A Rainforest Chronicle: A 30-Year Record of Change in Structure and Composition at El Verde, Puerto Rico

Thomas R. Crow[1]

Institute of Tropical Forestry, P. O. Box AQ, Rio Piedras, Puerto Rico 00928

ABSTRACT

Measurements over approximately a 30-year period in a *Dacryodes-Sloanea* forest indicate two distinctive phases in stand development. Secondary species were common in the early stand (1940's), and rapid accumulations of biomass and basal area were measured. Many new species entered the stand, and the number of stems increased. In contrast, the stand of the 1970's approached steady-state for biomass and basal area accumulations, and, relative to earlier measurements, fewer stems and fewer species were recorded in the plot. This apparent dichotomy can be correlated to the periodic disturbance caused by tropical storms. The last severe hurricane to strike Puerto Rico occurred in 1932, 11 years prior to the establishment of the El Verde plot. It is postulated that the early measurements reflect the rapid recovery of the stand following this hurricane, with both invading secondary species and residual primary species present in the stand. Subsequent perturbations (i.e., cutting and another storm) were insufficient to disrupt the unmistakable trend toward a mature forest and the stand quickly approached steady-state conditions.

RESUMEN

La mensura llevada a cabo por un período de 30 años en un bosque de *Dacryodes-Sloanea* indica que hay dos aspectos característicos en el desarrollo del rodal. En el primer rodal (en los años del 1940) las especies secundarias eran comunes y se midieron las acumulaciones rápidas de la biomasa y del área basal. Muchas especies nuevas entraron al rodal y el número de tallos aumentó. En contraste, en el rodal de los años del 1970, las acumulaciones para el área basal y la biomasa casi se estabilizaron y en comparación con las mensuras anteriores se observaron menos tallos y menos especies en dicha parcela. Esta dicotomía aparente puede ser correlacionada al disturbio periódico causado por las tormentas tropicales. El último huracán que azotó gravemente a Puerto Rico ocurrió en el 1932, once años antes del establecimiento de la parcela de El Verde. Se ha postulado que las mensuras tempranas reflejan la rápida recuperación del rodal después de este huracán, a pesar de haber tenido especies secundarias invasoras al igual que especies primarias residuales. Las perturbaciones subsiguientes (esto es, el corte y otra tormenta) no lograron interrumpir la inconfundible tendencia hacia un bosque maduro y el rodal alcanzó condiciones estables inmediatamente.

EXCELLENT SUMMARIES of the structural and compositional features of tropical forests are available (e.g., Beard 1944, 1949, Richards 1952, Holdridge *et al.* 1971, Walter 1971), yet few studies provide the dynamic aspect, the change in structure and composition through time. Such information is presented in this paper for the moist tropical forest near El Verde in the Luquillo Experimental Forest of eastern Puerto Rico (fig. 1), where periodic remeasurement of a plot provides a rare chronicle over a long period.

The specific objective of the study was to quantify variations in stand structure and species composition over a 33-year period using data obtained from a 0.72 ha plot established in 1943 and remeasured ten times between 1943 and 1976. The measurements taken in 1946, 1951, and 1976 included ingrowth as well as measurements of the trees tagged in 1943, and it is primarily these data that were used to quantify change in this stand.

The forests of the study area were classified by Beard (1944, 1949) as lower montane rainforest, and more specifically as the *Dacryodes-Sloanea* association found in Puerto Rico and the Lesser Antilles. A number of biologic investigations have been conducted in the Luquillo Mountains in Puerto Rico (Odum and Pigeon 1970, Wadsworth 1970), resulting in an abundance of descriptive material on the flora, fauna, climate, soils, topography, and geology of the study area (table 1).

METHODS

The sample population was obtained from a 60 x 120 m plot in which all trees greater than 4.0 cm dbh were tagged, diameters measured, and species identified. Measurements in 1946 and 1976 also included total height of the trees greater than 4.0 cm dbh.

Stand parameters used to quantify change included number and diversity of species, basal area, number of stems, ingrowth-mortality, and biomass.

For diversity (H), an information measure for finite populations was used

$$H = \frac{1}{N} \log \frac{N!}{N_1!\ N_2!\ \text{- - - -}\ N_S!}$$

with N individuals of S different species (Pielou 1969). Because the factorials were difficult to cal-

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[1] Present address. Forestry Sciences Laboratory, 1030 Wright Street, Marquette, Michigan 49855, U.S.A.

culate for species with many individuals, log approximations were used (Pielou 1969).

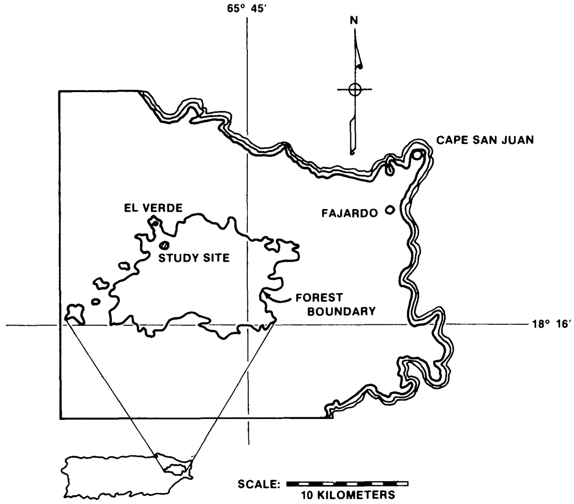


FIGURE 1. Location of study area within the Luquillo Experimental Forest in Puerto Rico.

To measure evenness or equitability of individuals among species, the ratio of observed diversity to the maximum value possible if the same number of individuals were evenly distributed among the species was calculated, i.e. $J = H/H\ \text{max}$.

Total biomass and aboveground biomass (dry weight) were estimated for individual trees and summed for a stand total. Biomass was expressed as an allometric function of dbh:

$$\log_e Y = -2.749 + 2.634 \log_e \text{dbh(cm)};$$ where Y = aboveground dry weight in kg ($R = 0.962$; $N = 33$);

$$\log_e Y = -2.703 + 2.731 \log_e \text{dbh(cm)};$$ where Y = total dry weight in kg ($R = 0.960$; $N = 30$).

These functions were derived from weight-dimensional data listed by Ovington and Olson (1970), but with sample trees less than 4.0 cm dbh eliminated. The sample size differs slightly for the two regressions because root biomass was not determined for all sample trees.

The biomass of the palm (*Prestoea montana*) was estimated as a function of tree height using a regression published both by Ovington and Olson (1970) and Bannister (1970):

$$\log_e Y = 3.846 + 2.912 \log_e \text{ht(m)};$$ where Y = total dry weight in g.

Aboveground dry weight for the palm was obtained by taking 80 percent of the total dry weight. All destructive sampling on which the above relations are based was done in the vicinity of the El Verde plot.

Basal area, number of stems, ingrowth-mortality, and biomass were also determined for seven "indicator" tree species. These species were selected to provide as wide a spectrum of roles within the community as possible. The species, with descriptions taken from Little and Wadsworth (1964), are:

(i) *Dacryodes excelsa* Vahl (Burseraceae). A dominant tree in the mature forest, this evergreen species reaches 30 to 35 m in height and over 1 m in dbh when mature. Distinguishing features are the smooth, whitish bark; the fragrant whitish resin that often exudes from the trunk; the pinnate leaves with 5 to 7 leaflets; and an oblong fleshy brown fruit.

