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Secondary Forest Succession and Tree Planting at the Laguna Cartagena and Cabo Rojo Wildlife Refuges in Southwestern Puerto Rico

Secondary forest succession and tree planting are contributing to the recovery of the Cabo Rojo refuge (Headquarters and Salinas tracts) and Laguna Cartagena refuge (Lagoon and Tinaja tracts) of the Fish and Wildlife Service in southwestern Puerto Rico. About 80 species, mainly natives, have been planted on 44 ha during the past 25 y in an effort to reduce the threat of grass fires and to restore wildlife habitat. A 2007 survey of 9-y-old tree plantings on the Lagoon tract showed satisfactory growth rates for 16 native species. Multiple stems from individual trees at ground level were common. A sampling of secondary forest on the entire 109 ha Tinaja tract disclosed 141 native tree species, or 25% of Puerto Rico's native tree flora, along with 20 exotics. Five tree species made up about 58% of the total basal area, and seven species were island endemics. Between 1998 and 2003, tree numbers and basal area, as well as tree heights and diameter at breast height values (diameter at 1.4 m above the ground), increased on the lower 30 ha of the Tinaja tract. In this area, much of it subject to fires and grazing through 1996, exotic trees made up 25% of the species. Dry forest throughout the tropics is an endangered habitat, and its recovery (i.e., in biomass, structure, and species composition) at Tinaja may exceed 500 y. Future forests, however, will likely contain some exotics.

INTRODUCTION

The US Fish and Wildlife Service (F&WS) of the Department of the Interior administers the national wildlife refuge system, which grew from a single 1.2 ha refuge in 1903 to 390 refuges totaling 137 380 km^2 by 1979 (1). With the addition of the Salinas tract to the Cabo Rojo National Wildlife Refuge in October 1999, refuges numbered more than 500 and covered nearly 380 000 km^2 (2, 3). Today, refuges are scattered in all states throughout the continental United States and in Alaska, Hawaii, Puerto Rico, the US Virgin Islands (4), and Navassa Island near Haiti's southwestern shore (5).

Initially, the purpose of the refuge system was to protect wildlife, especially migratory waterfowl, from the devastating impacts of a growing society (1). In 1924, a provision allowed for hunting and fishing. In 1934, during the Great Depression, an effort was made to purchase and restore habitats. At the same time, the refuges faced pressure for greater public use, including recreation. In 1973, the US Congress passed, and subsequently amended, the Endangered Species Act to protect endangered and threatened species. Today, the main use of many refuges is for environmental education, fishing, wildlife observation, hiking, and photography rather than hunting.

A stated mission of the F&WS is "to administer a national network of lands and waters for the conservation, management, and where appropriate, restoration of the fish, wildlife, and plant resources and their habitats within the United States for the benefit of present and future generations of Americans" (2, pp. 135–136). Since many important migratory bird habitats in the eastern Caribbean have been lost through development, refuges in Puerto Rico and the Virgin Islands have become increasingly more important in the conservation of migratory wildlife.

For most of the twentieth century, natural forests in Puerto Rico were replaced by farmland on which subsistence crops, fruit trees, coffee and coffee shade, tobacco, and a few ornamentals were grown. During this period, native vegetation was severely reduced, and exotics increased in numbers and extent (6). Past use of the refuge lands included frequent fires, overgrazing, and sugar cane production accompanied by heavy fertilization, all of which contributed to severe soil erosion and sedimentation. The refuges today are covered with pasture interspersed with native and exotic trees and grasses, some areas of secondary forest, and increasingly larger patches of tree plantings of various species.

The Cabo Rojo and the Laguna Cartagena National Wildlife Refuges occupy nearly 1180 ha (7) (Fig. 1). The Headquarters and Salinas (salt flats) tracts are in the Cabo Rojo refuge, which also includes the current F&WS regional office in the Caribbean. The Salinas tract is the most important area for shorebirds in Puerto Rico (8). The Laguna Cartagena refuge includes the Lagoon and Tinaja tracts. About one-half of the Lagoon tract is occupied by the Cartagena Lagoon, which is one of the island's most important waterfowl habitats.

