

Secondary Subtropical Dry Forest at the La Tinaja Tract of the Cartagena Lagoon National Wildlife Refuge, Puerto Rico

PETER L. WEAVER¹ AND J. DANILO CHINEA²

¹International Institute of Tropical Forestry, USDA Forest Service, Río Piedras, Puerto Rico 00928-5000

²Biology Department University of Puerto Rico, Mayagüez, Puerto Rico 00681-9012

ABSTRACT.—A vegetation survey using 109 circular plots (3.4% sample) of the recently acquired 110-ha La Tinaja tract in the Cartagena Lagoon Wildlife Refuge disclosed 103 dicotyledonous tree species. Another 58 tree species were tallied within the tract but outside of the plots. The cactus, *Pilosocereus royenii* (L.) Byles & Rowley, occurring on 44% of the plots, had the greatest number of stems. *Leucaena leucocephala* (Lam.) DeWit had the greatest number of individual trees. The 10 most common tree species accounted for nearly 60% of the stems, and the 43 least common species, each with ≤ 5 individuals, for only 2.2% of the stems. Five species accounted for 58.5% of the total basal area, and 19 species were represented by a single plant. Seven endemic, 20 exotic, and three endangered species were tallied. A canonical correspondence analysis (CCA version 4, using a direct gradient analysis of species densities by plot) showed that land use history was the most important factor in explaining species' distribution. Slope and distance to drainages also added significantly to the explained variability. Aerial photos from 1998 show that the current ground cover is about 50% shrubs, 43% open canopy forest, and 7% grass cover.

INTRODUCTION

The U.S. Department of the Interior Fish and Wildlife Service manages three properties totaling 1,120 ha in southwestern Puerto Rico, among them the La Tinaja (hereafter, Tinaja) tract acquired in 1996. Tinaja, once covered by dry forest, was used during the 20th century for timber removal, fuel wood harvest, and livestock grazing similar to the activities that occurred in the nearby Guánica Forest (Wadsworth 1990). Several years ago, the upper slopes were abandoned and reverted to shrubs and secondary tree species. Grazing continued for a longer period on Tinaja's lower slopes where the most recent burn, about 15 ha, occurred in 1997.

One of the major goals of the Fish and Wildlife Service is the protection of wildlife habitat. An initial survey of the tract's vegetation disclosed 196 species in 59 families, with 9 species or varieties endemic to Puerto Rico (Proctor 1996). The relative abundance of tree species and the recovery rate in different parts of the tract were unknown. Our objectives were to initiate permanent monitoring of the vegetation, to de-

termine tree species diversity, and to explore tree species-site relationships as influenced by past land use, topographic features, and elevation.

SETTING

The Tinaja tract of the Cabo Rojo National Wildlife Refuge occupies 110 ha in the Subtropical Dry Forest Life Zone (Holdridge 1967; Ewel and Whitmore 1973) of southwestern Puerto Rico. Tinaja's long dimension measures 1.6 km and ranges from 20 to 290 m in elevation (Fig. 1). The highest point on the property lies a few meters below Cerro Mariquita, the highest peak in the Sierra Bermeja range. The northern-most 20% of the tract is gently sloped and contrasts with the higher, steeper, southern portion. Drainages are prominent at middle to lower elevations.

The mean annual temperature at Tinaja is about 27°C (Calvesbert 1970). The nearest rain gauges to Tinaja are located at Cabo Rojo, about 7 km to the west, and at Carta-

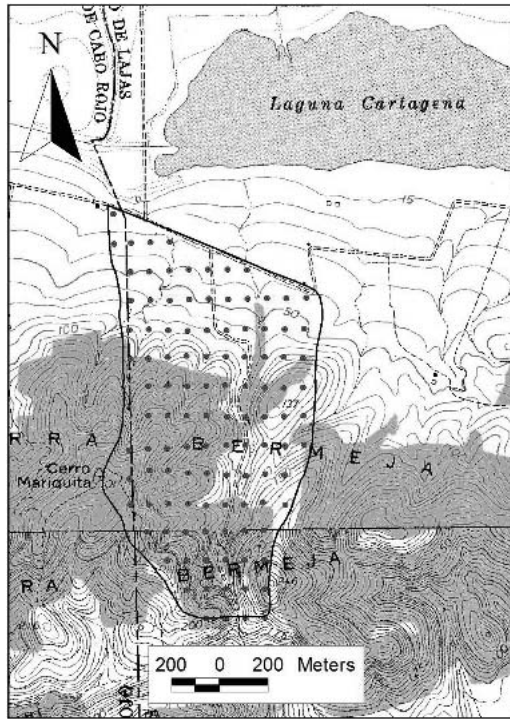


FIG. 1. Location of the 109 circular sampling plots on the Tinaja tract in 1998. The plots, geographically referenced, are superimposed on a U.S. Geological Survey topographic map. Shading indicates the amount of forest or shrub cover in 1966.

gena Lagoon, about 1 km to the north. During the 10-year period between 1991 and 2000, mean annual rainfall at Cabo Rojo, averaged about 840 mm/yr (Table 1). For the same period, mean annual rainfall at Cartagena Lagoon, averaged about 1040

mm/yr. Rainfall at Cabo Rojo averaged 81% of that at Cartagena Lagoon, ranging from 65% to 90%. At Cabo Rojo, rainfall in particular years varied from 55 to 175% of the 10-year mean (Table 1). At Cartagena Lagoon, the range was from 68 to 162%. The driest and wettest years during the period were 1997 and 1998, respectively.

Puerto Rico's southwest has escaped most of the island's major hurricanes during the past three centuries (Salvia 1972), but recently two traversed the region. The first, Hortense, passed over on September 10, 1996 (Monzón 1996). A category 1 hurricane on the Saffir-Simpson Scale, it had sustained winds of 135 km/hr. The second, Georges, a category 3 hurricane with sustained winds of 180 km/hr, traversed the area on September 22, 1998 (USGS 1999). Both hurricanes caused flooding, uprooted trees, and damaged crowns and branches.