(ii) *Manilkara bidentata* (A. DC.) Chev. (Sapotaceae). A common member of the mature forest, with a dense crown of horizontal branches; dark-green, simple, elliptic leaves; reddish-brown bark; and a buttressed base. A milky latex is evident for all plant parts. When mature, this is a large forest tree and was once the most important timber species in Puerto Rico.

(iii) *Sloanea berteriana* Choisy (Elaecarpaceae). Another dominant species in the upper story of the mature forest, which may be recognized by the mostly large, simple, elliptic leaves; the smooth, dark-gray bark with reddish-brown warts; and the pronounced buttresses at the base of the trunk.

TABLE 1. *A summary of important biotic and abiotic features of the El Verde study area.*

Parameter	Mean values
Climate: diurnal ranges[a]	
temperature	21-25°C
relative humidity	81-96%
absolute humidity	18.0-19.6 g H_2O/m^3
wind velocity	0-6 kph
Climate: annual[a]	
temperature	22.3°C
rainfall	3760 mm
Elevation above sea level	500 m
Soils-deep acid clays on ridges and slopes; stoney clays in drainages.	
Mean stand dbh (1976)[b]	13.6 cm
Mean stand height (1976)[b]	10.54 m
Basal area (1976)[b]	35.7 m^2/hectare
Total biomass (1976)[b]	378.9 dry weight, metric tonnes/hectare
Floristic richness (1976)[b]	49 # tree species/1000 stems 71 # tree species/hectare

[a] Based on 1963-1966 period; measurements were taken above the forest canopy; Source: Odum, Drewry, and Kline (1970).

[b] Includes only trees > 4.0 cm dbh.

(iv) *Cecropia peltata* L. (Moraceae). A common pioneer tree throughout much of the humid American tropics, this tree is found in secondary forests and in gaps within the primary forest. *Cecropia* is a medium-sized evergreen tree, growing to 20 m in height and 60 cm in dbh, with a very thin, spreading crown with large umbrella-like leaves, 30 to 75 cm across.

(v) *Didymopanax morototoni* (Aubl.) Decne & Planch. (Araliaceae). This tree resembles *Cecropia*, but has palmately compound leaves and is botanically unrelated. Like *Cecropia*, it is a light-demanding, pioneer species and ranges throughout most of the humid neotropics.

(vi) *Croton poecilanthus* Urban (Euphorbiaceae). This species is endemic to the mountains of eastern Puerto Rico, where it is common in the understory.

(vii) *Prestoea montana* (R. Grah.) Nichols (Palmae). A palm that forms pure stands in the upper mountains of Puerto Rico, but an understory component in the lower forest. It is often associated with rocky or unstable soils.

RESULTS

COMMUNITY DEVELOPMENT:—The results indicate two distinctive phases in development of the El Verde stand during the measurement period. The first phase was characterized by an increase in the number of stems (fig. 2A), and a rapid increase in basal area (fig. 2B) and stand biomass (fig. 2C). Diversity also increased during this early period (fig. 2D), a result of many new species entering the stand. Comparing the 1946 species list to the 1943 list indicated 17 new species with only 3 species lost. Comparing 1951 to 1943 also indicated a net gain in number of species (table 2).

The second phase had reduced rates of basal area and biomass increments and a decline in the total number of stems and species (fig. 2). From 1951 to 1976, stand basal area increased only 2.5 percent from 24.4 m^2 to 25.0 m^2 (0.7 hectare); in contrast, basal area increased 37.2 percent in the short period from 1943 to 1951. If expressed on a yearly basis, these differences, and parallel differences in biomass accumulation, are most dramatic. From 1943 to 1951, basal area increment per hectare averaged 1.18 m^2/year and biomass increment (total tree) averaged 13.25 mt/year; from 1951 to 1976, these rates averaged only 0.04 m^2/year and 0.97 mt/year, respectively. In contrast to the rapid increments early in the measurement period, this stand approached steady-state conditions for biomass and basal area increments during approximately the last 25 years.

It is also apparent that tree diversity declined during the latter part of the measurement period. During the last 20 to 25 years, the rate at which tree species were lost to this tropical stand greatly accelerated, while the number of new species found since 1943 were less than in previous measurement years (table 2). In addition to the net loss of species, evenness or equitability of distribution of individuals among species also declined. Fewer species accounted for greater proportions of the total stems, basal area, and biomass in 1976 than in any other measurement year. In 1946, the 10 most abundant species accounted for 66 percent of the total stems and 65 percent of the stand basal area; in 1976, the 10 most abundant species accounted for 80 percent of all stems and 77 percent of the stand basal area (table 3).

Among stand parameters, number of stems and species diversity were at a maximum in 1946, the second measurement year (fig. 2). Between 1943 and 1946, a large flux of ingrowth of many different species occurred, while mortality was relatively low. The net result was greater species diversity, a substantial increase in number of small stems within the stand, and a lower mean stand dbh in 1946 than in 1943.

This surge of ingrowth can best be seen in the stand dbh tables (table 4). The number of stems in the smallest dbh class, $> 4 \leqq 8$ cm, increased by 216 during the first three years of plot establishment, with decreases in this dbh class recorded in subsequent measurement years. A comparison of the 1946 and 1976 tables indicates substantial change in the smallest and intermediate dbh classes, but little change in the largest classes. In the 1946 stand, 62 stems or 5.0 percent of the population was larger than 32 cm dbh. These proportions had increased only slightly by 1976 to 67 stems representing 6.6 percent of the total. In 1946, 75 percent of the stems were in the 4-12 dbh range, and this decreased to 58

TABLE 2. *Number of tree species gained and lost to the El Verde plot during five time periods.*(Determined by comparing the species lists from 1943 to that for 1946, etc. Inventories were restricted to trees $>$ 4.0 cm dbh.)

Time period	Number of species gained	Number of species lost
1943-1946	17	3
1943-1951	11	3
1943-1976	12	19
1946-1951	7	13
1951-1976	8	23

percent by 1976, with the proportion of stems in the 12-24 cm dbh range almost doubling during this period.

Changes also occurred in height distribution (fig. 3). A narrow range of heights existed in 1946, with the majority of stems within the 3-9 m range and the tallest trees in the 21-24 m range. By 1976, many trees had moved into the 12-24 m class, and several trees exceeded 30 m in height. Canopy stratification was more discernible in 1946 than in 1976. In 1946, an understory and overstory layer could be readily delineated at 12 m; in 1976, a more even distribution of heights made the delineation of strata more difficult.

The 1019 stems in the > 4.0 cm dbh sample population in 1976 consisted of 481 from the 1943 population (41 percent of the total stems in 1976); 188 stems that were recorded as ingrowth between 1943 and 1951, and survived until 1976 (18 percent); and 350 stems that were not tagged and thus represented ingrowth that occurred since 1951 (34 percent).

