FOREST CHANGES AFTER HURRICANES IN PUERTO RICO'S LUQUILLO MOUNTAINS[1].

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Cyclones and hurricanes with 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 120km/hr, are plotted on a basin-wide map of the Caribbean, all islands are obscured by black ink (Neumann *et al.*, 1978).

Hurricanes commonly cause defoliation, breakage, and windthrow in forest (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 adequate sampling on permanent plots (Bormann and Likens 1979; Callahan 1984). Such monitoring in the neo-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. In the past, 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). This study is the first to provide a detailed analysis of all data sets for a specific forest.

In 1928, hurricane San Felipe, with maximum winds of 240 km/hr and 36 hours duration, passed over Puerto Rico southwest of the Luquillo Mountains, and in 1931 San Nicolas, with 140km/hr winds and 40 hours duration, pased just north of the island (Salivia 1972). The only precise data available on recovery after San Felipe dealt with the elapsed time before certain tree species refoliated at lower elevations in the Luquillo Mountains (Bates 1929). San Cipriano of 1932, with 200km/hr winds and more than 43cm of rainfall during 18 hours, passed directly over the Luquillo Mountains (Crow 1980). Although all storms had some effect on the colorado forest, especially San Cipriano, no field observations of damage were made. Considerable defoliation, windfall, stem breakage, and mortality, however, are normal consequences of hurricanes. A later hurricane, Santa Clara of 1956, crossed the island southwest of the Luquillo Mountains and caused only slight, localized damage within the Luquillo Forest (Wadsworth and Englerth 1959).

If the damage caused by San Cipriano was considerable, systematic changes in forest structure and composition should be evident over time. The existence of 7 permanent plots established in the colorado forest in 1946 and 1947 provided the basis for testing this hypothesis. A knowledge of the colorado forest's 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.

The Study Site

The 11,200ha Luquillo Experimental Forest of northeastern Puerto Rico (18°N, 66°W) is located in the Luquillo Mountains, an isolated range of resistant Cretaceous and Tertiary rocks (Mitchell 1954) that rise abruptly to 1075m only 8km from the ocean. The soils of the colorado forest are mainly clays and some silty clay loams, classified principally as ultisols and inceptisols. The soils are saturated most of the year and contain large amounts of organic matter (Wadsworth and Bonnet 1951).

The mountains' abrupt rise from the coast profoundly influences local climate. Rainfall increases from 2300mm/yr at 200m near the northern

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forest boundary (Crow and Weaver 1977) to 4600mm/yr at La Mina, in the colorado forest near 715m elevation (Wadsworth 1948). Rainfall averages 4450mm/yr on Pico del Este at 1050 m. The mean annual temperatures decline from 23°C to 19°C over the same gradient. Transpiration, evapotranspiration, and solar insolation decrease with altitude but cloud cover, fog, interception, relative humidity, and wind velocity increase (Baynton 1968; Briscoe 1966; Weaver 1972; Weaver et al., 1973).

Hurricanes in the Caribbean Basin occur mainly in the summer. September is the month of most frequent occurrence, followed by August and July (Salivia 1972). About 70 hurricanes have passed over Puerto Rico since the early 1700's (Fig. 1). Of these, 13 were A storms, those whose vortexes passed directly over the island with hurricane force winds. Ten were B storms, those whose vortexes may or may not have passed over the island, but only part of the island experienced hurricane force winds. Of the A storms, 4 had trajectories directly over the Luquillo Mountains. The last of these 4 was San Cipirano in 1932.

The Luquillo forest is divided into tabonuco forest (72%) that lies between 120 and 600m in elevation, colorado forest (25% that lies between 600 and 900m, and dwarf forest (3%) from 900 to 1075m (Wadsworth 1951). Tabonuco forest is Beard's (1944, 1949) lower montane rain forest and generally corresponds to Holdridge's (1967) subtropical wet forest. Colorado forest is Beard's montane rain forest and generally corresponds to Holdridge's lower montane wet forest. The dwarf forest is also called dwarf by Beard and is an atmospheric association in Holdridge's life zone system. The lack of an emergent story in all of the forests has been attributed to recurrent hurricanes (Odum 1970).

The colorado forest, the subject of this study, is lower montane wet forest (Ewel and Whitmore 1973) and is characterized by 2 strata, evergreen foliage and an abundance of superficial roots (Wadsworth 1949). A representative sample of trees greater ≧10cm in diameter on 4ha contained 60 species averaging 830 stems/ha, 95% of which were < 45cm in diameter (Wadsworth 1951). Forests similar in physiognomy to the colorado forest, according to the Holdridge system, occupy about 100,000 km² and constitute a little over 2% of the Caribbean and

