whatsoever. Eight species had fewer than 770 seedlings/ha.

Relative understory and seedling density ratios, seed size and wood density were used to rank the canopy species from most secondary to most primary in characteristics. The groupings recognized were: shade intolerant pioneers, two; shade intolerant gap or late secondary species, five; and shade tolerant species, 13. Of the latter, one species was capable of growing to maturity in shade, seven benefited from gaps, and five required them to mature after regeneration. Thus gaps in the canopy are critical to the regeneration and growth of nearly all of the colorado forest species.

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APPENDIX TABLES

Appendix Table 2. Alphabetical listing of tree species abundance in the ordination study.

No.	Species name[1/]	Species Total	
		No. Stems	Percent stems
1	Alchornea latifolia Sw.	44	0.16
2	Alchorneopsis portoricensis Urban	2	0.02
3	Antirhea obtusifolia Urban	5	0.06
4	Ardisia luquillensis (Britton.) Alain	12	0.15
5	Beilschmiedia pendula (Sw.) Benth. & Hook F.	7	0.09
6	Buchenavia capitata (Vahl) Eichl.	9	0.11
7	Byrsonima coriacea (Sw.) De.	1	0.01
8	Byrsonima wadsworthii Little	66	0.81
9	Calycogonium squamulosum Cogn	1,103	13.48
10	Calyptranthes krugii Kiaersk	37	0.45
11	Casearia arborea (L.C. Rich) Urban	1	0.01
12	Casearia guianensis (AVBL.) Urban	3	0.04
13	Casearia sylvestris Sw.	1	0.01
14	Cassipourea guianensis AVBL.	2	0.02
15	Cecropia peltata L.	60	0.73
16	Cestrum macrophyllum Vent.	3	0.04
17	Citharexylum caudatum L.	34	0.42
18	Cleyera albopunctata (Griseb.) Krug + Urban	2	0.02
19	Clusia krugiana Urban	190	2.32
20	Coccoloba swartzii Meisn.	2	0.02
21	Corbia borinquensis Urban	370	4.52

Appendix Table 2 (continued)

22	Croton poecilanthus Urban	326	3.98
23	Cyathea arborea L.J.E. Smith	108	1.32
24	Cyrilla racemiflora L.	234	2.86
25	Dacryodes excelsa Vahl	41	0.50
26	Daphnopsis philippiana Krug + Urban	170	2.08
27	Dendropanax arboreus L. Decne. + Planch	2	0.02
28	Dendropanax laurifolius (E. March) R.C. Schneid	1	0.01
29	Didymopanax morototoni Aubl. Decne. + Planch	14	0.17
30	Ditta myricoides Griseb.	66	0.81
31	Drypetes glauca Vahl	48	0.59
32	Eugenia borinquensis Britton	265	3.24
33	Eugenia eggersii Kiaersk.	4	0.05
34	Eugenia jambos L.	4	0.05
35	Eugenia stahlii Kiaersk. Krug + Urban	30	0.37
36	Ficus trigonata L.	3	0.04
37	Ficus laevigata Vahl	3	0.04
38	Ficus sintenisii Warb.	2	0.03
39	Grammadenia sintenisii Urban Mez	2	0.03
40	Guarea ramiflora Vent.	12	0.15
41	Guettarda valenzuelana A. Rich.	27	0.33
42	Haenianthus salicifolius Griseb.	169	2.07
43	Hedyosmum arborescens Sw.	19	0.23

Appendix Table 2 (continued)

44	Hirtella rugosa Pers.	121	1.48
45	Homalium racemosum Jacq.	11	0.13
46	Ilex nitida Vahl. Maxim.	2	0.02
47	Ilex sideroxyloides Griseb	10	0.12
48	Ilex sintenisii (Urban) Britton	6	0.07
49	Inga laurina (Sw.) Willd	28	0.34
50	Inga vera Willd	10	0.12
51	Ixora ferrea (Jacq.) Benth.	18	0.22
52	Linociera dominguensis (Lamb.) Knobb.	3	0.04
53	Magnolia splendens Urban	71	0.87
54	Manilkara bidentata (A. DC.) Chev.	2	0.02
55	Marliera sintenisii Kiaersk.	25	0.31
56	Matayba domingensis	108	1.32
57	Mecranium amygdalinum (Desr) C. Wright	6	0.07
58	Meliosma herbertii Rolfe.	17	0.21
59	Miconia laevigata (L.) DC.	42	0.51
60	Miconia pachyphylla Cogn.	11	0.13
61	Miconia prasina (Sw.) DC.	1	0.01
62	Miconia tetandra (Sw.) D. Don	140	1.71
63	Micropholis chrysophylloides Pierre	350	4.28
64	Micropholis garciniaefolia Pierre	818	10.00

Appendix Table 2 (continued)

65	Myrcia fallax Rich. DC.	95	1.16
66	Myrcia deflexa (Poir) DC.	11	0.13
67	Myrcia splendens (Sw.) DC.	1	0.01
68	Ocotea leucoxylon (Sw.) Mez	52	0.64
69	Ocotea moschata (Meisn.) Mez	7	0.09
70	Ocotea portoricensis Mez	5	0.06
71	Ocotea spathulata Mez	410	5.01
72	Ormosia krugii Urban	18	0.22
73	Palicourea riparia Benth	1	0.01
74	Prestoea montana (R. Grah) Nichols.	1,365	16.69
75	Psychotria berteriana DC.	51	0.62
76	Rapanea ferruginea Ruiz + Pav. Mez	1	0.01
77	Rheedia portoricensis Urban	55	0.67
78	Rondeletia portoricensis Krug + Urban	9	0.11
79	Sapium laurocerasus Desf.	30	0.37
80	Sloanea berteriana Choisy	28	0.34
81	Tabebuia heterophylla (DC.) Britton	7	0.09
82	Tabebuia rigida Urban	686	8.38
83	Tetragastris balsamifera (Sw.) Kuntze	1	0.01
84	Tetrazygia urbanii Cogn.	8	0.10
85	Torralbasia cuneifolia (C. Wright) Krug + Urban	28	0.34

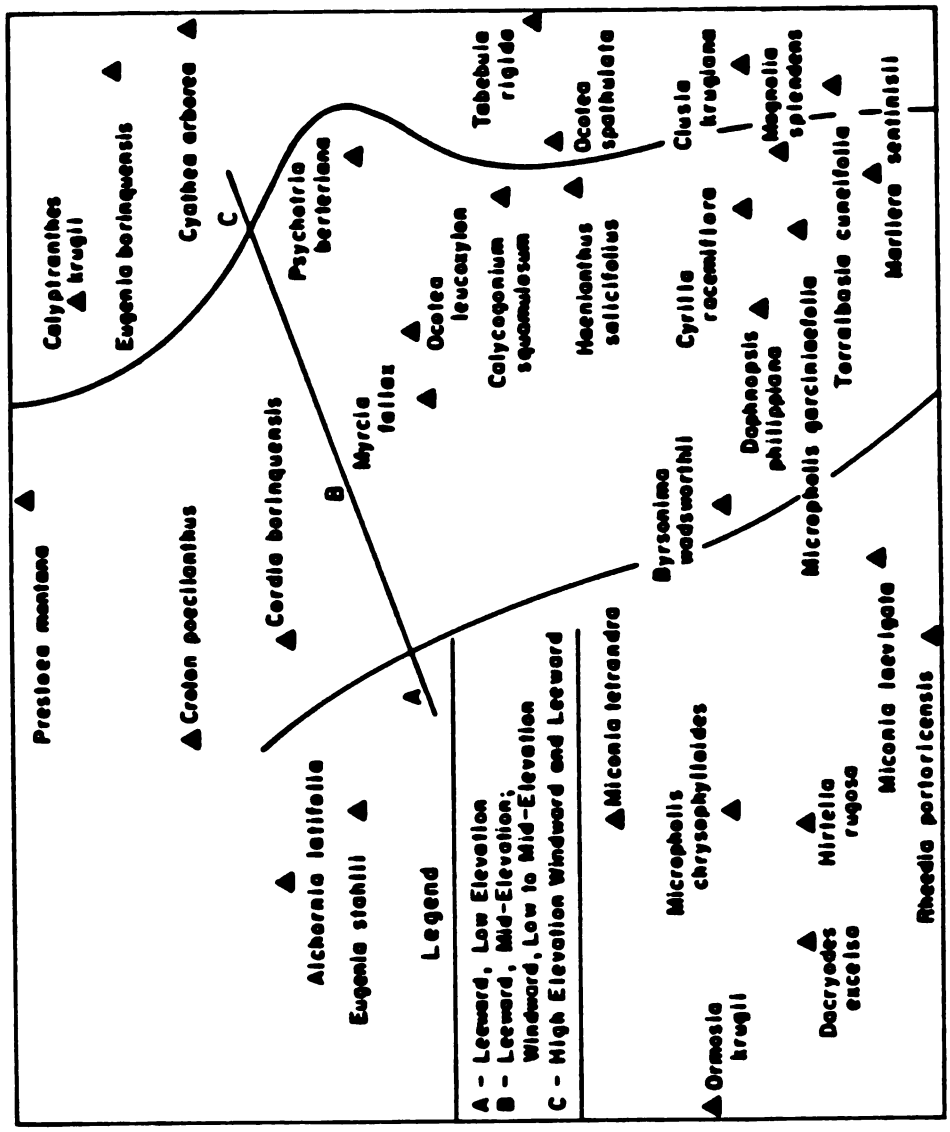
Appendix Table 2 (continued)

86 *Vitex divaricata* Sw.	2	0.02
87 *Xylosma schwaneckeanum* (Krug + Urban) Urban	8	0.10
TOTALS	8,183	100.00

1/ Source: Little and Wadsworth 1964; Little *et al*. 1974.

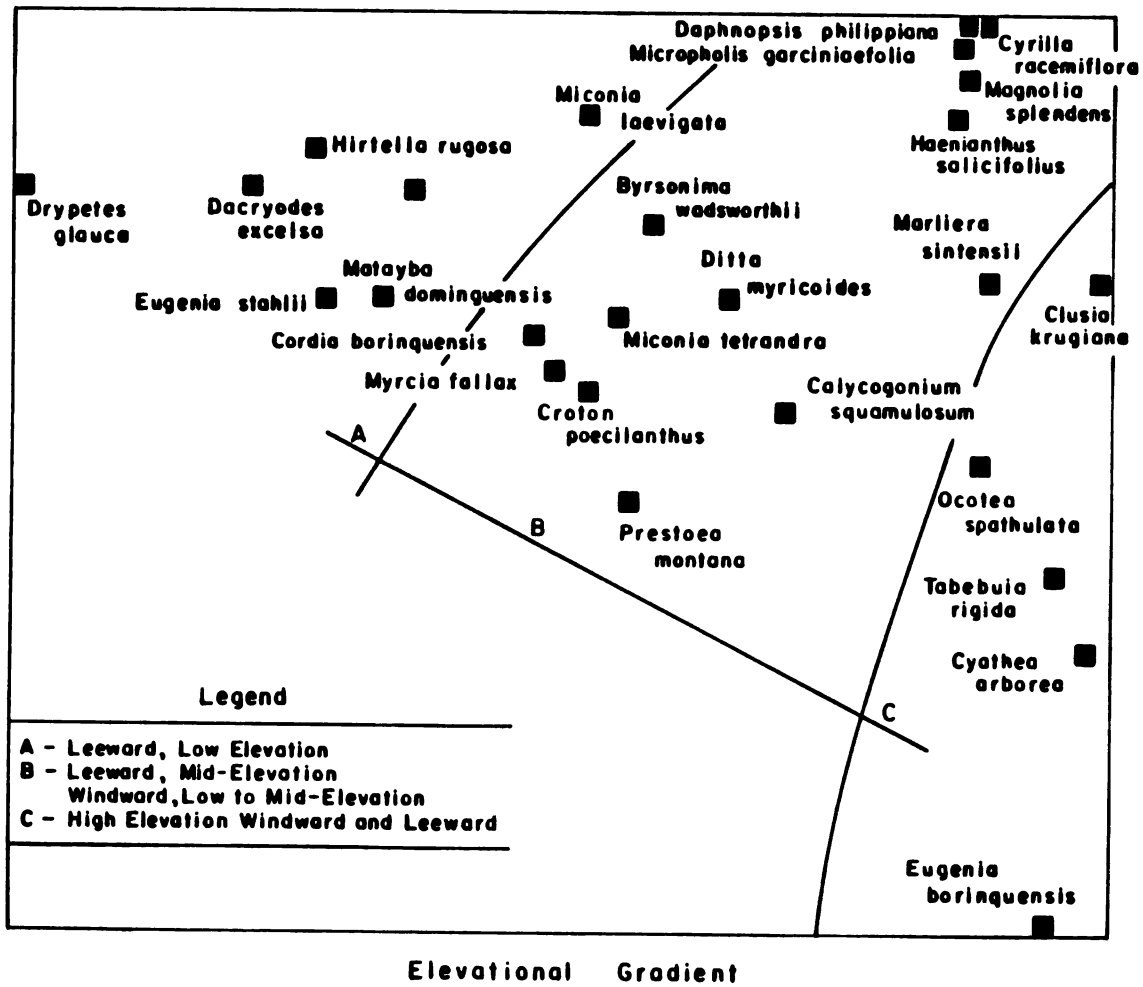
APPENDIX FIGURES

Appendix Figure A-2. Reciprocal averaging ordination: species ordination of 27 windward and 30 leeward plots and 30 species on ridge topography.