The turnover rate during the 30-year period was 50 percent, i.e., 481 of the original 955 stems survived

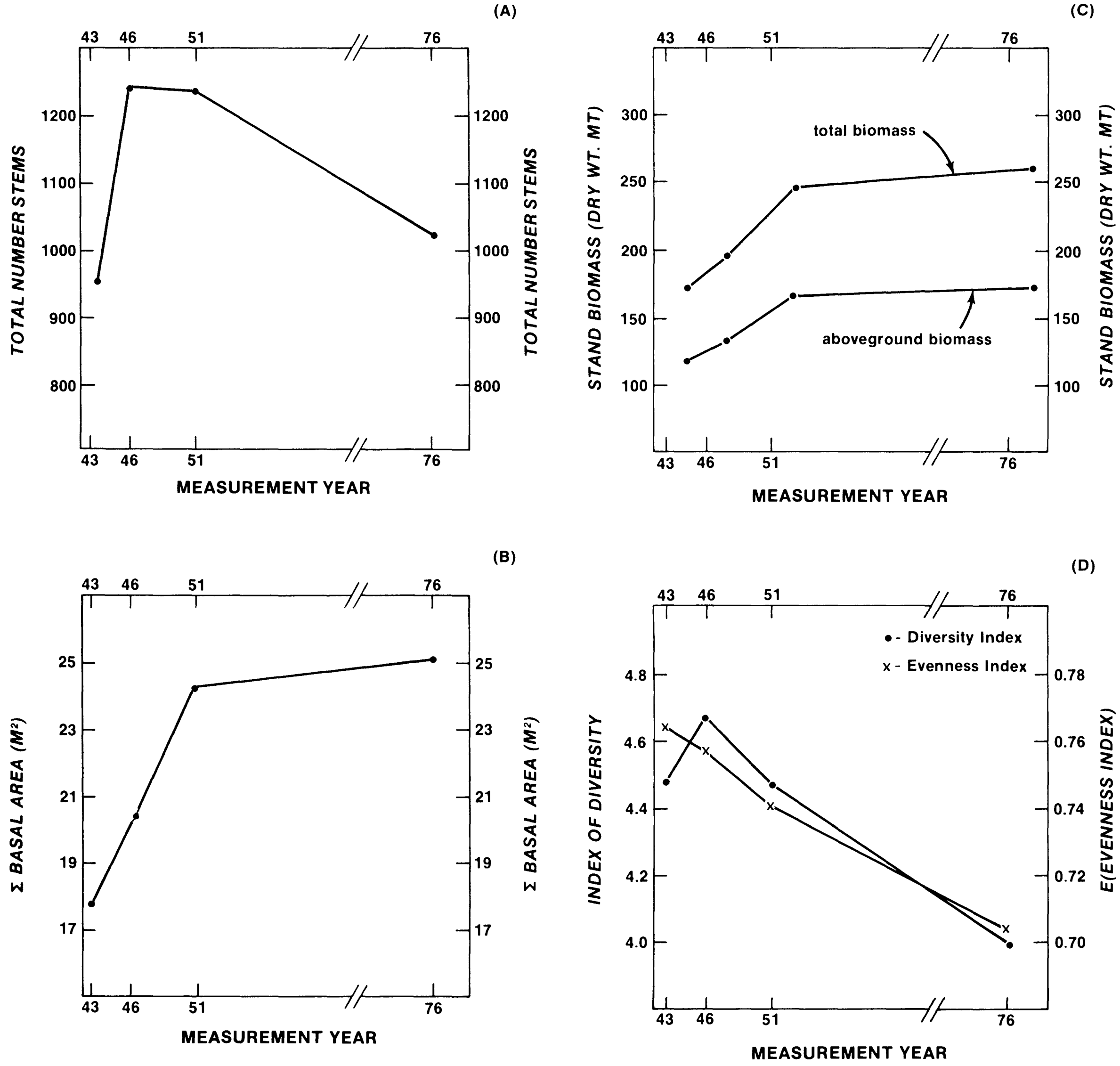


FIGURE 2. Changes in stand characteristics for the El Verde plot during approximately the last 30 years. All measures are based on the population of trees > 4.0 cm dbh within the 0.72 ha plot. Parameters include: (A) number of stems, (B) stand basal area, m^2, (C) total biomass and aboveground biomass, metric tonnes of dry weight, (D) species diversity, bits.

TABLE 3. *Relative abundance and dominance of prominent tree species in the El Verde plot by sample year.*

Species	Percent of stand total Number of stems	 Basal area (m^2)
1943		
Dacryodes excelsa	19.0	36.2
Sloanea berteriana	15.1	5.0
Manilkara bidentata	11.7	5.1
Tetragastris balsamifera	4.8	6.1
Cecropia peltata	4.1	5.5
Croton poecilanthus	3.5	2.2
Inga vera	3.0	3.6
Miconia prasina	2.9	0.1
Drypetes glauca	2.6	0.1
Prestoea montana	2.2	3.2
Sum (% of total stand) =	68.9	67.1
1946		
Sloanea berteriana	16.5	5.9
Dacryodes excelsa	16.4	34.5
Manilkara bidentata	9.0	5.6
Psychotria berteriana	5.2	0.1
Tetragastris balsamifera	4.1	6.2
Cecropia peltata	4.0	5.8
Croton poecilanthus	3.4	2.4
Inga vera	3.0	4.1
Cordia borinquensis	2.1	0.1
Miconia prasina	2.1	0.1
Sum =	65.8	64.8
1951		
Dacryodes excelsa	18.2	33.9
Sloanea berteriana	16.5	6.4
Manilkara bidentata	11.8	6.1
Tetragastris balsamifera	4.7	5.8
Drypetes glauca	4.5	1.1
Croton poecilanthus	3.9	2.5
Inga vera	3.1	4.4
Cecropia peltata	3.1	5.9
Miconia prasina	2.9	0.8
Prestoea montana	1.8	2.4
Sum =	70.5	69.3
1976		
Dacryodes excelsa	23.3	41.1
Manilkara bidentata	14.5	10.7
Prestoea montana	14.3	9.8
Sloanea berteriana	8.5	4.6
Tetragastris balsamifera	6.1	6.3
Quararibaea turbinata	4.9	1.3
Croton poecilanthus	2.7	1.8
Guarea ramiflora	2.1	1.1
Miconia prasina	1.9	0.1
Cordia borinquensis	1.6	0.1
Sum =	79.9	76.9

this period. As expected, the survivors were generally the larger trees and accounted for 96 percent of the total stand biomass and 84 percent of the stand basal area in the 1976 stand.

The constant turnover among smaller trees and the increased dominance by fewer species produced changes in the floristics of the stand. True, the dominants of the stand changed little, but their importance within the stand certainly did not remain constant. Impressive are the number of species that entered the stand during early periods of measurement and the number that were lost to the stand in the latter period (table 2). With a few exceptions, this flux consisted of species with few individuals in the sample population at any time during the roughly 30-year measurement period.

BEHAVIOR OF INDIVIDUAL SPECIES:—Among the prominent species listed in table 3, there was a trend of increasing dominance by the primary species (e.g., *D. excelsa* and *M. bidentata*) and decreasing dominance by secondary species (e.g., *C. peltata*) that is indicative of a maturing stand. The performance of the "indicator" species (fig. 4) provides additional information regarding this trend.

Although ingrowth of *C. peltata* was recorded in both 1946 and 1951 (table 5), and at least a limited amount of niche space was still available for this light-demanding species early in the measurement period, both *D. morototoni* and *C. peltata* declined in importance as stand components (figs. 4A and 4B). Their 1976 sample populations consisted primarily of large, mature individuals with crowns above the surrounding trees. The rapid mortality, especially for *C. peltata* which declined from a peak of 50 stems in 1946 to only 6 stems in 1976, reflects high mortality among mature individuals of these relatively short-lived species.