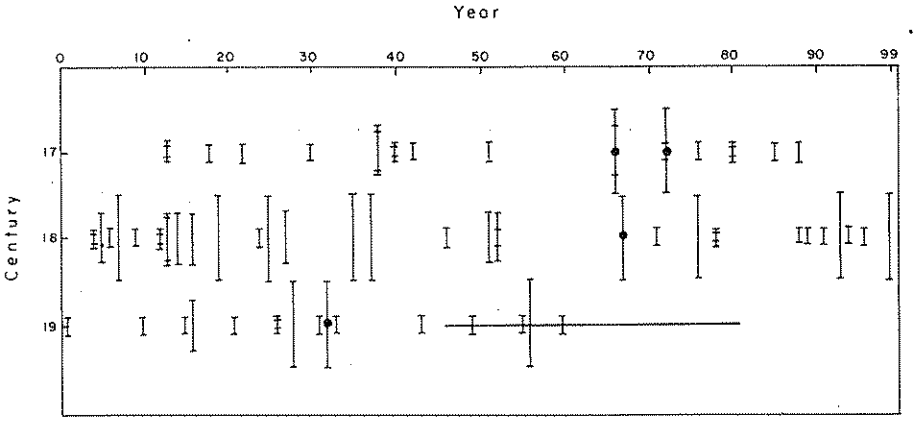

Fig. 1. Hurricane record for Puerto Rico from 1700 to 1970 (Salivia 1972). Long vertical I bar - type A storm (vortex of hurricane passes directly over the island with hurricane force winds); intermediate vertical I bar - type B storm (vortex of hurricane may or may not have passed over the island; but 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 Forests; black circle - type A storms that directly hit the Luquillo Forest.

Central and South American region (Weaver 1987). In addition, several islands of the Lesser Antilles not yet classified in 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. Of the 225 tree species native to the forests of the Luquillo Mountains, 41% are also found on continental areas (South America, Central America, Mexico, and F'orida), 28% are found in the West Indies but not on the continents, and 31% are endemic to Puerto Rico (Little and Woodbury 1976).

Methods

The 7 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 750m in elevation, occasionally flooded in riparian areas. Four plots, located on s'ope topography ranging from 700 to 900m in elevation, had better drained soils.

All trees ≧4.1cm at breast height (dbh, or 1.4cm above the ground) were measured to the nearest 0.1 inch (0.25cm). Height was estimated visually to the nearest 0.5m and checked occasionally with a hand level. Crown classes were recorded as dominant, codominant, intermediate or suppressed (Baker 1950). After the initial survey, some of the plots were visited in 1951, 1956, and 1976, but neither tree nor stand measurements were complete. Species were tallied, but height was not recorded. Moreover, ingrowth by recruitment, or by trees that grew into the minimum diameter class, was partially recorded: New trees, however, were never tagged.

Detailed tree measurements on all plots were made again in 1981 when all trees were retagged. Diameter was measured to the nearest 0.1cm and height was estimated by an optical rangefinder to the nearest 0.1m. 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. There were 5,271 trees recorded in 1946-47 and 5,266 trees recorded in 1981 for all plots combined.

Basal area, volume, and biomass were determined for each plot. The heights required for calculation of volume and biomass of mortality recorded the years 1951, 1956 and 1976 were estimated by a height vs. diameter curve. This curve was based on data for dicot species from other plots where diameter 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

TABLE I

RELATIVE DENSITY [1], RELATIVE FREQUENCY [2], RELATIVE BASAL AREA [3], AND PERCENT IMPORTANCE [4] FOR MAJOR TREE SPECIES ON PERMANENT PLOTS IN THE COLORADO FOREST IN 1946 AND 1981. SPECIES ARE RANGED FROM HIGHEST TO LOWEST PERCENT IMPORTANCE BASED ON THE 1946 VALUES

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	0.024	0.297	11.9	0.034	0.024	0.168	7.5
Micropholis garciniafolia	0.116	0.024	0.176	10.6	0.116	0.024	0.218	11.9
Calycogonium squamulosum	0.157	0.024	0.113	9.9	0.164	0.024	0.094	9.4
Prestoea montana	0.124	0.024	0.107	8.4	0.128	0.024	0.109	8.8
Micropholis chrysophylloides	0.072	0.020	0.049	4.7	0.089	0.020	0.083	6.5
Croton poecilanthus	0.084	0.024	0.031	4.7	0.091	0.024	0.057	5.7
Ocotea spathulata	0.052	0.024	0.031	3.5	0.029	0.024	0.014	2.2
Magnolia splendens	0.026	0.024	0.046	3.2	0.017	0.024	0.044	2.8
Haenianthus salicifolius	0.028	0.024	0.028	2.7	0.039	0.024	0.043	3.5
Cordia borinquensis	0.035	0.020	0.010	2.2	0.046	0.024	0.013	2.7
Daphnopsis philippiana	0.033	0.024	0.004	2.0	0.040	0.024	0.005	2.3
Tabebuia rigida	0.013	0.024	0.011	1.6	0.017	0.024	0.014	1.9
Miconia laevigata	0.019	0.024	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
Ditta myricoides	0.016	0.024	0.003	1.4	0.019	0.024	0.005	1.6
Hedyosmum arborescens	0.019	0.020	0.002	1.4	0.002	0.017	0.001	0.7
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	0.024	0.004	1.1	0.008	0.024	0.005	1.2
Dacryodes excelsa	0.005	0.014	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	0.024	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 prasina	0.006	0.017	0.005	0.9	0.001	0.014	0.001	0.6
Myrcia splendens	0.005	0.017	0.001	0.8	0.003	0.014	0.001	0.6
Linociera dominguensis	0.005	0.017	0.003	0.8	0.002	0.010	0.004	0.6
Myrcia deflexa	0.001	0.017	0.002	0.8	0.001	0.010	0.000	0.4
Ternstroemia luquillensis	0.006	0.014	0.003	0.8	0.002	0.014	0.000	0.5
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
Subtotals	0.937	0.600	0.977	84.3	0.925	0.601	0.965	83.2
Remaining species	0.063	0.387	0.021	15.7	0.075	0.399	0.035	16.8
Totals	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.