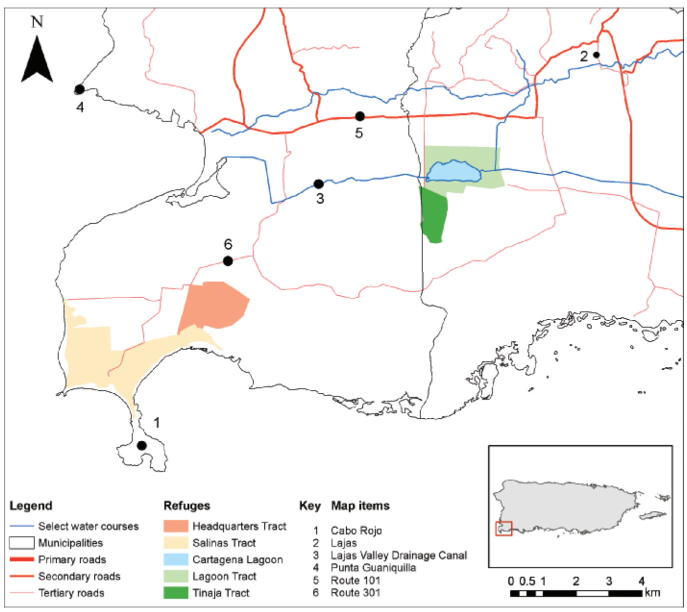

Figure 1. Locations of the US Fish and Wildlife refuges in southwestern Puerto Rico: Cabo Rojo (Headquarters and Salinas tracts), 751 ha, and Laguna Cartagena (Lagoon and Tinaja tracts), 426 ha.

Table 1. Land cover on the US Fish and Wildlife Service refuges in southwestern Puerto Rico.

	Vegetative cover (ha)					
	Cabo Rojo		Laguna Cartagena			
Land class	Headquarters	Salinas	Lagoon	Tinaja	Total	Percent of area
Grassland	124.7	97.2	93.0	32.8	347.7	29.5
Shrubland	17.2	14.2	31.5	7.2	70.1	5.9
Shrubland-woodland	82.6	58.9	0	39.0	180.5	15.3
Forest*	10.9	5.4	12.3	29.9	58.5	5.0
Wetlands						
Fresh water	0.1	0	177.5	0	177.6	15.0
Saline	0.1	322.2	0	0	322.2	27.3
Developed†	0.5	20.9	0.1	0.1	21.6	1.8
Beach	0	2.6	0	0	2.6	0.2
Total	236.1	521.4	314.4	109.0	1180.9	100.0

* Grouping of different forest types. † Roads, buildings, and salt extraction operations at Salinas.

Wetlands cover >40% of both refuges (i.e., about 15% fresh water at Laguna Cartagena and 25% saline water at Cabo Rojo) (Table 1). Land classed as forest or woodland-shrubland combined covers about 20% of the total area, whereas grassland and shrubland together cover about 35%. The remaining 2% is either beach or developed areas, including the salt flats at Salinas. Each of the refuge tracts, however, varies with regard to land cover. More than 50% of the Headquarters tract and nearly 20% of the Salinas tract are grass covered. The Lagoon tract is nearly 40% in grass and shrubs. Tinaja, the smallest tract, is more than two-thirds covered by forest and woodland-shrubland combined.

The main purpose of this paper is to report recent observations of tree growth on the Laguna Cartagena refuge and to evaluate the survival, growth, and future potential of different tree species used for habitat restoration in both refuges. Current monitoring of secondary forest on the Tinaja tract is also reviewed.

SITE INFORMATION

Both refuges are situated in the subtropical dry forest life zone (9, 10). From 1991 through 2000, the mean annual rainfall on the Headquarters and Lagoon tracts averaged 840 mm and 1040 mm, respectively (11). February and March are the driest months; May and September through November are the wettest months. Mean temperature is about 26°C and varies only slightly during the year (12).

All tracts on both refuges lie between sea level and 290 m in elevation. Nearly three-quarters of the Cabo Rojo refuge are composed of deposits of beach and quartz sand, along with areas of limestone and alluvium (13). In contrast, the soils at the Laguna Cartagena refuge are mainly clays, silty clays, and clay loams. Situated at elevations between 10 and 40 m, the alluvial soils of the Lagoon tract are generally fertile, heavy, difficult to drain, and affected by salt, particularly in areas that have been previously irrigated (14).

The Tinaja tract varies in elevation between 20 and 290 m and includes high-elevation, steep, eroded slopes with shallow, stony, well-drained, and dry soils (15), and lower slopes with deeper, colluvial soils. Tinaja's highest slopes and ridges, in general, contain sparse vegetation. Much of the area on mid- to upper-level slopes has had tree cover since the 1930s (i.e., evident on old aerial photos). The gentle lower slopes, where grasses are more common, also have deeply incised and more humid arroyos that support trees approaching 10 m in height (16). Trees growing in these drainages, along fence lines demarcating property boundaries, and bordering the dirt road within the property have for years provided habitat and forage for bats and birds, and a source of seeds for dispersal to surrounding areas.

