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**TREE GROWTH IN SEVERAL TROPICAL FORESTS  
OF PUERTO RICO**

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## SUMMARY

About 2400 individual stems  $\geq 4.1$  cm d.b.h., and representing about 100 species, from six plots in three Life Zones, some with edaphic variation and/or silvicultural treatment, scattered throughout Puerto Rico, were studied for varying periods, usually ranging from 24 through 30 years but in one instance for only 2 years. Also, more than 11,000 mangrove stems  $\geq 1$  cm at ground level were followed after clearcutting on 3 plots consisting of two separate treatments and a control.

The periodic annual increment for all stems  $\geq 4.1$  cm, regardless of species or crown class, ranged from about 0.05 cm/yr in the Guanica dry limestone forest of the southwest (Subtropical Dry Life Zone) to about 0.45 cm/yr in the Piñones mangrove and early secondary rainforest at Saint Just, both in Subtropical Moist Life Zone.

The species diversity of forests in Puerto Rico is intermediate between those of continental temperate forests of the United States and continental tropical forests. Ten species accounted for 70 to 95 percent of the stems on all sites, exclusive of Piñones mangrove and Guanica.

## RESUMEN

Alrededor de 2400 tallos individuales  $\geq 4.1$  cm d.a.p., localizados en 6 parcelas en 3 Zonas de Vida, y representando unas 100 especies, algunos de ellos en parcelas con una variación edáfica y/o tratamiento silvícola, fueron estudiados por periodos variables fluctuando entre 24 a 30 años, aunque en una ocasión por solo 2 años. Además, después de limpiar 3 rodales consistentes de 2 tratamientos diferentes y un control, se estudiaron la regeneración de 11,000 tallos de mangle  $\geq 1$  cm a nivel del suelo.

El incremento periódico anual del d.a.p. (IPA) para todos los tallos  $\geq 4.1$  cm, haciendo caso omiso de la especie y clase de copa, fluctuó desde 0.05 cm/año en el bosque seco de piedra caliza de Guanica en el sudoeste de Puerto Rico (Zona de Vida Seca Subtropical) hasta 0.45 cm/año en el manglar de Piñones y el bosque pluvial secundario en St. Just, ambos en Zona de Vida Húmeda Subtropical.

La diversidad de especies en Puerto Rico intermedia entre las de los bosques templados continentales de los Estados Unidos y los bosques tropicales continentales. Diez especies respondieron por el 70 al 95 por ciento de los tallos en todos los sitios, sin contar el mangle de Piñones y el bosque de Guanica.

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# Tree Growth in Several Tropical Forests of Puerto Rico

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## INTRODUCTION

From 1943 to 1951, the staff of the Institute of Tropical Forestry established plots in several forests throughout Puerto Rico to determine periodic annual d.b.h. increment (PAI) and to evaluate the potential of different species and forest types for timber production. Initial results disclosed that d.b.h. growth was comparable to that of temperate forests. Subsequently, many of the studies were discontinued after 5 or 10 years.

Since little is known about long-term PAI, stand changes over time, or stand diversity in tropical forests, and since this information is vital to forest planning and management, the plots were remeasured during the mid-70's.

The principal purpose of this paper is to summarize PAI's by species and crown class for several modified or natural stands in Puerto Rico. Also, baseline data on rates of ingrowth, mortality, and stand diversity are provided. Such information will serve as a standard for comparison with other tropical and temperate zone forest types, and with the results of future research in secondary forests of Puerto Rico.

## THE STUDY AREA AND RESEARCH PLOTS

Puerto Rico is located at 18°N latitude and 66°W longitude in the West Indies archipelago. It is about 165 km long by 55 km wide and has a highly diverse physical environment (Pico 1950).

The island comprises a central mountain range that is oriented east to west and varies from 600 m to over 1200 m in elevation. The northern foothills and northern coastal lowlands encompass a large region of limestone origin in which karst hills are the dominant land form. Limestone is also found in the southwestern coastal region.

The island receives an average of 1900 mm/yr of rainfall, mostly orographic, with marked differences in amount over short distances. The southwest, or leeward coastal areas, receive about 800 mm/yr; the northeast, east and southeast, or windward coastal areas, about 1500 to 2000 mm/yr. In the mountains, rainfall varies with location, gradually increasing with elevation to over 5000 mm/yr.

Surrounding ocean temperatures vary from 25.5°C to 27.8°C seasonally, and as a result, mean air temperatures have a small range between the warmest and coldest months. Potential evapotranspiration is estimated at 2000 mm/yr in the coastal areas and 1000 mm/yr or less in the interior mountains (Calvesbert 1970). February, March, and April are drier than the other months.

Mangrove, dry, deciduous, rain, lower montane, upper montane, palm, and elfin forest are terms that indicate the variability of the island's vegetation types. Several authors have described them according to their preferred classification schemes (Gleason and Cook 1927, Beard 1944, Stehlé 1945, Dansereau 1966, Ewel and Whitmore 1973). The last classification recognized six Life Zones (Holdridge 1947, 1967) of which the Subtropical Dry, Subtropical Moist, and Subtropical Wet Life Zones comprised 98.6 percent of the island's land area (fig. 1).

Nine research plots were selected within three Life Zones (fig. 1): one in Subtropical Dry at Guanica on azonal limestone soil; six in Subtropical Moist, two at Cambalache on azonal limestone soil with different exposures, three at Piñones mangrove, and one on zonal soil at St. Just; and two in the Lower Montane Wet Colorado association, one at Toro Negro on zonal soils, and one at Maricao on serpentine. Mean monthly and mean annual rainfalls and temperatures for each plot are provided in figure 2.

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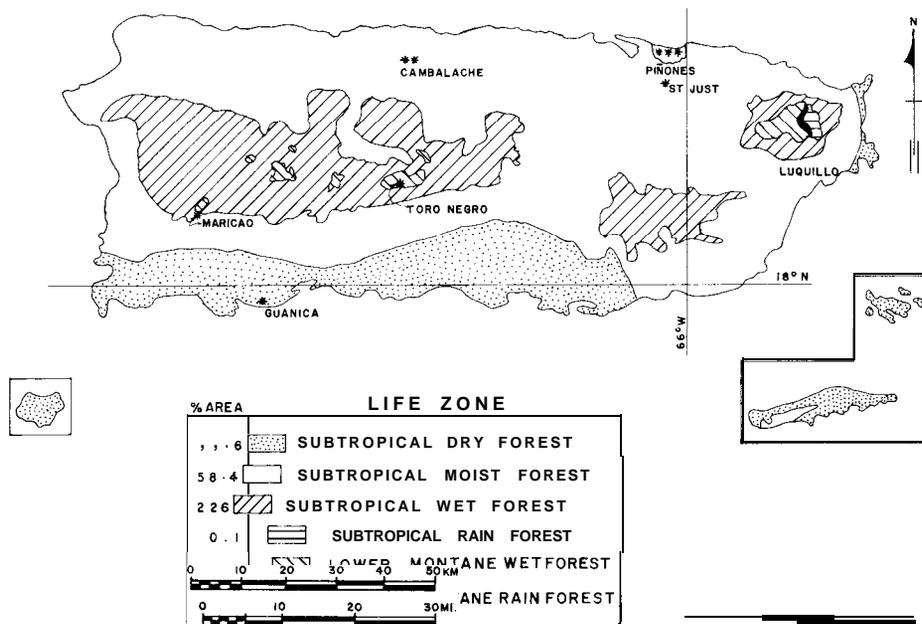


Figure 1.-Ecological Life Zones of Puerto Rico and location of study sites indicated by asterisk (adapted from Ewel and Whitmore, 1973).