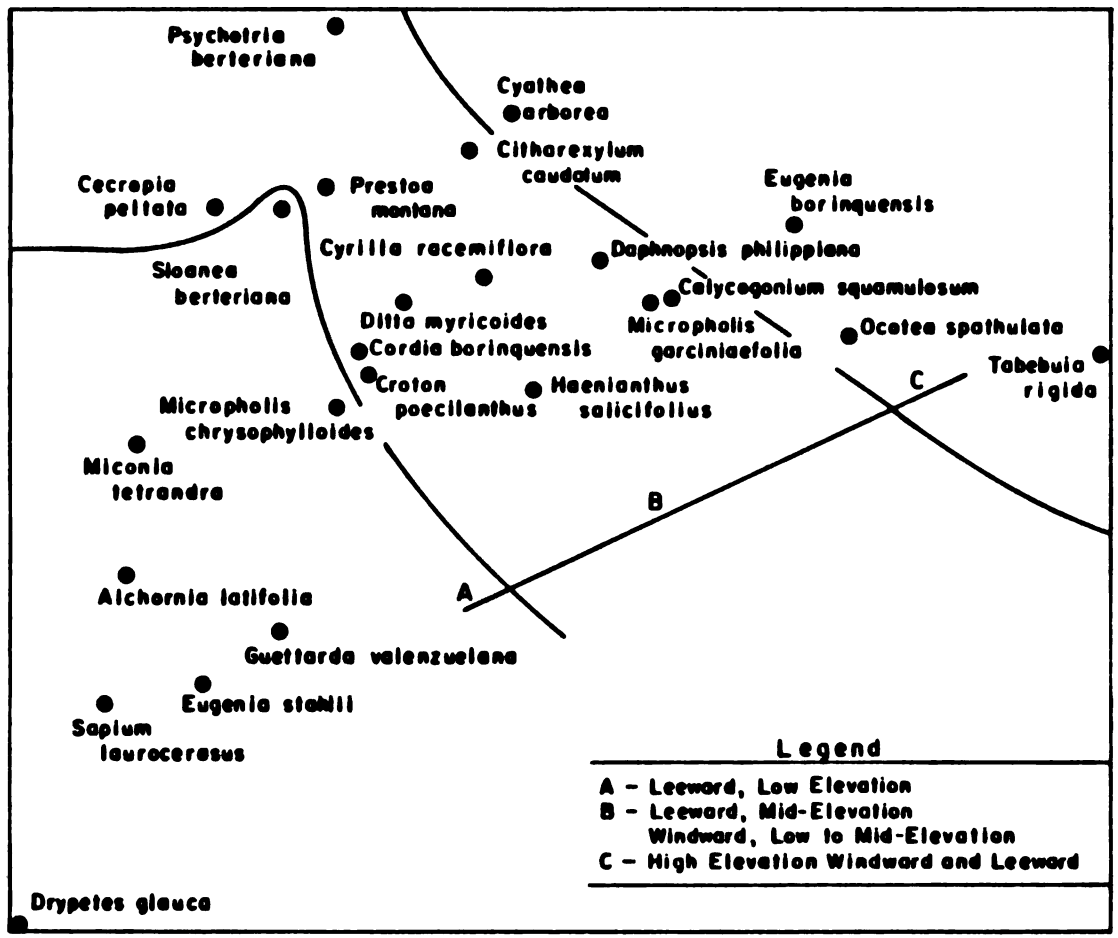
Appendix Figure A-2

Appendix Figure A-3. Reciprocal averaging ordination: species ordination of 27 windward and 30 leeward plots and 26 species on slope topography.



Appendix Table A-3

Appendix Figure A-4. Reciprocal averaging ordination: species ordination of 27 windward and 30 leeward plots and 24 species on valley topography.



Appendix Figure A-4

PART III

FOREST STRUCTURE AND PRODUCTIVITY

INTRODUCTION

The diversity of plant life in the tropics, where plant communities range from the lowlands through montane areas to timberline and paramo, in humid and dry environments, exceeds that of other latitudes. Of the world's 116 life zones according to Holdridge's (1967) classification of plant formations, 66 are located within the tropics. Nearly half of these support forests. Moreover, tropical forests constitute about half of the world's forests on an areal basis (UNESCO 1978) and make significant contributions to human welfare, yet remain poorly studied. For example, information on total annual net primary productivity (total NPP), or the rate of storage of organic matter in excess of respiratory utilization during the measurement period (Odum 1971), was available from only 20 tropical forests about a decade ago (Murphy 1975).

The purpose of this study was to determine NPP in the colorado forest by summing the rates of litterfall, herbivory, and biomass increment (Medina and Klinge 1981; Weaver et al. 1986). Over the gradient from low elevations to the summits of the Luquillo Mountains, temperature decreases, and cloud cover and rainfall increase, resulting in a decline in forest structure and complexity (Baynton 1968; Weaver et al. 1973; Wadsworth 1951). The existence of information on forest structure and dynamics for each of the forest types in the Luquillo Mountains including the tabonuco forest at 450 m in elevation, through the palm brake (Frangi and Lugo 1985) and the colorado forest (this study) at 750 m, to the dwarf forest at 1050 m in elevation (Weaver et al. 1986), provided a rare

opportunity to compare changes along a 600 m elevational gradient in the subtropical latitudes of the Caribbean.

METHODS

The re-measurement of the permanent plots and their data analyses were described in the methods of Part I. Soil data collection and analyses were outlined in the methods of Part II.

Leaf area index (LAI) measurements were made on two permanent plots located at mid-elevations in the colorado forest, slope plot B, and mixed topography plot E, once during April which is drier than most months (Fig. 2, General Introduction), and again in June. Of primary interest was the LAI of the woody vegetation since ground vegetation may have been disturbed by previous tree measurements. A modified plumb-bob technique was used (Benedict 1976). Fifteen sampling stations were spaced about 10 m apart within each stand. At each station, a ladder was positioned against the nearest tree and an extension pole was used to lower four plumb-bob lines 90^{o} apart through the canopy to the ground. All leaf contacts were recorded. Because ground area is reduced to a point, each contact per line represents 1 m^2 of leaf surface per 1 m^2 of ground surface. An adjacent area was also selected and the measurements were repeated at 10 stations. In this instance, canopy vegetation was partitioned between trees and epiphytes, and the ground vegetation among herbs, grasses and bryophytes.

Litterfall was collected periodically for two years starting in January 1981. Twenty 0.25 m^2 baskets were placed about 10 m apart in the center of both permanent plots. During the first year they were emptied twice per month and during the second year on a monthly basis.

Litterfall was partitioned into leaves, wood, fruits and flowers, and miscellaneous categories, and dried to a constant weight and recorded.

Loose litter, or unincorporated detritus composed of leaves, other plant materials and woody fragments, was collected monthly for one year starting in January 1982. Twenty 0.25 m^2 collections were made from areas adjacent to both permanent plots. All samples were partitioned into woody and miscellaneous categories, dried to a constant weight, and recorded.

Herbivory was evaluated in two ways. Standing herbivory, or the amount of herbivory evident at a particular moment, was determined once by sampling the eaten portions and total areas of 1439 leaves on 153 branches of 35 trees. Twelve of the most common species were represented. In order to convert standing herbivory estimates by species to a value representative of the entire colorado forest, a weight factor was used. First, the relative density and relative basal area of each species sampled were determined. These percentages of density and basal area were based on the species composition of all seven of the natural forest permanent plots. Next, these percentages for density and basal area were summed, and then divided by two to yield a value that was weighted by both the number of individuals (density) and size of the trees (basal area). The standing herbivory for the forest species not sampled was assumed equal to the weighted mean of the 12 species that had been sampled. These weighted species values were converted to ecosystem values by multiplying by the LAI of the arborescent vegetation.

Herbivory rate, or the amount of herbivory during a given period, was determined by sampling 418 leaves on 111 branches of 41 trees. Nine of the most common species were represented. In this instance, fully

developed young leaves without evidence of herbivory were selected. Each was numbered and tagged with plastic tape that was stapled across the midrib on the underside of the leaf. After 90 days, the leaves were removed from the trees and the amount of herbivory was determined. Herbivory rate for the ecosystem was estimated using the same weighting procedure mentioned above.

Leaf weight was determined by removing 30 leaves for each of 18 common species. Leaves were then placed in numbered bags and dried to a constant weight. The same weighting procedure outlined above was used to convert individual species values to ecosystem values.

For standing herbivory, herbivory rate and leaf weight, leaves were selected from trees of different crown classes, and at different heights within the canopy. Leaf area in each instance was determined with a Li-Cor Model 3100 Area Meter. In all cases, weights were to the nearest 0.01 g and areas to the nearest 0.01 cm^2.

Seventeen dicotyledenous trees ranging in size from 6.5 to 36.7 cm in diameter and representing seven different species were selected for biomass determinations. For sampling purposes, biomass was partitioned into trunks, branches >2.5 cm, branches $\leq$2.5 in diameter, and leaves. Wet weights were determined in the field. For each tree, four sample discs of the trunk taken at different heights and six sample discs of branches >2.5 cm were oven-dried along with four samples of branches $\leq$2.5 cm and leaves. Leaves were dried for three days and the remaining materials for six weeks at $70^{o}C$, at which time no decrease in dry weight was observed. Sample dry/wet weight proportions were then used to determine the dry weight of all classes of material. Regressions in which dry weight was expressed as an allometric function of tree diameter squared

times tree height were developed for leaves, branches, trunks, aboveground woody material and total biomass (leaves and woody fractions combined). The regressions were used to determine the standing biomass of the leaf and aboveground woody compartments for all measured trees. Root biomass was not sampled. Rather, it was estimated as 30 percent of the aboveground woody biomass. This value has been used frequently for humid forests when root data are lacking (Murphy 1975). The value slightly exceeds the estimate of 22 percent determined for root biomass on a palm plot (Frangi and Lugo 1984) adjacent to one of the colorado forest plots used in this study. The percent root biomass estimate on the palm plot, however, may be low because of poor drainage and the dominance of palms which characterize these sites.

In all instances, the above regression equations were compared with data for the tabonuco forest (Ovington and Olson 1970) using standard statistical techniques (Freese 1967). Significance was defined as $P \leq 0.05$. Cecropia peltata and Didymopanax morototoni, both very light woods, were removed from the data set of the tabonuco forest so as not to distort the regression estimates.

Net primary productivity (NPP) was estimated as the sum of litterfall, herbivory, and biomass increment. Herbivory was determined as the annual herbivory rate times the leaf biomass. Biomass increment during the 35-year period was partitioned into the accrual of the leaf, the aboveground woody, and the root compartments. Net biomass increment for leaf and aboveground woody compartments was determined as the 1981 standing biomass minus the 1946 standing biomass divided by 35 years. The increase in root biomass was estimated as 0.3 times the aboveground net woody increment.

Palms were treated separately. Total palm biomass (leaves, stems, and roots) was estimated by the equation $\ln Y = 3.85 + 2.91 \ln X$ where Y is the dry weight of the palm in grams and X is its height in meters (Bannister 1970). Palm trunk biomass was estimated independently as basal area times height times the specific gravity. These values were added, respectively, to total aboveground biomass and aboveground woody biomass estimates. The weight of palm leaf stalks, inflorescences, and roots was determined as the residual of total palm biomass minus palm trunk biomass, both derived by the aforementioned relations.

RESULTS

Leaf Characteristics in the Forest

Leaf area index

There was no significant difference in LAI for trees measured on the same plot in different months, nor was there a significant difference in tree LAI between plots measured in the same month. Therefore, all data were combined into a single estimate of 3.01 m^2/m^2 (Table 16). Epiphytes averaged 0.30 m^2/m^2, herbs and grasses 1.18 m^2/m^2, and ground bryophytes 0.47 m^2/m^2. The total for all vegetation was 4.96 m^2/m^2.

Leaf weights

Mean oven-dry leaf weights for dicotyledons ranged from 0.06 g for Ditta to 1.61 g for Clusia. Palm leaflets (Prestoea) averaged 1.75 g (Table 17). Mean leaf areas for dicotyledons ranged from 8.10 cm^2 for Ditta to 135.89 cm^2 for Cordia, with palm leaflets at 236.90 cm^2. Specific leaf areas for the dicots ranged from 36.01 cm^2/g for Clusia to 163.73 cm^2/g for Cordia, with palm leaflets at 135.37 cm^2/g. The mean oven-dry leaf weight values for all dicotyledons combined was 0.67 g; the mean area was 56.38 cm^2; and the mean specific leaf area was 90.96 cm^2/g. The weighted mean specific leaf area for all dicotyledons, a value more representative of the forest, was 67.79 cm^2/g. All dicotyledonous leaves were within Raunkiar's mesophyll size class (Richards 1966). The palm leaves were classified as megaphylls.

Table 16. Leaf area indices by compartment in the colorado forest

Compartment	Number of lines	LAI, m^2/m^2 Mean ± SE
Canopy		
Trees[1]	280	3.01 (0.12)
Epiphytes[2]	40	0.30 (0.14)
Ground		
Herbs + grasses[2]	40	1.18 (0.16)
Bryophytes[2]	40	0.47 (0.08)
Total	---	4.96 (----)

[1] This figure is derived from 60 measurements on each of 2 plots made in April and June plus an additional 40 measurements on a third plot in June. Neither plots nor dates showed significant differences, therefore, the data were combined.

[2] Three epiphytes and herbs + grasses and bryophytes were determined only on the third plot which had not been disturbed by previous dbh measurements.