test (Steel and Torrie 1960). Dicot tree volumes, icluding branches ≥2.5cm in diameter, were determined using an existing equation derived in English units or the construction of volume tables in the colorado forest (Wadsworth 1949). 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 14.8% and an aggregate difference of 1.1% (Wadsworth 1949). These are mensurational measures (Chapman and Meyer 1949). The mean deviation is equal to approximately 80% of the standard deviation and the aggregate difference indicates goodness of fit to sample data to the developed volume table charts. Above-ground woody biomass estimates were derived by multiplying individual tree volumes by their respective specific gravities. The specific gravities 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 0.6g/cm³, the weighted average specific gravity for the forest. The stem volumes of palms 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.

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 obtain species trends. Percent similarity, the summation of the lowest percentages (percentage = the number of individuals per species/ total number of individual per plot) by species within each pair of stands being compared, was used to estimate community similarity among plots. A species count was also made for each plot.

Trends in species composition were studied by determining the survival rates and changes in stem numbers and basal areas of 10 "indicator"

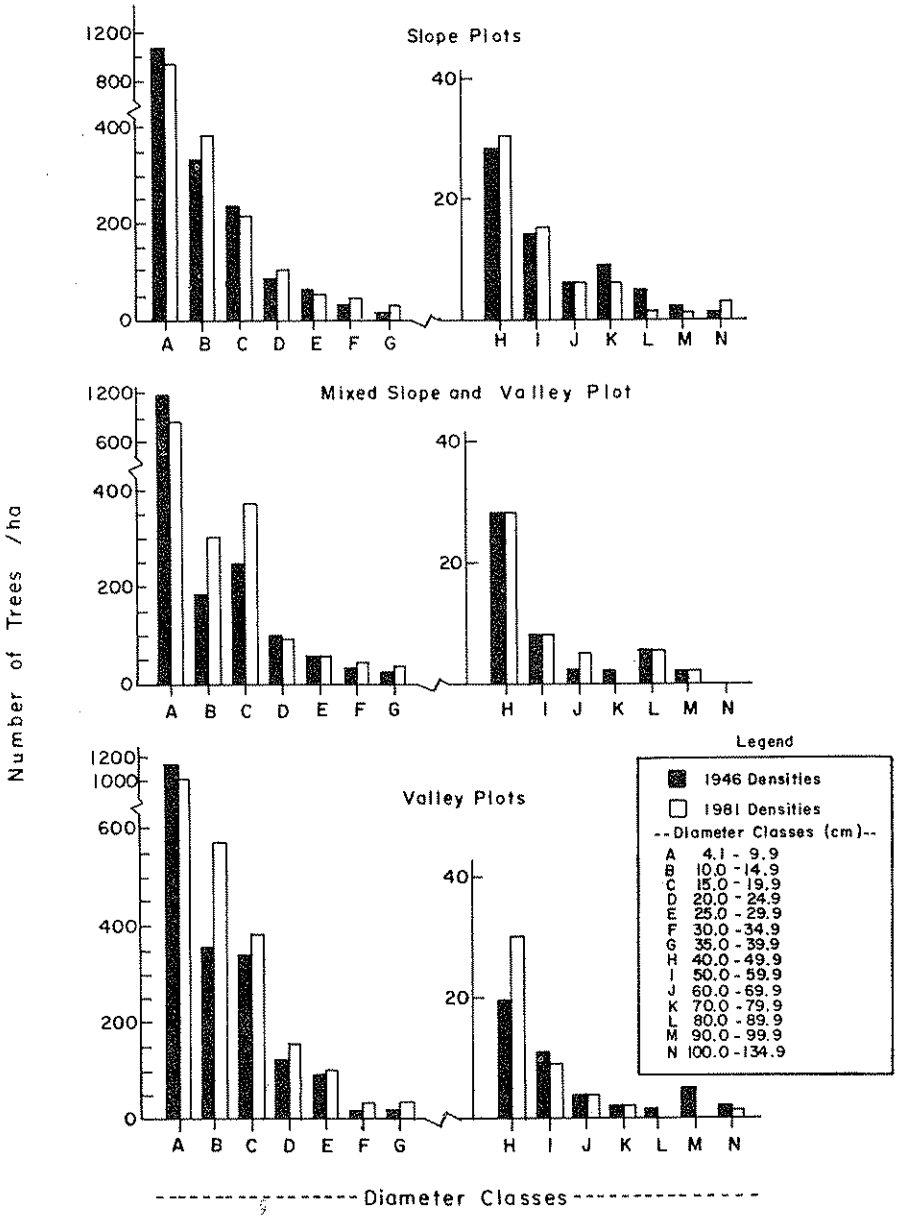

Fig. 2. Diameter class distributions by topography for natural forest permanent plots in the colorado forest in 1946 and 1981.

