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REGENERATION OF NATIVE MARIANA ISLAND FOREST IN DISTURBED HABITATS

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Abstract. I studied the present vegetation of a habitat disturbed ca. 45 years ago on Saipan, Mariana Islands to determine the extent to which native trees have become reestablished, to gain insights into the mechanisms involved in natural reforestation and to determine if natural reforestation offers any management lessons. In ten 10 x 5 m plots, I enumerated all tree species present and measured their basal areas in four vertical strata (canopy, sapling, shrub, seedling). Introduced species, particularly *Leucaena leucocephala* and *Carica papaya*, were proportionately most dense in the canopy and seedling layers, whereas native species, particularly *Melanolepis multiglandulosa* and *Aidia cochinchinensis*, reached their highest proportionate density in the shrub and sapling layers. Moreover, introduced species increased and native species declined in proportionate basal area from the shrub layer to the canopy. The great majority of native trees present were characterized by having, small, fleshy fruits and were probably dispersed into the area by indigenous forest birds. Native tree species appear to be successfully recolonizing this site and may eventually come to predominate if no additional human disturbance occurs. However, temporal shifts in vegetation composition seem likely to involve a complex interplay of seed dispersal agents, evolving microenvironments, plant competitive interactions and external events such as typhoons. Several potential management strategies are described.

The native vegetation of Saipan, Mariana Islands, has been greatly altered since human settlement. Agriculture, burning, cutting, feral ungulates, introduced plants and war-related damage (Fosberg 1960) have all contributed to this alteration. Some of the most extensive vegetation changes occurred during the Japanese administration (1914–1944), when much of the southern Marianas were cultivated. In addition, military-related land clearing followed the American invasion of Saipan in 1944 (Farrell 1990). After World War II, much of the agricultural and military land on Saipan was abandoned and began to revegetate with a largely alien mixture of plant species (Fosberg 1960). Presently, the introduced tangantangan (*Leucaena leucocephala*) is an especially prominent part of the island's flora on former agricultural land, particularly on limestone-derived soils. The small tree was aeri ally seeded following the U.S. invasion of Saipan to prevent erosion (Engbring et al. 1986). Papaya (*Carica papaya*), sosuge (*Acacia con-*

fusa), white monkeypod (*Albizia lebeck*), and flametree (*Delonix regia*) are also locally common introduced trees.

Despite this wholesale alteration of indigenous habitats, steep limestone escarpments have retained stands of native forest (Fosberg 1960). Such forest, termed limestone forest, is now widely recognized as a distinctive natural resource and efforts have been directed at revegetating disturbed sites with native trees (e.g. Villagomez 1987). Moreover, native trees have spontaneously spread from native forest into former cleared areas. However, there are no data on natural reestablishment of native trees and artificial revegetation efforts have had limited success. Therefore, I studied the present vegetation of tangantangan dominated land to determine the extent to which native trees have become reestablished, to gain insights into the mechanisms involved in natural reforestation and to determine if natural reforestation offers any management lessons. The taxonomic nomenclature of Raulerson and Rinehart (1992) is followed in this study.

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FIG. 1. The Marpi region, showing introduced elephant grass (*Miscanthus giganteus*) in the foreground, alien tangantangan thickets in the midground and native limestone forest in the background.

METHODS

The limestone escarpments of the Marpi region, Saipan have the most extensive and among the best developed native forest remaining on the island. The forest is characterized by two strongly dominant canopy (*Pisonia grandis*, *Cynometra ramiflora*), and understory (*C. ramiflora*, *Guamia marianae*) species, although at least 40 native tree species are present (Craig 1992). Canopy height is relatively low in this typhoon-influenced forest, averaging ca. 10 m, although individual trees grow to 16 m. Saipan residents report that no feral ungulates have been known from the vicinity in ca. 30 years.

Aerial photographs from 1945 indicate that this forest received little disturbance during the Japanese administration (see Pangelinan and Kapileo 1971) except perhaps for logging of the valuable timber tree *Intsia bijuga*. However, before World War II, level areas throughout much of the island were cultivated for sugarcane (*Saccharum officinarum*) (Fosberg 1960). Wartime activities at Marpi resulted in construction directly adjacent to the forest of an airfield and storage facilities for military ordinance (Pangelinan and Kapileo 1971).