METHODS

Since 1996, the F&WS has increased efforts to restore wildlife habitat in the refuges, including the representation of uncommon and rare tree species. The approach has involved tree planting in open areas and the stimulation of secondary succession on the slopes of Sierra Bermeja. First, seeds of many common tree species were collected and germinated at the Headquarters nursery, while other seedlings were purchased from a nearby commercial nursery. Next, control of recurrent fires and livestock grazing was initiated to protect tree plantings and to promote secondary forest recovery. Several steps were involved, among them, mending damaged fences, the development and maintenance of fire lanes, the formulation of a fire-management program, training of fire personnel, the purchase of fire-control equipment, and regular patrols, especially during the dry season. Periodic monitoring was then initiated to determine tree growth and to assess changes in composition of secondary forest species and their growth. This paper combines both previously unreported tree-growth measurements and a partial review of past monitoring research.

Twelve species planted on the Lagoon tract in June 1998 and four species planted on the Tinaja tract in February 2001 were remeasured in August and February of 2007, respectively (Figs. 2 and 3). Site preparation on the Lagoon tract consisted of grass

Figure 2. Restoration activities. Tree planting is initiated on the Lagoon Tract of the Laguna Cartagena Wildlife Refuge, southwestern Puerto Rico (Photo: Fish and Wildlife Services).

Figure 3. Field monitoring. Trees planted during June 1998 are measured on the Lagoon Tract of the Laguna Cartagena Wildlife Refuge, southwestern Puerto Rico (August 2007). (Photo: P. L. Weaver)

cutting and plowing. Seedlings were planted on top of the furrows in 3 × 4 m spacing and watered on an irregular basis for one year. At Tinaja, the grass was cut in strips to clear space for the seedlings, which were planted 6 m apart and watered immediately. In the Lagoon tract, stems with a minimum diameter at breast height (d.b.h.) of 4 cm (d.b.h. = diameter at 1.4 m above the ground) were identified to species and measured with a tape to the nearest 0.1 cm (multiple stems from single trees at ground level were common). Heights were determined to the nearest 0.1 m with an extension pole. Measurements at Tinaja were similar, except that all stems ≥2.5 cm were included.

In addition, recent habitat restoration studies carried out on the refuges were summarized, including: *i*) the 1998 survey of structure and species composition of secondary forest using 109 circular plots (i.e., a 3.4% sample) for the entire 109 ha Tinaja tract (Fig. 4); *ii*) the 2003 survey of Tinaja's lower slopes (i.e., the lowest 32 plots, or 30 ha of the tract) to determine short-term vegetation changes; and *iii*) the 2003 measurement and evaluation of native and exotic tree species planted on both refuges between 1980 and 1998. Plant nomenclature in all studies followed local taxonomy texts (17, 18).

RESULTS

Recent Study at Laguna Cartagena

The recent surveys carried out at Laguna Cartagena showed tree survival rates averaging greater than 90% for 12 species on the Lagoon tract and more than 80% for four species on the Tinaja tract. In addition, mean d.b.h. growth for stems varied from 0.50 to 1.39 cm y^{-1} on the Lagoon tract and between 0.71 and 2.00 cm y^{-1} on the Tinaja tract (Table 2). Mean height growth ranged between 0.58 and 1.10 m y^{-1} on the Lagoon tract and between 0.65 and 0.87 m y^{-1} on the Tinaja tract.

Multiple stems with measurable d.b.h. growing from much larger individual trunks near ground level were common, notably for *Crescentia cujete*, *Guazuma ulmifolia*, *Pisonia subcordata*, and *Stahlia monosperma*. The largest *Crescentia*, for example, had a trunk diameter near ground level of 27.1 cm with four stems at d.b.h. between 8.0 and 10.8 cm. Similar data for the largest trees of the remaining species are: *Guazuma*, 46.2 cm, with seven stems between 7.3 and 12.8 cm; *Pisonia*, 21.2 cm, with seven stems between 4.8 and 7.4 cm; and *Stahlia*, 15.5 cm, with eight stems between 4.5 and 6.5 cm. In addition, regeneration of a couple of native tree species not present in the canopy was observed.