## METHODS

On each plot, all trees were measured with a steel tape at diameter at breast height and permanently marked with sequentially numbered tags at 15 cm below diameter at breast height to avert errors due to swelling. Crown classes were also recorded. In some instances, thinnings or clearcuts were made. Periodically thereafter, the plots were revisited, and the surviving trees measured again. Simultaneously, mortality was observed, and during the final measurement, both ingrowth and mortality were tallied.

Details about plot sizes, number of stems, soil types (U.S. Dep. Agric. 1972), and silvicultural treatments are compiled in table 1. The Life Zone system is used as a framework for analysis because results are often applicable in corresponding Life Zones elsewhere.

Statistical testing of PAI's by crown classes was done with Tukey's Omega Procedure (Steel and Torrie 1960). Statistical testing of PAI's among species, however, was considered inappropriate because of possible confounding due to unequal replication, grouping without respect to crown class, and differential effects of previous silvicultural treatments.

The Shannon-Weiner Index, which is influenced by both the variety and equitability of

the species sampled (Krebs 1972), was used to determine species diversity. All species names were derived from *Common Trees of Puerto Rico and the Virgin Islands* (Little and Wadsworth 1964, Little and others 1974).

## RESULTS

### Subtropical Dry Life Zone

Subtropical Dry Forest on limestone occupies 210 km<sup>2</sup> or 13 percent of the Life Zone, which in turn occupies 1650 km<sup>2</sup> or 18 percent of Puerto Rico.

In 1944, 66 stems of *Bucida buceras* were measured in secondary forest; by 1975, only 34 stems remained. Mortality was highest in the small diameter classes, and in the suppressed and intermediate crown classes. Since the plot was dimensionless, ingrowth was impossible to determine.

The PAI for the 34 surviving stems is only 0.06 cm/yr, with dominants averaging 0.11 cm/yr, codominants 0.08, intermediates 0.04, and suppressed stems 0.02 cm/yr (table 2). Previous measurements of PAI on the same plot showed that the "thriftiest and most vigorous" trees averaged only 0.13 cm/yr during the first 17 years of measurement (Briscoe 1962).

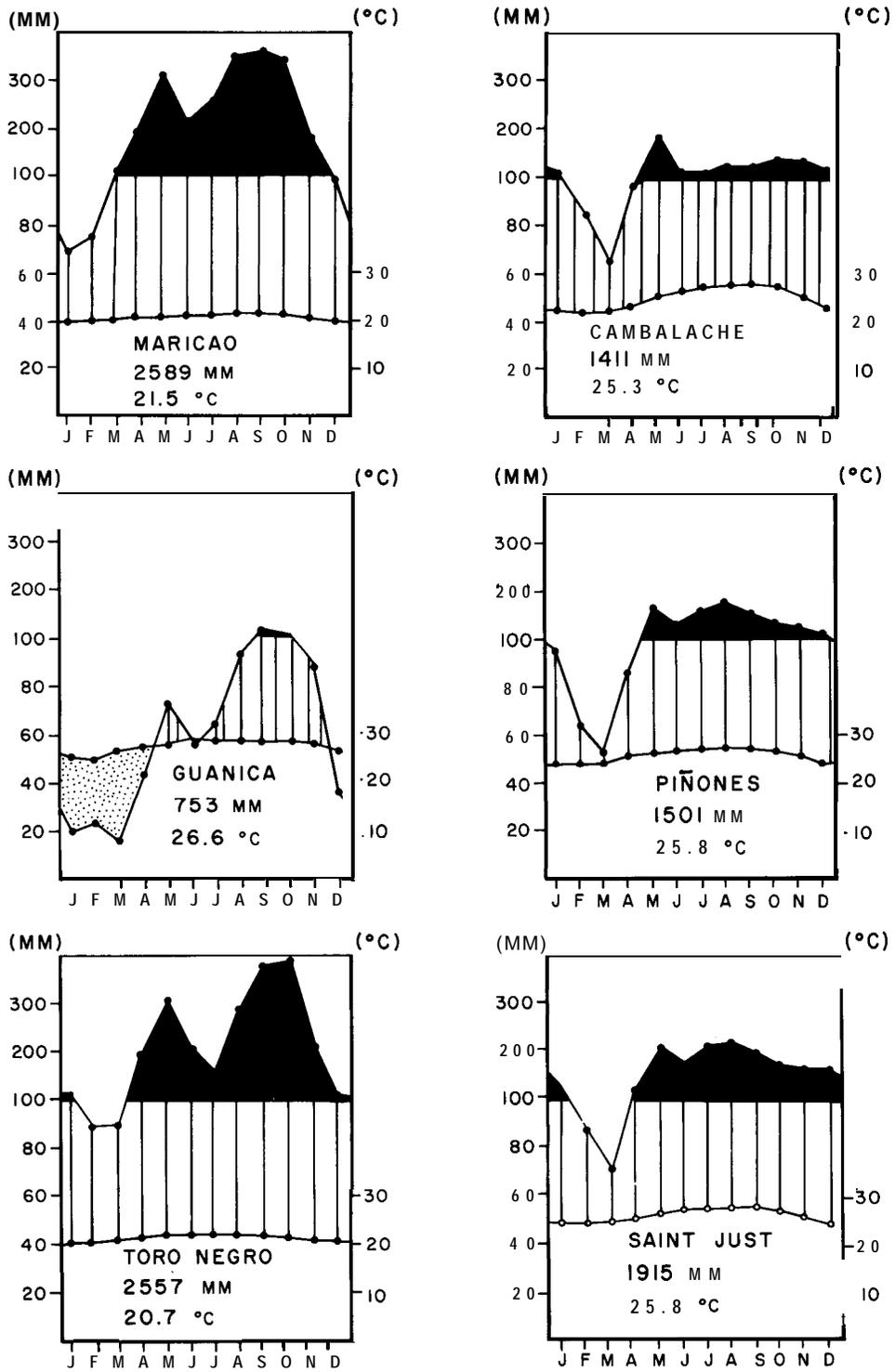


Figure Z.-Climatic diagrams for six plots in natural forests of Puerto Rico.