I chose as a study site a tangantangan thicket bordering the northwest-facing limestone escarpment known as Suicide Cliff (Fig.1). The thicket borders limestone forest here for ca. 300 m and extends out 30–60 m to a paved road. Similar habitat occupied the opposite side of the road until 1988, when much of that area became altered by ranching activities. On a 1945 aerial photograph (Pangelinan and Kapileo 1971) the study site was deforested, and appeared to have been mowed at least in part. The site presently has clear evidence of previous disturbance, including an overgrown apparent roadbed, remains of air raid shelters, rows of decaying metal drums and sandbag piles. It appears representative of disturbed areas grown up to tangantangan thickets except that the close proximity of an extensive native seed source has maximized the probability of reforestation by native trees.

Following the recommendation of Mueller-Dombois and Ellenberg (1974), I used study plots placed with their long axis perpendicular to the forest border to gather data on vegetative structure and composition in this habitat. I gathered data for ten plots on vegetation in four vertical strata that for the most part also appeared to correspond to age classes. These strata were: (1) canopy—trees first inter-

cepting sunlight and at least 3 m tall, (2) sapling—trees shaded by canopy trees and 2–<3 m in height, (3) shrub—all woody plants other than vines 1–<2 m in height, (4) persistent seedlings—all woody plants other than vines 0.5–<1 m tall. Based on previous observation, I judged smaller seedlings too ephemeral in composition to provide clear insights into longer term patterns and, therefore, I did not measure them. I subdivided each 10 x 5 m plot into ten 1 x 2.5 m quadrats to ensure complete enumeration of all plants present in the plot. In each quadrat, I recorded the number of individuals of each species present in each stratum. I recorded a measure of above ground biomass, the basal area, for all plants larger than seedlings by measuring their diameter at the base of the stem.

RESULTS

Introduced species significantly differed among strata in density (Kruskal-Wallis $H = 15.1, 3 \text{ df}, P < 0.005$). They reached their greatest abundance by far in the seedling layer, but they were similarly abundant in the remaining three strata. Basal areas of introduced trees also significantly differed among strata (One way ANOVA $F = 22.2, 2,27 \text{ df}, P < 0.001$). They declined sharply from the canopy to sapling and shrub layers and the conservative Tukey test indicated that the divergence in mean basal area of the canopy and lower strata was significant ($W = 559.0, P = 0.05$). Native trees similarly differed significantly in density among strata ($H = 22.8, 3 \text{ df}, P < 0.001$), although their distributional pattern diverged from that of the intro-

TABLE 1. Tree species presence in ten 50 m² plots. Density (D) = trees/500 m², basal area (BA) = tree cm²/500 m².

Species	Layer							
	Canopy		Sapling		Shrub		Seedling	
	D	BA	D	BA	D	BA	D	
Introduced:								
<i>Leucaena leucocephala</i>	54	643.4	38	247.7	56	115.1		213
<i>Carica papaya</i>	5	89.6	1	9.7	21	75.7		152
<i>Albizia lebbbeck</i>	5	64.7	10	46.9	5	7.0		4
<i>Pithecellobum dulce</i>					1	2.2		
<i>Lantana camara</i>					1	1.1		
Total:	64	797.7	49	304.3	84	201.2		369
Native:								
<i>Melanolepsis multiglandulosa</i>	17	126.7	85	326.5	60	122.0		5
<i>Aidia cochinchensis</i>			20	65.8	94	150.6		56
<i>Pouteria obovata</i>	1	6.7	5	14.6	13	18.5		17
<i>Psychotria mariana</i>					5	6.3		32
<i>Guamia mariannae</i>	5	54.3	13	70.4	8	19.0		6
<i>Eugenia palumbis</i>			2	7.4	9	15.6		14
<i>Ochrosia mariannensis</i>			1	5.4	5	10.1		1
<i>Cynometra ramiflora</i>			3	13.7	1	1.0		5
<i>Pisonia grandis</i>	1	109.2			4	7.3		
<i>Ficus</i> spp.	1	19.5	3	21.5				
<i>Morinda citrifolia</i>					2	3.9		2
<i>Callicarpa candicans</i>					1	2.5		1
<i>Erythrina variegata</i>	1	9.3						
<i>Pandanus dubius</i>			1	8.8				
<i>Pipturus argenteus</i>	1	11.2						
<i>Maytenus thompsonii</i>					1	2.5		
Total:	27	336.9	133	534.1	203	359.2		139