Table 17. Leaf characteristics for common species found throughout the colorado forest.[1/]

Species	Unweighted Mean ± SE		Specific leaf area (cm^2/g)	Weight factor[2/]	Weighted specific leaf area value[3/] (cm^2/g)
	Dry weight (g)	Area (cm^2)			
Brysonima wadsworthii	0.21 (0.01)	23.36 (1.20)	111.24	0.12	13.35
Calycogonium squamulosum	0.29 (0.01)	26.85 (1.19)	92.59	2.62	242.58
Clusia krugiana	1.61 (0.10)	57.98 (3.50)	36.01	0.41	14.76
Cordia borinquensis	0.83 (0.04)	135.89 (5.71)	163.72	0.62	101.51
Croton poecilanthus	0.96 (0.03)	80.86 (2.26)	84.23	1.51	127.19
Cyrilla racemiflora	0.37 (0.01)	20.81 (0.77)	56.24	2.15	120.92
Daphnopsis philippiana	0.52 (0.03)	55.92 (2.59)	107.54	0.46	49.47
Ditta myricoides	0.06 (0.00)	8.10 (0.25)	135.00	0.25	33.75
Haenianthus salicifolius	0.21 (0.02)	17.56 (0.85)	83.62	0.84	70.24
Hedyosmum arborescens	0.30 (0.01)	40.22 (1.41)	134.07	0.04	5.36
Magnolia splendens	1.46 (0.06)	132.97 (6.29)	91.08	0.62	56.47
Miconia tetrandra	0.91 (0.06)	99.30 (4.68)	109.12	0.02	2.18
Micropholis chrysophylloides	0.46 (0.02)	27.17 (0.89)	59.06	1.76	103.94
Micropholis garciniaefolia	0.80 (0.03)	38.96 (1.27)	48.70	3.39	165.09
Ocotea leucoxylon	0.77 (0.06)	88.22 (6.39)	114.57	0.02	2.29
Ocotea spathulata	0.53 (0.03)	20.10 (1.41)	37.92	0.43	16.30
Prestoea montana	1.75 (0.12)	236.90 (8.86)	135.37	2.41	326.24
Tabebuia rigida	1.03 (0.08)	84.12 (5.60)	81.66	0.33	26.95
Total/Mean	0.67[a/] - - -	56.38[a/] - - -	90.96[a/]	18.0	67.79[b/]

[1/] Estimates based on 30 leaves per species taken from different levels within the forest.

[2/] Weights based on (percent of total stems sampled in forest + percent of total basal area sampled in forest) divided by two.

[3/] Weighted values for determining the mean specific leaf area for the colorado forest ecosystem.

[a/] The unweighted means for all species exclude palm leaflets (Prestoea). When the palm is included, the values are, respectively, 0.73, 66.41, and 93.43.

[b/] The weighted specific leaf area with palm leaflets is 82.15.

Litterfall and Loose Litter

The litterfall data from the two plots were not significantly different on a monthly basis, and were therefore combined into a single monthly estimate of litterfall. The same was true of the loose litter data. The mean annual rate of litterfall was 680 g/m^2 (Fig. 39). Leaves constituted 74 percent of the total, wood fall about 18 percent, and flowers, fruits and miscellaneous fragments accounted for 8 percent. Leaf fall exhibited a peak between March and June (Fig. 40), but monthly rates did not exceed 75 g/m^2. Flower and fruit fall showed a peak in July (Fig. 41) with generally higher values from April through August. Woody litterfall showed considerable monthly variation (Fig. 40) and miscellaneous litterfall did not demonstrate any consistent trends (Fig. 41).

The mean standing crop of loose litter was about 875 g/m^2 (Fig. 42). The first three months of the year showed a notable decline in loose litter, while the rest of the year it ranged between 800 to 1000 g/m^2. A peak in loose litter high is evident in June and July just after peak leaf fall.

Because the loose litter values were low during the first three months of the first year of measurement, loose litter was sampled the following year during January, February and March. Again, these values were consistently lower, and compared favorably with the results of the first year.

Figure 39. Total litterfall for the colorado forest by month, from January 1, 1981 through December 31, 1982.

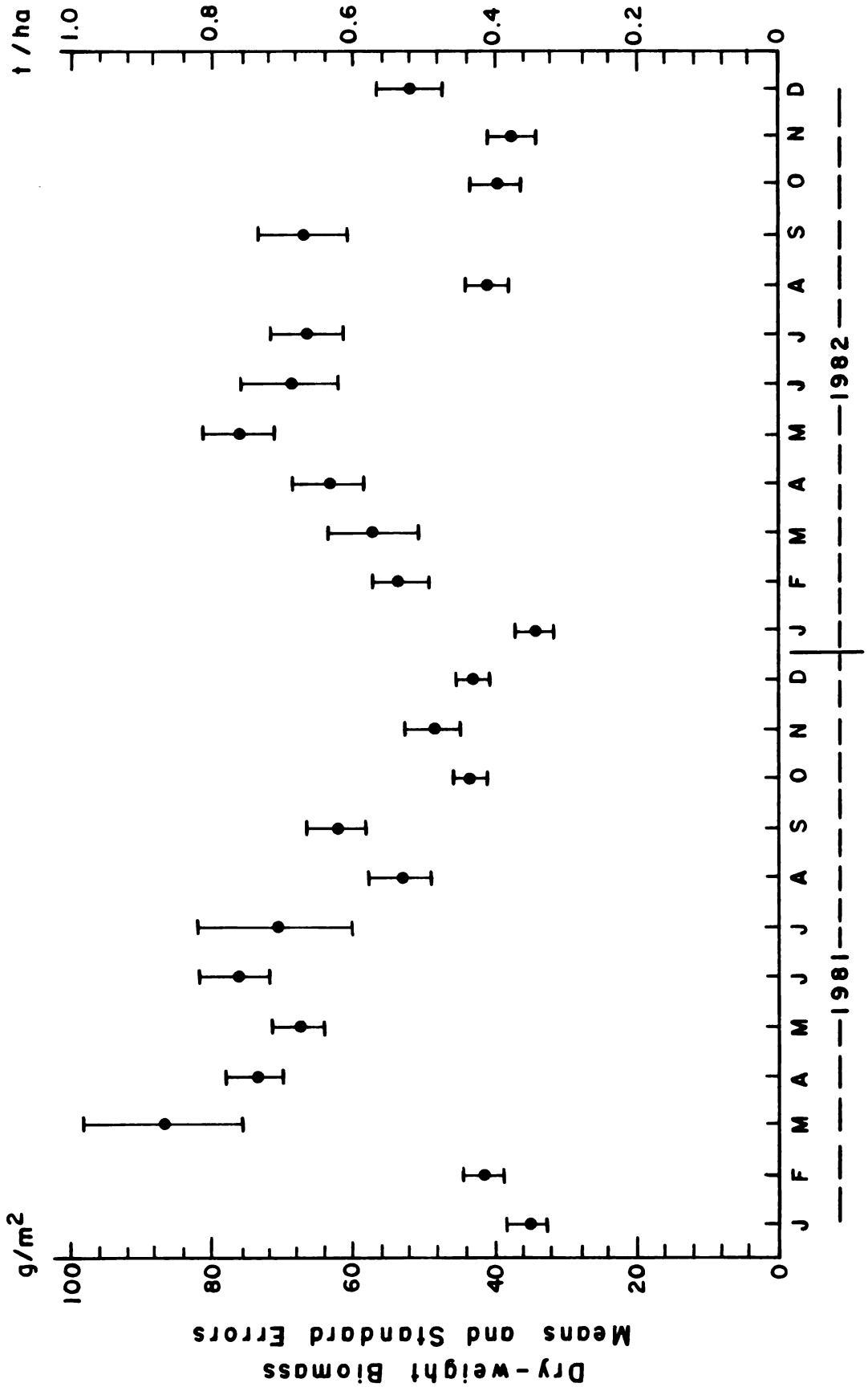

Dry-weight Biomass
Means and Standard Errors
g/m²
t/ha
100
80
60
40
20
0
1.0
0.8
0.6
0.4
0.2
0
J F M A M J J A S O N D J F M A M J J A S O N D
1981
1982
Months

Figure 39

Figure 40. Leaf litterfall and woody litterfall for the colorado forest by month, from January 1, 1981 through December 31, 1982.

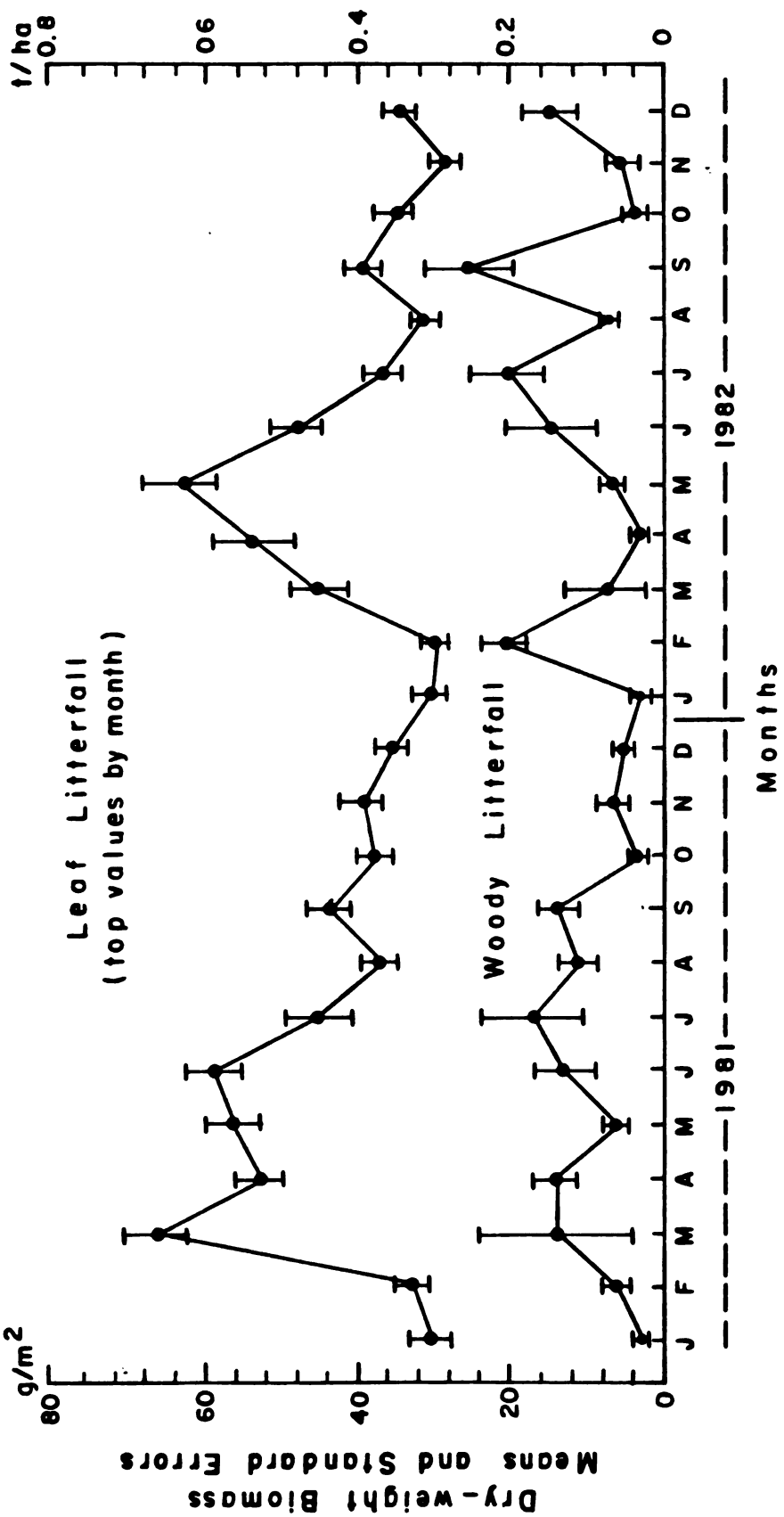

Dry-weight Biomass
Means and Standard Errors
g/m2
80
60
40
20
0
t/ha
0.8
0.6
0.4
0.2
0
Leaf Litterfall
(top values by month)
Woody Litterfall
J F M A M J J A S O N D J F M A M J J A S O N D
1981
1982
Months

Figure 40

Figure 41. Flower/fruit litterfall and miscellaneous litterfall for the colorado forest by month, from January 1, 1981 through December 31, 1982.

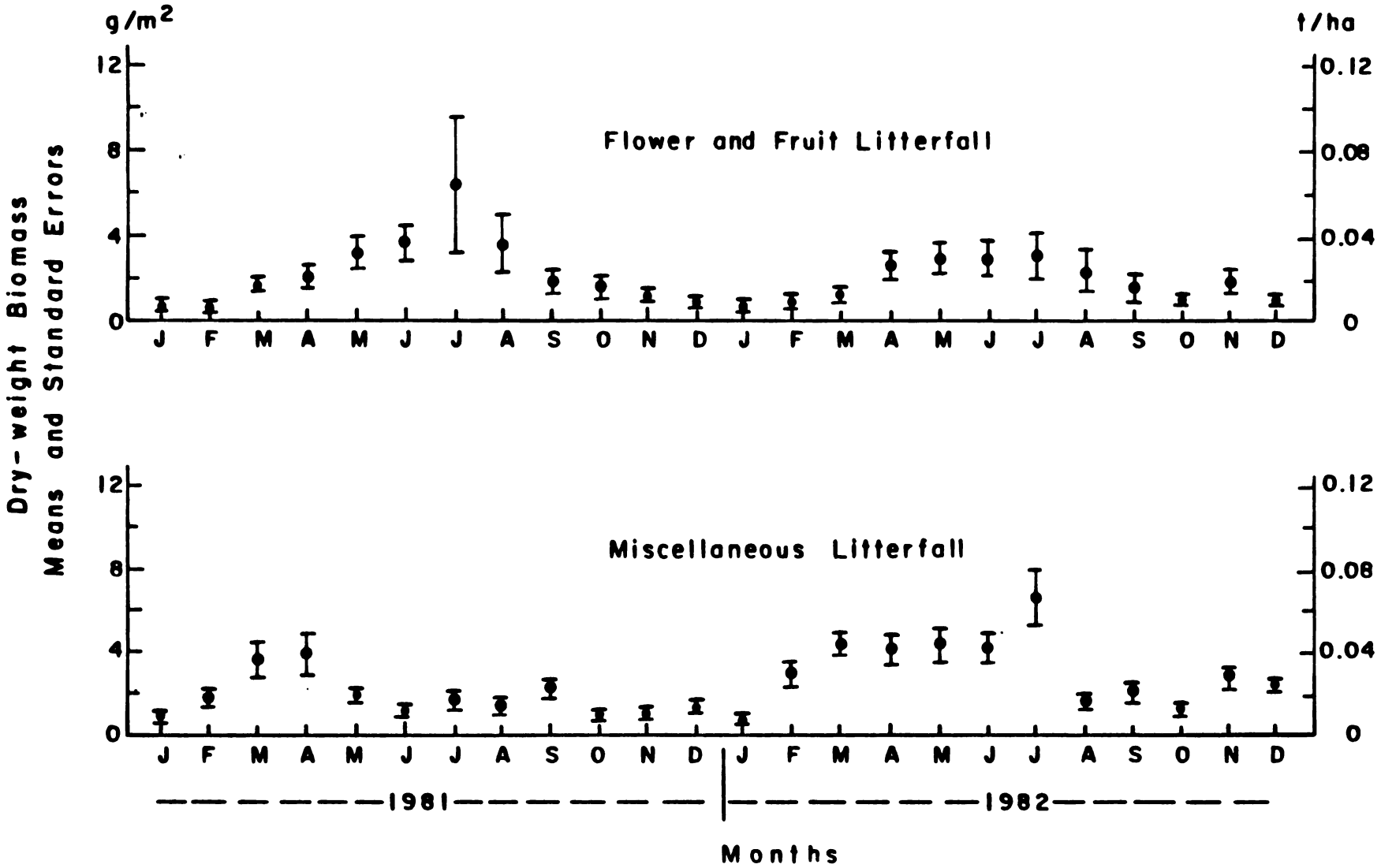

g/m²
t/ha
Dry-weight Biomass
Means and Standard Errors
Flower and Fruit Litterfall
Miscellaneous Litterfall
12
8
4
0
0.12
0.08
0.04
J F M A M J J A S O N D J F M A M J J A S O N D
1981
1982
Months

Figure 41

Figure 42. Woody looselitter, miscellaneous looselitter and total looselitter for colorado forest by month, from January 1 through December 31, 1982.