Table 1.— Selected sites for comparative ecosystem growth study in Puerto Rico

Holdridge Life Zone (association)	Name of public forest and plots	Number of trees	Plot size in ha (m X m)	Plot Data: Seral stage: soils; elevation; silviculture
Subtropical Dry (Limestone)	Guánica	65	None	Secondary; shallow dry limestone; 150 m; none
Subtropical Moist (Rain forest)	St. Just	1018	0.40 (40 x 100)	Early secondary; shallow, humid volcanic; 60 m; selective thinning before study
Subtropical Moist (Limestone)	Cambalache	402	0.10 (20 x 50)	Secondary: lower slopes and ridges of "pepino hills." wet limestone soils; 30 m and 60 m; abandoned agricultural land in mid 1930s
Subtropical Moist (Mangrove)	Piñones		0.10 (31.6 X 31.6)	Mangrove reproduction; deep organic (mangrove) soils; sea level; plot A and plot C basal area reduced by 50 percent in 1937-38 and again in 1949; Plot A thinned to basal area of 20 m <sup>2</sup> /ha in 1951, and Plot C to 14 m <sup>2</sup> /ha; Plot E kept as control
	1. Plot A	3789		
	2. Plot c	4098		
	3. Plot E	3317		
Lower Montane Wet (Colorado)	Toro Negro	245	0.10 (20 x 50)	Late secondary colorado transition; deep, red, acid clay; 930 m; selective thinning in 1947 and 1957
Lower Montane Wet (Colorado)	Maricao	228	0.10 (20 x 50)	Climax: deep, red, acid clay, 670 m; selective thinning in 1951

Table 2.— Periodic annual diameter increment (PAI) by crown class for *Bucida buceras* from 1944 through 1975 in Guánica Forest (Subtropical Dry Forest) on all trees that survived the entire period

Crown Class	1944-54	1954-75	1944-1975 statistics <sup>1</sup>			D.b.h. range 1944 (cm)
			Mean	CV (%)	Stems (No.)	
Dominant	0.20	0.06	0.11	24	4	8-11
Codominant	0.15	0.04	0.08	30	15	6-10
Intermediate	0.08	0.02	0.04	63	13	4- 9
Suppressed	0.04	0.02	0.02	94	2	5
Total	0.12	0.04	0.06	53	34	4-11

<sup>1</sup>CV = Coefficient of variation.

### Subtropical Moist Life Zone

Subtropical Moist Forest occupies 5400 km<sup>2</sup> or 58 percent of the island.

*St. Just.* The St. Just forest is an early secondary stand that was selectively thinned before the first measurement. During 2 years of observation, the number of stems decreased from 2460/ha to 1845/ha, and basal area decreased from 12.2 m<sup>2</sup>/ha to 10.3 m<sup>2</sup>/ha (table 3). In both years, 10 species accounted for 90 percent of the stems and basal area. Ingrowth and mortality did not appreciably change species composition.

The PAI for all 685 stems during the brief 2-year period of measurement was 0.47 cm/yr, and ranged from a low of 0.15 cm/yr to a high of 0.91

cm/yr for *Buchenavia capitata*, a fast growing species (table 3). The codominant crown class averaged 0.66 cm/yr, followed by intermediates at 0.56, dominants at 0.48, and suppressed stems at 0.40 cm/yr.

*The Cambalache Forest.* The Cambalache stand is secondary forest on limestone, which occupies 800 km<sup>2</sup> or 14 percent of the Subtropical Moist Life Zone. Measurements spanned 26 years.

1. The Lower Slope Forest — In 1950, the 10 most common species accounted for nearly 90 percent of the stems and basal area, and by 1976, about 80 percent of each (table 4). During the same period, stems decreased by nearly half while the basal area increased only slightly.

Table 3.— Ranking of species by density and basal area (BA) dominance in St. Just Forest (Subtropical Moist Forest) from 1952 to 1954

Species	1952		1954		Ingrowth <sup>1</sup> 1952-54		Mortality by d.b.h. class, 1952-54 <sup>2</sup>				1952-54 statistics <sup>2</sup>		D.b.h. range	
	Stems	BA	Stems	BA	Stems	BA	5	10	20	Total	Mean	CV	Stems	1952
	(No./ha)	(m <sup>2</sup> /ha)	(No./ha)	(m <sup>2</sup> /ha)	(No./ha)	(m <sup>2</sup> /ha)	No./ha				(cm/yr)	(%)	(No.)	(cm)
<i>Inga laurina</i>	765	3.70	654	3.91	42	0.07	62	83	8	153	0.63	51	242	4-16
<i>Ocotea leucoxylo</i>	355	1.80	213	0.96	13	0.02	58	84	13	155	.38	80	80	4-19
<i>Nectandra coriacea</i>	245	1.30	176	0.74	13	0.02	41	23	18	82	.20	105	64	4-22
<i>Byrsonima coriacea</i>	205	1.40	148	1.01	2	0.00	17	27	15	59	.35	76	56	4-20
<i>Tetragastris balsamifera</i>	198	0.57	172	0.76	28	0.04	43	11		54	.58	42	66	4-20
<i>Casearia arborea</i>	125	0.30	64	0.18	11	0.03	51	21		72	.40	82	23	4-10
<i>Miconia prasina</i>	90	0.19	48	0.11	7	0.05	46	3	—	49	.20	85	16	4-10
<i>Manilkara bidentata</i>	85	0.27	80	0.35		—	5	—		5	.58	35	31	4-13
<i>Hymenaea courbaril</i>	82	1.14	81	1.28	7	0.02	5	3	—	8	.53	78	29	4-45
<i>Casearia guianensis</i>	48	0.09	42	0.01	2	0.00	8	—		8	.25	73	15	4- 8
<i>Chrysophyllum argenteum</i>	45	0.12	29	0.10	2	0.00	16	2		18	.40	52	11	4-12
<i>Andira inermis</i>	39	0.12	35	0.14	3	0.01	7	—		7	.28	99	13	4-12
<i>Symplocos martinicensis</i>	38	0.29	20	0.15		—	2	11	5	18	.28	96	8	4-12
<i>Zanthoxylum martinicense</i>	22	0.15	12	0.05		—	3	5	2	10	.15	77	4	4-16
<i>Buchenavia capitata</i>	18	0.24	15	0.27		—		3		3	.90	38	6	8-22
<i>Pouteria multiflora</i>	15	0.10	13	0.11		—	2	—		2	.38	62	5	4-17
<i>Tabebuia heterophylla</i>	13	0.05	8	0.03		—	2	3		5	.25	100	3	5- 8
<i>Citharexylum fruticosum</i>	12	0.06	5	0.01		—	2	5		7	.12	0	2	4- 7
<i>Ficus citrifolia</i>	10	0.08	5	0.01		—		3	2	5	.12	0	2	4- 5
10 remaining species	49	0.24	26	0.14	2	—	12	11	2	25	.40	72	9	4-18
Total	2459	12.21	1846	10.32	132	0.26	382	298	65	745	0.47	69	685	4-45

<sup>1</sup>Ingrowth refers to stems present in final survey but absent in initial survey; mortality, stems recorded initially but absent in the final survey. Mortality d.b.h. classes increase geometrically from the 5 cm through 20 cm class: 5 cm (4.1-6.5), 10 cm (6.6-14.1), 20 cm (14.2-26.8). Stems which entered the lowest d.b.h. class (i.e. 4.1 cm) after the initial survey, but died before the final survey, were not tallied.

<sup>2</sup>CV = coefficient of variation.