Among the primary species, *D. excelsa* increased its relative dominance within the stand, both in terms of stem density and basal area, at a slow but steady rate (fig 4C). From 1943 to 1976, the proportion of

TABLE 4. *Absolute and relative distributions of trees among dbh classes.*

	1943		1946		1951		1976	
Diameter class (cm)[a]	Number of stems	% of stand	Number of stems	% of stand	Number of stems	% of stand	Number of stems	% of stand
4-8	470	49	686	55	584	47	407	40
8-12	214	22	247	20	259	21	181	18
12-16	70	7	97	8	123	10	139	14
16-20	60	6	67	5	83	7	107	11
20-24	44	5	34	3	50	4	55	5
24-28	24	3	33	3	37	3	27	3
28-32	13	1	18	1	31	3	32	3
> 32	60	7	62	5	69	5	67	6
Sums	955		1244		1236		1015	

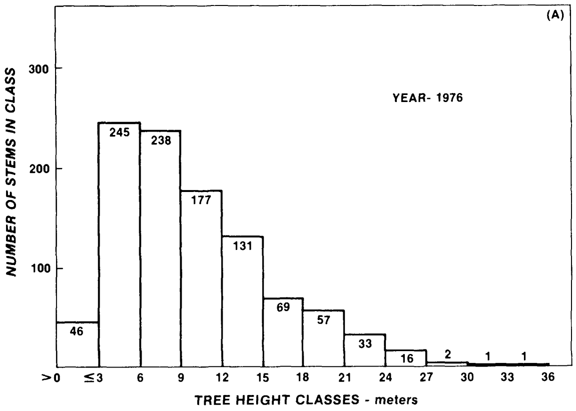
[a] Diameter classes are $> 4 \leq 8$ cm, etc.

this species increased from 19.0 to 23.2 percent of the total number of stems and from 36.2 to 41.1 percent of the stand basal area. *Manilkara bidentata* increased only slightly in number of stems during the same period (fig. 4D), but existing stems grew rapidly relative to other species, and a number of trees moved into the larger-dbh classes. In 1943, the largest trees of *M. bidentata* were in the 24-28 cm dbh class; in 1976, the largest trees were in the 44-48 cm class (table 6). As a result, this species doubled its proportion of stand basal area from 5.1 percent in 1943 to 10.7 percent in 1976, and tripled its proportion of stand biomass from 3.0 to 9.1 percent during the same period.

The other primary species, *S. berteriana*, differed in its response. After early increases, declines occurred in basal area, biomass, and stem density (fig. 4E). Throughout the early measurements, *S. berteriana* accounted for 15-16 percent of the total stems, but declined to 8 percent by 1976 (table 3). In early measurements, *S. berteriana* was the most abundant species tallied as ingrowth, but in 1976 it dropped to fifth in frequency tallied, with one-third as many stems (table 5). This trend contrasts to the increasing numbers of *D. excelsa* and *M. bidentata* tallied each measurement year. The lack of ingrowth combined with continued high mortality resulted in fewer stems of this species in the smaller dbh classes (table 6). Between 1951 and 1976, the frequency of *S. berteriana* in the 4-8 cm dbh class declined by 50 percent and in the 8-12 cm class, a 6-fold reduction occurred.

Croton poecilanthus likewise first gained but then declined slightly in relative basal area and number of stems (fig. 4G). Ingrowth for this species was recorded for each measurement year, providing a constant but not abundant supply of new individuals into the population. The performance of this species is indicative of its role as a common understory species—a species able to compete in a shaded environment, always present, but never dominant.

Perhaps the most dramatic change that occurred in this stand was the increased abundance of the palm, *Prestoea montana*. Measurements in 1943, 1946, and 1951 (fig. 4F) indicate this species to be a minor, almost quiescent member of the community. Between 1957 and 1976, this species surged, increasing from 1.8 to 14.1 percent of the total stems, and from 2.4 to 9.8 percent of stand basal area. In assessing the importance of a species within the community, estimates of biomass were generally parallel and supportive of basal area measurements, therefore only the directly measured basal area (ba) was plotted in figure 4. An exception to this generalization occurred with *P. montana*. In this case, the morphology and physiognomy of this monocot produces a low dry weight per stem, and thus its importance within the community as indicated by total biomass was much less, only 1.1 percent of the stand total in 1976, as compared to frequency or basal area. Thus, the biomass measurement underestimated its relative importance.



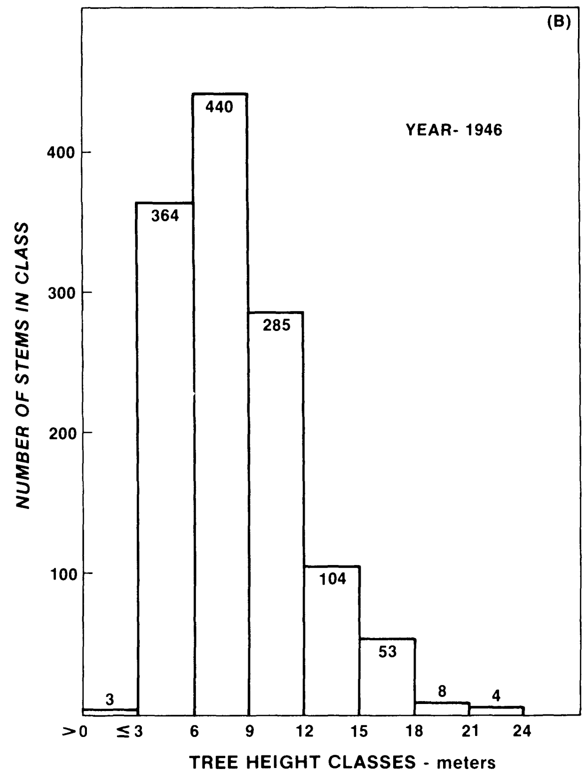


FIGURE 3. Changes in the distribution of tree heights in the El Verde plot between 1976 (A) and 1946 (B). The actual number of trees within each class is given at the top of each bar.

The fate of the stems tagged in 1943 was determined at 10-year intervals beginning in 1946 and the percentage of survival plotted in figure 5 for each of the "indicator" species. To some extent, the different patterns in figure 5 can be related to the autecology of the species. *Dacryodes excelsa* and *M. bidentata* are long-lived species that can persist for extensive periods under very competitive conditions. These characteristics along with the abundant ingrowth recorded (table 5) would seem to indicate increasing domination of this stand by these species. Again, *S. berteriana* differed in its response relative to other primary species.

Other interesting patterns in species behavior are evident in table 3. Occasionally, a species would suddenly surge and become a prominent member of the community, only to decline abruptly to lower levels of abundance. Examples of this population "spike" include *Psychotria berteriana*, the fourth most abundant species in 1946, but only a minor stand component in 1943 and 1951, and *Drypetes glauca*, the fifth most abundant species in 1951, but an uncommon species in either 1946 or 1976.