species that 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 6m tall, found mainly in small opening in the forest; *Cecropia peltata and Didymopanax morototoni,* common, intermediate to canopy-sized pioneer trees, found in secondary forests and in gaps in primary forests in the American tropics growing to 30 to 50cm in diameter and 15 to 20m tall; *Miconia laevigata,* a small to intermediate-sized tree, reaching 15cm in diameter and 8m 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 15m tall, whose regeneration is tied to gaps in the mature forest; *Cordia borinquensis,* a common, shade tolerant, understory tree, to 15cm in diameter and 7m 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 chrysophylloides* and *M. garciniaefolia,* both shade tolerant, canopy trees reaching 50 to 60cm in diameter and 15m

tall. 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 for all plots combined at the beginning and end of the study was virtually the same. The means and standard errors of stem numbers/ha were 1860 ± 73 in 1946 and 1858 ± 89 in 1981. 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% of the original stem density. When stem density on plots is considered by topography, density on the 4 slope plots declined by 6% while that on the two valley plots increased by 9% from 1946 to 1981. Stem density on the plot with mixed slope and valley topography also increased, but only by 2%. The survival rate of stems that were measured in 1946 varied between 50 and 70% per plot.

Diameter Class Distribution. All plots, regardless of topography, showed a decrease in the smallest diameter class, ranging from 11% in the valleys through 13% on the slopes, to 23% on the mixed plot (Fig. 2). Moreover, all showed an increase in the 10.0-to-14.9-cm diameter class, varying from 13% on the slopes through 61% in the valleys to 66% on the mixed plot. The valley plots showed an increase in all diameter classes from 15.0 to 49.9cm, 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 ≧ 50cm for all groupings of plots fluctuated slightly between measurements but demonstrated a general decline because of mortality of larger stems.

Height Class Distribution. The trend in height class distribution on all plots parallels that of the diameters. The smallest class, 0-to-2.9-m, decreased between 10 and 84%, with the smallest decline on the mixed plot (Fig. 3). The next size class, from 3.0-to-5.9-m, also showed a decline, ranging from 35 to 81%. All remaining 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.

Crown Class Distribution. The dominant and intermediate crown classes on all plots decreased by about 70 stems/ha, or 3%, from 1946 to 1981. The suppressed crown class increased by about 175 stems/ha, or 6%. The codominant crown class remained virtually unaltered. Despite these changes, the pattern of crown class distribution in both years is similar: 45 to 50% in the suppressed class, 25 to 30% in the intermediate class, and 10 to 12% in the dominant and codominant classes.

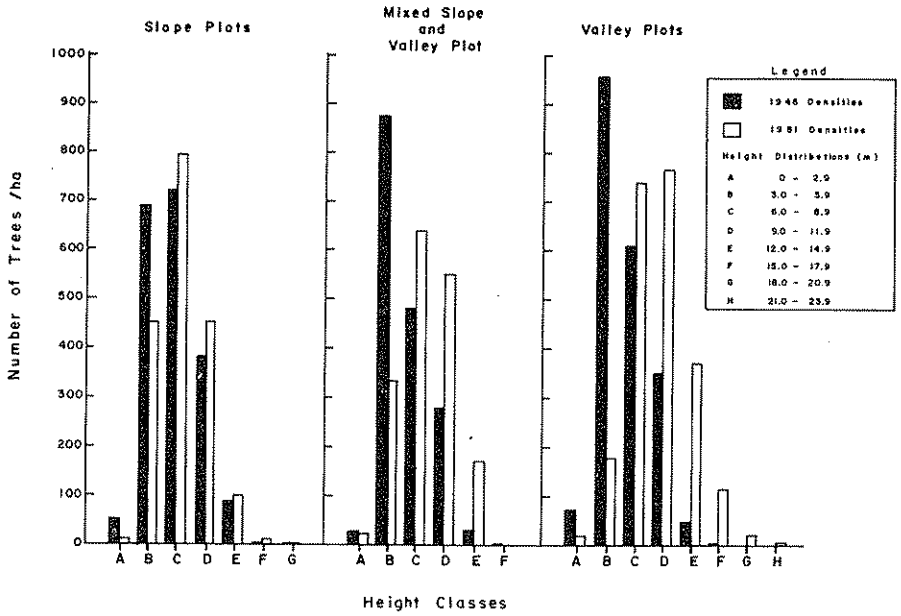

Fig. 3. Height class distribution by topography for natural forest permanent plots in the colorado forest 1946 and 1981.

Specific Gravity Distributions. About 35% of all stems was in the specific gravity class from 0.60 to 0.69g/cm³ in 1946 and 1981. Another 30% was between 0.70 and 0.79g/cm³. When volume was substituted for number of stems, however, 43% was found in the 0.50-to-0.59g/cm³ class in 1946 and about 30% in the same grouping in 1981. The 0.60-to-0.69g/cm³ class had about 28% in 1946 and about 35% in 1981.

The weighted mean specific gravity for all trees, based on their respective volumes, showed a 1.9% increase from 0.563 to 0.574g/cm³ between 1946 and 1981 for all plots combined. 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% increase from 0.608 to 0.632g/cm³.