Table 4.— Ranking of species by density and basal area (BA) dominance in the Cambalache Slope Forest (Subtropical Moist Forest) from 1950 to 1976<sup>1</sup>

Species	1950		1976		Ingrowth 1950-76		Mortality by d.b.h. class, 1950-76			Total
	Stems (No./ha)	BA (m <sup>2</sup> /ha)	Stems (No./ha)	BA (m <sup>2</sup> /ha)	Stems (No./ha)	BA (m <sup>2</sup> /ha)	5 -----	10 -----	20 -----	
<i>Tetrazygia elaeagnoides</i>	760	3.64	20	0.12			240	490	10	740
<i>Sabinea florida</i>	620	1.43	490	3.16	120	0.23	140	110		250
<i>Ardisia obovata</i>	580	1.94	40	0.10	30	0.07	250	320		570
<i>Phyllanthus nobilis</i>	430	1.30	300	2.06	110	0.46	140	100		240
<i>Thouinia striata</i>	280	0.63	270	2.28	50	0.22	50	10	—	60
<i>Coccoloba diversifolia</i>	200	0.56	100	0.39	30	0.05	100	30	—	130
<i>Cuettarda scabra</i>	190	0.40	190	0.58	50	0.13	40	10		50
<i>Andira inermis</i>	160	0.49	110	0.56			10	40	—	50
<i>Bursera simaruba</i>	140	0.47	30	0.29			90	20		110
<i>Dipholis salicifolia</i>	130	0.76	100	1.65	—		—	30		30
<i>Eugenia rhombea</i>	60	0.14	30	0.08	30	0.07	30	30		60
<i>Terebraria resinosa</i>	40	0.15	80	1.06	50	0.24		10	—	10
<i>Cupania americana</i>	40	0.08	40	0.25	20	0.03	20	—	—	20
<i>Plumeria alba</i>	40	0.07	10	0.05			30	—		30
<i>Montezuma speciosissima</i>	30	0.13	10	0.13	—	—		20		20
<i>Citharexylum fruticosum</i>	30	0.12	10	0.06	—	—	10	10		20
<i>Cordia nitida</i>	30	0.06	20	0.08				10	—	10
<i>Eupatorium portoricense</i>	30	0.06		—			30	—	—	30
<i>Clusia rosea</i>	20	0.42	10	0.02				—	10	10
<i>Maytenus elliptica</i>	20	0.12	20	0.24	10	0.02	—	10		10
<i>Xylosma buxifolium</i>	20	0.04	30	0.13	10	0.02		—		
<i>Picramnia pentandra</i>	20	0.04	20	0.18				—	—	
<i>Allophylus racemosus</i>	20	0.03	160	0.34	140	0.28		—	—	—
<i>Comocladia glabra</i>	20	0.03	20	0.04	20	0.04	20	—		20
<i>Exothea paniculata</i>	20	0.03	10	0.02	—		10	—		10
<i>Dendropanax arboreus</i>	20	0.03	40	0.18	20	0.03		—		—
11 remaining species	70	0.17	120	0.78	120	0.37	60	10		70
Total	4020	13.34	2280	14.83	810	2.26	1270	1260	20	2550

<sup>1</sup>Ingrowth refers to stems present in final survey but absent in initial survey; mortality, stems recorded initially but absent in the final survey. Mortality d.b.h. classes increase geometrically from the 5 cm through 20 cm class: 5 cm (4.1-6.5), 10 cm (6.6-14.1), 20 cm (14.2-26.8). Stems which entered the lowest d.b.h. class (i.e. 4.1 cm) after the initial survey, but died before the final survey, were not tallied.

Ingrowth and mortality resulted in changes in the dominance ranking: *Tetrazygia elaeagnoides*, *Ardisia obovata*, and *Bursera simaruba*, all secondary species, nearly disappeared from the stand. *Sabinea florida*, *Phyllanthus nobilis*, both present in the original stand, regenerated well.

The PA1 for all stems that survived the short term from 1950 to 1956 was 0.16 cm/yr. Dominants grew fastest at 0.26 cm/yr followed by codominants at 0.22, intermediates at 0.14, and suppressed stems at 0.08 cm/yr. The PA1 for the 150 stems that survived the entire period of measurement was 0.14 cm/yr, and ranged from 0.02 to 0.39 cm/yr (table 5).

2. The Ridge Forest — From 1950 to 1976, the number of stems increased by 10 percent and the basal area by over 50 percent (table 6). In both years, the 10 most common species accounted for

over 95 percent of the stems and basal area.

Ingrowth and mortality, however, changed the dominance ranking: *Ardisia obovata*, a previously abundant secondary species, disappeared entirely from the stand, while *Coccoloba diversifolia*, *Dipholis salicifolia*, *Terebraria resinosa*, *Eugenia rhombea*, *Sabinea florida*, and *Cuettarda scabra*, major constituents of the wet limestone forest type, and all present in the original stand, regenerated well. *Bursera simaruba*, *Andira inermis*, and *Tabebuia heterophylla*, generally recognized as secondary species, regenerated within the stand.

The PA1 for all stems that survived the 1950-56 period was 0.09 cm/yr, with dominants growing the fastest at 0.17 cm/yr followed by codominants at 0.11, intermediates at 0.08, and suppressed stems at 0.03 cm/yr. The PA1 for the 237 trees that survived the entire period of

Table 5.— Periodic annual diameter increment (PAI) by species from 1950 to 1976 in Cambalache Slope Forest (Subtropical Moist Forest) on all trees that survived the entire period

Species	PAI			1950-76 statistics <sup>1</sup>			D.b.h. range 1950 (cm)
	1950-56	1956-67	1967-75	Mean	CV	Stems	
	-----cm/yr-----				(%)	(No.)	
<i>Tetrazygia elaeagnoides</i>	0.20	0.16	0.02	0.12	40	2	7-14
<i>Sabinea florida</i>	.18	.14	.09	.13	55	37	4-18
<i>Ardisia obovata</i>	.08	.12	.08	.09	—	1	6
<i>Phyllanthus nobilis</i>	.19	.12	.14	.14	62	19	4-17
<i>Thouinia striata</i>	.22	.19	.16	.19	57	22	5-18
<i>Coccoloba diversifolia</i>	.05	.05	.06	.06	108	7	4-11
<i>Guettarda scabra</i>	.05	.08	.02	.05	78	14	4- 8
<i>Andira inermis</i>	.14	.05	.04	.07	75	11	4-12
<i>Bursera simaruba</i>	.00	.12	.15	.09	50	3	9-11
<i>Dipholis salicifolia</i>	.31	.17	.11	.19	58	10	8-20
<i>Terebraria resinosa</i>	.24	.47	.40	.39	79	3	5-24
<i>Cupania americana</i>	.29	.22	.19	.23	69	2	8-14
<i>Pluvneria alba</i>	.13	.15	.05	.12	—	1	8
<i>Montezuma speciosissima</i>	.51	.05	.05	.14	—	1	12
<i>Citharexylum fruticosum</i>	.15	.00	.00	.04	—	1	8
<i>Cordia nitida</i>	.10	.10	.00	.07	21	2	6- 7
<i>Clusia rosea</i>	.05	.00	.02	.02	—	1	4
<i>Maytenus elliptica</i>	.83	.00	.00	.22	—	1	16
<i>Xylosma buxifolium</i>	.11	.11	.11	.11	69	2	4- 9
<i>Picramnia pentandra</i>	.25	.23	.14	.20	52	2	8
<i>Allophyllus racemosus</i>	.08	.06	.02	.05	30	2	6
<i>Exothea paniculata</i>	.05	.02	.02	.03	—	1	5
<i>Dendropanax arboreus</i>	.22	.19	.09	.16	9	2	9
<i>Ilex nitida</i>	.12	.33	.20	.24	—	1	10
<i>Phyllanthus nobilia</i>	.36	.25	.18	.25	—	1	12
<i>Zanthoxylum martinicense</i>	.28	.20	.12	.20	—	1	10
Total	.18	.13	.10	.14	76	150	4-24

<sup>1</sup>CV = coefficient of variation.