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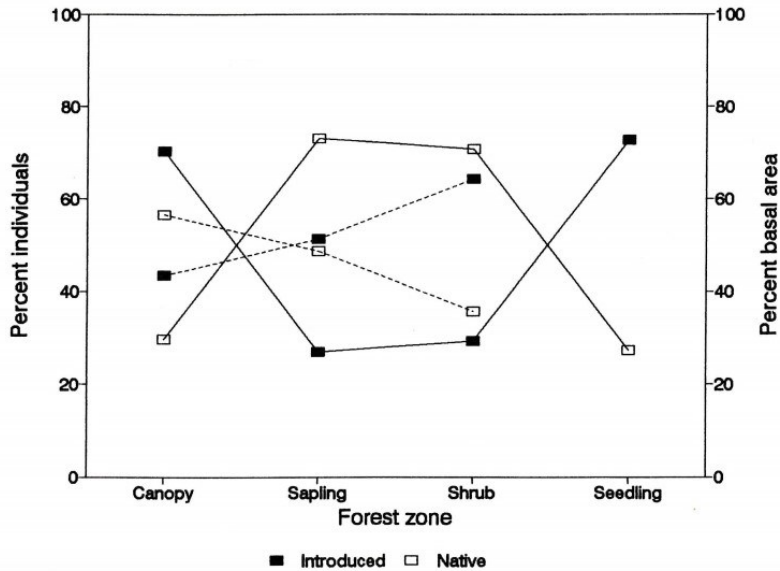


FIG. 2. Comparison of the relative density (solid lines) and basal area (dashed lines) of introduced and native tree species in four tangantangan thicket strata.

duced species. They were most abundant in the lower three strata but were comparatively uncommon in the canopy. Basal areas of native trees showed no significant difference among strata ($F = 1.0, 2, 27 \text{ df}, P > 0.25$), although they averaged highest in the canopy, primarily because single large *P. grandis* and *Ficus prolixa* were present (Table 1).

The abundant, introduced *L. leucocephala* did not differ significantly among strata in density ($H = 3.1, 3 \text{ df}, P < 0.1$), although it significantly differed in basal area ($F = 14.2, 2, 27 \text{ df}, P < 0.001$). *L. leucocephala* averaged most frequent in the seedling layer and had its greatest basal area in the canopy. The second common (but occurring too irregularly for statistical testing) introduced species, *C. papaya*, was also most abundant in the seedling layer but its basal area in the sapling layer was low (Table 1).

The abundant, native *Melanolepsis multiglandulosa* (growing to canopy height) increased in density from the seedling to the sapling layer but declined in the canopy. Basal area showed a similar pattern. The second most common native species, the small understory tree *Aidia cochinchinensis*, reached its greatest density and basal area in the shrub layer. Other regularly encountered native species were *Pouteria obovata*, which grows to tree size, and the two understory species *Psychotria mariana* (occasionally growing to canopy height) and *Eugenia palumbis* (a small understory tree). These latter three species occurred primarily in the shrub and seedling layers. Notably, the predomi-

nant canopy species of the adjacent native forest (Craig 1992), *P. grandis* and *C. ramiflora*, were uncommon in the thickets. *G. mariannae*, an abundant understory species of the limestone forest, was present but relatively uncommon in all thicket strata. All these native species occurred too irregularly for their distributions to be examined statistically (Table 1).

When I compared percent contributions to stratum density, introduced species greatly predominated in the canopy and seedling layers, whereas native species predominated in the shrub and sapling layers. Differences in percent density between strata (Fig. 2) were statistically significant ($H = 27.0, 3 \text{ df}, P < 0.001$). In contrast, proportionate basal area increased for introduced species but declined for native species from the canopy to the shrub layer ($H = 7.0, 2 \text{ df}, P < 0.05$).

Among introduced species, *L. leucocephala* showed a significant difference among strata in its proportionate contribution to vegetation density ($H = 16.2, 3 \text{ df}, P < 0.005$). It was the most abundant species in the canopy and seedling layers but it was relatively infrequent in the shrub and sapling layers. Percent basal area, although averaging greatest in the sapling layer, just missed being significantly different between strata ($H = 5.2, 2 \text{ df}, P > 0.05$). *C. papaya*, in comparison, was an important component of the shrub (basal area) and seedling (density) layers (Fig. 3). Among native species, the proportionate contribution of *M. multiglandulosa* to the vegetation strata increased from the seedling to sap-

TABLE 2. Percent distribution of fruit types among introduced and native tree species occurring in study plots; *n* in parentheses.