Species Changes

Changes in Composition. The relative density, relative frequency, relative basal area, and percent importance for 30 species in 1946 and 1981 are given in Table I. The first 7 species accounted for more than half of the total percent importance in both years. A major decline of 4.4 in percent importance was shown by *Cyrilla racemiflora,* mainly in basal area, because of the loss of several large stems. Other species that declined by ≧0.4 in percent importance, in order of magnitude were: *Ocotea spathulata, Heydyosmum arborescens, Psychotria berteriana, Miconia laevigata, Cecropia peltata, Calycogonium squamulosum,* and *Magnolia splendens.* The greatest increase, 1.8 in percent importance, was shown by *Micropholis chrysophylloides,* because of increases in density and basal area. Other increases of ≧0.4 in percent importance, in order of magnitude, were observed for *Micropholis garciniaefolia, Miconia tetrandra, Clusia krugiana, Croton poecilanthus, Haenianthus salicifolius,* and *Prestoea montana.*

Indicator Species. Nearly all of the *Hedyosmum arborescens* and all of the *Psychotria berteriana* stems originally found on the plots in 1946 had disappeared by 1981 (Fig. 4). When ingrowth was added to survival, however, the 1981 populations of these species amounted to 10 and 19%, respectively, of the 1946 populations. Moreover, the percent importance of *Hedyosmum* and *Psychotria* had declined from 1.4 to 0.7 and from 1.5 to 0.7, respectively (Table I). The 1981 total basal area (growth on residual trees +

ingrowth) was 30% of the 1946 value for *Hedyosmum* and 23% for *Psychotria*.

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

Cyrilla racemiflora lost 45% 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% 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% for its 1946 population. With regeneration, this species increased to 130% of its original population. Total basal area in 1981 was also nearly 130% of that in 1946 due to ingrowth and increment on residual stems. Its percent importance also increased from 2.2 to 2.7.

In contrast, *Prestoea montana, Micropholis garciniaefolia,* and *M. chrysophylloides* showed survivals ranging from 65 to 90% 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% of the 1946 populations. The 1981 total basal areas were also greater than in 1946, ranging from 125 to over 160% of the 1946 values for both species of *Micropholis*. *Prestoea* only increased to 105% of the 1946 value because it lacks diameter increment. Percent importance values also increased for each of these species, ranging from 0.4% for *Prestoea* to an average of 1.5% for both species of *Micropholis*.

The abundance of species by topography is also shown in Fig. 4. *Hedysomum, Cyrilla* and both species of *Micropholis* are more common on slope plots while *Cecropia, Didymopanax,* and *Prestoea* are found mainly on valley plots. The remaining species, *Psychotria, Miconia,* and *Cordia,* are wel represented on both topographic positions.

Species Richness. The total number of tree species found on all plots declined from 86 in 1946 to 81 in 1981 (Fig. 5). Three observations may be made. First, the variability of species' numbers for plots of the same size is considerable. Second, the 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 the species' numbers on basis of topography. The species' totals on slope plots A through D ranged from 33 to 46 in 1946 and from 37 to 43 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.

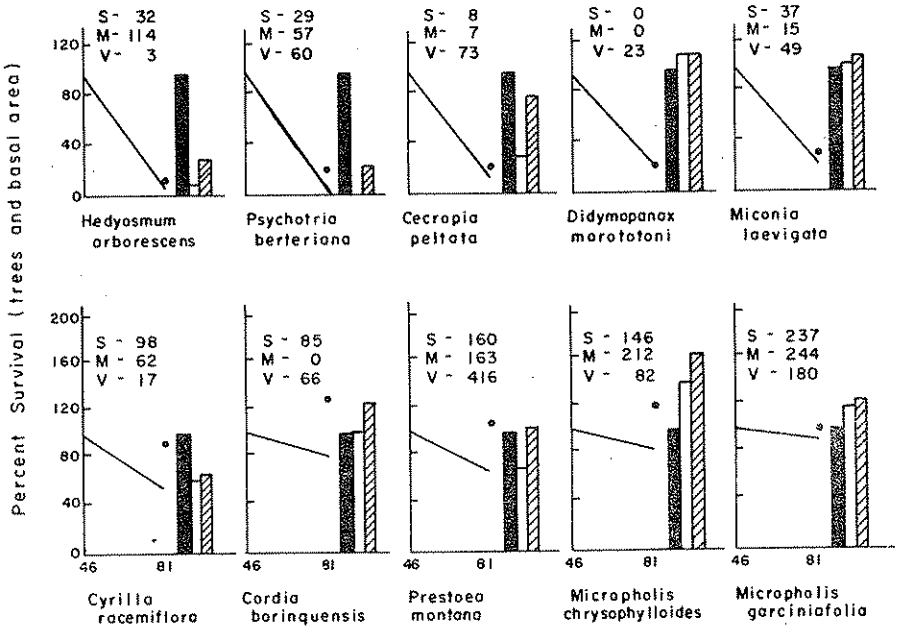

Fig. 4. Percent survival of indicator species in the colorado forest from 1946 to 1981. Lines indicate survival of original trees. Dot is 1981 population of trees (survival of residual trees and ingrowth). Bars indicate basal area: shaded bars, 1946 basal area; unshaded bars, 1981 basal area survivors and growth on survivors; and obliquely-lined bars, 1981 total basal area, growth of residual basal area and ingrowth. Number of trees/ha in 1946 indicated for slope (S), slope and valley (M), and valley (V) plots.

The decline of five tree species between 1946 and 1981 represents a flux in which 12 species were lost and 7 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 2 unidentified species are assumed to be uncommon in the colorado forest. Of the 7 species gained, *Beilschmiedia pendula* is more common in the tabonuco forest and *Grammadenia sintenisii* in the dwarf forest. The remaining species are components of the colorado forest and include *Mecraneum amygdalinum, Miconia pachyphylla* and *Miconia mirabilis,* which are uncommon, and *Ouratea striata* and *Ardisia luquillensis,* which are rare.