Table 6.— Ranking of species by density and basal area (BA) dominance in Cambalache Ridge Forest (Subtropical Moist Forest) from 1950 to 1976<sup>1</sup>

Species	1950		1976		Ingrowth 1950-76		Mortality by d.b.h. class, 1950-76			
	Stems	BA	Stems	BA	Stems	BA	5	10	20	Total
	(No./ha)	m <sup>2</sup> /ha)	(No./ha)	(m <sup>2</sup> /ha)	(No./ha)	(m <sup>2</sup> /ha)	-----No./ha-----			
<i>Coccoloba diversifolia</i>	1040	4.12	1580	7.27	910	2.49	100	260	10	370
<i>Ardisia obovata</i>	950	2.56	—	—	—	—	650	300	—	950
<i>Dipholis salicifolia</i>	710	2.50	810	4.94	230	0.91	90	40	—	130
<i>Terebraria resinosa</i>	680	2.02	810	3.93	250	0.68	70	50	—	120
<i>Eugenia rhombea</i>	380	0.65	970	2.34	740	1.53	130	20	—	150
<i>Bursera simaruba</i>	190	0.56	140	0.79	60	0.15	70	40	—	110
<i>Sabinea florida</i>	160	0.31	220	0.62	140	0.28	50	30	—	80
<i>Andira inermis</i>	110	0.52	60	0.33	20	0.04	50	20	—	70
<i>Tabebuia heterophylla</i>	100	0.41	50	0.31	10	0.02	40	10	10	60
<i>Citharexylum fruticosum</i>	90	0.15	40	0.08	20	0.04	60	10	—	70
<i>Guettarda scabra</i>	80	0.13	190	0.40	130	0.27	20	—	—	20
<i>Tetrazygia elaeagnoides</i>	30	0.10	—	—	—	—	10	20	—	30
14 remaining species	50	0.11	250	0.66	220	0.53	—	20	—	20
Total	4570	14.14	5120	21.67	2730	6.94	1340	820	20	2180

<sup>1</sup>Ingrowth refers to stems present in final survey but absent in initial survey; mortality, stems recorded initially but absent in the final survey. Mortality d.b.h. classes increase geometrically from the 5 cm through 20 cm class: 5 cm (4.1-6.5), 10 cm (6.6-14.1), 20 cm (14.2-26.8). Stems which entered the lowest d.b.h. class (i.e. 4.1 cm) after the initial survey, but died before the final survey, were not tallied.

Table 7.— Periodic annual diameter increment (PAI) by species from 1950 to 1976 in Cambalache Ridge Forest (Subtropical Moist Forest) on all trees that survived the entire period

Species	PAI				1950-76 statistics <sup>1</sup>			D.b.h. range
	1950-56	1956-67	1967-75	Mean	CV	Stems	1950	
	cm/yr				(%)	(No.)	(cm)	
<i>Coccoloba diversifolia</i>	0.16	0.09	0.07	0.10	72	67	4-13	
<i>Diphotis salicifolia</i>	.11	.11	.07	.10	74	58	4-14	
<i>Terebraria resinosa</i>	.09	.09	.06	.08	71	56	4-12	
<i>Eugenia rhombea</i>	.06	.09	.05	.07	45	23	4-6	
<i>Bursera simaruba</i>	.07	.14	.12	.12	69	8	4-10	
<i>Sabinea florida</i>	.13	.09	.07	.09	46	8	4-6	
<i>Andira inermis</i>	.02	.01	.00	.01	148	4	5-15	
<i>Tabebuia heterophylla</i>	.08	.14	.14	.13	84	4	5-8	
<i>Citharexylum fruticosum</i>	.00	.05	.02	.03	52	2	4-5	
<i>Guettarda scabra</i>	.05	.05	.00	.03	100	6	4-5	
<i>Myrcia leptoclada</i>	.13	.15	.10	.12	—	1	6	
<i>Picramnia pentandra</i>	.08	.20	.18	.17	—	1	5	
<i>Adelia ricinella</i>	.05	.00	.00	.00	.01	1	5	
Total	.11	.10	.07	.09	74	237	4-15	

<sup>1</sup>CV = the coefficient of variation.

Table 8.— Ranking of species by density and basal area (BA) dominant for all trees from 1938 through 1975 on plots A, C, and E in Piñones Forest

Plot	Species	1938		1945		1949 <sup>1</sup>		1951 <sup>1</sup>		1955		1975	
		Stems (No./ha)	BA (m <sup>2</sup> /ha)	Stems (No./ha)	BA (m <sup>2</sup> /ha)	Stems (No./ha)	BA (m <sup>2</sup> /ha)	Stems (No./ha)	BA (m <sup>2</sup> /ha)	Stems (No./ha)	BA (m <sup>2</sup> /ha)	Stems (No./ha)	BA (m <sup>2</sup> /ha)
A	<i>Laguncularia racemosa</i>	—	26458	18.55	23125	29.73	72	0.61	445	3.67	1285	17.12	
	<i>Avicennia nitida</i>	—	1300	2.43	1198	4.18	322	2.80	438	5.13	395	6.76	
	Total	38920	19.72	27758	20.98	24322	33.91	394	3.41	882	8.80	1680	23.88
C	<i>Laguncularia racemosa</i>	—	39450	20.13	26460	28.79	52	0.38	585	3.21	1448	22.01	
	<i>Avicennia nitida</i>	—	1720	3.42	958	4.91	292	2.96	320	4.20	322	6.68	
	Total	42096	15.15	40720	23.55	27418	33.70	344	3.34	905	7.41	1770	28.69
E	<i>Laguncularia racemosa</i>	—	31615	26.38	22178	30.07	178	1.32	458	3.85	1235	18.04	
	<i>Avicennia nitida</i>	—	698	2.73	435	3.88	395	4.65	405	6.57	260	5.83	
	Total	34092	18.78	32313	29.11	22613	33.95	573	5.97	863	10.42	1495	23.87

<sup>1</sup>The apparent discrepancy between the 1949 and 1951 entries is due to a change in sampling procedure. In 1949, all stems were measured; in 1951, only stems  $\geq 9.1$  cm.

measurement was also 0.09 cm/yr, and ranged from 0.01 to 0.17 cm/yr (table 7).

The PAI for all surviving stems on the slope exceeded that on the ridge. Also, the PAI's of each crown class were higher on the slope than the ridge, and in general, individual species grew faster on the slope. The exceptions were *Coccoloba diversifolia* and *Bursera simaruba* (tables 5 and 7).

Previously reported PAI's also varied by site. Two hundred codominant trees of several species, selected at random, on both lower slope and summit, averaged 0.30 and 0.15 cm/yr respectively, (U.S. Dep. Agric. For. Serv. 1954).

*Piñones Mangrove Forest.* Originally, mangroves covered about 27,000 ha in the Subtropical Moist and Subtropical Dry Life Zones of which slightly over 3000 ha remain today.

In 1937, three plots in the Piñones Forest were cleared (table 1). Regeneration after clearing yielded about 40,000 stems/ha (table 8). In 1945 and 1949, less than 5 percent of the stems were *Avicennia* although the basal area ranged from 10 to 15 percent of the stand. In 1951, after a change in sampling procedure (table 8), 70 percent or more of the total stems  $\geq 9.1$  cm, as well as 80 percent or more of the basal area,

belonged to *Avicennia*. By 1975, *Laguncularia* once again dominated the stand in stem numbers and basal area, although *Avicennia* was well represented among the larger stems.

The PAI of *Avicennia* exceeded that of *Laguncularia* from 1938 to 1955 (table 9), but this trend was reversed from 1955 through 1975. An overall estimate of PAI for both species on all three plots over the 37-year duration of the study is 0.45 cm/yr.