DISCUSSION

The trends observed in the El Verde stand can be

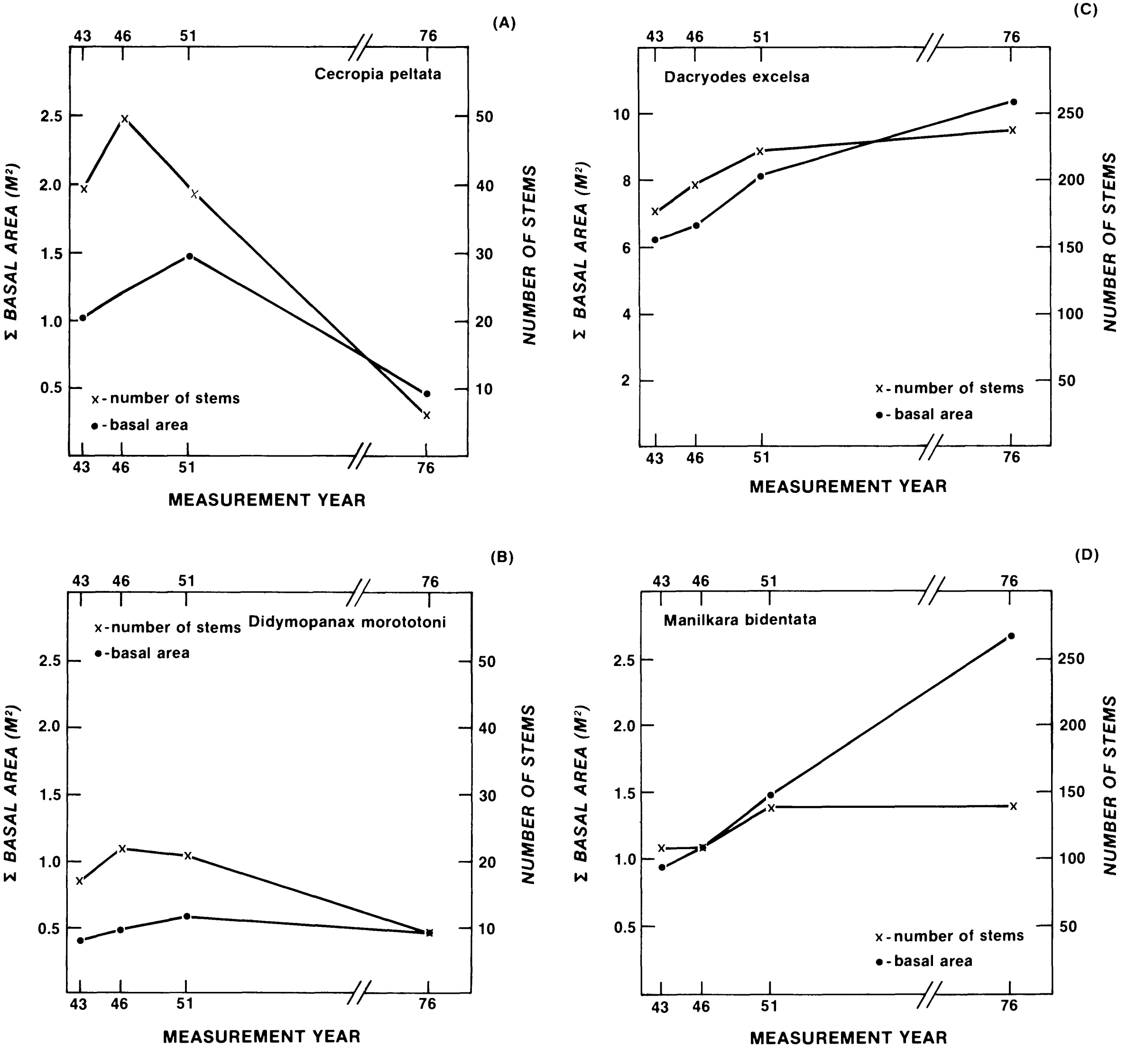
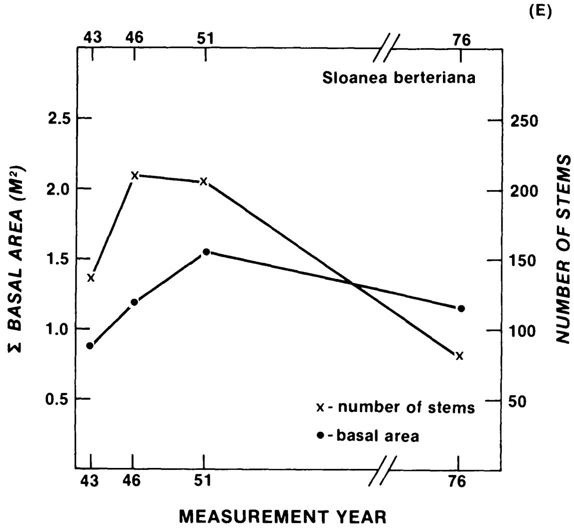


FIGURE 4. Performance of "indicator" species as measured by Σ basal area (.) and number of stems (x). Measurements apply to those portions of the total populations > 4.0 cm dbh within the 0.72 ha plot. When making comparisons among species, note the differences in scale.

correlated with periodic disturbance, both natural and man-caused. These events, scaled along a time line in figure 6, include three severe hurricanes, San Felipe, San Nicolás, and San Ciprian, during a period from 11 to 15 years before plot establishment and a single hurricane, Betsy (locally called Santa Clara), during the measurement period. Several cuttings have also occurred in this stand. A selection harvest occurred in 1937, and a silvicultural treatment (timber-stand improvement) was applied in 1959.

All three hurricanes which occurred during the late 1920's and early 1930's probably damaged the forest to some extent. San Felipe is considered to be a benchmark hurricane to which all other hurricanes are compared (table 7). High winds and flooding associated with San Felipe caused extensive property damage and loss of life in Puerto Rico. Although San Nicolás did not match San Felipe in terms of maximum winds and rainfall, it had a long duration (table 7). The center of both hurricanes struck somewhat south of the Luquillo Mountains on the southeastern coast of Puerto Rico and traveled on a diagonal path across the Island to the northwest coast. In contrast, the Luquillo Mountains were directly in the path of San Ciprian, and records indicate that the high winds and heavy rains damaged the forests of these mountains. Defoliation, windfall, and stem breakage were common, and tree mortality was extensive (Wadsworth and Englerth 1959).



These tropical storms provide logical explanations for the youthful characteristics of the El Verde stand early in the measurement period. It is apparent that ample "growing space" was still available in the 1940's. Early secondary species (e.g., *Cecropia peltata*) continued to enter the stand, and many new species were recorded, while few species were lost. In addition, stand biomass and basal area accumulated at rapid rates.

The 1937 selection harvest constituted another disruptive factor in the period before plot establishment. Records do not indicate the exact number of trees removed from the El Verde stand, but the prescription called for a very light cutting in order to minimize the impact on the watershed (F. H. Wadsworth, pers. comm.). The harvesting of a few trees

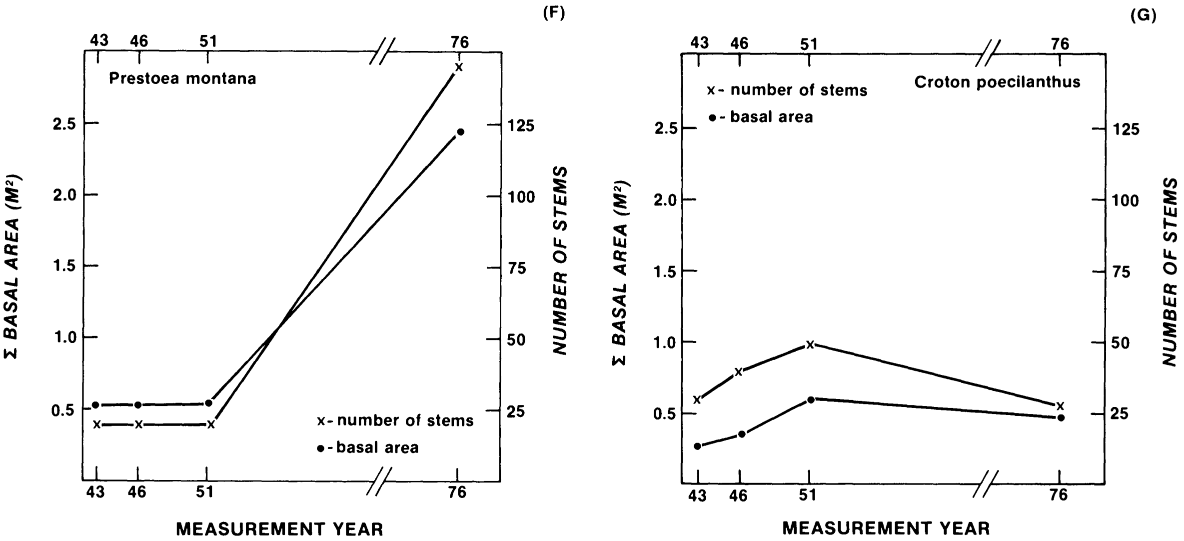


FIGURE 4. Continued

was probably a minor factor in the observed trends, and, at most, the cutting extended the period in which youthful stand characteristics persisted.