Similarity of the Plots. Similarity changes ≥2 percentage points occurred for 20 species found on the plots. They are the first 17 species listed in Table I and *Clusia krugiana, Miconia tetrandra* and *Guettarda valenzuela.* The most frequent and largest percent changes, in descending order, were for *Prestoea montana, Calycogonium squamulosum, Micropholis chrysophylloides, Cyrilla racemiflora,* and *Croton poecilanthus.*

Similarity comparisons between pairs of plots in 1946 and 1981 are shown in Table II. Of the 21 comparisons between plots, 14 showed greater similarity in 1981 than in 1946 and 6 showed less similarity. One comparison set was the same in both years. In general, the loss of secondary and late secondary indicator species (Fig. 4, top row and *Cyrilla*) contributed to greater dissimilarity between comparisons whereas the gain in climax indicator species (Fig. 4, bottom row except *Cyrilla*) contributed to greater similarity between

comparisons. The 6 comparisons that showed increases in dissimilarity had either large percentage changes among declining secondary species or percentage changes among both secondary and climax species.

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

Growth and Production

Diameter Growth. When all survivors regardless of species or crown class were compared, a significant decline in MAI from 0.14 ± 0.004 to 0.09 ± 0.004cm/yr was noted between the 1946-51 and 1976-81 periods. When considered by crown class, a significant decline in MAI was also observed in the intermediate and suppressed crown classes: intermediate trees slowed from 0.14 ± 0.006 to 0.09 ± 0.004cm/yr, and suppressed trees from 0.12 ± 0.005 to 0.05 ± 0.004cm/yr. The dominant crown class also declined in growth from 0.15 ± 0.011 to 0.12 ± 0.012cm/yr, but the difference was not significant. In contrast, codominant trees showed a significant increase in diameter growth from 0.14 ± 0.009 to 0.16 ± 0.010 cm/yr.

Biomass, Volume and Basal Area Changes. The mean increase in aboveground woody biomass, including branches ≥2.5cm, on the 7 plots was 0.67 t/ha/yr (Fig. 6). Biomass accrual on 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 4 slope plots averaged only 0.22 t/ha/yr while the 3 valley plots and mixed topography plot averaged 1.27 t/ha/yr.

When mortality was added to ingrowth (in this case, ingrowth was equal to growth on the residual stems in the stand plus recruitment, or stems which reached the minimum diameter class used to tally trees) to determine biomass growth, biomass growth ranged from 1.33 to 3.07 t/ha/yr with a mean value of 1.90 t/ha/yr for all plots. The 4 slope plots averaged 1.45 t/ha/yr while the 3 valley plots and mixed topography plots averaged 2.49 t/ha/yr.

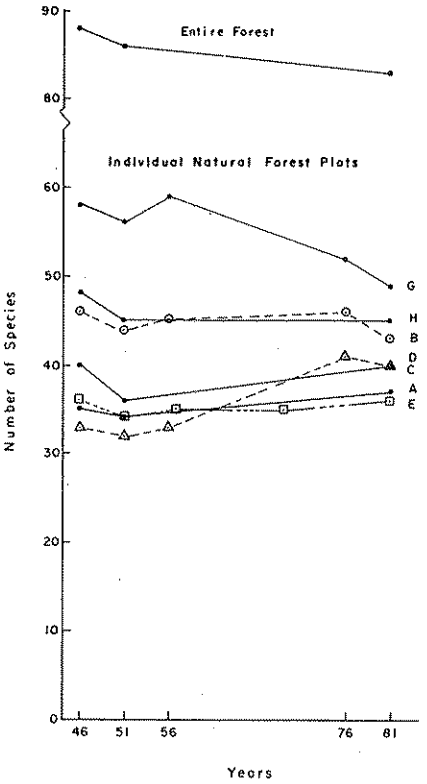

Fig. 5. Change in number of species by plot and for the entire forest from 1946 to 1981.

The mean increase in aboveground woody volume for all plots was 1.06 m^3/ha/yr during the period of measurement (Weaver 1987). When mortality was added to ingrowth to determine woody volume growth, it averaged 3.37 m^3/ha/yr for all plots. In contrast, basal area for all plots decreased by an average of 0.01m^2/ha/yr. When mortality was added to ingrowth, however, it increased by 0.43m^2/ha/yr.

Discussion

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. 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, considerable damage is concentrated into a short period of time during hurricanes. Immediately after the storms, 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 insolation, reduced transpiration, and direct contact of the biotic components of the soil and litter with fallen debris creates an environment favorable for increasing both the rate of debris decomposition and nutrient availability (Bormann and Likens 1979; Maser and Trappe 1984; Canham and Marks 1985).

In response to improved environmental conditions, secondary species increase in prominence (White 1979) by means of 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 (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 after storms 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% of the total stems were in the smallest diameter class (Fig. 2). 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 I and Fig. 4).