Previously reported mean annual d.b.h. increments (MAI) at Piñones are high. In a sapling stand, dominants averaged 0.82 cm/yr, codominants 0.49, intermediates 0.32, and suppressed stems 0.16 cm/yr during 4 years; in a pole stand these averages were 0.46, 0.40, 0.24, and 0.17, respectively, during 3 years (Wadsworth 1959).

Table 9.—Mean annual diameter increment by species from 1938 through 1975 in Piñones Forest on trees that survived the entire period

Plot	Species	Mean annual diameter increment				Trees <sup>1</sup> (No.)
		1938	1951	1955	1938	
		-51	-55	-65	-75	
-----cm/yr-----						
A	<i>Laguncularia racemosa</i>	0.77	0.42	0.30	0.48	6
	<i>A vicennia nitida</i>	0.79	0.63	0.13	0.42	14
	Subtotal	0.78	0.57	0.18	0.44	20
C	<i>Laguncularia racemosa</i>	0.74	0.62	0.38	0.54	5
	<i>Avicennia nitida</i>	0.85	0.69	0.14	0.46	17
	Subtotal	0.82	0.67	0.19	0.48	22
E	<i>Laguncularia racemosa</i>	0.71	0.36	0.33	0.47	8
	<i>A vicennia nitida</i>	0.97	0.55	0.20	0.51	4
	Subtotal	0.80	0.42	0.28	0.48	12
	Total	0.80	0.58	0.21	0.46	54

<sup>1</sup>More trees survived, but only those trees that could be positively identified by tags were used.

### Lower Montane Wet Life Zone

This Life Zone, scattered in the summits of the Cordillera Central and Luquillo Mountains, occupies 110 km<sup>2</sup> or about 1 percent of the island.

**Toro Negro.** The late secondary colorado forest at Toro Negro was harvested for fence posts in 1947, and had all stems  $\leq$  12 cm removed in 1957.

During the 24-year period of measurement, the number of stems decreased by 30 percent while basal area increased only slightly (table 10). In 1951 and 1975, over 90 percent of the stems and over 85 percent of the basal area belonged to only

10 species. During that same period, ingrowth, mortality, and selective thinning resulted in compositional changes: *Solanum rugosum*, *Cecropia peltata*, *Policourea riparia*, and *Miconia prasina*, secondary species that invaded the plot after thinning, largely disappeared; *Myrcia splendens*, *Byrsonima wadsworthii*, *Guatteria blanii*, and *Ocotea leucoxylon*, all climax species common in the understory, were probably removed in the 1957 thinning of small stems; and, *Micropholis garciniaefolia*, *Dacryodes excelsa*, both climax overstory species, and *Casearia arborea*, a common understory tree in both secondary and climax forests, reproduced well within the stand.

The PAI for all stems that survived the 1951-56 interval was 0.24 cm/yr with codominants growing the fastest at 0.32 cm/yr followed by the intermediates at 0.29, the dominants at 0.25, and the suppressed stems at 0.11 cm/yr. The PAI for the 109 stems that survived the entire period of measurement was 0.15 cm/yr, and ranged from 0.05 to 0.50 cm/yr (table 11).

**Maricao Serpentine Forest.** Serpentine soils occupy 65 km<sup>2</sup> on the island, a small part of which is in the Lower Montane Wet Life Zone. In 1951, suppressed stems were removed on the Maricao plot to provide growing space for remaining trees.

During the 24-year period of measurement, the number of stems decreased by about 10 percent while the basal area increased by over 35 percent (table 12). In 1951 and 1975, the 10 most common species accounted for over 70 percent of the stems and 75 percent of the basal area. Ingrowth, mortality, and the effects of selective thinning had an effect on composition: *Drypetes alba*, a persistent understory climax species, reproduced well. *Pseudolmedia spuria*, *Eugenia jumbos*, *Cecropia peltata*, *Rapanea ferruginea* and *Casearia sylvestris*, all secondary species, as well as nine additional species, regenerated within the stand in limited numbers.

The PAI for all stems that survived the 1951-56 interval was 0.10 cm/yr, with only slight differences among crown classes. Codominants grew the fastest at 0.15 cm/yr followed by dominants at 0.11, suppressed at 0.09, and intermediate stems at 0.08 cm/yr.

The PAI for those stems that survived the entire period of measurement was 0.12 cm/yr and ranged from 0.03 cm/yr for *Ocotea leucoxylon* to 0.58 cm/yr for *Ficus citrifolia*, the strangler fig (table 13).

Table 10.—*Ranking of species by density and basal area (BA) dominance in Toro Negro Forest from 1951 to 1976<sup>1</sup>*

Species	1951		1975		Ingrowth 1951-75		Mortality by d.b.h. class, 1951-75				Total
	Stems	BA	Stems	BA	Stems	BA	5	10	20	40	
	(No./ha)	(m <sup>2</sup> /ha)	(No./ha)	(m <sup>2</sup> /ha)	(No./ha)	(m <sup>2</sup> /ha)	-----No./ha-----				
<i>Micropholis garciniaefolia</i>	1050	6.32	1010	10.41	250	0.48	160	120	10	—	290
<i>Solanum rugosum</i>	390	1.06	10	0.15	10	0.15	170	220	—	—	390
<i>Cecropia peltata</i>	260	2.25	20	0.28	—	—	40	110	90	—	240
<i>Eugenia stahlia</i>	170	1.26	90	1.44	10	0.01	50	40	—	—	90
<i>Dacryodes excelsa</i>	120	5.32	110	5.99	—	—	10	—	—	—	10
<i>Myrcia splendens</i>	100	0.50	—	—	—	—	30	70	—	—	100
<i>Matayba dominguensis</i>	40	2.14	30	1.63	—	—	—	—	—	10	10
<i>Rapanea ferruginea</i>	40	0.11	20	0.49	—	—	—	20	—	—	20
<i>Calycogonium squamulosum</i>	30	0.89	—	—	—	—	10	20	—	—	30
<i>Byrsonima wadsworthii</i>	30	0.56	—	—	—	—	—	20	10	—	30
<i>Guatteria blanii</i>	30	0.31	—	—	—	—	—	30	—	—	30
<i>Casearia arborea</i>	30	0.05	180	0.68	170	0.58	—	20	—	—	20
<i>Didymopanax mortotoni</i>	20	0.26	20	0.46	10	0.20	—	—	10	—	10
<i>Ocotea leucoxyton</i>	20	0.07	—	—	—	—	10	10	—	—	20
<i>Cordia sulcata</i>	20	0.05	10	0.10	—	—	—	10	—	—	10
<i>Palicourea riparia</i>	20	0.03	—	—	—	—	20	—	—	—	20
<i>Miconia prasina</i>	20	0.03	50	0.33	50	0.33	10	10	—	—	20
<i>Cedrela odorata</i>	20	0.03	10	0.13	—	—	10	—	—	—	10
<i>Buchenavia capitata</i>	10	2.06	10	2.47	—	—	—	—	—	—	10
8 remaining species	30	0.10	120	1.01	100	0.57	10	—	—	—	10
Total	2450	23.40	1690	25.57	600	2.32	530	700	120	10	1360

<sup>1</sup>Ingrowth refers to stems present in final survey but absent in initial survey; mortality, stems recorded initially but absent in the final survey. Mortality d.b.h. classes increase geometrically from the 5 cm through 40cm class: 5 cm (4.1-6.5), 10 cm (6.6-14.1), 20 cm (14.2-26.8), 40 cm (26.9-54.6). Stems which entered the lowest d.b.h. class (i.e. 4.1 cm) after the initial survey, but died before the final survey, were not tallied.