However, these conditions did not persist for long. By the 1950's, 20 years after San Ciprian, early secondary species no longer were entering the stand, but only a remnant population of large, mature individuals remained. Species characteristic of the mature

TABLE 5. *Species and number of stems that grew into the > 4.0 cm dbh class (ingrowth). In each case, a single inventory was taken at the end of the time period. Note that the second period also begins in 1943. Although ingrowth was tallied in 1946, the new trees were not tagged, thus making the concurrent time period necessary.*

1943-1946		1943-1951		1951-1976	
Species	Number of stems	Species	Number of stems	Species	Number of stems
Sloanea berteriana	66	*Sloanea berteriana*	67	*Prestoea montana*	144
Psychotria berteriana	65	*Dacryodes excelsa*	42	*Dacryodes excelsa*	55
Dacryodes excelsa	23	*Manilkara bidentata*	32	*Manilkara bidentata*	43
Manilkara bidentata	17	*Drypetes glauca*	30	*Tetragastris balsamifera*	22
Drypetes glauca	14	*Croton poecilanthus*	18	*Sloanea berteriana*	22
Cecropia peltata	13	*Cecropia peltata*	13	*Quararibaea turbinata*	14
Miconia prasina	12	*Tetragastris balsamifera*	13	*Palicourea riparia*	14
Croton poecilanthus	9	*Guarea ramiflora*	12	*Croton poecilanthus*	6
Cordia borinquensis	9	*Miconia prasina*	10	*Miconia prasina*	5
Inga vera	8	*Inga vera*	9	*Guarea trichilioides*	5
36 other species	86	40 other species	101	20 other species	42
stand total	322	stand total	347	stand total	347

TABLE 6. *Diameter distributions for "indicator" species expressed as number of trees by diameter class and measurement year.*

	Diameter Classes (cm)[a]								
Species	4-8	8-12	12-16	16-20	20-24	24-28	28-32	32-36	> 36
1943									
Sloanea berteriana	104	25	6	5	2			1	
Dacryodes excelsa	64	39	17	11	13	5	2	4	27
Didymopanax morototoni	3	1	3	4	4	1	1		
Manilkara bidentata	59	31	11	8	1	2			
Cecropia peltata	14	12	4	1		2	2	2	2
Croton poecilanthus	12	12	4	1	2	2			
Prestoea montana			3	12	6				
1946									
Sloanea berteriana	144	44	6	6	2	2		1	
Dacryodes excelsa	73	44	21	14	8	10	3	3	28
Didymopanax morototoni	7	2	3	4	2	3	1		
Manilkara bidentata	50	31	17	10	1	2	1		
Cecropia peltata	13	17	8	4	1		2	3	2
Croton poecilanthus	20	11	6	1	2		2		
Prestoea montana			3	11	7				
1951									
Sloanea berteriana	116	61	14	5	4	1	1	2	
Dacryodes excelsa	75	42	26	16	11	11	8	3	31
Didymopanax morototoni	5	1	2	4	4	3	2		
Manilkara bidentata	68	35	20	13	4	3		1	
Cecropia peltata	1	5	9	7	7	4	2	3	1
Croton poecilanthus	23	7	12	1	2	1	2		
Prestoea montana			3	14	5				
1976									
Sloanea berteriana	51	10	12	4	4	1		1	3
Dacryodes excelsa	77	38	25	19	15	13	13	7	28
Didymopanax morototoni	1			1	2	1	1	3	
Manilkara bidentata	74	17	18	12	9	4	4	3	5
Cecropia peltata		2		1			1		2
Croton poecilanthus	9	5	5	3	4	2			
Prestoea montana	5	39	45	46	9				

[a] Diameter classes are $> 4 \leq 8$ cm, etc.

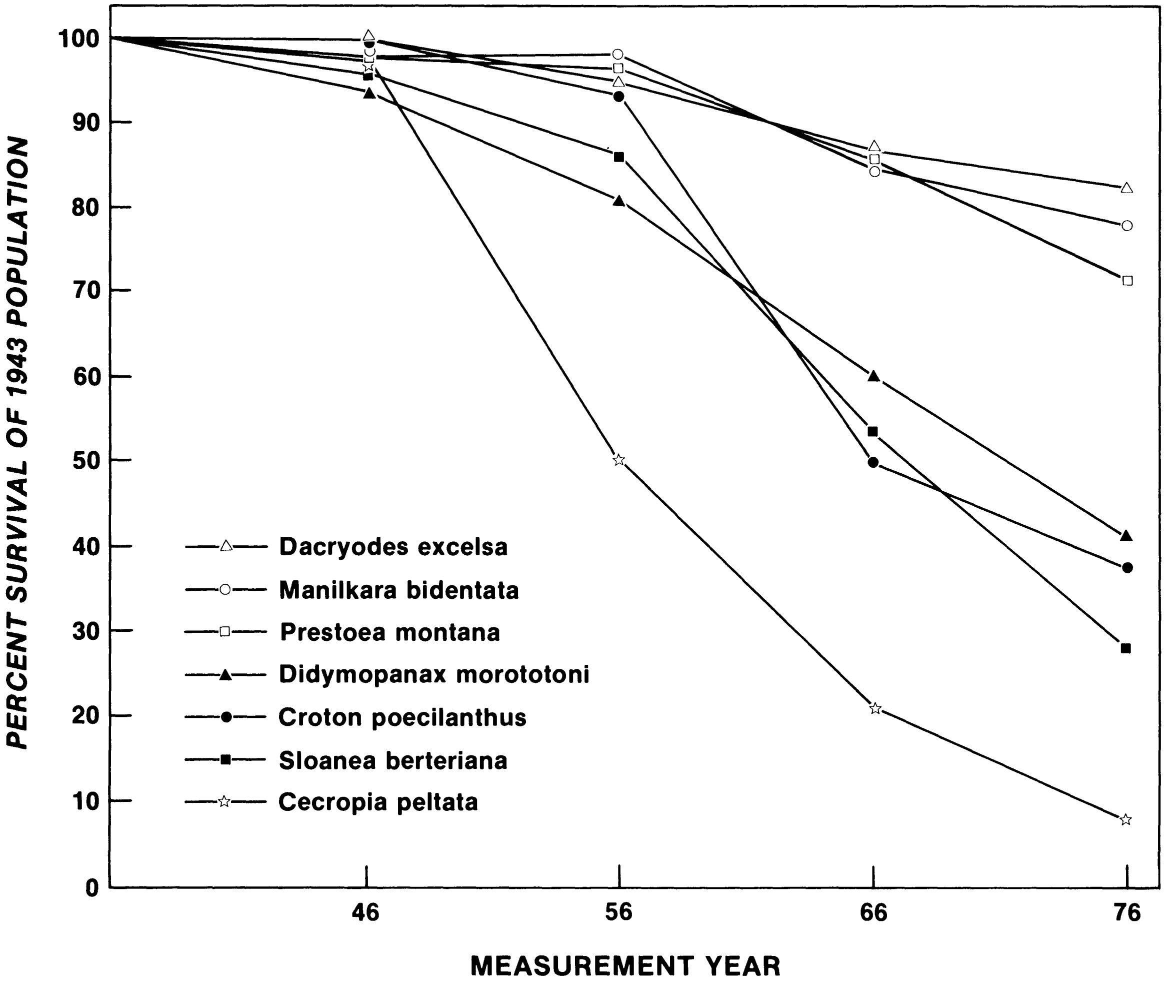


FIGURE 5. Survivorship curves for the 1943 populations of the "indicator" species.

forest (e.g., *D. excelsa* and *M. bidentata*) gained in both the overstory and the understory. Increments of biomass and basal area during the last 20 years were much reduced compared to the first 10-year period, and stand biomass approached asymptotic levels.