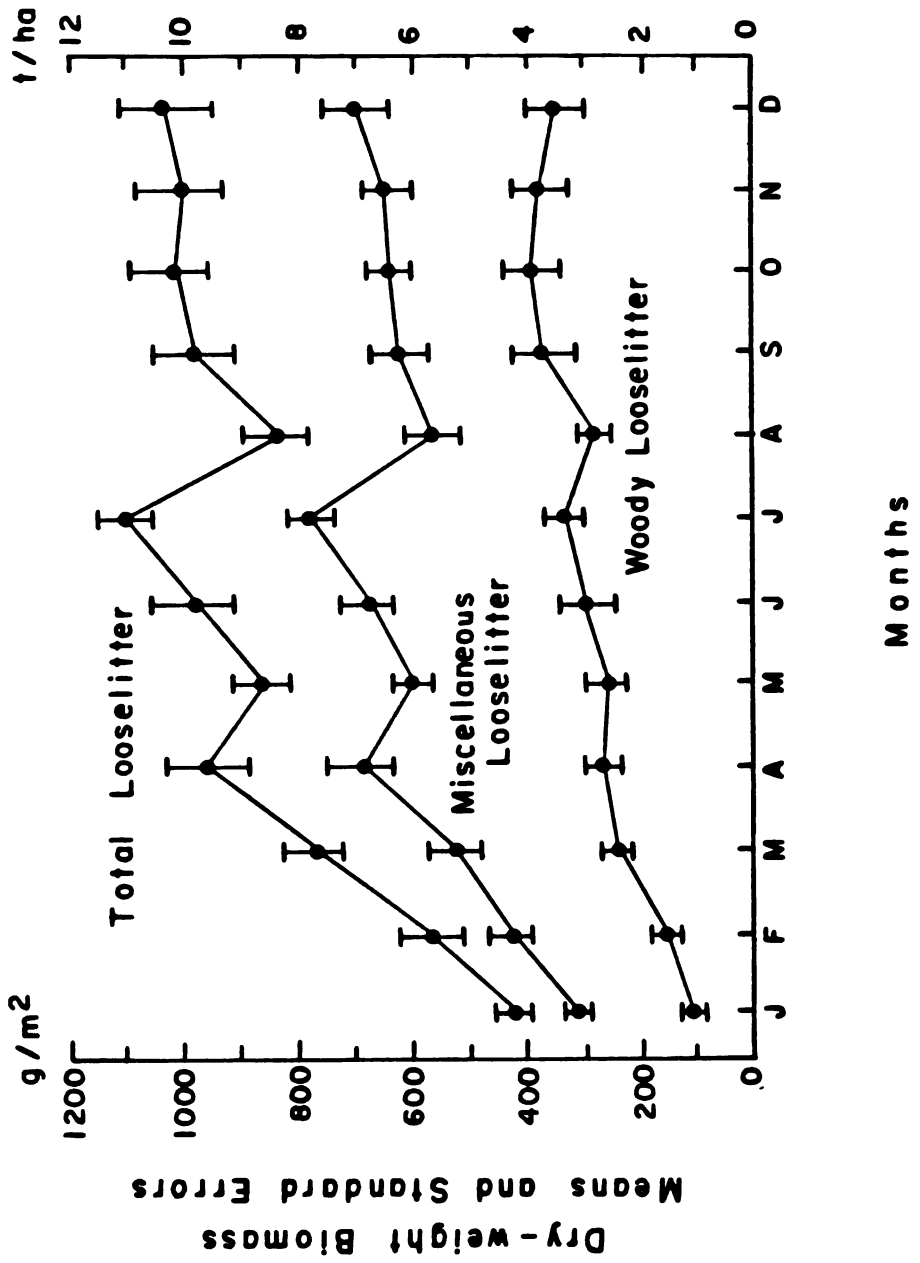

Dry-weight Biomass
Means and Standard Errors
g/m2
t/ha
1200
1000
800
600
400
200
0
12
10
8
6
4
2
0
J
F
M
A
M
J
J
A
S
O
N
D
Months
Total Litter
Miscellaneous Litter
Woody Litter

Figure 42

Standing Herbivory and Herbivory Rates

Of the 686.9 cm^2 of leaf area sampled of 12 common tree species in the colorado forest, 37.0 cm^2, or 5.5 percent of the total, were eaten (Table 18). Standing herbivory varied from 0.6 percent for Cordia to 11.1 percent for Magnolia. A simple mean of species values, however, is not the best estimate of herbivory in the forest because tree species are not equally common nor of the same size. Conversion of individual species values to a value representative of the forest yielded an estimate of 5.1 percent standing herbivory.

Sampling of standing herbivory gives an estimate of the amount of foliage consumed. However, because the age of the leaves is not known, herbivory rates cannot be calculated from these data.

Herbivory rates ranged from virtually zero for Croton and Prestoea to 1.20 ± 0.31 $cm^2/90$ days, or 3.6 percent for Clusia (Table 19), with a mean for all species sampled of 0.5 ± 0.10 $cm^2/90$ days, or 0.9 percent of the leaf area. Conversion of individual species values to a value representative of the entire forest yielded an estimate of 1 percent over a 90-day period. Assuming that herbivory will continue at the same rate for the rest of the year, the annual rate of herbivory may be extrapolated at four percent of the foliage.

Biomass

Leaf weight, branch weight, trunk weight, aboveground woody weight and total aboveground tree weight, expressed as an allometric function of D^2H, all demonstrated significant relations in the colorado forest

Table 18 : Standing herbivory sample for 12 tree species in the colorado forest.

Species	Number Sampled			Leaf Area		Percent Herbivory by species	Weight Factor [1]	Percent Herbivory by forest
	Trees	Branches	Leaves	Total $\bar{X}$+SE (cm^2)	Eaten $\bar{X}$+SE (cm^2)			
Calycogonium squamulosum	4	15	55	29.4± 1.65	2.5±0.47	8.5	1.92	16.3
Clusia krugiana	3	10	183	43.4± 1.45	3.3±0.37	7.6	0.41	3.1
Cordia borinquensis	2	4	29	77.9± 4.17	0.5±0.16	0.6	0.43	0.3
Croton poecilanthus	2	16	148	45.8± 1.46	2.5±0.37	5.5	0.71	3.9
Cyrilla racemiflora	4	25	248	11.2± 0.25	0.6±0.01	5.4	1.42	7.7
Daphnopsis philippiana	2	6	31	30.3± 2.10	1.2±0.34	4.0	0.24	1.0
Magnolia splendens	2	10	50	101.3± 3.58	11.2±1.54	11.1	0.41	4.6
Micropholis chrysophylloides	4	20	237	14.8± 0.36	0.4±0.06	2.7	0.88	2.4
Micropholis garciniaefolia	4	25	248	6.8± 0.14	0.1±0.02	1.5	1.88	2.8
Ocotea spathulata	3	8	73	21.4± 0.88	2.0±0.28	9.3	0.60	5.6
Prestoea montana	2	4 [a]	32 [a]	219.8±15.06	7.2±2.02	3.3	2.21	7.3
Tabebuia rigida	3	10	105	84.8± 3.52	5.5±0.65	6.5	0.89	5.8
Totals	35	153	1439	686.9 ----	37.0 ----	---	12.00	---
Means	—	---	-----	34.8± 1.13	1.7±0.12	5.5	------	5.1

[1] Weights based on (percent of total stems sampled in forest + percent of total basal area sampled in forest) divided by two.

[a] In this instance, the leaf rachis was considered as a branch and the palm leaflets as leaves.

Table 19: Herbivory rate sample for nine tree species in the colorado forest over 90 days.

Species	Number Sampled			Leaf Area		Percent Herbivory by species	Weight Factor	Percent Herbivory by forest
	Trees	Branches	Leaves	Total $\bar{X}$+SE (cm^2)	Eaten [1] $\bar{X}$+SE (cm^2)			
Calycogonium squamulosum	3	8	47	24.9± 0.91	0.86±0.32	3.5	1.58	5.5
Clusia krugiana	3	11	51	33.4± 3.6	1.20±0.31	3.6	0.33	1.2
Croton poecilanthus	5	14	10[a]	42.0± 4.4	0.01±0.01	0.0	0.58	0
Cyrilla racemiflora	4	14	51	17.8± 0.7	0.05±0.01	0.3	1.17	0.4
Micropholis chrysophylloides	5	10	39	34.5± 1.5	0.02±0.02	0.1	0.72	0.1
Micropholis garciniaefolia	6	16	78	31.1± 3.4	0.04±0.02	0.1	1.57	0.2
Ocotea spathulata	7	15	36	29.4± 1.7	0.06±0.02	0.2	0.49	0.1
Prestoea montana	3	8[b]	40[b]	241.6±26.8	0.08±0.04	0.0	1.82	0
Tabebuia rigida	5	15	66	78.3± 3.0	1.7 ±0.05	2.2	0.74	1.6
Totals	41	111	418	533.0	4.02	---	9.0	---
Means	---	---	---	57.0± 4.1	0.5± 0.10	0.9	---	1.0

[1] Eaten portions include brown spots. These are rate values, or areas eaten/90 days.

[a] Forty leaves were not recovered.

[b] In this instance, the leaf rachis was considered as a branch and the palm leaflets as leaves.

(Figs. 43 to 47). The r^2 values were all $\geq$0.89 with the exception of that for leaves which showed a value of 0.60.

The comparison of least squares linear regressions for leaf, branch, and total aboveground woody biomass, at the 95 percent level, between colorado and tabonuco forests, yielded significant differences. The regressions for trunk and total aboveground biomass, however, were not significantly different.

Biomass estimates for the leaves, aboveground woody, and root compartments are shown in Table 20. Palm estimates were derived with other equations (see Methods).

Net Primary Production (NPP)

The total annual NPP for the colorado forest between 1946 and 1981 using the definition that NPP is equal to the sum of litterfall, forest herbivory rate, and biomass increment (including leaf, aboveground woody, and estimated root increment) was 7.83 t/ha/yr (Table 20). Litterfall accounted for nearly 87 percent of the total, biomass increment more than 10 percent, and the herbivory rate nearly three percent (Table 20).

A simple model depicting the storage of organic matter aboveground and in the soil to a depth of 50 cm is shown in Figure 48. The four measured compartments, contained 55,584.6 g/m^2, or 555.8 t/ha. Of this, about 70 percent was stored in the soil or on the soil surface, and the remainder was found in leaves and in aboveground wood. The litter turnover rate was once per 1.28 years, or 0.78 times per year.

Figure 43. Leaf weight expressed as an allometric function of D^2H. Tabonuco data were obtained from Ovington and Olson (1970) and the colorado data from this study.