Table 11.—*Periodic annual diameter increment (PAI) by species from 1951 through 1976 in Toro Negro Forest on all trees that survived the entire period*

Species	PAI				1951-76 statistics <sup>1</sup>		D.b.h. range	
	1951-56	1956-62	1962-67	1967-75	Mean	CV	Stems	1951
	-----cm/yr-----				-----	(%)	(No.)	(cm)
<i>Micropholis garciniaefolia</i>	0.19	0.18	0.11	0.08	0.14	51	76	5-23
<i>Cecropia peltata</i>	.30	.24	.04	.14	.19	48	2	5-10
<i>Eugenia stahlia</i>	.24	.17	.02	.11	.12	79	8	5-23
<i>Dacryodes excelsa</i>	.12	.08	.10	.09	.09	126	11	10-48
<i>Matayba dominguensis</i>	.32	.28	.22	.16	.25	76	3	10-36
<i>Rapanea ferruginea</i>	.82	.57	.28	.26	.50	18	2	5
<i>Casearia arborea</i>	.55	.40	.22	.04	.27	—	1	5
<i>Didymopanax morototoni</i>	.80	.57	.31	.38	.50	—	1	5
<i>Cordia sulcata</i>	.70	.31	.04	.00	.23	—	1	5
<i>Cedrela odorata</i>	.65	.44	.09	.34	.37	—	1	5
<i>Buchenavia capitata</i>	.10	.18	.31	.20	.20	—	1	51
<i>Guarea ramiflora</i>	.00	.40	.00	.04	.11	—	1	8
<i>Ocotea moschata</i>	.05	.09	.04	.04	.05	—	1	8
Total	.21	.19	.11	.09	.15	71	109	5-51

<sup>1</sup>CV = coefficient of variation.

Table 12.—*Ranking of species by density and basal area (BA) dominance in Maricao Forest from 1951 to 1975<sup>1</sup>*

Species	1951		1975		Ingrowth 1951-75		Mortality by d.b.h. class, 1951-75		
	Stems (No./ha)	BA (m <sup>2</sup> /ha)	Stems (No./ha)	BA (m <sup>2</sup> /ha)	Stems (No./ha)	BA (m <sup>2</sup> /ha)	5	10	Total
							-----No./ha-----		
<i>Micropholis chrysophylloides</i>	280	2.72	200	3.00	30	0.05	40	70	110
<i>Terebraria resinosa</i>	230	1.62	140	1.78	10	0.03	30	70	100
<i>Linociera dominguisis</i>	230	1.31	110	1.50		—	30	90	120
<i>Homalium racemosum</i>	190	0.70	170	1.29	30	0.06	20	30	50
<i>Tabebuia schumanniana</i>	180	0.74	130	0.71	10	0.02	20	40	60
<i>Eugenia stahlii</i>	130	1.10	100	1.40		—	10	20	30
<i>Myrcia splendens</i>	120	0.68	80	0.93	20	0.08	40	20	60
<i>Matayba dominguisis</i>	120	0.47	90	0.76	10	0.03	20	20	40
<i>Cordia borinquensis</i>	50	0.15	20	0.11	—	—	20	10	30
<i>Plumeria alba</i>	40	0.16	40	0.35	—	—	—	—	—
<i>Guettarda ovalifolia</i>	40	0.14	40	0.08	40	0.08	30	10	40
Myrtaceae	30	0.17	30	0.39	—	—	—	—	—
<i>Guatteria blainii</i>	30	0.13	10	0.04	—	—	20	—	20
<i>Ocotea leucoxydon</i>	30	0.07	50	0.12	20	0.03	—	—	—
<i>Myrcia deflexa</i>	30	0.06	40	0.18	20	0.03	10	—	10
<i>Micropholis garciniaefolia</i>	20	0.27	20	0.38	—	—	—	—	—
<i>Coccoloba swartzii</i>	20	0.12	20	0.27	—	—	—	—	—
Lauraceae	20	0.05	10	0.02	—	—	10	—	10
<i>Drypetes glauca</i>	20	0.04	—	—	—	—	20	—	20
<i>Ficus citrifolia</i>	10	0.34	10	0.95	—	—	—	—	—
<i>Drypetes alba</i>	10	0.06	130	0.34	130	0.34	—	10	10
24 remaining species	120	0.39	280	1.06	230	0.59	60	10	70
Total	1950	11.49	1720	15.66	550	1.34	380	400	780

<sup>1</sup>*Ingrowth* refers to stems present in final survey but absent in initial survey; *mortality*, stems recorded initially but absent in the final survey. Mortality d.b.h. classes increase geometrically from the 5 cm to 10 cm class: 5 cm (4.1-6.5), 10 cm (6.6-14.1). Stems which entered the lowest d.b.h. class (i.e. 4.1 cm) after the initial survey, but died before the final survey, were not tallied.

Both plots in the Lower Montane Wet Forest share species, but Maricao contains some that are also found in the drier coastal forests: *Terebraria resinosa*, *Tabebuia schumanniana*, *Guettarda ovalifolia*, *Ocotea cuneata*, *Coccoloba sintenisii*, *Eugenia monticola*, and *Cassipourea elliptica*.

#### Species Diversity on Plots

The number of species per plot ranged from a low of two in the Piñones mangrove forest to a high of 39 at the end of the study in the Maricao serpentine forest (table 14). In the mangrove forest, the Shannon-Weiner species diversity index was below 1.0 and in the Maricao serpentine forest, above 4.0; other forests were intermediate in both species numbers and diversity (table 14).

## DISCUSSION

### Increment

The reported PAI's corroborate previous studies in Puerto Rico and are similar to those of

the temperate zone. For example, *Acer saccharum*, *Quercus rubra*, *Pinus strobus*, and *P. taeda*, common species in the United States, average from 0.15 to 0.50 cm/yr (U.S. Dep. Agric. For. Serv. 1965), even though the growing season ranges from under 200 to 300 days/yr. Furthermore, Jordan (1971) suggests that the rate of woody production in intermediate age stands on mesic sites, regardless of latitude, is similar.

The fastest PAI's for all measured stems were found in St. Just and Piñones forests. St. Just is a selectively thinned early secondary stand measured over 2 years. As the stand develops, competition among stems will probably reduce PAI considerably. The Piñones stands are mangrove regeneration plots that were measured after clearing. An earlier study that summarized the development of the stands from 1938 to 1953 found that the control plot grew rapidly with stems equal in form and quality to the crop trees of the thinned plots (U.S. Dep. Agric. For. Serv. 1954). In 1975, plot C had from 5 to 18 percent more stems, and about 20 percent more basal area

Table 13.— *Periodic annual diameter increment (PAI) by species from 1951 through 1975 in Maricao Forest on all trees that survived the entire period*