Vegetative cover on Tinaja is not uniform. In general, mid- to high-elevation slopes on the tract have tree and shrub cover (Fig. 1). Some upper ridges are occupied by shrubs and grass cover and the lower portion of the tract, grazed sporadically until 1996, is mainly in shrubs and grass, with some scattered trees. In all instances, trees growing along drainages, or along tract boundaries at lower elevation, are larger.

Three major rock types occur in Tinaja (Volckmann 1984a, 1984b). Mariquita chert, lower Cretaceous and Upper Jurassic in age, occupies about 90% of the area. Maguayo porphyry, lower Cretaceous in origin, covers about 9%, and serpentine,

TABLE 1. Comparison of rainfall records between Cabo Rojo and Cartagena Lagoon.

Refuge	Rainfall (mm) by year										
	1991	1992	1993	1994	1995	1996	1997	1998	1990	2000	Mean ¹
Cabo Rojo	575	1032	870	715	668	877	459	1464	740	980	838
Cartagena	707	1149	1135	870	918	878	709	1687	1140	1094	1039
Percentage ²	81	90	77	82	73	90	65	87	65	90	81
Percentage ³											
Cabo Rojo	69	123	104	85	80	104	55	175	88	117	100
Cartagena	68	111	109	84	88	94	68	162	110	105	100

¹Mean for 10 years; data recorded by Fish and Wildlife Service.

²Percentage is the annual rainfall at Cabo Rojo divided by corresponding annual rainfall at Cartagena Lagoon.

³Percentage is the rainfall in the cited year divided by the 10-year mean annual rainfall on the same refuge.

lower Cretaceous and Upper Jurassic in age, covers <1% of the area.

The lower, 5 to 12% slopes of Tinaja, have alluvial and colluvial, gravelly clay loam soils (Carter 1965). Higher elevations, with slopes ranging from 5 to 60%, are comprised mainly of cherty clay loams. Outcrops of acid volcanic rock also cover small areas at middle to higher elevations.

METHODS

From April to June 1998, 109 circular plots (a 3.4% sample) were systematically sampled and geographically referenced (GPS readings) throughout the Tinaja tract (Fig. 1). Each plot, permanently marked with a 1.9 cm reinforcement bar as a center stake, measured 10 m in radius, or 0.0314 ha in size. All individual stems ≥ 2.5 in cm dbh (diameter at breast height), including multiple stems arising from a single tree at ground level, were identified to species and measured with a diameter tape or calipers to the nearest 0.1 cm, but not tagged. Heights were estimated to the nearest 0.1 m with a height pole or rangefinder. The position of the crowns in the canopy (Baker 1950) were noted as dominant, codominant, intermediate, or suppressed. Plot environmental data were also recorded: elevation in meters, percent slope, aspect in degrees, and topographic features (ridge, mid-slope, drainage, and combinations such as ridge-upper slope and lower slope-drainage). All trees were identified and classified using Little and Wadsworth 1964; Little et al. 1974; Little and Woodbury 1980; Liogier 1985-97 and Francis and Liogier 1991. Tree species growing between the plots, if not previously tallied, were also recorded. Aerial photos taken in 1936, 1977, and 1998 were examined to classify Tinaja's vegetation into three broad categories: grass cover, shrubs, and forest.

A canonical correspondence analysis (CCA version 4) using a direct gradient analysis of species densities by plot (ter Braak and Smilauer 1998) was employed to determine the geophysical and land-use history correlates of compositional variability. Prior to vegetation analyses, all uniden-

tified and rare species that occurred in less than 5% of the samples were removed. Editing reduced the original data matrix from 109 plots and 103 species to 97 plots and 40 species for the analysis. All species recorded in the 109 plots are listed in Table 2. Five independent variables were used: land use history, distance to roads, elevation, percent slope, and distance to drainages. Land use history was determined from land use maps based on aerial photos in 1936, 1977, and 1998. The data were digitized and geo-referenced and areas were calculated from the GIS data layer. CCA was performed through forward selection of the independent variables. A Monte Carlo permutation test evaluated their significance with 1,000 random permutations at a 5% confidence level. Geological and edaphic variables were not used in the analyses. These variables are strongly related spatially to the distribution of slopes and elevations and their inclusion would not improve the results.

The samples were also classified by species matrix with a K-means procedure (Legendre and Legendre 1998) to detect community types and their distinct species assemblages. One procedure calls for several classification runs with different numbers of clusters, the most meaningful run being selected through an objective index. We selected the run that maximized the sum of squared distances of the samples to their group's own class centroids. This procedure was used to generate a maximum of 20 clusters and a minimum of two. The runs were repeated by initially assigning samples to the cluster centroids a 100 times at random to avoid local minima. Distinct species were determined by computing the difference in percentage occurrence of a species within a pair of clusters. An arbitrary value of 25% difference was considered sufficiently large to distinguish these species.

RESULTS

The aerial photos showed that the current ground cover is about 50% shrubs, 43% open canopy forest, and 7% pasture. Survey totals from the sample plots revealed

TABLE 2. Complete tree species list for La Tinaja, ranked by stem numbers, with information on size and occurrence.^{1,2}