Fruit type	Layer				Total
	Canopy	Sapling	Shrub	Seedling	
Introduced:					
small fleshy	0	0	1.2 (1)	0	0.2 (1)
large fleshy	7.8 (5)	2.0 (1)	26.2 (22)	41.2 (152)	33.0 (190)
dry woody	92.2 (59)	98.0 (48)	72.6 (61)	58.8 (217)	66.8 (385)
Native:					
small fleshy	70.4 (19)	86.5 (115)	89.7 (182)	89.9 (125)	87.8 (441)
large fleshy	0	1.5 (2)	3.4 (7)	2.2 (3)	2.4 (12)
dry woody	29.6 (8)	12.0 (16)	6.9 (14)	7.9 (11)	9.8 (49)

ling layer but then declined in the canopy. *A. cochinchinensis* increased from the seedling to the shrub layer but declined in the sapling layer and was absent from the canopy (Fig. 4).

Of the 502 native trees encountered in the study plots, the great majority, including *M. multi-glandulosa*, *A. cochinchinensis*, *P. obovata*, *P. mariana*, and *E. palumbis*, were characterized by having relatively small (ca. 1–2 cm), fleshy or semi-fleshy fruits. The number of trees in the ten plots with such fruits was significantly greater than those with other types of fruits (dry pods, large fruits) (Wilcoxon Rank Sum $Z = 3.7$, $P < 0.0005$). Only a small proportion of native trees had large fruits (> 3 cm; e.g. *Ochrosia mariannensis*, *Pandanus dubius*, *C. ramiflora*) or dry pods (e.g. *Erythrina variegata*). Of the introduced species, only *C. papaya* had fleshy fruits and occurred regularly. *L. leucocephala* has dry pods (Table 2).

DISCUSSION

Without data on stratum recruitment dynamics, definitive predictions about plant succession are impossible. However, insights into vegetation development in this disturbed habitat may be obtained, and hypotheses advanced, from existing patterns. For example, the present canopy apparently developed from colonization of the abandoned site by weedy introduced species, particularly *L. leucocephala*. Although *L. leucocephala* is common in all strata, suggesting that its populations are presently maintained in the thicket, the *L. leucocephala* canopy has likely altered the micro-environment sufficiently to permit recolonization by certain native forest species. Indeed, native species now numerically dominate the shrub and sapling layers. Many native species presently in the understory are capable of invading the canopy and, therefore, over time natives might increase

their presence in the canopy. Some recruitment into the canopy by native species, particularly *M. multi-glandulosa*, has already occurred.

In addition to native species possessing a high relative density in the understory, the few native trees in the canopy already predominate in relative basal area. Native tree species are in many instances capable of growing far larger than *L. leucocephala* and, as these species become established and mature, they will likely shade the understory to a degree unsuitable for *L. leucocephala* reproduction. Because the thicket understory is also being recolonized by native understory species, a community may eventually develop that resembles the adjacent native forest.

In addition to the potential influence of such site-specific factors as evolving microenvironments and plant competitive interactions in native tree reestablishment, plant dispersal agents also appear to have exerted an important impact on reforestation. Native tree species at the study site represented a subset of those present in the immediately adjacent limestone forest. Notably, species with small, fleshy or semi-fleshy fruits were particularly abundant in the thickets. Such fruits are popular food items of the indigenous forest birds (Craig 1990, unpubl. data). In contrast, native trees with large fruits were infrequent in the thickets. Some rat (*Rattus* spp.) dispersal of the large-fruited *Ochrosia mariannensis* seemed probable, based on my observation of partially rat-chewed fruits of this tree species. However, other species with large, fleshy fruits like *Neisosperma oppositifolia*, though regularly occurring in the adjacent limestone forest (Craig 1992), were undetected in the thickets.

In disturbed sites on the Mariana Island of Rota, I have observed that *N. oppositifolia* and other large, fleshy-fruited species are common seedlings and saplings. This difference between the islands may exist because the Marianas Fruit Bat (*Pteropus*