Past Research: Entire Tinaja Tract

The 1998 survey of secondary forest on the entire Tinaja tract showed that 141 of the 161 tree species tallied were native (19). Other observations included:

- Twenty exotics accounted for about 12% of the tallied tree species and about 18% of the tallied stems; *Leucaena leucocephala* (Lam.) DeWit was the most common tree.
- The mean stem density was 1510 ha^{-1}, and the mean tree density was 823 ha^{-1}, including the cactus *Pilosocereus royenii* (L.) Byles & Rowley. Without the cactus, mean stem density was 1271 ha^{-1}, and mean tree density 744 ha^{-1}.
- Multiple stems below d.b.h. were common; the average was 1.84 per tree including the cactus, and 1.71 per tree excluding the cactus.
- The mean basal area for the tract was 6.9 m^2 ha^{-1}, including the cactus, and it ranged from 0 to 28.0 m^2 ha^{-1} on individual plots.
- The 10 most common tree species accounted for 63.4% of the stems, and the 43 least common species accounted for only 2.2% of the stems.
- Five species accounted for 58% of the total basal area.
- The largest tree tallied was a *Ceiba pentandra* at 20 m in height and 77 cm in d.b.h.
- Seven endemic tree species were tallied: *Eugenia woodburyana* Alain, *Garcinia hessii* (Britton) Alain, *Leptocereus quadricostatus* (Bello) Britton & Rose, *Machaonia portoricensis* Baill, *Rondeletia inermis* (Spreng.) Krug & Urban, *Tabebuia haemantha* (Bert.) DC, and *Thouinia striata* Radlk.

Past Research: Lower Tinaja Tract

Several changes occurred between 1998 and 2003 with the elimination of grazing and fire on Tinaja's lower slopes (Table 3) (16):

- In 2003, tree species numbered 31, with 1175 stems and 701 individual trees. The four most common species—*Leucaena leucocephala*, *Pithecellobium dulce* (Roxb.) Benth, *Pilosocereus royenii*, and *Prosopis pallida* (H&B ex Willd.) HBK—accounted for 80% of both stems and trees, whereas the nine least common species were represented by a single tree. *Leucaena leucocephala* made up 35% of the stems and 50% of the trees.
- In 2003, exotics accounted for about 25% of the species, 75% of the stems, and 80% of the trees.
- Only one endemic tree species, *Thouinia striata* Radlk., was recorded and it was observed on both dates.
- From 1998 to 2003, the number of stems and trees per hectare increased 3.3 times and 2.6 times, respectively, and basal area doubled; moreover, residual trees increased in height and d.b.h.

DISCUSSION

Recent Survey at Lagoon Tract

The high survival rate of trees with minimal watering is encouraging since it indicates that reforestation efforts using this technique should be successful in all but the driest years. The initial d.b.h. and height growth rates for all tree species on both tracts are satisfactory, and in the case of *Ceiba pentandra*, *Bucida buceras*, and *Guazuma ulmifolia*, impressive. *Bucida buceras*, along with *Crescentia cujete*, *Guazuma ulmifolia*, and *Pisonia subcordata*, rapidly attained canopy closure on the Lagoon tract, reducing grass cover to a level insufficient to sustain ground fires. The tendency for multiple branching is

Table 2. Growth rates of planted trees at Laguna Cartagena National Wildlife Refuge in Puerto Rico.

Tree species	Number of trees*	Number of stems*	Range in stem size d.b.h. (cm)	Range in stem size Height (m)	Stem growth rates d.b.h. (cm y^{-1})	Stem growth rates Height (m y^{-1})
Laguna Cartagena—Lagoon						
Andira inermis	25	32	4.5–17.8	3.5–10.1	0.96 ± 0.06	0.65 ± 0.03
Bucida buceras	23	25	5.0–18.9	8.8–11.8	1.39 ± 0.09	1.10 ± 0.02
Cordia collococca	17	30	4.3–21.0	3.8–8.6	1.12 ± 0.09	0.70 ± 0.02
Cresentia cujete	13	50	4.4–18.0	4.4–8.0	0.86 ± 0.03	0.58 ± 0.01
Ficus citrofiolia	5	6	4.1–11.3	5.6–8.4	0.95 ± 0.12	0.72 ± 0.05
Guazuma ulmifolia	9	45	5.0–17.0	6.4–9.6	1.11 ± 0.05	0.95 ± 0.02
Pisonia subcordata	4	16	4.2–12.7	6.0–7.9	0.82 ± 0.07	0.74 ± 0.02
Sapindas saponaria L.†	4	4	3.9–5.8	5.0–9.2	0.50 ± 0.04	0.69 ± 0.10
Sideroxylon foetidissum	3	3	3.5–8.3	3.9–7.5	0.64 ± 0.15	0.60 ± 0.11
Spondias mombin	15	24	4.6–25.0	4.7–8.3	1.04 ± 0.09	0.67 ± 0.02
Stahlia monosperma	20	62	3.0–7.7	3.5–7.8	0.57 ± 0.01	0.64 ± 0.01
Tabebuia heterophylla	25	48	3.6–12.0	4.1–7.7	0.82 ± 0.04	0.70 ± 0.01
Subtotal	163	345				
Laguna Cartagena—Tinaja						
Bursera simaruba	126	219	1.5–15.0	1.3–8.2	1.10 ± 0.03	0.87 ± 0.01
Ceiba pentandra	5	5	7.5–15.5	4.2–5.2	2.00 ± 0.24	0.86 ± 0.04
Citharexylum fruticosum	39	70	1.5–11.5	2.2–7.3	0.71 ± 0.04	0.81 ± 0.03
Cordia sulcata DC.†	41	98	1.5–10.4	1.5–5.5	0.78 ± 0.03	0.65 ± 0.02
Subtotal	211	392				
Total	374	737				