Species name	Stems (no.)	Trees (no.)	Maximum size ³		Basal area (m ² /ha)	Plots ⁴ (%)
			Diameter (cm)	Height (m)		
<i>Pilosocereus royerii</i> (L.) Byles & Rowley	819	271	13.6	6.5	1.066	49
<i>Trichilia hirta</i> L.	336	136	15.6	11.0	0.194	33
<i>Leucaena leucocephala</i> (Lam.) DeWit ⁵	335	319	9.3	7.5	0.162	33
<i>Pithecellobium dulce</i> (Roxb.) Benth ⁵	333	86	32.3	8.2	0.235	32
<i>Guapira fragrans</i> (Dum. Cours) Little	308	225	29.4	11.0	0.524	25
<i>Hymenaea courbaril</i> L.	294	168	48.7	12.5	0.814	20
<i>Eugenia pseudopsidium</i> Jacq.	291	243	11.4	8.5	0.139	16
<i>Clusia rosea</i> Jacq.	215	124	27.8	12.5	0.524	24
<i>Securinega acidoton</i> (L.) Fawl. & Rendle	192	120	9.5	10.0	0.105	28
<i>Myrciaria floribunda</i> (West ex Willd.) Berg.	155	77	12.4	6.5	0.053	15
<i>Prosopis juliflora</i> (Sw.) DC. ⁵	133	44	19.0	8.0	0.122	16
<i>Eugenia biflora</i> (L.) DC.	129	89	8.4	8.0	0.051	22
<i>Bucida buceras</i> L.	119	25	55.0	17.0	0.762	13
<i>Bursera simaruba</i> (L.) Sarg.	91	77	44.3	12.0	0.336	25
<i>Acacia farnesiana</i> (L.) Willd. ⁵	74	22	7.6	4.5	0.019	10
<i>Coccoloba microstachya</i> Willd.	73	24	7.8	6.5	0.038	6
<i>Bourreria succulenta</i> Jacq.	72	45	24.2	13.0	0.157	18
<i>Capparis indica</i> (L.) Fawc. & Rendle	68	43	15.7	6.5	0.048	19
<i>Capparis amplissima</i> Lam.	63	46	26.1	11.5	0.058	15
<i>Leptocereus quadricostatus</i> (Bello) Britton & Rose ⁶	60	41	9.2	4.2	0.036	7
<i>Capparis baducca</i> L.	59	49	5.3	6.5	0.150	10
<i>Melicoccus bijugatus</i> Jacq.	49	28	18.9	11.0	0.074	7
<i>Capparis hastata</i> Jacq.	48	31	11.2	5.0	0.024	8
<i>Amyris elemifera</i> L.	45	23	8.7	6.0	0.021	11
<i>Andira inermis</i> (W. Wright) HBK	44	33	28.2	13.0	0.215	8
<i>Zanthoxylum monophyllum</i> (Lam.) P. Wilson	44	15	15.0	7.5	0.033	9
<i>Erythroxylum rotundifolium</i> Lunan	40	26	5.7	5.0	0.011	14
<i>Eugenia woodburyana</i> Alain ^{6,7}	36	13	8.5	8.0	0.017	6
<i>Machaonia portoricensis</i> Baill. ⁶	33	13	7.4	5.5	0.010	6
<i>Randia aculeata</i> L.	33	24	5.6	7.0	0.010	13
<i>Licaria parvifolia</i> (Lam.) Kostermans	32	18	10.2	7.5	0.023	6
<i>Coccoloba swartzii</i> Meisner	28	16	20.5	11.0	0.042	3
<i>Thouinia striata</i> Radlk. ⁶	28	9	4.4	5.3	0.007	6
<i>Guaiacum officinale</i> L.	27	7	19.0	17.0	0.071	4
<i>Piscidia carthaginensis</i> Jacq.	27	10	10.9	6.0	0.015	3
<i>Guazuma ulmifolia</i> Lam.	26	14	33.1	10.5	0.091	2
<i>Exostema caribaeum</i> (Jacq.) R&S	25	17	18.9	10.0	0.021	6
<i>Ouratea littoralis</i> Urban	24	11	8.8	4.5	0.009	6
<i>Albizia lebbek</i> (L.) Benth ⁵	21	18	23.2	9.5	0.084	6
<i>Myrcianthes fragrans</i> (Sw.) McVaugh	21	11	6.0	5.0	0.008	6
<i>Citharexylum fruticosum</i> L.	20	13	12.7	9.5	0.014	10
<i>Rauwolfia nitida</i> Jacq.	17	4	30.9	7.5	0.030	4
<i>Cordia alliodora</i> (R. & P.) Oken	15	14	12.5	8.5	0.019	6
<i>Tetragastris balsamifera</i> (Sw.) Kuntze	15	6	15.2	10.0	0.036	1
<i>Capparis flexuosa</i> L.	14	7	7.0	4.5	0.006	6
<i>Calotropis procera</i> (Ait.) f. ⁵	14	11	9.5	5.0	0.009	4
<i>Krugiodendron ferreum</i> (Vahl) Urban	14	12	19.5	6.5	0.019	4
<i>Guettarda elliptica</i> Sw.	13	3	4.6	6.0	0.004	2
<i>Celtis trineroia</i> Lam.	11	4	10.5	11.5	0.011	4
<i>Plumeria alba</i> L.	10	9	7.9	3.9	0.005	5
<i>Erithalis fruticosa</i> L.	9	1	14.5	5.7	0.011	1

TABLE 2. Continued.