The third stage of recovery, that of building, is characterized by a gradual decline in the number of secondary species. This is 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. 4). The observed shifts in the distributions of diameter, height, and specific gravity classes are all consistent with forest recovery. The decline of stems in the smallest diameter and height classes is due in part to growth of survivors, as well as the mortality of short-lived secondary species. Intermediate size trees, usually vigorous when adequate light is available, increase in numbers because of additions

from smaller diameter classes and because of the continued survival of trees within the class. The general decline in the largest diameter classes is due mainly to senescence and mortality of large trees that survived the hurricane. The increased number of suppressed stems in 1981, 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 lightweight pioneer and early secondary species and 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 nearly equal, although the increases on the mixed plot and valley plots balanced the overall decline on the slope plots. *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 once more due to increasing competition among surivivors. This trend is apparent on the slope plots to different degrees, although one of the 4 slope 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 and the fact that the colorado forest is a dense formation of small-sized, slow-growing trees (Wadsworth 1951; Weaver 1983). Change in stem numbers during recovery within this forest is not as rapid as in the tabonuco forest where an 18% 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. 3). When these die, they may create large openings, or growing space for saplings, Six tree with dbs's >90cm died during 35 years on valley plots but none that size were lost on the mixed or slope plots (Fig. 2). Moreover, the ingrowth of palms on the mixed plot and valley plots averaged 150 trees/ha compared to only 50 trees/ha on the slope plots during the period of measurement. The average number of palms in 1981 on the mixed plots and valley plots was 380/ha while on the slope plots it was only 140/ha. The Sierra Palm is not only shade tolerant, slow growing, and persistent for long periods (Bannister 1970), but it requires less space to mature than the larger dicot species.

TABLE II

PERCENT SIMILARITY[1] INDICES FOR THE COLORADO FOREST PERMANENT PLOTS IN 1946 AND 1981

Plot	*A*	*B*	*C*	*D*	*E*	*G*	*H*
A	——	62-69	52-59	65-65	61-62	53-56	43-46
B	——	——	57-54	51-49	66-71	42-43	47-57
C	——	——	——	64-57	63-56	37-39	44-48
D	——	——	——	——	64-51	41-38	45-47
E	——	——	——	——	——	53-58	48-54
G	——	——	——	——	——	——	69-72
H	——	——	——	——	——	——	——

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 = Σ (lowest percentage for each species). The first number refers to 1946 and the second number to 1981.

The 6% decline in the number of tree species for the entire forest is also a trend evident during the building phase (Fig. 5). Individual 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 near the transition between tabonuco and colorado forests at 650m in elevation. The disturbance of this area during and after the hurricane led to colonization from both forest types and gave these plots a higher species richness about 15 years after the storm. Perhaps the most interesting trend in the colorado forest is the apparent convergence of species' numbers on all plots during recovery. 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. For all plots combined, the floristic richness appears greatest a few years after disturbance. During this phase of colonization and growth, both primary and secondary species are components of the stand. During the building phase, the gradual dominance of shade tolerant species leads to a decline of secondary species and may locally exclude some of the uncommon species.

Growth. The 35% decline in the rate of diameter growth on the trees that survived the 35-year period of measurement probably indicates that the forest building phase has ended and the mature phase is underway. 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).

The growth rate (basal area, volume, and biomass) may be estimated from differences in the standing crop of trees in 1946 and 1981, yielding an estimate of net change, or by summing net change and mortality over the same period. The second method provides a better estimate of actual stand production because it includes all trees that exploited growing space at some time within the stand. Mortality is not estimated in most studies because they span short periods and little mortality is evident. Omission of mortality underestimates actual forest production. This is analogous to excluding intermediate thinnings in studies of plantation production.

Mean basal area changed litt'e on the plots. This indicates a long-term dynamic balance between the loss of secondary species along with mortality of large stems that had 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.

The mean net volume growth for all plots was 1.06m³/ha/yr during 35 years, and was positive on 6 of the plots, suggesting recovery from previous 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 between slope and va'ley growth rates may be partly attributab'e to better site conditions and partly to different species compositions. Valley plots in colorado forest, especially at lower elevations such as these, contain *Dacryodes excelsa, Manilkara bidentata, Buchenavia capitata, Matayba dominguensis* and *Miconia laevigata* from the tabonuco forest. All attain larger size than most colorado forest species and grow at faster rates.

Several other estimates of net volume growth in previously disturbed tropical moist and wet forests range between 1 to 5m³/ha/yr. Virgin tabonuco forest in Puerto Rico recovering from disturbance by San Cipriano had a net volume growth of 2.5m³/ha /yr (Wadsworth 1957). Partially cutover or disturbed rain forest in Malaysia yielded 1 to 3m³/ha/yr, the rain forest in Nigeria 2, and the dipterocarp forest in the Philippines from 2.9 to 4.3m³/ ha/yr (Johnson 1976). Tropical high forest in Uganda appeared incapable of yielding >1.4m³/ha/yr under any management system involving multiple cutting or >4.2m³/ha/yr under a simple 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 6 of the plots, with a mean rate of 0.67 t/ha/yr. Again, the valley plots exceeded the slope plots, averaging 1.41t/ha/yr. The plots are located only 2km horizontally and 200m 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).