* Multiple stems at d.b.h. growing from single trees at ground level. † Remaining species authorities appear in Table 4.

noteworthy since it appears to be partially dependent on species. Satisfactory tree survival and growth rates validate both the selection of species and the planting techniques. Moreover, local wildlife was using the new forest as witnessed by the presence of native tree seedlings normally dispersed by birds or bats.

Previous monitoring of tree d.b.h. growth rates on several sites at both refuges ranged from satisfactory to excellent, despite the dry climate and land-use history of the refuges (11). *Bucida buceras*, widely planted on the Headquarters tract, averaged 0.51 cm y^{-1} in d.b.h. and 0.37 m y^{-1} in height over 23 y. Six other natives planted on the Lagoon tract, *Andira inermis*, *Ceiba pentandra*, *Cordia collococca*, *Guazuma ulmifolia*, *Stahlia monosperma*, and *Tabebuia heterophylla*, averaged between 0.62 to 3.00 cm y^{-1} in d.b.h. and 0.59 to 1.28 m y^{-1} in height over 5 to 7 y.

More than 60 y ago, experimental tree planting was initiated by the US Forest Service at Guánica Forest in southwest Puerto Rico using tree species with possible timber potential (20). The natives *Cordia alliodora* (R&P) Oken and *Guaiacum officinale* as well as the exotics *Casuarina equisetifolia* J.R & J.G. Forster, *Prosopis pallida*, *Senna siamea* (Lam.) Irwin & Barneby, and *Swietenia mahogoni* were rated as promising; five other species, however, were considered unsuccessful (21). Measurements made at 30 cm height after 18 y showed that *Haematoxylon campechianum* L. averaged nearly 1 cm y^{-1} (22). The d.b.h. growth of *Bucida buceras* was found to vary considerably by crown class (i.e., crown size and position in the canopy) as well as measurement period and tended to slow over time (23).

Since 1980, the F&WS has planted nearly 17 500 trees of 80 species on both refuges, mainly during the past 10 y. About 88% of the total was planted on the Headquarters and Lagoon tracts (Fig. 5). The 33 most commonly planted tree species represented 94% of all plantings on the refuge sites; moreover, *Bucida buceras*, *Bursera simaruba*, *Swietenia mahagoni*, and *Stahlia monosperma* alone accounted for nearly 58% of the total (Table

Table 3. Comparison of structural parameters and species numbers for the secondary forest in the Tinaja tract in 1998 and 2003.*

Parameter (units)	Year 1998	Year 2003
Mean values by plot		
Trees (no. ha^{-1})	214	703
Stems (no. ha^{-1})	497	1283
Basal area (m^2 ha^{-1})	2.0	4.0
Range of plot values		
Trees (no. ha^{-1})	0–955	0–2325
Stems (no. ha^{-1})	0–2038	0–3599
Basal area (m^2 ha^{-1})	0–10.2	0–13.0
Species (total on all plots)	30	31
Species (no. per plot)	0–13	0–12
Size class of stems		
Height (m)		
1.4–3.9 (no. ha^{-1})	271	786
4.0–7.9 (no. ha^{-1})	219	372
≥8.0 (no. ha^{-1})	7	17
d.b.h. (cm)		
2.5–7.9 (no. ha^{-1})	397	986
8.0–14.9 (no. ha^{-1})	76	153
≥15.0 (no. ha^{-1})	24	36

* Weaver and Schwagerl (16).