Species name	Stems (no.)	Trees (no.)	Maximum size ³		Basal area (m ² /ha)	Plots ⁴ (%)
			Diameter (cm)	Height (m)		
<i>Eugenia rhombea</i> (Berg) Krug & Urban	9	6	6.2	8.0	0.004	1
<i>Casearia aculeata</i> Jacq.	8	5	5.4	6.0	0.003	2
<i>Guettarda scabra</i> (L.) Vent.	8	8	5.1	4.2	0.002	3
<i>Myrcia citrifolia</i> (Aubl.) Urban	8	5	6.2	5.6	0.003	3
<i>Schaefferia frutescens</i> Jacquin	8	3	3.8	4.0	0.002	2
<i>Vitex divaricata</i> Sw.	7	5	17.1	5.0	0.015	3
<i>Coccoloba diversifolia</i> Jacq.	6	4	8.1	7.0	0.003	2
<i>Gymnanthes lucida</i> Sw.	6	6	6.8	6.0	0.002	3
<i>Savia sessilifolia</i> (Sw.) Willd.	6	4	4.0	4.0	0.001	2
<i>Zanthoxylum martinicense</i> (Lam.) DC.	6	4	25.9	9.5	0.039	3
<i>Bauhinia monandra</i> Kurz. ⁵	5	3	7.7	5.4	0.001	1
<i>Pictetia aculeata</i> (Vahl) Urban	5	3	9.5	10.0	0.003	2
<i>Spondias mombin</i> L.	5	4	25.8	11.5	0.021	2
<i>Tamarindus indica</i> L. ⁵	5	4	3.9	5.0	0.001	2
<i>Garsinia hessii</i> Britton (Alain) ⁶	4	4	11.0	3.8	0.002	1
<i>Rochefortia acanthophora</i> (DC.) Griseb.	4	1	5.0	5.0	0.002	1
<i>Sabinea florida</i> (Vahl) DC.	4	4	4.9	4.0	0.001	4
<i>Ziziphus reticulata</i> (Vahl) DC.	4	1	6.0	6.0	0.003	1
<i>Coccoloba venosa</i> L.	3	3	6.5	7.0	0.002	1
<i>Faramea occidentalis</i> (L.) A. Rich.	3	2	2.8	4.5	—	1
<i>Forestiera segregata</i> (Jacq.) Krug & Urban	3	2	3.9	5.0	0.001	1
<i>Lantana camara</i> L. var. <i>camara</i>	3	3	2.8	3.2	—	3
<i>Lonchocarpus domingensis</i> (Pers.) DC.	3	1	19.9	7.0	0.014	1
<i>Polygala penaea</i> L.	3	2	7.5	4.0	0.002	2
<i>Samyda dodecandra</i> Jacq.	3	3	2.6	3.6	—	3
<i>Capparis cynophallophora</i> L.	2	2	7.0	4.0	0.001	2
<i>Clusia minor</i> L.	2	2	11.7	9.5	0.006	2
<i>Cordia collococca</i> L.	2	2	42.0	15.0	0.046	2
<i>Comocladia dodonaea</i> (L.) Urban	2	2	4.4	2.5	0.001	1
<i>Gyminda latifolia</i> (Sw.) Urban	2	1	2.8	4.0	—	1
<i>Manilkara pleeana</i> (Pierre) Cron. ⁷	2	1	13.3	7.9	0.008	2
<i>Petitia domingensis</i> Jacq.	2	2	4.9	3.7	0.001	1
<i>Psychotria microdon</i> (DC.) Urban	2	2	3.0	5.0	—	2
<i>Byrsonima spicata</i> (Cav.) HBK.	1	1	2.5	3.0	0.001	1
<i>Castela erecta</i> Turb.	1	1	3.1	3.5	0.002	1
<i>Ceiba pentandra</i> (L.) Gaertn.	1	1	77.0	20.0	0.134	1
<i>Chionanthus compacta</i> Sw.	1	1	4.7	6.0	0.001	1
<i>Chrysolobanus icaco</i> L.	1	1	2.9	2.4	0.002	1
<i>Chrysophyllum oliviforme</i> L.	1	1	2.5	4.0	—	1
<i>Cordia laevigata</i> Lam.	1	1	11.8	9.5	0.001	1
<i>Cordia rickseckeri</i> Millsp.	1	1	13.8	8.5	0.001	1
<i>Croton astriotes</i> Dryand.	1	1	4.2	3.3	—	1
<i>Croton rigidus</i> (Muell. Arg.) Britton	1	1	2.7	3.3	—	1
<i>Cupania americana</i> L.	1	1	7.7	6.5	—	1
<i>Erythroxylum rufum</i> Cav.	1	1	2.8	2.0	—	1
<i>Eugenia ligustrina</i> (Sw.) Willd.	1	1	6.0	7.0	0.001	1
<i>Ficus citrifolia</i> Mill.	1	1	5.0	5.0	0.001	1
<i>Jaquinia armillans</i> Jacq.	1	1	4.6	3.2	0.001	1
<i>Margaritaria nobilis</i> L.f.	1	1	2.7	3.0	—	1
<i>Morinda citrifolia</i> L. ⁵	1	1	15.1	8.5	0.001	1
<i>Rauwolfia viridis</i> Willd. ex. Roem. & Schult	1	1	3.7	2.4	—	1
<i>Trichilia pallida</i> Sw.	1	1	6.4	4.0	0.001	1

TABLE 2. Continued.

Species name	Stems (no.)	Trees (no.)	Maximum size ³		Basal area (m ² /ha)	Plots ⁴ (%)
			Diameter (cm)	Height (m)		
Unknowns	4	4	6.5	6.5	0.003	2
Totals/mean ⁸	5,170	2,817	—	—	6.883	—
Totals/mean ⁸	4,351	2,546	—	—	5.817	—

¹Stem numbers: includes cactus species, tree species, and brush species where all vertical stems emerging from below dbh are tallied as separate stems. Tree numbers refers to the number of trees tallied, many of which contain multiple stems. The classification of plants as trees is based on Little and Wadsworth 1964 and Little et al. 1974.

²The data are for the entire 110 ha Tinaja tract of which 3.423 ha were sampled (a 3.11% sample).

³Maximum dbh and height sizes not necessarily for the same tree.

⁴Percent of plots on which species occurs, rounded to nearest integer.

⁵Exotic species.

⁶Endemic species.

⁷On Puerto Rican critical species list.

⁸Totals for stems (column 1) and trees (column 2) and mean values for basal area (column 5): upper value includes *Pilosocereus royenii*; lower values omits *Pilosocereus royenii*.

103 dicotyledonous tree species represented by 2,817 individual trees with 5,170 stems at breast height (Table 2). An additional 54 tree species were recorded between the plots (Appendix Table A). *Pilosocereus royenii* (L.) Byles & Rowley had the greatest number of stems and *Leucaena leucocephala* (Lam.) DeWit the greatest number of trees. The 10 most common tree species accounted for 59.6% of the stems and the 43 least common species, each with ≤ 5 individuals, for only 2.2% of the stems. Nineteen species were represented by a single tree.

Multiple stems below breast height were common. The average number of stems per tree was 1.84 when *P. royenii* was included (Table 2, totals), and 1.71 without it in the calculations. Of the 40 dicotyledonous species with stems recorded ≥ 20 times, *Bucida buceras* L., *Guaiacum officinale* L., *Pithecellobium dulce* (Roxb.) Benth., *Acacia farnesiana* (L.) Willd., *Thouinia striata* Radlk., and *Coccoloba microstachya* Willd., (in descending order) had stem-to-tree ratios ≥ 3.0 (Table 2).