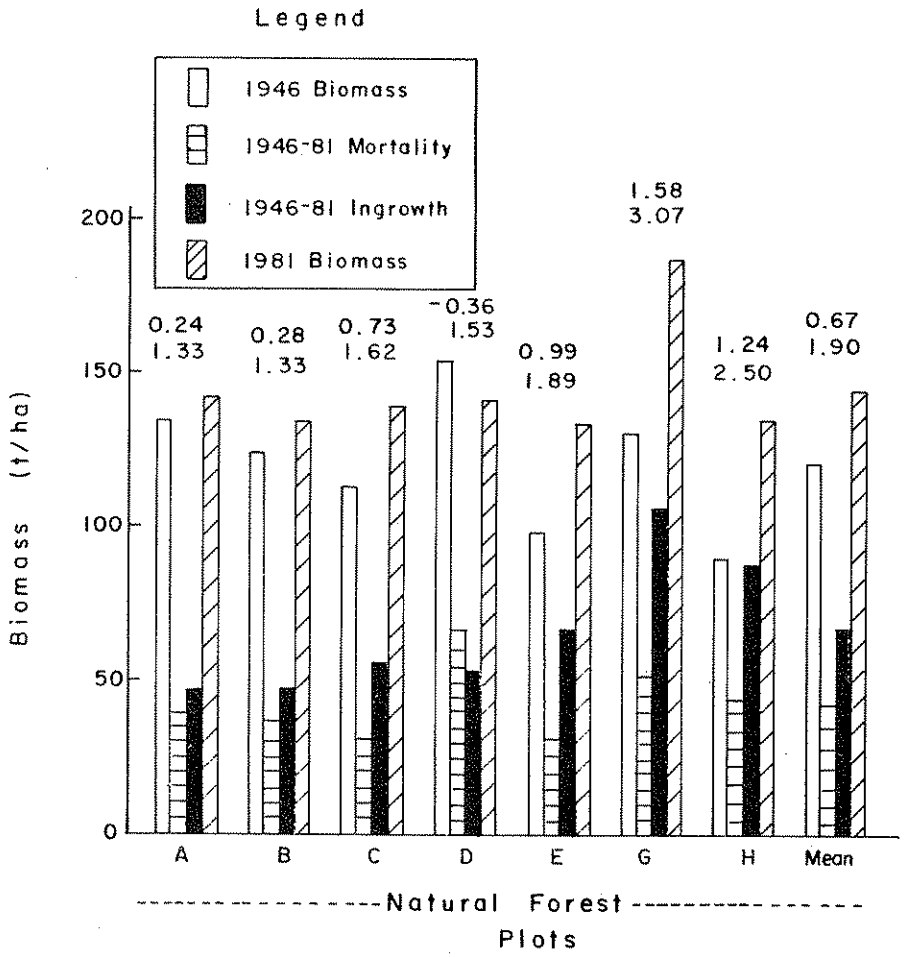

Fig. 6. Aboveground woody biomass changes for all natural forest permanent plots from 1946 to 1981. Mean is for all natural forest plots combined. Ingrowth includes recruitment and growth on residual stems. Mean annual biomass growth (in t/ha) is shown above the bars. The top value is for ingrowth alone. The bottom value sums both ingrowth and mortality as growth.

Net aboveground woody biomass accumulation rates for mature natural forests elsewhere in the American tropics are in the range of 0.5 to 3.5 t/ha/yr (Weaver 1986). Secondary net woody biomass accumulations are more variable but, except for stands less than 5 years old, exceed those in the mature forest, ranging from 5 to 12 t/ha/yr in tropical moist forests. Because all of the secondary forest sites reported (Weaver 1986) were cleared before establishment of the growth plots, their biomass accumulation rates should approach the maximum for the colonization growth, and early building phases of natural forests after disturbance.

Hurricane Damage and Recovery in the Luquillo Mountains

Hurricane damage should be a function of numerous factors among which are storm characteristics (wind velocity, total rainfall, and duration), storm recurrence, vegetation features (tree size, stem density, crown growth patterns, and tree specific gravities), soils, and topography. 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.

With an increase in elevation in the mountains, the soils become wetter, notably so above the rather abrupt transition between tabonuco and colorado forest (Wadsworth and Bonnet 1951). The number of stems per hectare increases and tree size declines along the same elevational gradient (Wadsworth 1951; White, 1963), 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 forests, windfall is most prevalent in valleys where the soils are wet and the trees have large crowns, while breakage prevails on ridges (Wadsworth and Englerth 1959). The small, dense vegetation on upper slopes and ridges in both colorado and dwarf forest (Weaver *et al.*, 1986) 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 from 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 valleys through slopes to ridges at any particular elevation.

Recovery after hurricanes in the tabonuco forest occurs with colonization of large pioneer trees such as *Cecropia peltata, Didymopanax morototoni, Alchornea latifolia, Alchorneopsis portoricensis* and smaller trees in the Rubaceae 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 more slowly. 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 that had been cleared by a plane wreck, showed a dense growth of grass and ferns with some tree sprouting after 6 years (Byer and Weaver 1977), a condition that prevailed for 15 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 the meadows are formed, their reversion to forest may span centuries. The facts that meadows are rare and that secondary tree species are largely absent (Byer and Weaver 1977) indicate that uprooting of trees and the creation of large gaps in the dwarf forest are uncommon.

The building phase in the tabonuco and colorado forests is characterized by a shift in the number of stems to larger diameter and height classes, and a proportional increase in the suppressed crown class. 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 these 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 should change little 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 forest recovery processes on a smaller scale.

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