Figure 4. Tinaja tract viewed from Cerro Mariquita. Secondary forest and shrubland-woodland vegetation cover two-thirds of the tract at mid- to upper-elevations, whereas the highest slopes and ridges contain sparse cover. The coastal village of Parguera lies in center background (February 2006). (Photo: P. L. Weaver)

Table 4. Thirty-tree species with ≥40 replicates used in restoration efforts at both US Fish and Wildlife Service refuges between 1980 and 1998.*

Tree species	Trees (no.)	Percent of trees (%)	Assessment† (S-G)
Andira inermis (W. Wright) DC.	161	1.8	G-G
Avicennia germinans (L.) L.	40	0.4	P-P
Bourreria succulenta Jacq.	88	1.0	G-G
Bucida buceras L.	2633	28.9	G-G
Bursera simaruba (L.) Sarg.	1198	13.2	G-G
Ceiba pentandra (L.) Gaertn.	184	2.0	G-G
Citharexylum fruticosum L.	179	2.0	G-F
Coccoloba uvifera (L.) L.	195	2.1	P-F
Cocos nucifera L.	82	0.9	P-I
Colubrina arborescens (Mill.) Sarg.	75	0.8	G-G
Conocarpus erectus L.	190	2.1	F-F
Cordia collococca L.	76	0.8	G-F
Cordia sulcata DC.	154	1.7	G-G
Cresentia cujete L.	64	0.7	G-F
Erythroxylum aerolatum L.	98	1.1	G-G
Ficus citrifolia (P. Miller)	164	1.8	P-P
Guaiacum officinale L.	471	5.2	G-P
Guazuma ulmifolia Lam.	88	1.0	G-G
Jaquinia armillaris Jacq.	61	0.7	P-P
Pisonia subcordata Sw.	41	0.4	G-F
Polygala cowelli (Britton) S.F. Blake	92	1.0	P-F
Samanea saman (Willd.) Merril	44	0.5	G-G
Sideroxylon foetidissimum Jacq.	45	0.4	F-F
Spondias mombin L.	76	0.8	G-F
Stahlia monosperma (Tul.) Urban	698	7.7	G-F
Swietenia mahogani (L.) Jacq.	716	7.9	G-G
Tabebuia heterophylla (DC.) Britt.	275	3.0	G-F
Thespesia populea (L.) Soland ex Correa	175	1.9	P-I
Trichilia hirta L.	84	0.9	G-G
Zanthoxylum flavum Vahl	109	1.2	P-I
Subtotals	8556	93.9	NA
48 other species	541	6.1	NA
Totals	9097	100.0	NA

* Weaver and Schwagerl (16). Authorities not in this table are provided in text or Table 2.
† Assessment for survival (S) and initial growth (G): P = poor, F = fair, G = good, I = insufficient data. NA = not applicable.

4). About 80% of the species survived and grew well initially and were considered promising for future use. Spacings varied, ranging from 3 × 4 m to 6 × 6 m. Assuming an average spacing of 5 × 5 m (i.e., 400 ha^{-1}), survival of the original plantings would have provided tree cover for about 44 ha.

Secondary Forest on the Tinaja Tract

The 141 native tree species tallied at Tinaja represents about one-quarter of the island's native tree species, an impressive figure for a small parcel of land, especially since portions of the lower slopes had been repeatedly burned and grazed through 1996. The occurrence of seven endemic tree species is also impressive. Tinaja's relatively high species diversity is due in part to the mosaic of habitats on the tract and to the survey technique. The sampling procedure tallied small trees and used plots systematically scattered throughout the tract. To better account for diversity, tree species that were absent from the plots but encountered between them were recorded separately.

The lower slopes of Tinaja are currently dominated by exotic tree species. The presence of exotics on wildlife refuge lands is a controversial issue, and some critics suggest that efforts should be made to eliminate them. *Leucaena leucocephala* is a prime example of an exotic that advances rapidly into grass-covered areas but gradually declines with the regeneration of native forest. Exotics common in the southwest will remain a part of the flora in the short-term but most, being intolerant of shade, will not persist as the native forest recovers (24).

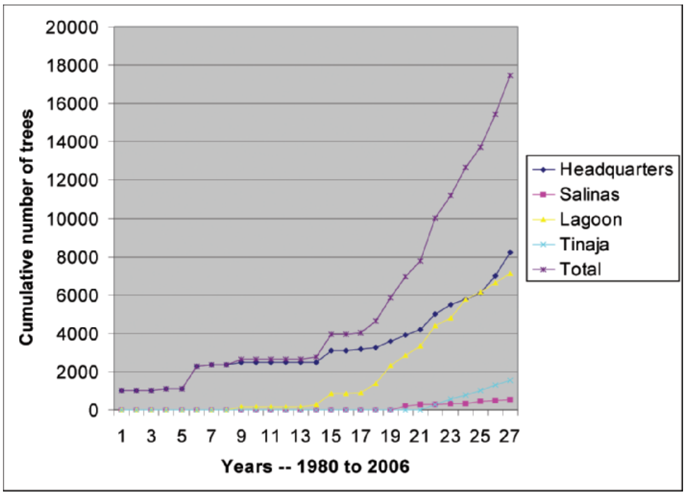

Figure 5. Planting history. Record of tree planting by tract and year for the US Fish and Wildlife Service refuges in southwestern Puerto Rico.