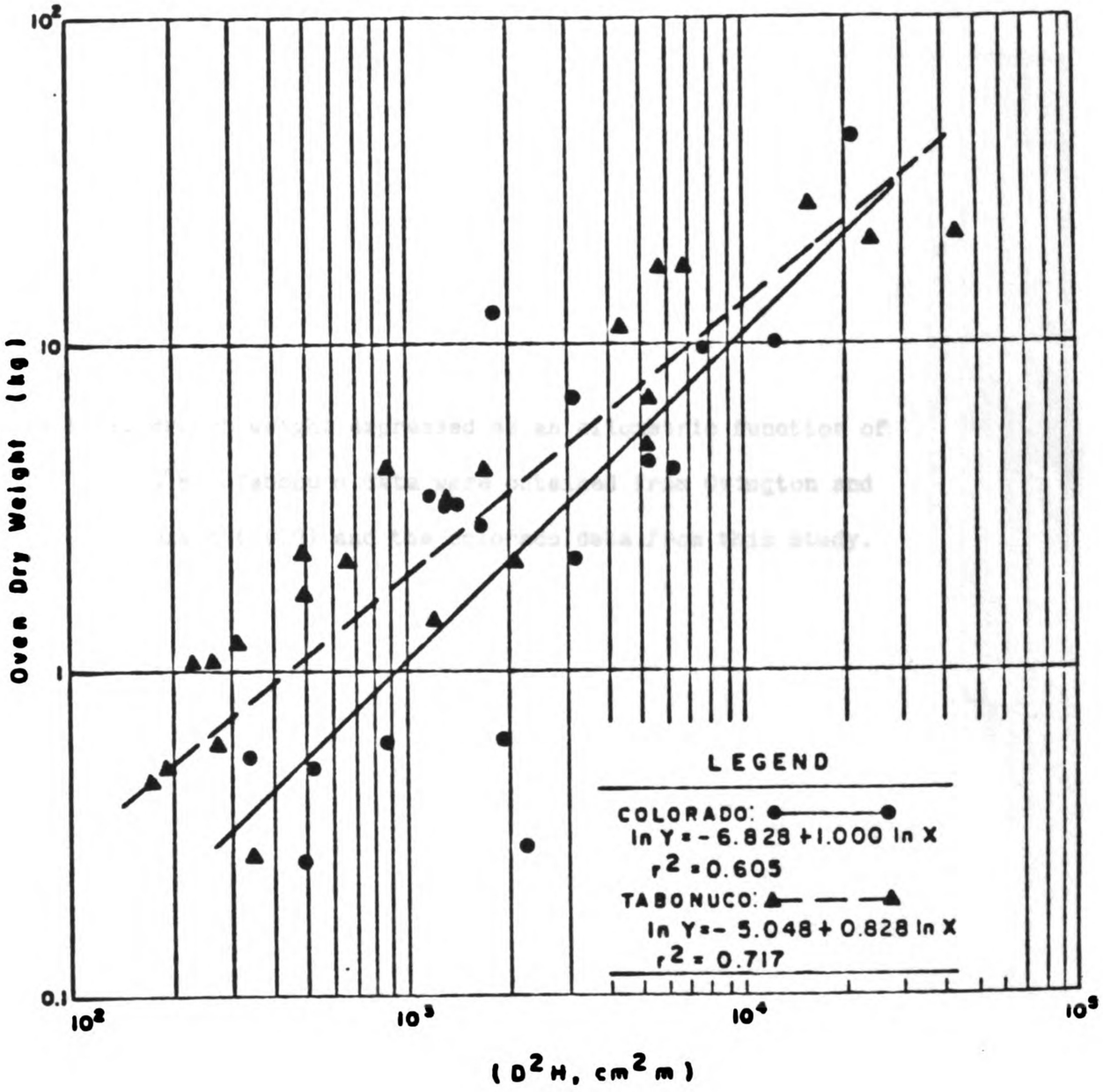

Oven Dry Weight (kg)
10^2
10
1
0.1
10^2
10^3
10^4
10^5
$(D^2H, cm^2 m)$
LEGEND
COLORADO:
ln Y = - 6.828 + 1.000 ln X
r^2 = 0.605
TABONUCO:
ln Y = - 5.048 + 0.828 ln X
r^2 = 0.717

Figure 43

Figure 44. Branch weight expressed as an allometric function of D^2H. Tabonuco data were obtained from Ovington and Olson (1970) and the colorado data from this study.

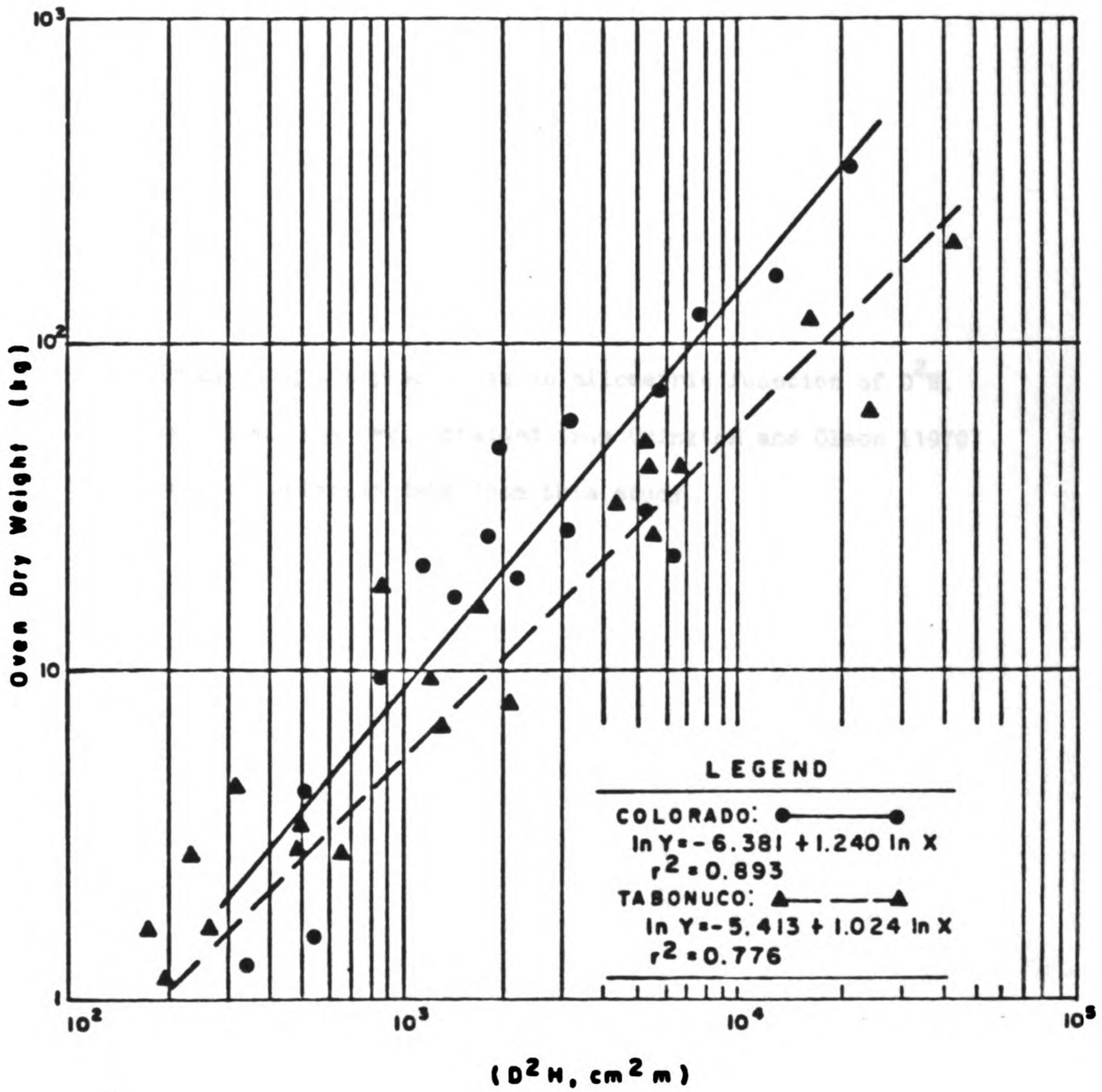

Oven Dry Weight (kg)
10^3
10^2
10
1
10^2
10^3
10^4
10^5
$(D^2H, cm^2 m)$
LEGEND
COLORADO:
ln Y = - 6.381 + 1.240 ln X
r^2 = 0.893
TABONUCO:
ln Y = - 5.413 + 1.024 ln X
r^2 = 0.776

Figure 44

Figure 45. Trunk weight expressed as an allometric function of D^2H. Tabonuco data were obtained from Ovington and Olson (1970) and the colorado data from this study.

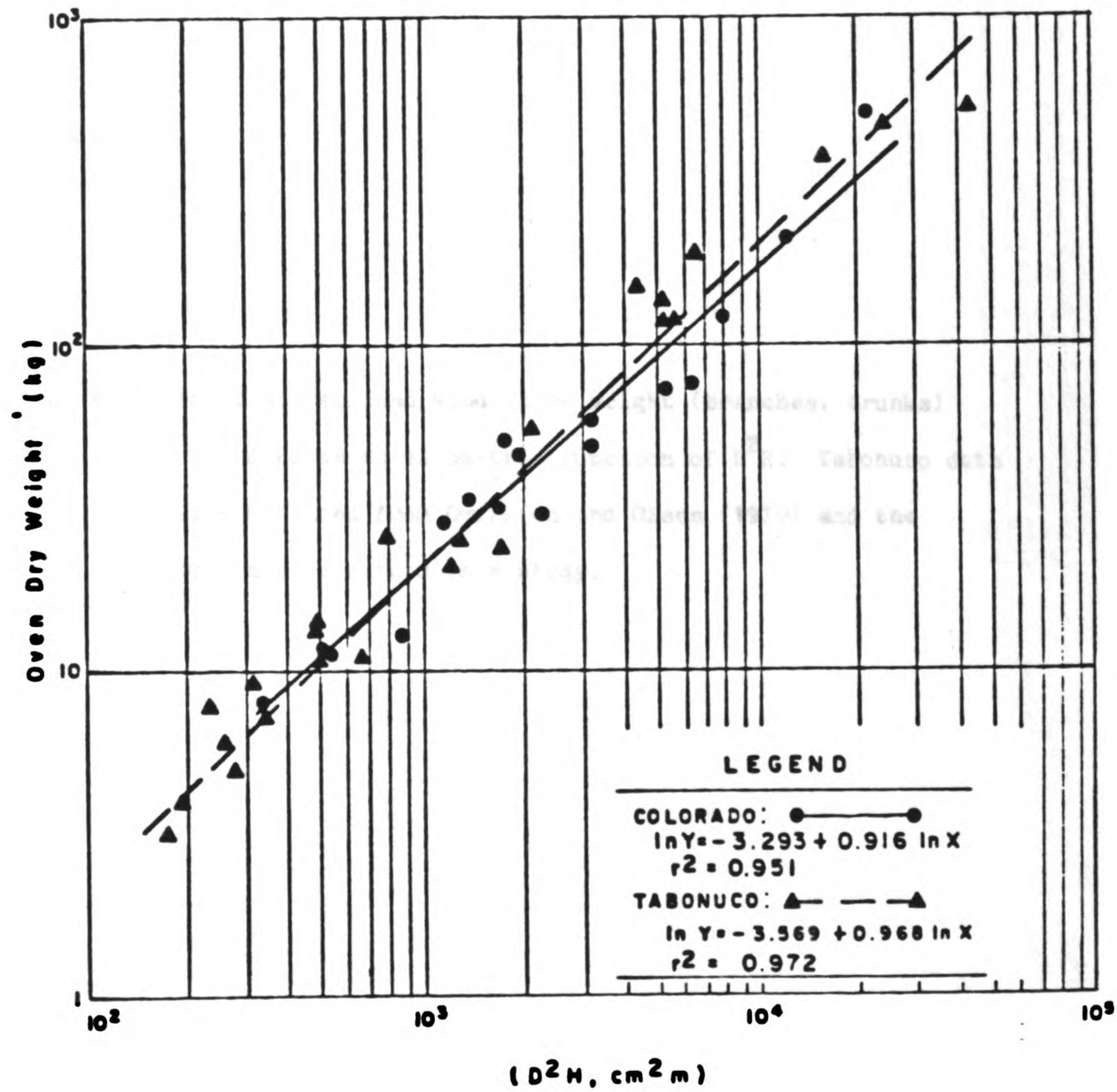

Oven Dry Weight (kg)
10^3
10^2
10
1
10^2
10^3
10^4
10^5
(D^2H, cm^2m)
LEGEND
COLORADO:
lnY = - 3.293 + 0.916 lnX
r^2 = 0.951
TABONUCO:
ln Y = - 3.569 + 0.968 ln X
r^2 = 0.972

Figure 45

Figure 46. Total aboveground woody tree weight (branches, trunks) expressed as an allometric function of D^2H. Tabonuco data were obtained from Ovington and Olson (1970) and the colorado data from this study.

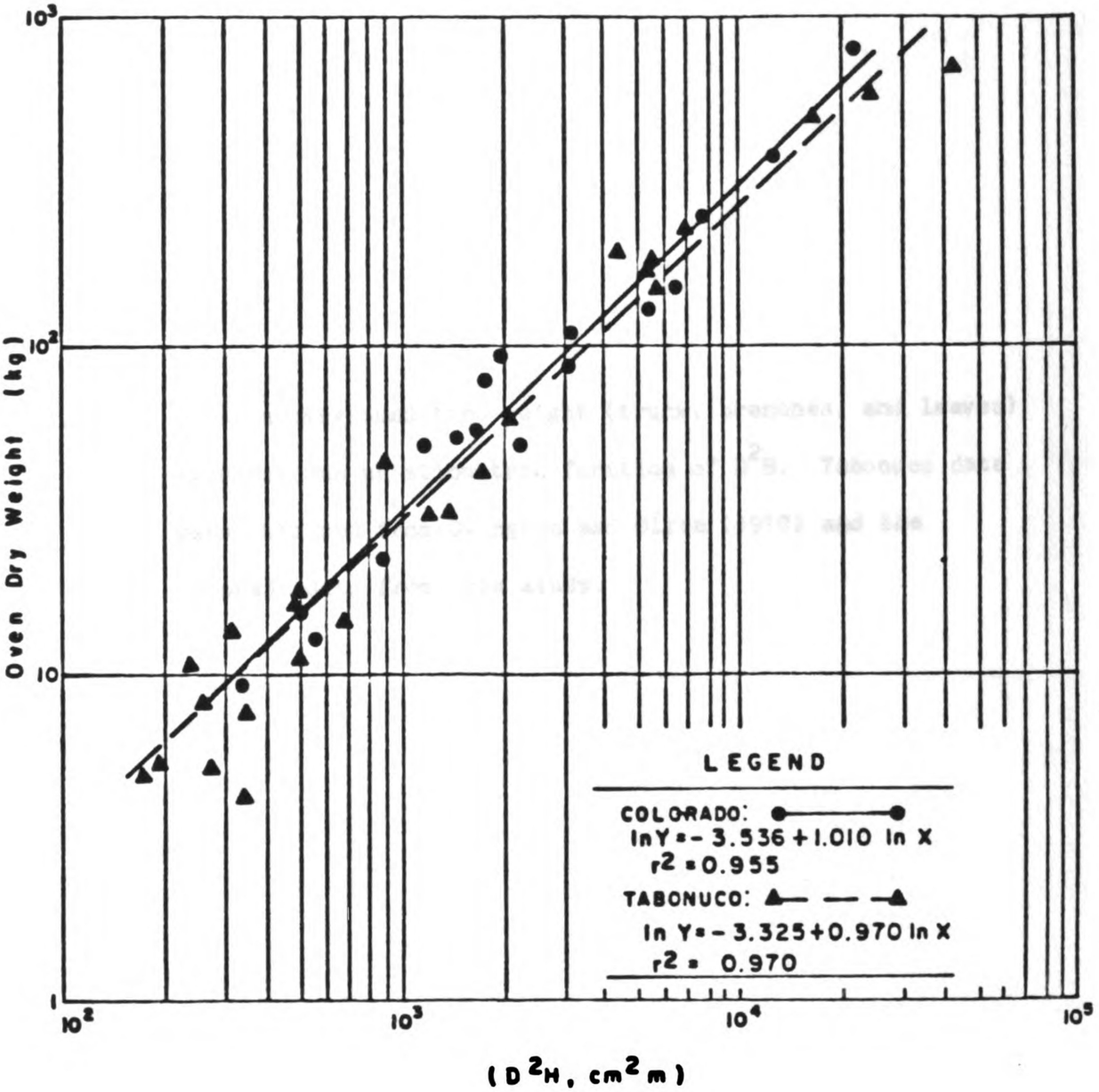

Oven Dry Weight (kg)
10^3
10^2
10
1
10^2
10^3
10^4
10^5
$(D^2H, cm^2 m)$
LEGEND
COLORADO:
$\ln Y = -3.536 + 1.010 \ln X$
$r^2 = 0.955$
TABONUCO:
$\ln Y = -3.325 + 0.970 \ln X$
$r^2 = 0.970$