The largest tree tallied was a *Ceiba pentandra* (L.) Gaertn. measuring 77.0 cm in dbh and 20 m in height (Table 2). Other sampled species >40 cm in dbh included one individual each of *B. buceras*, *Cordia collococca* L., *Hymenaea courbaril* L., and *Bursera simaruba* (L.) Sarg. About one-third of the

stem dbhs were between 2.5 and 3.9 cm, and $>90\%$ were <10 cm (Table 3). More than one-half of the stem heights were between 2.0 and 3.9 m, and $>95\%$ were <8 m (Table 3). Five species, *P. royenii*, *H. courbaril*, *B. buceras*, *Guapira fragrans* (Dum. Cours) Little, and *Clusia rosea* Jacq., ac-

TABLE 3. Distribution of stem heights and diameters at La Tinaja.

Category size class	Stems (no.)	%
Height (m)		
<2.0	304	5.9
2.0-3.9	2,442	47.3
4.0-5.9	1,660	32.1
6.0-7.9	534	10.3
8.0-9.9	150	2.9
10.0-11.9	53	1.0
12.0-13.9	20	0.4
≥ 14.0	7	0.1
Totals	5,170	100.0
Diameter (cm)		
2.5-3.9	1,764	34.1
4.0-5.9	1,456	28.2
6.0-7.9	956	18.5
8.0-9.9	488	9.5
10.0-11.9	168	3.2
12.0-13.9	95	1.8
14.0-15.9	70	1.4
16.0-17.9	39	0.8
18.0-19.9	37	0.7
20.0-29.9	75	1.4
≥ 30.0	22	0.4
Totals	5,170	100.0

counted for 58.5% of the total basal area (Table 2).

The mean density for the entire tract, including *P. royenii*, was estimated at 1510 stems/ha (Table 2), and 823 trees/ha. When *P. royenii* was removed from the totals, the estimates were 1271 stems/ha and 744 trees/ha, respectively. Individual plot values for stem density ranged from 0 to 5,350/ha.

The mean basal area for the entire tract, including *P. royenii*, was 6.88 m²/ha (Table 2). Individual plot values for basal area ranged from 0 to 28.01 m²/ha. Classification of crown position of each stem showed that 14% were dominant or co-dominant, 48% intermediate, and 38% suppressed.

Pilosocereus royenii was the best distributed species, occurring on nearly one-half of the plots (Table 2). *Trichilia hirta* L., *L. leucocephala*, *P. dulce* grew on one-third of the plots, and *G. fragrans* on one-quarter of them (Table 2). Fifty-five percent of the species were confined to three percent of the plots. Seven endemic species were recorded: *Eugenia woodburyana* Alain, *Garcinia hessii* Britton (Alain), *Leptocereus quadricostatus* (Bello) Britton & Rose, *Machaonia portoricensis* Baill., and *Thouinia striata* (Table 2); and *Rondeletia inermis* (Spreng.) Krug & Urban and *Tabebuia haemantha* (Bert.) DC. (Appendix Table A). *Eugenia woodburyana* with 13 trees and 36 stems and *Manilkara pleeana* (Pierre) Cron. with 1 tree and 2 stems (Table 2), and *Bourreria virgata* (Sw.) G. Don (Appendix Table A) sighted once between plots, are considered endangered. *Eugenia woodburyana* was concentrated in open forest on the east-facing slopes of Cerro Mariquita between 150 and 200 m. Because of the paucity of stems, it is impossible to generalize on the occurrences of the remaining endangered species.

Twenty exotics accounted for 12% of all recorded species. They were: *Acacia farnesiana* (L.) Willd., *Albizia lebbek* (L.) Benth., *Bauhinia monandra* Kurz, *Calotropis procera* (Ait.) f., *L. leucocephala*, *Morinda citrifolia* L., *Pithecellobium dulce*, *Prosopis juliflora* (Sw.) DC., and *Tamarindus indica* L. (Table 2); and *Citrus aurantifolia* L., *Delonix regia* (Bojer ex Hook) Raf., *Gliricidium sepium* (Jacq.) Kunth ex Walp, *Mangifera indica* L., *Melicoccus bi-*

jugatus Jacq., *Persea americana* Miller, *Pithecellobium saman* (Jacq.) Merr., *Psidium guajava* L., *Ricinus communis* L., *Spathodea campanulata* Beauv., and *Terminalia cattapa* L. (Appendix Table A). Exotic species comprised 17.8% of the tallied stems when cactus was included and 21.2% when cactus was excluded; similarly, exotics accounted for 18.0% of the tallied trees with cactus, and 20.0% without cactus (Table 2).

CANOCO forward selected percent slope, distance to drainages, and history of pasture changing to shrub, all non-correlated variables, and prior to the ordinations (Fig. 2). This combination of variables explained 13% of variance in species abundance. Species composition was also significantly explained by elevation but since elevation was strongly correlated with slope it was not included in the final analysis. The first axis of the ordination explained eight percent of the total variance (Monte Carlo permutation test; $p = 0.001$) while the second axis explained an additional four percent. The first axis showed a strong negative correlation with slope and a positive correlation with the history of pasture changing to shrub.

The most effective K-means classification resulted from generating two clusters. Cluster I samples occurred mostly on sites changing from pasture to shrub. Samples were commonly on flatter ground (with mean slope of 7 degrees) and closer to drainages (mean distance 105 m). Cluster II samples had a mean slope of 25 degrees and a mean distance to drainages of 194 m. Cluster I is characterized by a distinct community of two naturalized tree species, *P. juliflora* and *A. farnesiana*, and a few other generalist species such as *P. dulce*. In contrast, Cluster II was characterized by five native species *P. royenii*, *T. hirta*, *B. simaruba*, *C. rosea*, and *G. fragrans*, and by one naturalized species, *L. leucocephala*. Cluster II had five other species with at least 25% frequency, and several others of lower frequency.