Good records exist for the two perturbations following plot establishment. On August 12, 1956, hurricane Betsy (Santa Clara) struck Puerto Rico with heavy rains and high winds (table 7), and traveled on a diagonal path from the southeast coast to the northwest coast of the Island (Wadsworth and Englerth 1959). In San Juan, about 30 miles north of the storm's center, maximum winds were clocked at 148 kph (92 mph). The maximum rainfall reported for Puerto Rico on August 12, 22 cm (8.7 inches), occurred at El Verde, our study area.

Severe damage to forests in Puerto Rico was confined to an area within about 6 miles of the storm's center (Wadsworth and Englerth 1959), and in the Luquillo Mountains, damage was characterized as "local or slight." The most common damage was defoliation, with only limited breakage and windfall; mortality due to direct damage from this hurricane was not extensive. Records show a 5 percent loss (stems > 4 cm dbh) from 1955 to 1956, about average for that period.

A very definite oscillation in mortality did occur in 1958, and this can be attributed to the cultural treatment (timber stand improvement). All told, 146 stems were removed (or poisoned) from the plot, 109 trees of the total were from the smallest dbh class (4-8 cm), 26 were in the 8-16 cm dbh range, and 11 trees were larger than 16 cm dbh. *Sloanea berteriana*, *D. excelsa*, and *M. bidentata* were among the most prevalent species removed. The 1958 cultural treatment was not a significant factor in the decline in number of species for the 1946 to 1976 period. Records indicate that only two species, *Micropholis garciniaefolia* and *Beilschmiedia pendula*, were lost to the plot due to this treatment.

Alterations to stand composition and structure that resulted from the 1956 hurricane and the 1958 timber stand improvement were minor. For example, no new flux of secondary tree species occurred following these perturbations. Obviously, they did little to disrupt the unmistakable trend toward a mature forest.

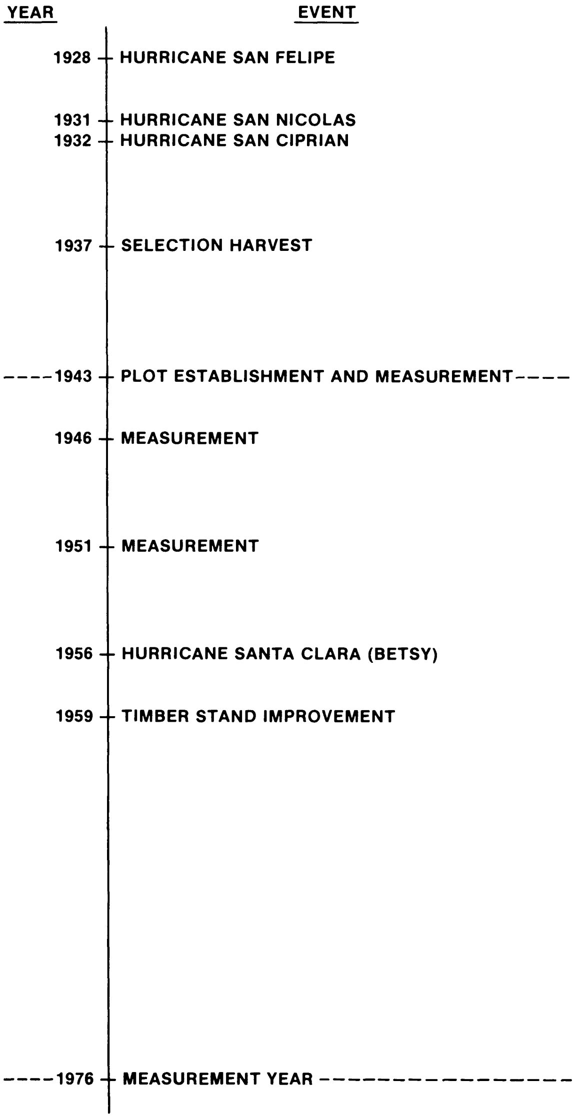


FIGURE 6. Stand history for the El Verde plot. Events are scaled along a time line.

TABLE 7. *Comparative hurricane data.*

Year	San Felipe 1928	San Nicolás 1931	San Ciprian 1932	Santa Clara 1956
Maximum amount of rainfall (inches)	29	5	17	9
Maximum wind velocity (mph)	150	90	120	90
Duration of hurricane winds (hrs)	36	40	18	10

In temperate and boreal forests, perturbations resulting from fires, windstorms, insects, or disease outbreaks are frequent and considered to be an integral part of the natural scheme (Stearns 1949, Rowe 1961, Loucks 1970, Dix and Swan 1971, Oliver and Stephens 1977), and, in general, very effective mechanisms for recovery have evolved, such as the availability of seeds from serotinous cones of jack pine (Cayford 1963), the abundant suckering of aspen after fire (Graham *et al.* 1963, Sandberg and Schneider 1953), and the long-term storage of viable pin cherry seeds in the soil (Marks 1971, Marquis 1975). Thus, dense stands of seral species develop rapidly, with early closure of canopy and rapid attainment of high net annual production and nutrient accumulations; the result is rapid development back toward steady-state conditions.

Periodic disturbance is also part of the natural scheme in the rainforest in Puerto Rico. Severe hurricanes are experienced on the average of once every 10 years (Wadsworth and Englerth 1959), making them an important factor in the development of these forests, and, as one would expect, in the presence of periodic disturbance, effective recovery mechanisms also operate in the El Verde stand. Colonizing species such as *Cecropia peltata* and *Didymopanax morototoni* account for a portion of the rapid stand growth during early measurement periods, but the survivors, the primary species, also responded rapidly to the changing environmental conditions and no doubt the canopy soon closed.

The understory shrubs, *Psychotria berteriana* and *Palicourea riparia*, played important roles in recovery of the El Verde stand. In a life-history study of *P. riparia,* Lebron (1977) concluded that it was an important component in disturbed areas but lower numbers are also found in the mature forest. By utilizing survival strategies characteristic of r-selection favoring high productivity and K-selection favoring conversion of limited resources into progeny (MacArthur and Wilson 1967), *P. riparia* can maintain a scattered population beneath the closed canopy; it is continually producing propagules and is readily able to respond with rapid growth and expanding population once the canopy is opened.

Psychotria berteriana, a genus closely related to

Palicourea, seems to fill a similar niche as that described by Lebron (1977) for *P. riparia*. *Psychotria berteriana* was prominent as ingrowth in early measurements (table 5), and *P. riparia* ingrowth in the last measurement (table 5) was one of the few indicators of a disturbance during the 1951-1976 period.