Figure 46

Figure 47. Total aboveground tree weight (trunk, branches, and leaves) expressed as an allometric function of D^2H. Tabonuco data were obtained from Ovington and Olson (1970) and the colorado data from this study.

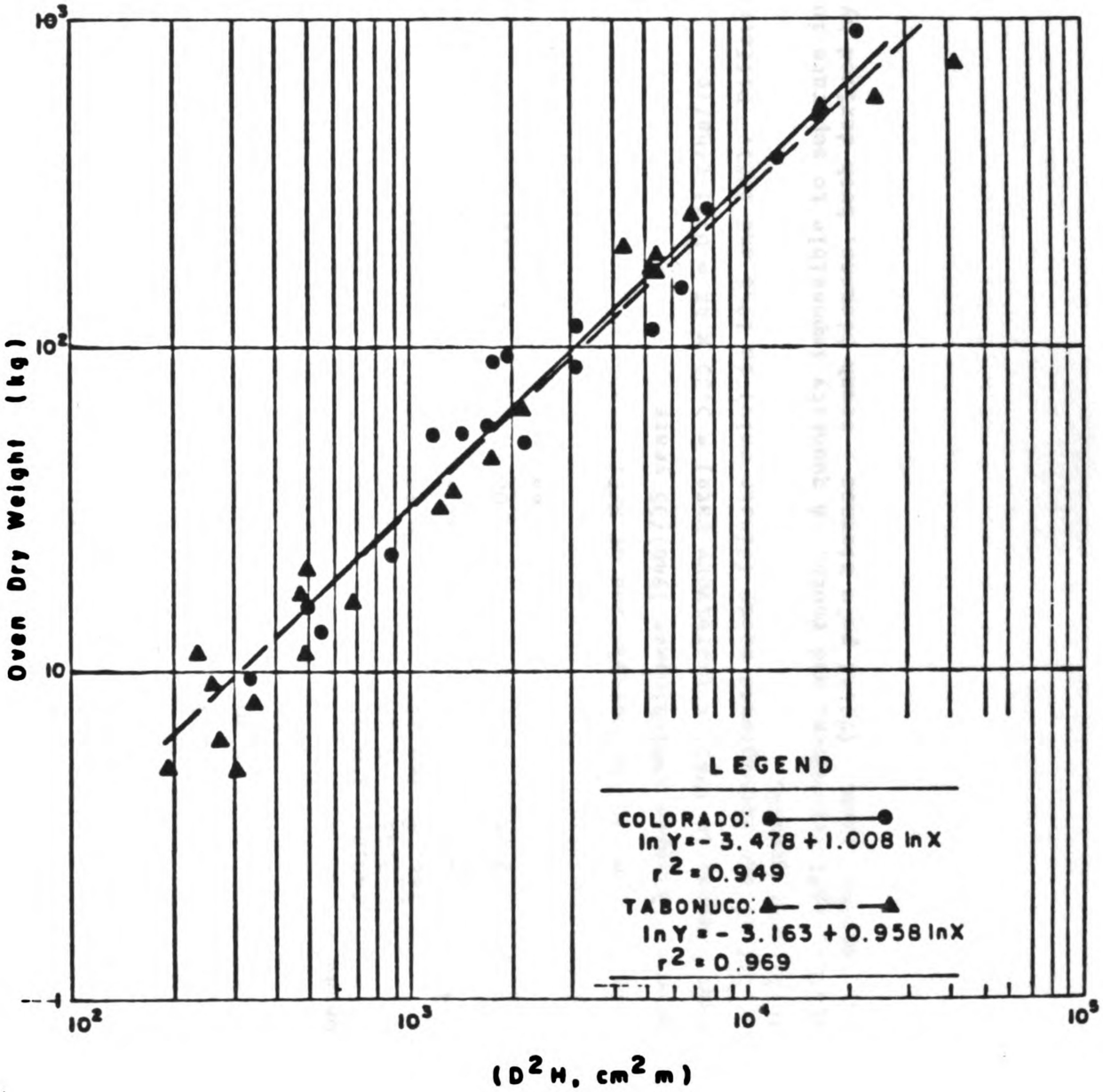

Oven Dry Weight (kg)
10^3
10^2
10
1
10^2
10^3
10^4
10^5
$(D^2H, cm^2 m)$
LEGEND
COLORADO:
ln Y = - 3.478 + 1.008 ln X
$r^2 = 0.949$
TABONUCO:
ln Y = - 3.163 + 0.958 ln X
$r^2 = 0.969$

Figure 47

Table 20. Detailed calculation of net primary productivity (NPP) for the colorado forest.

Factor	Year 1946	Year 1981	NPP[1] t/ha/yr	% of Total NPP
	----t/ha----			
Leaves[2]	4.75	5.35	0.02	0.26
Litterfall	----	6.80	6.80	86.85
Herbivory[3]	----	0.21	0.21	2.68
Aboveground woody[2]				
(dicots)	140.84	158.81	----	----
(palms)	3.44	5.43	----	----
Subtotal	144.28	164.24	0.57	7.27
Roots (dicots)[4]	42.25	47.64	0.15	1.92
Palm residual[5]	0.88	3.78	0.08	1.02
Total	------	------	7.83	100.00

[1] Independent values used in the calculation of NPP.

[2] NPP calculation: (Biomass 1981-biomass 1946)/35 years

[3] (Standing leaf biomass in 1981) x (herbivory rate) = 5.35 x 4% = 0.21 t/ha/yr.

[4] Estimated as 30% of the aboveground woody (dicots only) in 1946 and 1981. Differences divided by 35 years yields root growth.

[5] Palm leaf stalks, inflorescences, and roots. A quantity impossible to separate into other compartments. Derived from: (total palm biomass - trunk biomass, both derived by equations)/35 years.

Figure 48. Mean annual organic matter (O.M.) budget for two plots of 0.40 ha in size in the colorado forest.

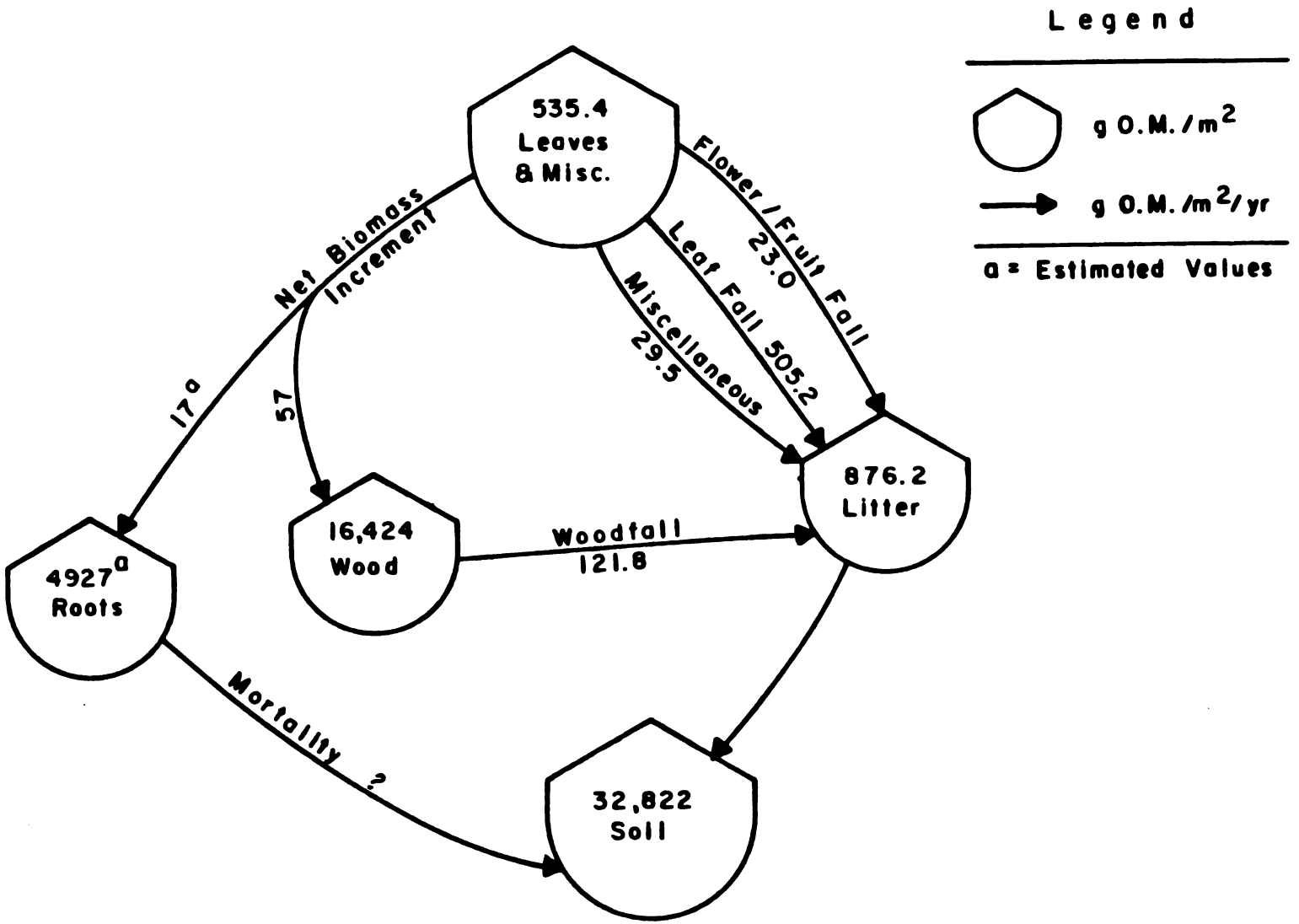

Legend
g O.M./m²
g O.M./m²/yr
a = Estimated Values
535.4
Leaves
& Misc.
Net Biomass
Increment
17ª
57
Miscellaneous
29.5
Leaf Fall 505.2
Flower / Fruit Fall
23.0
876.2
Litter
16,424
Wood
Woodfall
121.8
4927ª
Roots
Mortality ?
32,822
Soil

Figure 48

DISCUSSION

Forest structure and dynamics, including NPP, are related. The assessment of biomass increment in tropical regions is usually based on two successive estimates of total forest biomass made at the beginning and the end of the study period. Likewise, herbivory rates are related to leaf characteristics, and litterfall, the major component of NPP, reflects the entire aboveground structure of the forest. For these reasons, trends in forest structure are considered along with those of forest dynamics over the 600 m elevational gradient in the Luquillo Mountains.

Forest Structure

The number of trees per unit of land area and the weight of leaves per unit of leaf surface increase (the specific leaf area decreases) with elevation in the Luquillo Mountains (Table 21). The first trend is due to the greater number of smaller trees found at higher elevation. The second trend is because of a change in leaf structure with elevation. In general, montane leaves are smaller, have greater outer epidermal wall and lamina thickness, and have a lower non-palisade to palisade ratio (Tanner and Kapos 1982).

In contrast, canopy height, typical diameter range, forest volume and biomass, leaf area index and species richness, all decline with elevation. The fact that there is a greater reduction in forest canopy height than in aboveground biomass in montane forests was attributed to

Table 21. Comparison of stand structure for four forests within the Luquillo Mountains.

Structural Feature	Subtropical wet forest (Tabonuco)	Lower montane wet forest (Palm)	Lower montane wet forest (Colorado)	Lower montane rain forest (Dwarf)
Trees/ha	1750[a,b]	1620[a] (3050)[c]	1850	21,900[d]
Canopy height (m)	20-30[e]	17[e]	8-20[e]	3-5[e]
Typical dbh range (cm)	4-50[e]	4-30[e]	4-30[e]	4-15[e]
Basal area (m^2/ha)	40-45[a]	30[a] (42)[c]	40	45-65[d]
Aboveground volume (m^3/ha)	350[a,f]	210[a]	220	120[g]
Aboveground woody biomass (t/ha)	190[f]	174[c]	130	80[g]
Leaf biomass (t/ha)	7.9[f]	25.1[c]	5.8	2.9[g]
Leaf area index (m^2/m^2)	6-7[h]	3.3[c]	3-5	3-3.5[i]
Specific leaf area (cm^2/g)[1]	127[j]	- - -	91	47[g]
Total tree species	170[e]	50[e]	90[e]	40[e]
Tree species/ha	50[e]	30[e]	40[e]	15[e]
Soil organic matter (t/ha)	420[k]	316[l]	328[m]	550[n]

[1]Unweighted mean for species sampled, palm excluded.