Southwest Puerto Rico and the F&WS Refuges

Because of widespread conversion for agriculture and grazing, tropical dry forest has been called an endangered habitat (25). Recovery of dry forest implies biomass accumulation along with the development of a structure and species composition similar to the original forest. At Tinaja, biomass recovery, part of which is attributable to exotic species, might be approached in 50 y on many sites, notably the lower slopes. Typical structure, with a mixture of numerous small and large native and exotic trees will take longer, perhaps 200 y. The return of a species composition similar to that at the time of discovery (i.e., typical species-site relationships) could well exceed 500 y (19). At that time, shade tolerant exotics are likely to still be present. Moreover, unknowns such as climatic change could impose ecosystem changes. At a minimum, the time estimates highlight the importance of eliminating fires, which could set back succession to the grass stage and delay any type of recovery indefinitely.

Management alternatives exist to hasten the development of a more desirable species composition. Regeneration of native tree species has been observed in the shade of scattered large trees, including *Hymenaea courbaril* L., *Prosopis pallida*, and *Tamarindus indica* L., the last two of which are long-lived exotics (16). This regeneration, attributable mainly to seed dispersal by birds and bats, develops under partial shade where competition from grasses is reduced and moisture relationships may be more favorable. Restoration using clusters of different native species on the best sites has already yielded favorable results. Designing the clusters to contain fast-growing tree species to produce structure, and early flowering and fruiting species to attract dispersal agents, may enhance benefits through a positive interaction with local wildlife. In summary, trees, regardless of species, shade the ground, reduce grass cover and the threat of fire, provide nesting and roosting sites for birds and bats, and often facilitate the germination and early growth of native tree species.

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 during the past couple of centuries. Today's vegetation does not have the physical stature or biological diversity of the original forest; moreover, recurrent burning and erosion have reduced the soil's organic matter content and soil moisture holding capacity, making the entire region functionally drier for longer periods than it was at the time of discovery. The relative abundance of cactus on the refuges indicates drier growing conditions. Sometimes, planting-fast growing exotics is the most rational choice on badly degraded sites where native species are difficult or impossible to grow (26). Initial efforts should focus on reducing the threat of grass fires and restoring wildlife habitat, favoring, where possible, native tree species.

In conclusion, the F&WS refuges are successfully recovering from past agricultural activities through secondary forest succession and tree planting. In addition, the southwestern corner of Puerto Rico is currently experiencing land-use changes away from sugar cane production and subsistence farming to a landscape characterized by family residences, private summer homes, commercial enterprises, and hotels. Under such conditions, the F&WS properties become increasingly more important in sustaining Puerto Rico's resident and migratory wildlife.