Species	PAI			1951-75 statistics <sup>1</sup>			D.b.h. range 1951 (cm)
	1951-56	1956-67	1967-75	Mean	CV	Stems	
	-----cm/yr-----				(%)	(No.)	
<i>Micropholis chrysophylloides</i>	0.09	0.10	0.12	0.11	54	17	5-25
<i>Terebraria resinosa</i>	.13	.09	.09	.10	63	13	5-18
<i>Linocirra dominguensis</i>	.17	.16	.16	.16	56	11	5-12
<i>Homalium racemosum</i>	.12	.12	.20	.15	57	14	5-10
<i>Tabebuia schumanniana</i>	.05	.08	.10	.08	85	12	5-12
<i>Eugenia stahlia</i>	.12	.09	.08	.09	43	10	5-18
<i>Myrcia splendens</i>	.10	.10	.11	.10	45	6	5-18
<i>Matayba dominguensis</i>	.12	.13	.12	.12	92	8	5-10
<i>Cordia boriniensis</i>	.08	.06	.02	.05	42	2	5- 8
<i>Plumeria alba</i>	.06	.07	.23	.15	33	4	5-10
<i>Myrtaceae</i>	.16	.18	.17	.17	61	3	8-10
<i>Guatrria blainii</i>	.00	.15	.09	.09	—	1	5
<i>Ocotea leucoxylo</i>	.03	.02	.05	.03	115	3	5
<i>Myrcia deflexa</i>	.38	.20	.15	.22	—	1	5
<i>Micropholis garciniaefolia</i>	.07	.11	.11	.10	23	2	13
<i>Coccoloba swartzii</i>	.10	.08	.11	.10	17	2	12
<i>Lauraceae</i>	.05	.02	.06	.04	—	1	4
<i>Ficus citrifolia</i>	.50	.64	.55	.58	—	1	20
<i>Buchenavia capitata</i>	.43	.39	.31	.38	—	1	8
<i>Helicteres jamaicensis</i>	.24	.24	.25	.24	—	1	8
<i>Guapira fragans</i>	.05	.05	.03	.04	—	1	5
<i>Ardisia obovata</i>	.00	.05	.18	.07	—	1	8
Total	.11	.11	.13	.12	75	115	5-25

<sup>1</sup>CV = coefficient of variation.

than either A or E, which are remarkably similar (table 8). The effects of selective thinning have not been fully tested in this experiment.

The Guanica plot has the lowest rate of PAI. Since only one species was measured, generalities about the forest are difficult. It may be hypothesized, however, that since *Bucida* is one of the largest stems in the Guanica Forest, its PAI probably exceeds the average for all species. The remaining plots, Cambalache slope and ridge, Toro Negro, and Maricao, are uniform in size, of nearly equal duration of measurement, and have PAI's intermediate between those of St. Just and Guanica.

Comparisons among stands are difficult because of confounding due to many factors (species, soils, seral stages, age of stems, silviculture, and different durations of measurement), yet certain trends seem apparent. Early secondary forests represented by St. Just and Piñones, are comparatively fast growing. The PAI on surviving stems in secondary forests that have been measured over a long period shows a gradual decline probably due to closing of the stand and/or senescence. On Cambalache slope, for example, suppressed stems increased in

Table 14.— *Total numbers of species and Shannon-Weiner diversity indices (H) for several forests in Puerto Rico*

Public forests and plots	No. of Species		H <sup>1</sup>	
	Beginning	End	Beginning	End
St. Just	29	25	3.42	3.28
Cambalache				
1. slope	34	33	3.80	3.96
2. ridge	17	22	3.05	2.91
Piñones	2	2	0.15	0.67
Toro Negro	22	20	2.93	2.38
Mariacao	31	39	4.06	4.32

$$^1H = -\sum_{i=1}^s (p_i)(\log_2 p_i).$$

relative abundance from 20 to 50 percent, on Cambalache ridge from 10 to 20 percent, and at Maricao from 5 to 15 percent: at Toro Negro, 25 percent of the stems were suppressed throughout the period of measurement.

In the wet limestone hills represented by Cambalache, exposed summits have lower PAI's than the slopes, probably because of moisture stress. With ascent of the mountains, PAI's decrease. Saturated soils and reduced solar radiation have been suggested as causes

(Wadsworth 1952). In the dry limestone forest, lack of moisture again hinders tree growth (Lugo *et al.* 1979).

Crown classes appear useful as indicators of growth potential. On limestone soils, PA1 by crown class for all stems, regardless of species exhibits the pattern  $D > CD > I > S$ , probably reflecting the competitive advantage of larger stems in an environment where water is limiting. On mesic sites, the pattern  $CD = D = I > S$  prevails. This pattern does not corroborate previous work in the Subtropical Wet Forest of Luquillo (Crow and Weaver 1977) where  $D > CD > I > S$  was most common. The Luquillo study, however, dealt with thinned "crop trees" by species, whereas this study considered all stems by plot.

Although exceptional rates of growth have been reported for many plantations of exotics in the tropics, PAI's in excess of 1 cm/yr are rare in undisturbed tropical forests (Fernando 1962, Keay 1961, Crow and Weaver 1977). These modest growth rates have been attributed to the energetic costs of plant maintenance necessary for trees to survive in a highly competitive environment (Odum and Jordan 1970, Kira 1969).

Because controls were missing, the selective thinnings practiced in St. Just, Toro Negro, and Maricao do not lead to any firm conclusions about their effect on the residual stands. Nor do the PAI's reported herein reflect the growth potential of the stands under continuous management. First, the thinnings in Toro Negro and Maricao were conducted in stands that were late secondary or climax. Crown growth must be encouraged early in stand development since "big trees are unable to respond to silvicultural treatment much if at all" (Whitmore 1975). Second, as mentioned previously, from 15 to 50 percent of the stems in Cambalache and both montane forests were overtopped. Increment in the suppressed crown class, regardless of environment, is slow in comparison to dominant, codominant, and most intermediate stems.

### Species Diversity

In Puerto Rico, four species dominate mangrove soils: *Rhizophora mangle*, largely limited to the seaward or estuarine fringe; *Conorcarpus erecta*, at the landward edge; and *Laguncularia racemosa* and *Avicennia nitida*, in the central portion, or basin (Wadsworth 1959, Lugo and Snedaker 1974). The latter two species

probably constitute 95 percent of the stems in the Piiiones Forest.

In the Cambalache Forest, species numbers and diversity indices are greater on slopes than on ridges. This reflects the severe stress caused by well-drained limestone soils on the exposed hilltops (table 14). The comparatively low values for St. Just and Toro Negro are probably due to the selective removal of certain species during the improvement cuttings.

In the colorado type, which corresponds to the mature vegetation of the zonal association within the Subtropical Wet Life Zone, 57 species have been identified (Wadsworth 1951). The high number of species and high species diversity index on the Maricao plot (table 14) could reflect the well-drained and well-aerated nature of these serpentine soils (Tschirley *et al.* 1970). The sharing of species between the Cambalache and Maricao forests supports this hypothesis.

Investigations of species diversity within the southern mixed hardwoods and mixed mesophytic forest of the United States yielded indices from 2.0 through 3.4, with most values below 3.0 (Monk 1967). Within the tropics, Jin-, Bee (1960) reported that the mangrove forests of the Malay peninsula contained 17 principal species, and that a typical 0.4 ha patch of lowland rain forest would contain about 200 trees of about 100 species. Although direct comparisons are difficult to make, the forests of Puerto Rico apparently are intermediate in diversity between continental temperate and continental tropical forests.

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Presents periodic annual diameter increment for about 2400 stems  $\geq$  4.1 cm d.b.h., which were studied for periods ranging from 2 to 30 years. Over 100 tree species and three Life Zones on the island are represented.

Additional keywords: diameter increment, species composition, basal area, ingrowth, mortality, species diversity.