DISCUSSION

Of the 161 tree species tallied in the survey, 141 were natives (Table 2; Appendix

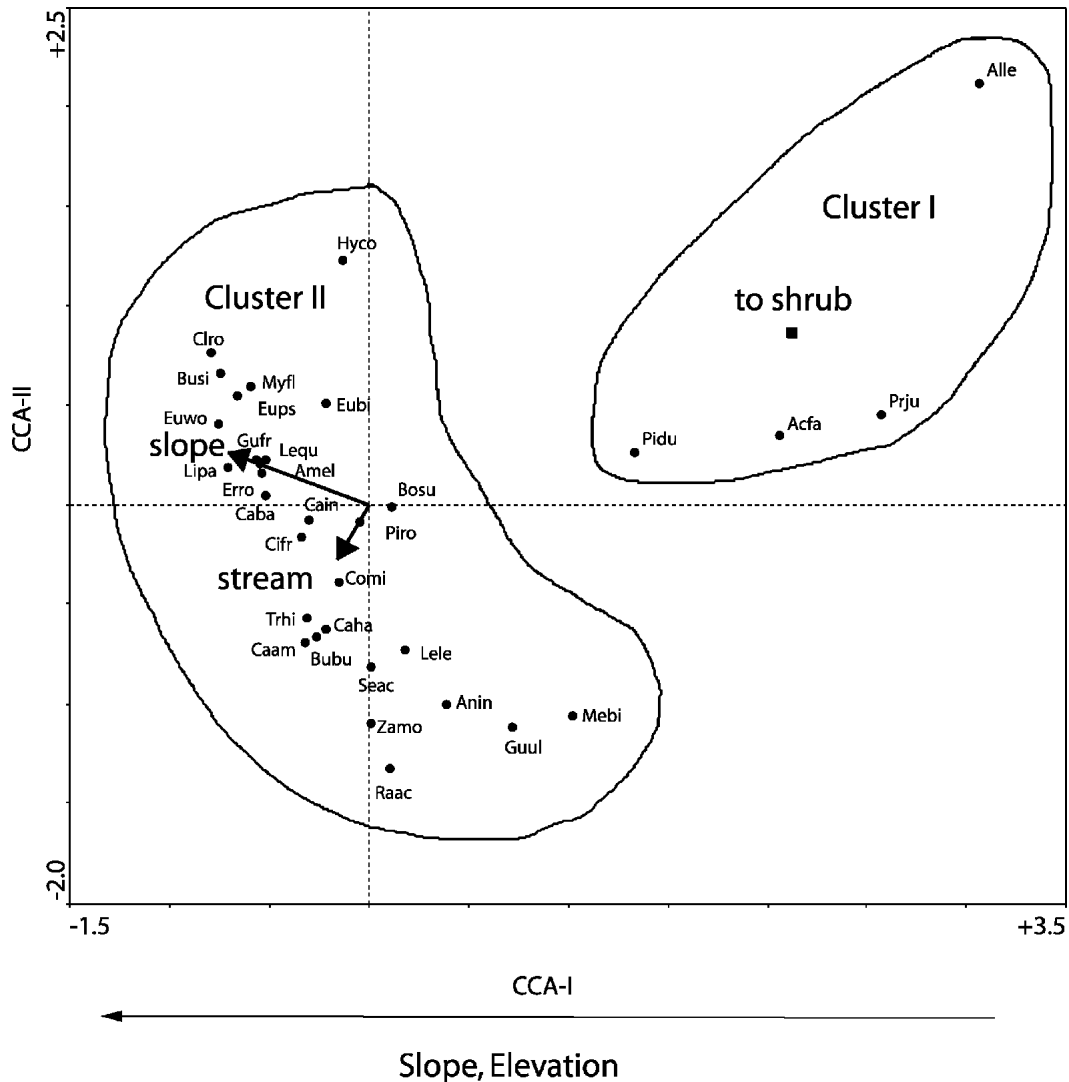


FIG. 2. Canonical correspondence analysis ordination diagram showing relationship among species with the forward selected physical (percent slope and distance from streams) and land use history variables. The centroid of the only forward-selected categorical variable (pasture changing to shrub) is indicated by a solid square. The 33 most frequent species are included in the diagram: *Acacia farnesiana*, *Albizia lebbek*, *Amyris elemifera*, *Andira inermis*, *Bourreria succulenta*, *Bucida buceras*, *Bursera simaruba*, *Capparis amplissima*, *Capparis baducca*, *Capparis hastata*, *Capparis indica*, *Citharexylum fruticosum*, *Clusia rosea*, *Coccoloba microstachya*, *Erythroxylum rotundifolium*, *Eugenia biflora*, *Eugenia pseudopsidium*, *Eugenia woodburyana*, *Guapira fragrans*, *Guazuma ulmifolia*, *Hymenaea courbaril*, *Leucaena leucocephala*, *Leptocereus quadricostatus*, *Licaria parvifolia*, *Melicoccus bijugatus*, *Myrciaria floribunda*, *Pithecellobium dulce*, *Pilosocereus royenii*, *Prosopis juliflora*, *Randia aculeata*, *Securinega acidoton*, *Trichilia hirta*, *Zanthoxylum monophyllum*.

Table A), or about 25% of Puerto Rico's 547 native tree species (Little and Wadsworth 1964, Little et al. 1974). This is an impressive figure for a relatively small parcel of land that has been repeatedly burned and

grazed, and is only partially covered with secondary forest. Nearby Guánica Forest with 4,000 ha is about 36 times the size of Tinaja. Guánica, designated as a Commonwealth Forest in 1919, and protected since

the 1930s, has 169 tree species (Murphy and Lugo 1986) including at least 23 exotics (China 1990). Two other properties managed by the Puerto Rican Conservation Trust also have relatively high tree species diversities: the 1,000-ha Cañon de San Cristóbal with about 150 (Francis et al. 1998), and the 178-ha Las Cabezas de San Juan Nature Reserve with nearly 100 (Weaver et al. 1999).