References and Notes

1. Doyle, R.E. 1979. Our national wildlife refuges: a chance to grow. *Natl. Geogr. 155, 342–349.*
2. Meretsky, V.J., Fischman, R.L., Karr, J.R., Ashe, D.M., Scott, J. M., Noss, R.F. and Schroeder, R.L. 2006. New directions in conservation for the National Wildlife refuge system. *Bioscience 56*, 135–143.
3. US Fish and Wildlife Service. 1999. *Las Salinas de Cabo Rojo se Convierten en Parte del Refugio Nacional de Vida Silvestre*. Release #R99-82. USDI, US Fish and Wildlife Service, Boquerón, Puerto Rico, 3 pp. (news release). Unpublished report on file at the US Fish and Wildlife Service, Boquerón, Puerto Rico.
4. Ogburn, C. 1979. Island, prairie, marsh, and shore. *Natl. Geogr. 155*, 350–381.
5. US Fish and Wildlife Service. 2002. *Caribbean Islands National Wildlife Complex Biological Review, January 14–25, 2002*. US Fish and Wildlife Service, Boquerón, Puerto Rico, 86 pp.
6. Birdsey, R.A. and Weaver, P.L. 1982. *The Forest Resources of Puerto Rico*. Resource Bulletin SO-85. US Department of Agriculture, Forest Service, Southern Forest Experiment Station, New Orleans, Louisiana, 59 pp.
7. Ventosa-Febles, E.A., Camacho Rodríguez, M., Chabert Llompart, J.L., Sustache Sustache, J. and Dávila Casanova, D. 2005. *Puerto Rico Critical Wildlife Areas*. Department of Natural and Environmental Resources, Bureau of Fish and Wildlife, Terrestrial Resources Division San Juan, Puerto Rico, 385 pp.
8. Collazo, J., Harrington, B.A., Grear, J.S. and Colón, J.A. 1995. Abundance and distribution of shorebirds at the Cabo Rojo Salt Flats, Puerto Rico. *J. Field Ornith. 66*, 424–438.
9. Holdridge, L.R. 1967. *Life Zone Ecology*. Tropical Science Center, San José, Costa Rica, 206 pp.
10. Ewel, J.J. and Whitmore, J.L. 1973. *The Ecological Life Zones of Puerto Rico and the US Virgin Islands*. Research Paper ITF-18. Institute of Tropical Forestry, Río Piedras, Puerto Rico, 71 pp.
11. Weaver, P.L. and Schwagerl, J. 2004. Tree planting in the national wildlife refuges of southwestern Puerto Rico. In: *Proceedings of the 7th Annual Caribbean Urban Forestry Conference & 11th Caribbean Foresters Meeting*. Zimmerman, T.W., Weaver, P.L., Miller, J.M. and Combie, V. (eds). University of the Virgin Islands Cooperative Extension Service, St. Croix, p. 127–141.
12. Calvesbert, R.J. 1970. *Climate of Puerto Rico and the US Virgin Islands*. US Department of Commerce, Environmental Services Administration, Environmental Data Service, Silver Spring, Maryland, 29 pp.
13. Bawiec, W.J. (eds). 2001. *Geology, Geochemistry, Geophysics, Mineral Occurrences and Mineral Resource Assessment for the Commonwealth of Puerto Rico*. Open-file Report 98-38. US Geological Survey, San Juan, Puerto Rico; Puerto Rico Department of Natural Resources; University of Puerto Rico at Mayaguez).
14. Carter, O.R. 1965. *Soil Survey of the Lajas Valley Area, Puerto Rico*. Series 1961, No. 23. US Government Printing Office, Washington, DC (US Department of Agriculture in cooperation with the University of Puerto Rico), 170 pp. + maps.
15. Picó, R. 1974. *The Geography of Puerto Rico*. Aldine Publishing Company, Chicago, Illinois, 439 pp.
16. Weaver, P.L. and Schwagerl, J. 2005. Early recovery of subtropical dry forest in the absence of grazing and fire. In: *Wildland Fire Management and Restoration,* Proceedings of the Twelfth Meeting of Caribbean Foresters in Puerto Rico, 7–11 June 2004.Weaver, P.L. and González, K.A. (eds). International Institute of Tropical Forestry, Río Piedras, Puerto Rico, p. 68–74.
17. Liogier, H.A. 1985–1997. *Descriptive Flora of Puerto Rico and Adjacent Islands. Spermatophyta*. Editorial de la Universidad de Puerto Rico, San Juan, Puerto Rico, *Vol. 1*, 352 pp.; *Vol. 2*, 481 pp.; *Vol. 3*, 461 pp.; *Vol. 4*, 617 pp.; *Vol. 5*, 436 pp.
18. Liogier, H.A. and Martorell, L.F. 1982. *Flora of Puerto Rico and Adjacent Islands: A Systematic Synopsis*. Editorial de la Universidad de Puerto Rico, Río Piedras, Puerto Rico, 343 pp.
19. Weaver, P.L. and Chinea, J.D. 2003. Secondary subtropical dry forest at the La Tinaja tract of the Cartagena Lagoon National Wildlife Refuge, Puerto Rico. *Carib. J. Sci. 39*, 273–285.
20. Wadsworth, F.H. 1990. Plantaciones forestales en el bosque estatal de Guánica. *Acta Científica 9*, 61–68.
21. Marrero, J. 1950. Resultados de la repoblación forestal en los bosques insulares de Puerto Rico. *Carib. Forest. 11*, 151–195.
22. Wadsworth, F.H. 1943. The Las Cobanitas campeche plantation. *Carib. Forest. 4*, 140–143.
23. Weaver, P.L. 1979. *Tree Growth in Several Tropical Forests of Puerto Rico*. US Department of Agriculture, Forest Service, Southern Forest Experiment Station, New Orleans, Louisiana, 15 pp.
24. Chinea, J.D. 1990. Árboles introducidos a la Reserva de Guánica, Puerto Rico. *Acta Ciéntifica 4*, 51–59.
25. Janzen, D.H. 1988. Guanacaste National Park: tropical ecological and biocultural restoration. Chapter 19. In: *Rehabilitating Damaged Ecosystems*. Cairns, J. Jr. (eds). CRC Press, Inc., Boca Raton, Florida, p. 143–192.
26. Lamb, D. 1998. Large-scale ecological restoration of degraded tropical forest lands: the potential role of timber plantations. *Restor. Ecol. 6*, 271–279.

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