In the tropical lowland rainforest of North Queensland, Australia, rampant vine growth obliterated most signs of widespread damage only nine months after a 1956 cyclone (Webb 1958). Vines are a conspicuous member of the forests in Puerto Rico, and they also play a role in stand recovery. After hurricane Betsy, some areas in the Luquillo Mountains (generally the severely disturbed areas in coves and valleys) were a mass of herbaceous vines for several years, and climber towers developed on trees which lost their crowns (F. H. Wadsworth, pers. comm.).

The increasing dominance of a few species in the El Verde stand was at the expense of many other species that were eliminated from the stand. The increased diversity often postulated with increased stand maturity (e.g., Odum 1962, 1969, Budowski 1965, Margalef 1968) may be valid in many cases, but results from this study suggest a different trend for the El Verde forest. Here the maximum floristic diversity was attained during recovery stages following disturbance when both secondary and primary species were present, and the distribution of individuals among species was more uniform.

The dominant species in 1943 were also dominant in 1976, with one exception, *P. montana*, the sierra palm. The dramatic increases for this species can be partially attributed to its role in succession. Beard (1949) described the palm brake, areas in the mountainous regions of the West Indies where palm occurs in nearly pure stands. He concluded that these were successional stands, and, therefore, sierra palm was a species occurring early in the development of a rainforest community. However, an ecological life-history study of sierra palm by Bannister (1970) and growth studies reported by Wadsworth (1951) provided new information. It was obvious from those studies that sierra palm was adaptive to the mature forest. The slow growth, the high moisture requirements, shade adaptation, and long survival of palm seedlings (Bannister 1970, Wadsworth 1951) are characteristic of species in the mature forest (Richards 1952).

Sloanea berteriana was still an abundant species in the El Verde in 1976, but results indicated a decline in its importance. *Sloanea* has been described as a co-dominant to *Dacryodes* in the climax forest (Beard 1949, Little and Wadsworth 1964). Yet in El Verde, *Sloanea* is not attaining great size, and it shows high rates of mortality and reduced levels of ingrowth. Much of this reduction has occurred in areas now dominated by palm. In a broad drainage with rocky soils, the 1943 records indicate 33 stems, 14 of which were *S. berteriana*, and three *P. montana*. In 1976, this drainage was totally dominated by palm, with only nine of the original (1943) 33 stems still present, none of which were *S. berteriana*. A survey in a second area dominated by palm showed similar results. No palms were present in 1943, yet this species dominated the area in 1976. Among the 39 stems in the 1943 stand, 16 were *S. berteriana*; none survived.

The timber stand improvement that occurred in 1958 most likely was a minor factor in the decline of *S. berteriana*. The 23 treees of *S. berteriana* cut or poisoned as part of this treatment were a small portion of the total decline within the plot from 204 stems in 1951 to 86 stems in 1976. One must conclude that the major factor is that sierra palm is better adapted to the rocky soils and low, poorly drained areas than is *S. berteriana*.

Richards (1952) makes a distinction between the mixed and single-dominant composition of climax rainforest communities. The mixed association is comprised of many different species, none of which dominates, but in which most species are represented by only a few individuals. The *Dacryodes-Sloanea* rainforest association of Puerto Rico and the Lesser Antilles is considered to be a single-dominant forest (Richards 1952). Moreover, Richards contends that there is an increasing domination by one species and a related decrease in species richness toward the periphery of the association. The *Dacryodes-Sloanea* association is floristically richest in Dominica (Beard 1949). Thus, Dominica is considered to be the center of distribution for the association (Richards 1952), and magnificant forests of huge *Sloanea* and *Dacryodes* do exist on this island. Puerto Rico is near the limit of distribution, and a single species (*Dacryodes excelsa*) does dominate at El Verde. It represented 18 percent of the total stems, 41 percent of the basal area, and half of the biomass in the 1976 stand. Most of the large trees in this stand were *D. excelsa*. The dominance by this species is a result of its competitive ability, longevity, and abundant reproduction.

Comparisons with other long-term plots within the Luquillo Forest indicate that most trends observed at El Verde are not unique. The abundance of *Cecropia peltata* and *Didymopanax morototoni* throughout the forest attests to extensive disturbance in the past, most likely the series of hurricanes around 1930 or perhaps cuttings within the forest. The maturity of these populations is evident from the very high rates of mortality measured in all long-term plots. Substantial increases in palm (*Prestoea montana*) have also been recorded elsewhere (P. L. Weaver, pers. comm.), indicating an increased status for this species throughout the Luquillo Forest. Although the severe declines for *Sloanea berteriana* may not be typical of the entire forest, this species definitely does not occupy a co-dominant position with *Dacryodes excelsa* in the forests of the Luquillo Mountains.

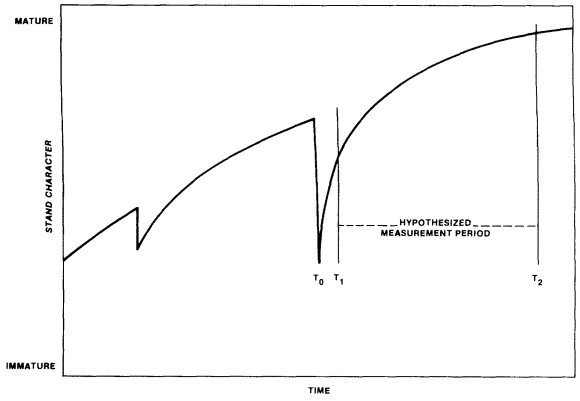


FIGURE 7. Hypothetical relationship between periodic disturbance caused by hurricanes and the character of the tropical rainforest in the West Indies. A storm occurs at T_0 and allows a flux of secondary species to enter the stand. Measurements beginning at T_1 indicate rapid change during the recovery phase. By T_2, the stand has again approached steady-state conditions.

Whitmore (1974) found disturbance (i.e., cyclones) to be the most important ecological factor affecting composition in the rainforests of the Solomon Islands, and cyclones are an important ecological factor, affecting both structure and composition in the tropical lowland rainforest of North Queensland, Australia (Webb 1958). To reiterate, similar conclusions also apply to the montane rainforest of Puerto Rico. These are examples that show that periodic disturbance is an integral part of stand development in tropical rainforests. The hypothesized relationship, characterized by figure 7, is one of partial destruction of a forest, followed by a rapid recovery characterized by a pulse of secondary species, with lower rates of biomass accumulation occurring when the primary species again dominate the stand. These trends are not unlike those reported for the disturbance forests of the northern latitudes.

Differences in the recovery process between a cyclone or hurricane-affected tropical rainforest and a rainforest removed from these storms (e.g., a continental rainforest in tropical America) are likely to be in scale only. In the latter, the recovery process operates on a smaller scale, but with continuous change as young trees replace an old tree, or secondary species fill a forest gap created by cropping or localized windfall.

An understanding of the regeneration system that has evolved during the last few million years is vital for developing rational land-use systems for tropical ecosystems. The inability of the rainforest throughout much of its extent to perpetuate itself under present land-use practices (Gómez-Pompa *et al.* 1972) reflects the fact that man-created disturbances exceed the spatial and temporal (frequency) scale of natural disturbances, thus the adaptive recovery process fails, and destruction of the resource ensues. From an ecological point of view, a rational system of resource exploitation is one in which the natural patterns of disturbance are emulated; in doing so, the evolved mechanisms for recovery remain intact and the resource is renewed.

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