Tinaja, with 12% of its tree species being exotics, is in the lower range of sample values for the island's secondary forests which vary from nine percent near Luquillo to 14, 18, and 20%, respectively, near Humacao (China 2002), Punta Guaniquilla, and Arecibo (China 2002; Vázquez and Kolterman 1998). By the mid-1940s, only 3,440 ha, or 0.4% of Puerto Rico, were still covered by climax vegetation (Wadsworth 1950). Throughout the island, natural forests had been replaced by farmland on which fruit trees, coffee shade, and ornamentals were cultivated. In 1980 and 1990, inventories of the island's secondary forests showed that five exotics, *Syzygium jambos* (L.) Alston, *Spathodea campanulata*, *Mangifera indica*, *Citrus sinensis* Osbeck, and *Erythrina peopigiana* (Walp.) O. F. Cook, ranked among the island's 10 most common tree species (Birdsey and Weaver 1982; Franco et al. 1997).

Tinaja's diversity, in part, is due to the variety of habitats found within the relatively small tract. Its elevation gradient extends from near sea level to just below the highest point in the Sierra Bermeja. Its topographic features include gentle lower slopes, steep upper slopes, ridges, and drainages of variable size. These sites consistently vary in soil moisture during the year. Moreover, the history of past land use indicates some tree cover since 1936, notably at middle and higher elevations, and along drainages. Mature boundary trees today are evident along fence lines and a dirt road that divides the lower one-quarter of the tract. These trees provided habitat for birds and served as a seed source during the past 65 years. The systematic sampling design used in this study required hiking the entire Tinaja tract. This allowed the identification of tree species growing between the samples plots (Appendix Table

A) in addition to those on the plots. A more detailed study of vegetation in Guánica Forest would likely reveal additional tree species at that site.

The tree species growing at Tinaja also grow in nearby Punta Guaniquilla Natural Reserve (Vázquez and Kolterman 1998), Guánica Forest (Quevedo et al. 1990), and the dry forests of Mona Island and Hispaniola (Little 1955). Guánica, because it has been protected, supports an average of 14,000 stems per hectare ≥ 2.5 cm in diameter and a basal area of nearly 20 m²/ha (Murphy and Lugo 1986). Both of these figures are about 3 times the average for the entire Tinaja tract. Only about 10% of Tinaja's sample plots have basal areas >20 m²/ha, and none approach Guánica's stem density (Table 4).

Although some investigations indicate a relatively rapid recovery after tree cutting or possibly the abandonment of agriculture in dry forest (Murphy et al. 1995), the recovery witnessed so far at Tinaja is more characteristic of dry forests with recurrent disturbance, a common condition in the Caribbean Basin. Tinaja's dry climate, dense grass cover, recurrent fires, and grazing, have all contributed to a slow recovery

TABLE 4. Number of stems and basal area at La Tinaja.

Category	Plots (no.)
Stems/ha (no.) ¹	
0	11
1-99	9
100-499	19
500-999	14
1000-1999	22
2000-4999	30
>5000	<u>4</u>
Totals	109
Basal area (m ² /ha) ²	
0	11
0.01-0.99	23
1.00-1.99	8
2.00-4.99	18
5.00-9.99	20
10.00-19.99	18
20.00-29.99	<u>11</u>
Totals	109

¹Maximum = 5,350 stems/ha.

²Maximum = 28.01 m²/ha.

of its natural vegetation. Fires used to clear vegetation on adjacent properties during the winter dry season sometimes escape and burn refuge lands. The most recent fires, in February, 2002, burned nearly 100 ha at Cabo Rojo and about 70 ha at Cartagena, including 60 ha of cattails in the lagoon.

Annual rainfall in Puerto Rico's dry southwest varied from about 300 to 1350 mm between 1920 and 1990 (Murphy and Lugo 1990). Notably dry years can cause unusual stress and play a critical role in tree regeneration, survival, and growth. Tinaja's multiple stemmed trees, a characteristic feature of Caribbean dry forests (Dunphy et al. 2000), may in part result from recurrent fires, grazing, and wood cutting, as well as recurrent droughts that kill terminal leaders but not root systems (Kolb and Davis 1994). Moreover, the low, open canopy characteristic of much of the Subtropical dry forest, allows light to reach ground level and increases soil temperatures, both factors that contribute to sprouting (Dunphy et al. 2000).

Although two physical variables, slope and distance to drainages, explain significant tree species variability on the Tinaja tract, land use history is of main importance in accounting for their distribution (Figure 2). Grazing was only recently abandoned on the lower, nearly level slopes, an area where drainages converge. Land use history was also shown to be correlated with physical variables and tree distribution near Humacao, Puerto Rico (China 2002).

The restricted occurrence of *P. juliflora* to recently abandoned pastures on land with gentle slopes confirms its requirement for deep soils with a water table. *Prosopis*, spread by cattle on disturbed areas, competes well with grass. Once established on dry sites, it is likely to survive long periods in full light. Species with shallower root systems tend to dominate the steepest slopes at higher elevations. *P. royenii*, *B. simaruba*, *G. fragrans*, and *C. rosea* thrive in these conditions.

Tropical dry forest, once widespread throughout the neotropics, has been referred to as an endangered habitat type

(Janzen 1988). Puerto Rico's refuge lands in the southwest, including Tinaja, are critical as nesting and foraging habitat for native and migratory bird species including endangered species such as the Puerto Rican Whip-poor-will (*Caprimulgus noctiterus*) and the Yellow-shouldered Blackbird (*Agelaius xanthomus*) (Raffaele 1983). The refuges also help protect native plant diversity, including threatened and endangered species, and provide educational opportunities for the public. Tinaja has seven endemic and three endangered tree species, yet also supports 20 exotics (Table 2; Appendix Table A) which might be considered as competitors for growing space. Not all exotics in Puerto Rico's dry southwestern forests are successful (China 1990). Of the 23 introduced through agriculture, forestry, or ornamental plantings in Guánica Forest, only 8 have survived and reproduced in sufficient numbers. Of the latter, *Calotropis procera* (Ait.) R. Br., *P. juliflora*, and *Gossypium barbadensis* L. also grow at Tinaja. Fifteen other exotics at Guánica were not successful. Among them were *D. regia*, *C. aurantifolia*, *M. bijugatus*, and *T. indica* which are also found at Tinaja.