Table 21 (continued).

[a]Weaver 1983, ≥ 4 cm in diameter

[b]Crow 1980, ≥ 4 cm in diameter

[c]Frangi and Lugo 1985, ≥ 1 cm in diameter

[d]Weaver 1972, ≥ 4 cm in diameter

[e]Several studies (Wadsworth 1950; Weaver 1983; Woodbury, personal communication)

[f]Ovington and Olson 1970

[g]Medina et al. 1981

[h]Odum 1970

[i]Benedict 1976

[j]Odum 1970, simple mean of 45 species

[k]Odum 1970, top 25 cm

[l]Frangi and Lugo 1985, top 100 cm

[m]Top 50 cm

[n]Figure 31, Part II, mean of 3 samples at 960 m elevation

the interaction of a decrease in canopy height with an increase in basal area (Edwards and Grubb 1977).

Comparisons of soil organic matter are more difficult because sampling was done at different depths (Table 21). The mean for the top 25 cm in tabonuco forest was 420 t/ha while those in the palm brake to 100 cm depth and the colorado forest to 50 cm depth were 316 and 328 t/ha, respectively. The mean for three values at highest elevation for colorado forest near 960 m, essentially at the border of dwarf forest, was about 550 t/ha (Fig. 31, Part II). Earlier studies (Lyford 1969) showed from 10 to 20% organic matter in dwarf forest soils, estimates corroborated for the sites at highest elevations in this study (Fig. 30, Part II).

Forest biomass equations

Leaf biomass for small stems in the tabonuco forest is higher than that of small stems in the colorado forest (Fig. 43). For larger trees, the leaf biomass estimates converge. Leaf biomass is related to many factors, among them the leaf area index, tree growth patterns, and the average leaf dry weight per unit area of leaf surface (Table 21). The most common large trees in the tabonuco forest regression were Dacryodes excelsa with an average dry weight for leaves of 162 g/m^2 (Odum 1970). The largest trees in colorado forest were Cyrilla racemiflora, Micropholis garciniaefolia, and M. chrysophylloides with average dry weights for leaves of 177, 206 and 172 g/m^2, respectively, all of which exceed the dry weight of Dacryodes leaves (Table 17). Moreover, Dacryodes frequently has a low crown-to-bole ratio and has unbranched boles for several meters while both species of Micropholis are shade tolerant, tend to branch low,

and bear leaves throughout the crown. These leaf and branching characteristics account for the convergence of the regression lines.

Branch biomass in the colorado forest is greater than branch biomass in the tabonuco forest, in particular, for larger trees (Fig. 44). Earlier accounts of this forest (Wadsworth 1951) described the trees as dense and 'branchy.' In comparison, numerous stems in the tabonuco forest, particularly in the intermediate crown class, are tall and slender with comparatively small crowns concentrated at the tops of the trees.

Trunk weight is greater in tabonuco forest than in colorado forest for larger trees although the converse is true for very small stems (Fig. 45). The average specific gravity of the species used in both regressions was 0.6 g/cm^3 with a range from 0.45 to 0.82 in the tabonuco forest and from 0.53 to 0.70 in the colorado forest. However, despite the overall similarities, Dacryodes, a tall, straight tabonuco forest dominant, was the only tree greater than 30 cm in diameter in the tabonuco regression. The proportionately greater trunk volumes of these large trees probably account for the trends.

Total aboveground woody biomass (Fig. 46) and the total aboveground biomass (Fig. 47) regressions for both forests are very similar. The reason for their similarity is due to the compensating effects of greater branch biomass in the colorado forest and greater trunk biomass in the tabonuco forest for trees of the same size class.

Forest Dynamics and Productivity

Dynamic features of the colorado forest are compared with other forest formations within the Luquillo Mountains in Table 22. Mortality rates in the palm and tabonuco plots measured during 30 years exceeded ingrowth while in the colorado plots measured during 35 years they were equal. These trends probably reflected differences in disturbance and recovery responses to past hurricanes. In the lower forests, trees are larger and openings caused by treefall provided "growing space." Competition among numerous fast growing stems caused greater mortality. In the higher forests, trees are smaller and damage was mainly by breakage creating smaller openings. Tree growth was slower. Moreover, a considerable proportion of the ingrowth was by palms which are shade tolerant and require less growing space to mature. Because of the short duration of measurement in the dwarf forest (Weaver 1983), comparable records were not available.

Loose litter tends to increase with elevation in the Luquillo Mountains, but there are notable exceptions in the dwarf forest at the summits and in the palm forest. Comparison with the only other collections made along an elevational gradient on a single tropical mountain, Khao Luang in Thailand, also showed an increase in loose litter with elevation except at the summit (Fig. 49A). In contrast, an increase in elevation in the Luquillo Mountains leads to a decline in litterfall with the notable exception of the palm forest (Fig. 49 B). A similar decline in litterfall is evident over an elevational gradient on Gunung Mulu in Sarawak.

Table 22. Comparison of stand dynamics for four forests within the Luquillo Mountains.

Dynamic feature	Subtropical wet forest (Tabonuco)	Lower montane wet forest (Palm)	Lower montane wet forest (Colorado)	Lower montane forest (Dwarf)
Ingrowth (stems/ha/yr)	21[a]	12[a]	20	---
Mortality (stems/ha/yr)	32[a]	23[a]	20	---
Litterfall (t/ha/yr)	8.61[b]	8.8[c]	6.8	3.1[d]
Leaf	4.94	6.26	5.05	2.45
Wood	1.38	0.86	1.22	---
Flower	0.17	0.18	(0.23)	(0.65)
Fruit	0.34	1.14		
Miscellaneous	1.78	0.36	0.30	---
Loose litter (t/ha)	6.0[e]	5.4[c]	8.76	4.34[d]
Standing herbivory (%)	7[g]	---	5	---
Herbivory rate (t/ha/yr)	0.38	---	0.25	0.13[d,f]
Litter turnover[1]	1.20[b,e]	1.62[c]	0.78	0.70[d]
Mean dbh growth (cm/yr)	0.15[h]	0.23[a]	0.10[a]	0.03[a,d]
Volume growth[2] (m^3/ha/yr)	2.26[i]	---	0.93	0.70[d]
Biomass growth[2] (t/ha/yr)	2.5[j]	3.3[c]	0.57	0.45[d]
NPP (t/ha/yr)				
Total aboveground	10.5	19.5[c]	7.66	3.70[d]
Root	0.75[k]	1.0[k]	0.17[k]	0.13[k]
Total (aboveground + roots)	11.3[l]	20.5[l]	7.83[m]	3.83[l]

Table 22 (continued)

[1]Litterfall/loose litter

[2]Total aboveground woody

[a]Weaver 1983; plots at 450 m elevation and measured for 30 years

[b]Reagan et al. 1982

[c]Frangi and Lugo 1985; plots at 750 m elevation and measured for 3 years

[d]Weaver et al. 1986; plots at 1000 m elevation

[e]Odum 1970

[f]Benedict 1976

[g]Odum and Ruiz-Reyes 1970

[h]Wadsworth 1951, 1952

[i]Briscoe and Wadsworth 1970; results from several plots

[j]Crow 1980

[k]Estimated root NPP = 0.3 x aboveground NPP (Murphy 1975)

[l]Total aboveground NPP + estimated root NPP

[m]From Table 20

Figure 49. A - Estimates of loose litter storage in montane tropical forests over an elevation gradient on the same mountain: dots - Khao (Mt.) Luang, peninsular Thailand (Yoda and Kira 1969); triangles - Luquillo Mountains, Puerto Rico (Table 22). Circled triangle, palm forest.

B - Estimates of litterfall in montane tropical forests over an elevation gradient on the same mountain; dots - Gunung Mulu, Sarawak (Proctor et al. 1983); triangles - Luquillo Mountains, Puerto Rico (Table 22). Circled triangle, palm forest.

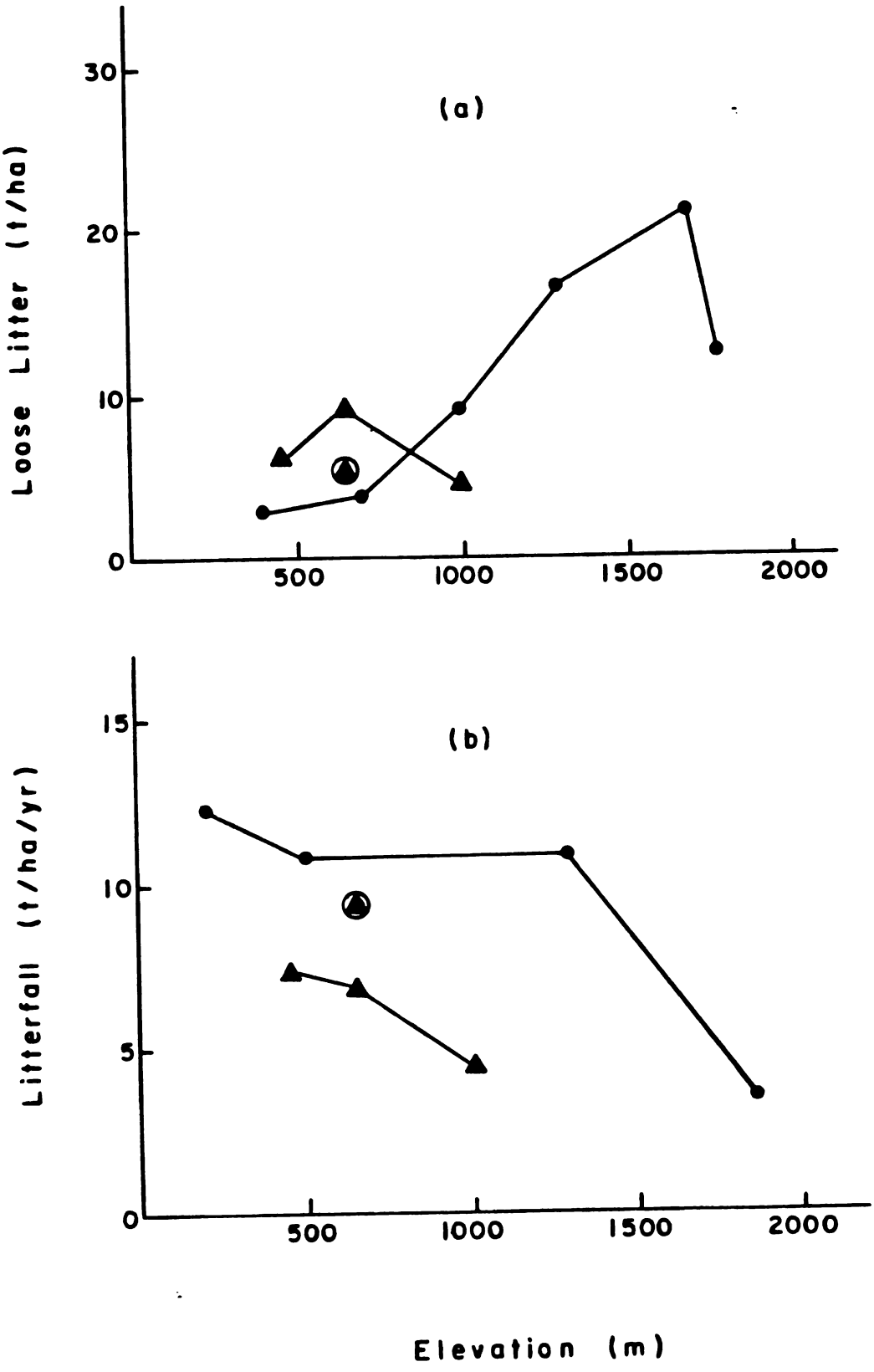

(a)
Loose Litter (t/ha)
30
20
10
0
500
1000
1500
2000
(b)
Litterfall (t/ha/yr)
15
10
5
0
500
1000
1500
2000
Elevation (m)

Figure 49

A gradual increase in elevation is accompanied by cooler, wetter, and cloudier environmental conditions where the breakdown of organic matter in the loose litter is slowed (Grubb 1971; Edwards 1977). The noticeable dip in loose litter at the summits is partially due to the smaller size, and lower productivity of the dwarf forest. It may also reflect some loss, or distribution, of litterfall to the leeward by winds in the exposed areas (Welbourn et al. 1981). The lower loose litter concentrations in the palm forest, in this instance, situated in a valley adjacent to a stream, reflects the low specific gravity of palm tissue at 0.26 g/cm^3 as well as frequent flushing of the forest floor by floods removing organic matter from the soil profile (Frangi and Lugo 1985).

The reduction of litterfall production with an increase in elevation correlates with a decline in tree size over the same gradient (Table 21). The exceptionally high litterfall production in the palm forest was attributed to the prevalence of palm which has a rapid turnover of large leaves combined with comparatively little wood production, due to the lack of secondary tissue growth (Frangi and Lugo 1985).

Litterfall and loose litter accumulations in the colorado forest also demonstrate temporal variation. The higher leaf and total litterfall observed between April and June occur just after the comparatively drier months of January through March (Fig. 2, General Introduction). They also coincide with a period of higher average wind velocity. January through March have average wind velocities between 6 and 11 km/hr while April though June have average wind velocities between 14 and 19 km/hr (Briscoe 1966). The unusually high value for leaf and total litterfall in March of 1981 may be the result of high winds over the span of a day or two.