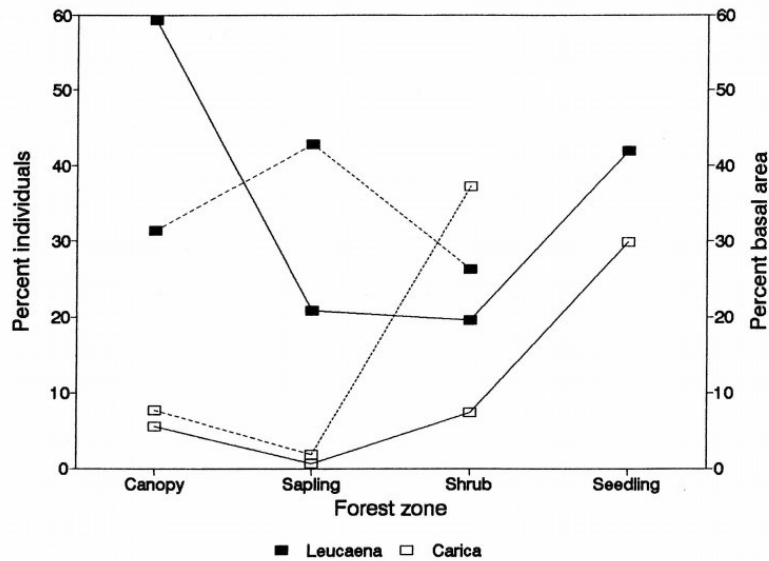


FIG. 3. Comparison of the relative density (solid lines) and basal area (dashed lines) of the introduced tree species, *Leucaena leucocephala* and *Carica papaya*, in four tangantangan thicket strata.

mariannus), which feeds on such fruits (Wiles et al. 1989), is reported by Saipan residents to have been virtually extirpated for ca. 30 years, whereas on Rota a large bat population persists. The introduced *C. papaya* was common in the thickets, but its large, fleshy fruits (but small seeds) are fed upon even by small forest birds (Craig 1990, Fig. 5).

The rarity of certain native tree species in the thickets, such as those that predominate in the adjacent native forest (e.g. *C. ramiflora*, *G. mariannae*) may be related at least in part to inadequate dispersal of their large, non-fleshy fruits. However, the rarity of other native species in the thickets requires alternate explanations. For example, even though the small, fleshy fruits of figs (*F. prolixa*, *F. tinctoria*) are a popular food of many forest bird species (Craig 1990, unpubl. data), *Ficus* was largely absent from the study area. Tree species such as these may find the microenvironments of thickets still unsuitable for growth. Although I made no quantitative measures, the interior of the adjacent limestone was noticeably darker, cooler, and wetter than that of the thickets. The occurrence of *P. mariana*, which also has small, fleshy fruits popular as food by forest birds, may provide evidence for continued evolution of the thicket microenvironment. It was absent in the sapling layer, uncommon in the shrub layer, but fairly common as a seedling. This suggests that it has invaded the thickets relatively recently, perhaps as the microenvironment, modified by the emergence of a sapling layer of *M. multiglandulosa*, has become more suitable.

If left undisturbed by human activity, temporal

shifts in the composition of thicket vegetation seem likely to involve a complex interplay of seed dispersal agents, evolving microenvironments, plant competitive interactions and external events such as typhoons. However, because the adjacent limestone forest appears resistant to invasion by introduced species (Craig 1992), colonizing native trees should ultimately prove competitively superior to weedy, introduced species. Efforts aimed at reestablishing native forest might make use of such competitive superiority in accelerating the reversion of thickets to native forest. Strategies that might be investigated include selectively thinning the tangantangan canopy to assist native understory species in assuming dominance, underplanting thickets with native canopy species that may have weak dispersal abilities and shading and irrigating thickets to simulate native forest microenvironments.

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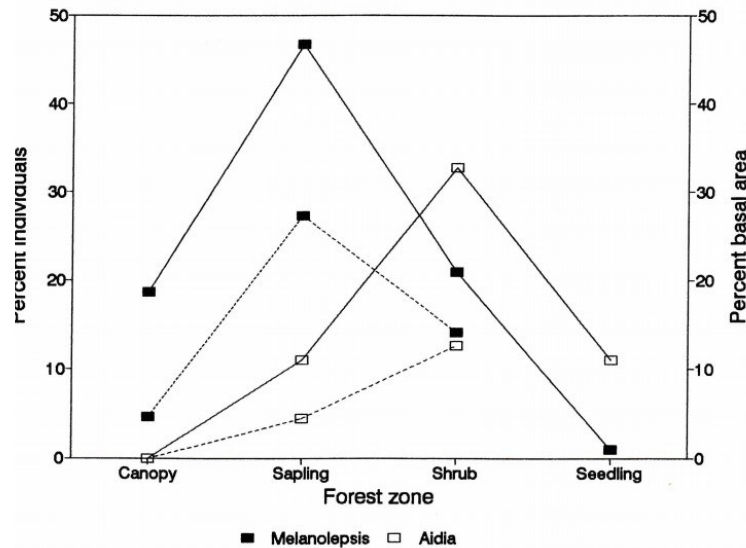


FIG. 4. Comparison of the relative density (solid lines) and basal area (dashed lines) of the native tree species, *Melanolepis multiglandulosa* and *Aidia cochinchinensis*, in four tangantangan thicket strata.

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FIG. 5. Golden White-eye (*Cleptornis marchei*) feeding on papaya fruits.