An often overlooked detail regarding the temporary role of exotics in ecosystem recovery is that many areas such as Puerto Rico's dry southwest have changed dramatically since the time of discovery and colonization. Today's vegetation doesn't have the physical stature or the biological diversity of the original forest; moreover, erosion and recurrent burning have reduced the soil's organic matter and moisture holding capacity, making the region functionally drier for longer periods. The relative abundance of *P. royenii* throughout the Tinaja tract is a sober reminder of drought.

The presence of exotic species on wildlife refuge lands will always be a controversial issue. However, planting exotics may facilitate succession and may be the most rational choice on some badly degraded sites where native species are difficult or impossible to grow (Lamb 1998). Initially, efforts should be made to assure forest habitat for wildlife, particularly bird species. Native tree species should be favored, but some

exotics such as *T. indica* offer size, considerable crown extension, drought tolerance, and longevity. The crown serves as a foraging substrate for birds and the area shadowed by the crown reduces grass cover and the threat of fires, a main obstacle to habitat recovery. The pods of another common exotic tree, *P. juliflora*, do not open on drying to release their seeds (Skolmen 1990). Instead, they open after decomposition of the pods or after passing through the digestive system of livestock. Now that cattle have been removed from Tinaja, it should decline in numbers.

Land use change was studied in and around the Guánica Forest (Lugo et al. 1996). Within the forest, between 1936 and 1989, urban (built-up) areas increased from less than one to about 10 ha; agricultural land declined from about 150 to 4 ha; and total forest cover increased from about 3,200 to 3,350 ha. Comparable figures for the Guánica Forest and vicinity were about 135 and 710 ha for the increase in urban land, from 3,520 to 1,800 ha for the decline in agricultural land, and from 5,400 to 6,850 ha for the increase in total forest cover. In summary, urban use and forest cover increased at the expense of agriculture showing the transition from an agrarian to urban society. The southwest corner of Puerto Rico, including the refuge lands and the Boquerón Forests, is currently experiencing similar changes.

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APPENDIX TABLE A. Tree species recorded within the La Tinaja tract but outside of sample plot boundaries.

Family	Species ¹
Anacardiaceae	<i>Mangifera indica</i> L. ²
Annonaceae	<i>Annona montana</i> Macf. <i>A. muricata</i> L.
Bignoniaceae	<i>Crescentia linearifolia</i> Miers <i>Spathodea campanulata</i> Beauv. ² <i>Tabebuia haemantha</i> (Bert.) DC. ³ <i>T. heterophylla</i> (DC.) Britton <i>Tecoma stans</i> (L.) Juss

APPENDIX TABLE A. Continued.

Family	Species ¹
Boraginaceae	<i>Bourreria virgata</i> (Sw.) G. Don ⁴ <i>C. sulcata</i> DC.
Canellaceae	<i>Canella winterana</i> (L.) Gaertn.
Celastraceae	<i>Cassine xylocarpa</i> Vent. <i>Crossopetalum rhacoma</i> Crantz
Combretaceae	<i>Terminalia catappa</i> L. ²
Erythroxylaceae	<i>Erythroxylum urbanii</i> D.E. Schultz
Euphorbiaceae	<i>Adelia ricinella</i> L. <i>Chamaecyce articulata</i> (Aubl.) Britton <i>Jatropha curcas</i> L. <i>Ricinus communis</i> L. ²
Flacourtiaceae	<i>Casearia decandra</i> Jacq. <i>C. guianensis</i> (Aubl.) Urban <i>C. sylvestris</i> Sw. <i>Prockia crucis</i> L.
Lauraceae	<i>Cinnamomum montanum</i> (Sw.) Bercht & Presl. <i>Ocotea coriacea</i> (Sw.) Britton <i>Persea americana</i> Miller ²
Leguminosae	
Caesalpinioideae	<i>Cassia polyphylla</i> Jacq. <i>Delonix regia</i> (Bojer ex Hook) Raf. ² <i>Parkinsonia aculeata</i> L.
Faboideae	<i>Gliricidium sepium</i> (Jacq.) Kunth ex Walp. ²
Mimosoideae	<i>Acacia tortuosa</i> (L.) Willd <i>Pithecellobium arboreum</i> (L.) Urban <i>P. saman</i> (Jacq.) Merr. ²
Malpighiaceae	<i>Bunchhosa glandulosa</i> (Cav.) L.C. Rich.
Malvaceae	<i>Gossypium barbadense</i> L. var. <i>barbadense</i>
Myrsinaceae	<i>Ardisia obovata</i> Hammilt.
Myrtaceae	<i>Eugenia monticola</i> (Sw.) DC. <i>E. procera</i> (Sw.) Poir <i>E. sessiliflora</i> Vahl. <i>Pimenta racemosa</i> (Miller) J.W. <i>Psidium guajava</i> L. ²
Nyctaginaceae	<i>Neea buxifolia</i> (Hook. f.) Heimerl.
Palmae	<i>Thrinax morrisii</i> H. Wendl.
Rubiaceae	<i>Guettarda ovalifolia</i> Urban <i>Hamelia patens</i> Jacq. <i>Rondeletia inermis</i> (Spreng.) Krug & Urban ³ <i>R. pilosa</i> Sw.
Rutaceae	<i>Citrus aurantifolia</i> L. ² <i>Zanthoxylum flavum</i> Vahl.
Sapindaceae	<i>Allophylus racemosus</i> Sw. <i>Melicoccus bijugatus</i> Jacq. ² <i>Sapindus saponaria</i> L.
Sapotaceae	<i>Mastichodendron foetidissimum</i> (Jacq.) H.J. Lam.
Solanaceae	<i>Solanum rugosum</i> Dunal
Sterculiaceae	<i>Helicteres jamaicensis</i> Jacq.
Thymeleaceae	<i>Daphnopsis americana</i> Mill.
Ulmaceae	<i>Trema micrantha</i> (L.) Blume
Verbenaceae	<i>Clerodendrum aculeatum</i> (L.) Schlecht

¹Several of these tree species were previously recorded (Proctor 1996).²Exotic species.³Endemic species.⁴On Puerto Rican critical species list.