Loose litter accumulations are notably less during the first three months of the year, a period that coincides with lower rainfall, lower average wind velocity, and less cloud cover. This period characterized by less litterfall input and generally drier and clearer conditions may foster greater biotic activity and facilitate the decomposition of organic matter. Elsewhere, the annual variation in litter accumulations has been considerable with climatic events accounting for much of it (Spain 1984).

An increase in the leafy portion of litterfall from 57.3 percent of the total litterfall in tabonuco forest through 74.3 percent in the colorado forest to 79 percent in the dwarf forest is evident (Table 22). This positive correlation of the percentage of leaf in litterfall with altitude has been observed elsewhere (Spain 1984). It appears related to the decrease in specific leaf area from tabonuco through colorado to dwarf forest combined with a decrease in the aboveground woody biomass (Table 21). Again, the palm forest is an exception because of the extremely large size and weight of the leaves, and generally low woody production. It should be pointed out, however, that similar trends were not apparent on Gunung Mulu in Sarawak (Proctor et al. 1983) where the leafy portion of litterfall varied between 52 and 64 percent over an elevational gradient, but did not display elevational trends.

An earlier summary of production of total litter for 226 forests of the world yielded estimates between 0.22 and 4.19 $g/m^2/day$, with cool temperate forests averaging about 0.93 $g/m^2/day$ (Bray and Gorham 1964). It also indicated that year to year variation in tropical rainforest litterfall was low in comparison to other forest types, that both total and leaf litterfall were significantly and negatively related to altitude and latitude, and that leaf litterfall was significantly related to mean

rainfall. A recent summary of mesic forests with a continuous canopy cover (Jordan and Murphy 1978) showed that the rate of litter production decreases in direct proportion to the decrease in light available during the growing season along a worldwide gradient. Similarly, within the Luquillo Mountains, a gradient exists. Between El Verde and Pico del Oeste (Pico del Oeste is located near Pico del Este and has similar climate and vegetation), a distance of 8 km horizontally and 550 m vertically, litterfall decreased by about 30 percent whereas solar insolation between the north coast and Pico del Oeste declined by about 40 percent (Briscoe 1966; Baynton 1968).

Comparison of colorado litterfall values with predictive equations showed excellent correlation of total annual litterfall with the temperature/precipitation ratio proposed by Brown and Lugo (1982). A previosuly suggested relationship between the common log of aboveground NPP vs. the common log actual evapotransportation (Rosenzweig 1968) overestimated litterfall. This discrepancy may be due to the inefficiency of actual evapotranspiration as a measure of productivity in very humid tropical environments with frequent cloud cover, generally cooler leaf temperatures, and frequent heavy rainfalls. Much of the moisture evapotranspired in wet forests follows the evaporation route because many of the rainfalls are light (Wadsworth 1948), or is lost as runoff during heavy rainfalls.

Litter turnover rate appears to decrease with elevation in the Luquillo Mountains, reflecting the cooler temperature, greater rainfall, and slower breakdown of organic matter. Litter turnover varies among forest types, but in the moist tropics, it usually takes one year (Olson 1963; Golley et al. 1975).

Standing herbivory and herbivory rate records are incomplete and thus difficult to compare. It appears, however, that both may decline slightly with elevation. It has been suggested that ecosystems with high NPP may have higher herbivory rates because of greater amounts of available food and more favorable climatic conditions for insects (Benedict 1977). In Panama, mature leaves of pioneer species were eaten three to 10 times more rapidly than mature leaves of 'persistent' species (Coley 1982). Growth of these species is usually faster, and less energy is expended on defensive mechanisms and, therefore, the leaves are more palatable. Moreover, with higher elevations in the Luquillo Mountains, the leaves become smaller and thicker, and may be more difficult for insects to consume. Also the climatic limits for insect infestation may be approached in the dwarf and other high elevation forests. It is probable that short leaf lifespan, high NPP, low energy investment in leaves, high palatability, and high herbivory rates are all related (Benedict 1976).

Diameter, volume and biomass increment all decrease with elevation as do aboveground NPP and total NPP estimates. The unique exception is that of the palm plot with a comparatively high value for each category. Wetland ecosystems have been shown to have high NPP rates (Brown and Lugo 1982). In general, the NPP rates in the forests of the Luquillo Mountains are low in comparison to other tropical moist, wet and rain forests (Murphy 1975; Medina and Klinge 1982; Brown and Lugo 1982), most of which fall in the range of 5 to 32 t/ha/yr. Environments characterized by high precipitation and humidity, intense soil leaching and generally lower temperatures are those in which productivity may be limited (Murphy 1975).

The Luquillo Forest Continuum

The structural and floristic impoverishment of forests with an increase in elevation on small, wet, tropical mountains, such as the isolated, coastal mountains in the West Indies, has been attributed to the Massenerhebung Effect (Richards 1966; Grubb 1971), a phenomenon first recorded in the European Alps. Many investigators have forwarded ideas to account for this phenomenon in Puerto Rico and elsewhere, among them, saturated soils and reduced root respiration (Holdridge 1967), impeded soil drainage (Wadsworth and Bonnet 1951), physiological drought (Beard 1944), high winds in summit areas (Roy O. Woodbury, pers. comm.), leaching of the soils combined with high fog incidence (Baynton 1969), reduced transpiration rates (Beard 1944; Odum 1968; Leigh 1975), fog, high soil water content and reduced mineralization of organic matter (Grubb 1971), and shallow soils (Gleason and Cook 1926).

The soils are not shallow in most areas of the Luquillo Mountains so this explanation to account for a decline in size and species richness of the forests does not seem satisfactory. Soil leaching has also been questioned. The high cation exchange capacity characteristic of high elevation soils rich in organic matter should hold nutrients so that they would not be rapidly leached (Lyford 1971). Physiological drought, or "the difficulty of drawing water from the soil coupled with increasing atmospheric power of evaporation from the leaves" (Beard 1941) is an idea that seems contrary to recent observations. Transpiration rates have been measured (Gates 1969; Weaver et al. 1973; Medina et al. 1981) and are generally low. With the frequent cloud cover in the summit areas, relative humidity is high, saturation pressure deficits are low (Odum 1968), and there is a positive addition of cloud water to the moisture

balance (Kerfoot 1968; Baynton 1969; Weaver 1972). None of these observations supports physiological drought. Yet the leaves are distinctly coriaceous and xeromorphic in appearance, and presumably adapted to occasional high winds and pronounced changes in environmental conditions characterized by cloud cover one moment and intensive solar isolation another.

Saturated soils and impeded drainage have been observed (Wadsworth and Bonnet 1951), and such conditions would influence root aeration. Roots in the higher elevation forests are largely superficial (Wadsworth 1951; Lyford 1971) and spreading on the forest floor. Recent work with roots of food crops like tomatoes has shown that these plants decrease water use when oxygen is excluded from the root zone (Sojka and Stozy 1981). As the diffusion rate of oxygen in the soil decreases, the stomates close, independent of other factors such as soil water or light intensity.

Forests at higher elevation in the Luquillo Mountains were called the "hurricane hardwood" type (Murphy 1916) suggesting that wind might play a role in their growth and survival. Specific reference was made to the contorted trees characteristic of the summits. Average wind velocities for El Yunque peak at 1050 m in elevation do not exceed 19 km/hr in any month (Briscoe 1966) although gusts of 100 km/hr were observed on El Toro peak at 1065 m during a period of normal winds elsewhere on the island (Wadsworth 1948). Hurricanes have had an influence on the species composition and dynamics of the colorado forest (Part I). Despite this influence, observed windfalls at higher elevations are rare, and gaps in the forest are not common. Indirect evidence of this is also available in

that pioneer tree species are notably lacking in the dwarf forest (Byer and Weaver 1977) and are not abundant in the colorado forest.

Among the possible adaptations to minimize the effects of hurricane damage in higher elevation forests is the development of denser woods. On windy sites, tree species with dense wood should experience lower rates of mortality, windthrow and snapping than less dense species (Lawton 1984). The mean specific gravity of trees considered to be climax for the upper forests average about 0.65 g/cm^3 in the dwarf forest and about 0.60 g/cm^3 in the colorado forest, the latter figure applying to slopes and ridges. In valleys, the average specific gravity is lower. Consequently, growth would be slower due partly to the investment in wood density and partly, perhaps, to the demands for nutrients to produce the denser wood.

Another factor related to high winds is the energetic cost of replacing foliage after storms. Direct observation of the effects of Hurricane Eloise of September 1975 showed an eight percent defoliation of the standing leaf area in the dwarf forest (Benedict 1976). Despite the fact that the trajectory of the storm was at a considerable distance from the island, the effects were noticed in the high elevation forests.

Relatively cool temperatures, frequency of fog and heavy rainfalls characterize the higher elevation forests, and interact to retard the mineralization of organic matter. It has been suggested that these environmental factors may effectively lower the elevational level at which shorter forest, mainly controlled by temperature, would occur (Grubb 1971, 1977; Weaver et al. 1986). Ascent of the Luquillo Mountains shows a gradual impoverishment of the forests both in stature and species composition. Indeed, the progressively cooler, wetter, and cloud-covered forests of higher elevations appear to constitute a stress environment for

trees, reflected in a continuum that is compressed into a narrow altitudinal range that extends from tabonuco forest at lower elevations to dwarf forest at the summits.

SUMMARY

A total net primary production (NPP) of 7.83 t/ha/yr was estimated for the colorado forest at 750 m elevation in the Luquillo Mountains of Puerto Rico. NPP was determined by summing litterfall (6.80 t/ha/yr), herbivory (0.21 t/ha/yr), and net biomass accrual above and below ground (0.82 t/ha/yr).

Several structural and dynamic components of the colorado forest were also estimated:

(1) a total leaf area index of 4.96 m^2/m^2 partitioned into aerial components of tree leaves (3.01) and epiphytes (0.30), and ground components of herbs and grasses (1.18) and bryophytes (0.47);

(2) a mean leaf weight for 17 dicotyledonous species of 0.67 g with a mean leaf area of 56.4 cm^2 (mesophyll size class) and a mean specific leasf area of 91.0 cm^2/g of leaf surface;

(3) an aboveground volume (trunks and branches) of 220 m^3/ha and aboveground woody biomass of 130 t/ha;

(4) an estimate of standing herbivory of 5.1 percent of the leaf area and herbivory rates of 4.0 percent of total leaf area per year, both on a forest-wide basis; and

(5) a mean litterfall rate of 680 $g/m^2/yr$ with a mean standing crop of 875 g/m^2 of litter and a turnover rate of 0.78 times per year.

Information on the structure and dynamics of other forest types in the Luquillo Mountains was compiled and compared with the results of this study to highlight the effects of a 600 m elevational gradient. Of the

structural features considered, the number of stems per hectare, basal area, and soil organic matter, all increased with an increase in elevation whereas canopy height, range of tree diameters, forest volume and biomass, leaf area index, specific leaf area, and species richness declined. Of the dynamic features studied, ingrowth and mortality of trees, litterfall, loose litter, standing herbivory and herbivory rates, litter turnover, growth in diameter, volume and biomass, aboveground woody NPP, and total NPP, all appeared to decline with an increase in elevation.

The structural and floristic impoverishment of the forest types with ascent, and their compression into a narrow altitudinal range, reflect the effects of numerous environmental factors among which the relatively cooler temperatures, frequency of fog, and heavier rainfalls interact to produce saturated soils and a retardation in the mineralization of organic matter.

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APPENDIX TABLES

Appendix Table 3 : Summary of biomass field data.

Species	Tree Dimensions		D^2H	Biomass-Dry Weight (kg)						
	dbh (cm)	ht (m)		Leaves	Branches <2.5 cm	Branches >2.5 cm	Branches Total	Trunk	Woody Above ground	Total Entire Tree
Cordia borinquensis	6.5	7.9	333.77	0.55	0.98	0.27	1.25	8.05	9.30	9.85
Cordia borinquensis	7.5	9.2	520.31	0.50	1.05	0.47	1.52	11.33	12.85	13.35
Croton poecilanthus	11.0	11.7	1421.75	3.44	7.45	9.52	16.97	34.74	51.71	55.15
Croton poecilanthus	16.1	12.2	3162.36	2.21	9.91	17.60	27.51	59.02	86.53	88.74
Croton poecilanthus	19.1	14.1	5143.82	4.46	7.66	23.68	31.34	75.48	106.82	111.28
Cyrilla racemiflora	9.8	9.1	878.77	0.61	2.09	7.56	9.65	13.03	22.68	23.29
Cyrilla racemiflora	12.8	10.1	1654.78	2.77	8.86	14.04	22.90	32.25	55.15	57.92
Cyrilla racemiflora	15.2	9.6	2217.98	0.28	3.68	16.17	19.85	30.49	50.34	50.62
Cyrilla racemiflora	23.4	11.7	6433.83	4.11	13.26	60.18	73.44	77.55	150.99	155.10
Cyrilla racemiflora	30.7	13.4	12629.37	10.27	32.82	130.18	163.00	218.11	381.11	391.38
Miconia tetrandra	15.6	12.9	3139.34	6.86	11.58	49.30	60.88	49.44	110.32	117.18
Micropholis garciniafolia	24.9	12.5	7750.12	9.83	14.32	111.36	125.68	125.92	251.60	261.43
Micropholis chrysophylloides	10.0	11.7	1170.00	3.50	13.57	7.49	21.06	29.61	50.67	54.17
Micropholis chrysophylloides	12.5	11.4	1781.25	12.41	17.55	8.78	26.33	52.99	79.32	91.73
Micropholis chrysophylloides	36.7	15.9	21415.55	43.91	84.87	278.31	363.18	519.72	882.90	926.81
Tabebuia rigida	7.7	8.4	498.03	0.26	3.28	0.95	4.23	11.67	15.90	16.16
Tabebuia rigida	14.6	9.1	1939.76	0.63	11.10	36.94	48.04	46.70	94.74	95.37

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