Micronesica 25(1): 85–97, 1992

Ecological Characteristics of a Native Limestone Forest on Saipan, Mariana Islands

ROBERT J. CRAIG[1]

Division of Fish and Wildlife,
Commonwealth No. Mariana Islands,
Saipan, MP 96950

Abstract—A remnant native limestone forest in the Marpi region, Saipan, was studied to characterize the species composition, relative species importance, tree basal area, and tree density in that habitat. Using the point-quarter sampling technique on 400 canopy and understory trees each, I found that mean canopy and understory basal area were, respectively, 45140 ± 24144 and 1460 ± 749 m^2/ha. Mean trees/ha in the canopy and understory were, respectively, 794 ± 174 and 2579 ± 770. *Pisonia grandis* overwhelmingly dominated in canopy basal area, whereas *Cynometra ramiflora*, *Pouteria obovata*, and *Guamia mariannae* dominated in the understory. *Cynometra ramiflora* occurred most densely in the canopy, and *C. ramiflora* and *G. mariannae* had the highest densities in the understory. The relative measure of forest prevalence, the importance value, showed that *P. grandis* and *C. ramiflora* were the principal canopy species, and *C. ramiflora* and *G. mariannae* were the major understory species. A model of forest dynamics is proposed in which *P. grandis* and other species largely absent from the understory may be maintained in the forest through disturbance, which might facilitate vegetative propagation, flowering, or survival of seedlings. Commonly fruiting, shade tolerant species like *C. ramiflora*, which were frequent in both the canopy and understory, may come to predominate under conditions of low forest disturbance. Despite centuries of human-related disruption, forest composition remains overwhelmingly native, suggesting that native forest is resistant to invasion by alien species.

Introduction

With the exception of the Hawaiian Islands (summaries in Mueller-Dombois 1985, Gerrish 1990), the quantitative ecology of tropical Pacific island forests remains largely unstudied. Plant ecological investigations often have been de-

---

[1] *Present address*: Northern Marianas College, Box 1250, Commonwealth No. Mariana Islands, Saipan, MP 96950.

scriptive accounts of distributions and plant associations (e.g. Maxwell 1982, Woodroffe 1985, 1987), although Ash (1987), Merlin (1991), and Franklin & Steadman (in press) provided quantitative data on Pacific islands south of the equator. Most botanical studies that include the Mariana Islands, Micronesia, have concerned plant systematics and floristics (e.g. Stone 1970, Fosberg et al. 1975, 1980). In addition, Fosberg (1960) gave descriptions of the principal plant associations of Micronesia, and Moore (1973) and Muniappan (1976) each characterized native forest found along single transects on Guam.

To begin providing comprehensive quantitative data on Mariana Island forests, I studied the native limestone forests of Saipan. I characterized the species composition, relative species importance, tree basal area, and tree density in this habitat. From comparative data on the canopy and understory components of the forest, inferences were made concerning future trends in forest composition. Furthermore, qualitative comparisons of this study area were made with other tracts of limestone forest to assess the generality of my findings.

Native forest on Saipan is estimated to cover 5% (Engbring et al. 1986) to 19% (Young 1989) of the island. Most surviving native forest occurs on steep limestone escarpments and may be classified as limestone forest (forest that grows on limestone-derived soil), although examples of ravine forest growing on volcanic soil, *Casuarina-Pandanus* savanna, mangrove swamp, freshwater swamp, and strand forest are also present (Fosberg 1960).

Because the native forests of Saipan have been subjected to centuries of human-related alteration, including cutting, burning, browsing by feral ungulates, war-related damage, and virtual extirpation of seed-dispersing Marianas Fruit Bats (*Pteropus mariannus*) (Fosberg 1960, Wiles et al. 1989), the present appearance of Saipan's limestone forest likely reflects the combined effects of these factors. Hence, the following analysis must be considered in light of anthropogenic alterations. In this study, the taxonomic nomenclature of Raulerson & Rinehart (1991) has been followed.

Study Area and Methods

The Marpi region of Saipan has the most extensive and among the best developed native forest remaining on Saipan. However, before World War II, level areas were cultivated for sugarcane (*Saccharum officinarum* L.) (Fosberg 1960), which largely isolated the Marpi forest from other tracts of native forest. There are no feral ungulates in this area, even Sambar Deer (*Cervus unicolor*) which have been introduced to Saipan, but local residents report that pigs (*Sus scrofa*) were present ca. 1960.

To obtain data on the structure and species composition of the Marpi forest, I established 10 transects with starting points about 250 m apart. The first transect was located near the northern corner of the steep limestone escarpment known as Suicide Cliff. Others were placed south along the escarpment's west slope and the last near its southern end. Transects were parallel to the slope contours at mid- to lower elevations, where forest was usually best developed. High elevation forest on steep slopes was often characterized by stunted, exposed forest. On each transect, I placed 10 sample points paced about 12 m apart (108 m total), which was sufficient to make each point independent (i.e. no overlap in trees between points). For comparison, limestone forests were studied qualitatively elsewhere on Saipan, particularly at Tapotchau, Gualo Rai, Naftan, Dandan, Talufofo, and Kagman, as well as on Guam, Rota, and Tinian.

The plotless point-quarter sampling technique (Cottam and Curtis 1956) was used to measure 4 canopy and 4 understory trees/point. Canopy trees were defined as those first intercepting sunlight, and understory trees were those growing below the canopy but taller than 2 m. For each tree, I measured the distance from the sample point to the center of the tree and the diameter at breast height (dbh). For the variety of tree growth forms encountered in the limestone forest, dbh proved the most equitable measure of diameter.

Point-quarter analysis yields data on the horizontal area covered by tree stems (basal area), no. stems/unit area (density), and dispersion of trees in the forest (frequency). From these 3 measures, I computed a relative importance index for each species known as the importance value (reviewed by Mueller-Dombois & Ellenberg 1974). For broad-leaved forests, the importance value is related to proportionate contribution of a species to forest foliage volume (Holmes & Robinson 1981). Tree density and basal area were also examined separately, because they are distinct, absolute measures of overall tree occurrence.

For each species, a ratio of importance values in the canopy versus the understory was computed by dividing the smaller value by the larger, and subtracting the quotient from 1. For graphical clarity, positive values were assigned to species predominating in the canopy, and negative values were assigned to those predominating in the understory. The more strongly a species was represented in the canopy, the closer its ratio was to 1 and, similarly, the more strongly it was represented in the understory, the closer its value was to -1. The importance value ratio highlights those species which predominate in either the canopy or understory, thereby providing insights into shifting patterns of forest species composition.

Results and Discussion

The 2 absolute measures of overall tree occurrence in the Marpi limestone forest, basal area (Figure 1) and density (Figure 2), varied substantially between transects, with the relative variance (as measured by the coefficient of variation, CV) similar in the canopy and understory. Canopy trees dominated in basal area but understory trees had the greatest density (canopy basal area (m^2/ha: $\bar{x} \pm$ SD $= 45140 \pm 24144$, CV $= 53$, understory basal area: $= 1460 \pm 749$, CV $= 51$; canopy trees/ha: $\bar{x} = 794 \pm 174$, CV $= 22$, understory trees/ha: $\bar{x} = 2579 \pm 770$, CV $= 30$).

Pisonia grandis R. Br. showed overwhelming canopy dominance among trees in basal area (Table 1). It was the largest species in the forest, with massive individuals to 242 cm dbh present. In contrast, the abundant but slender-trunked

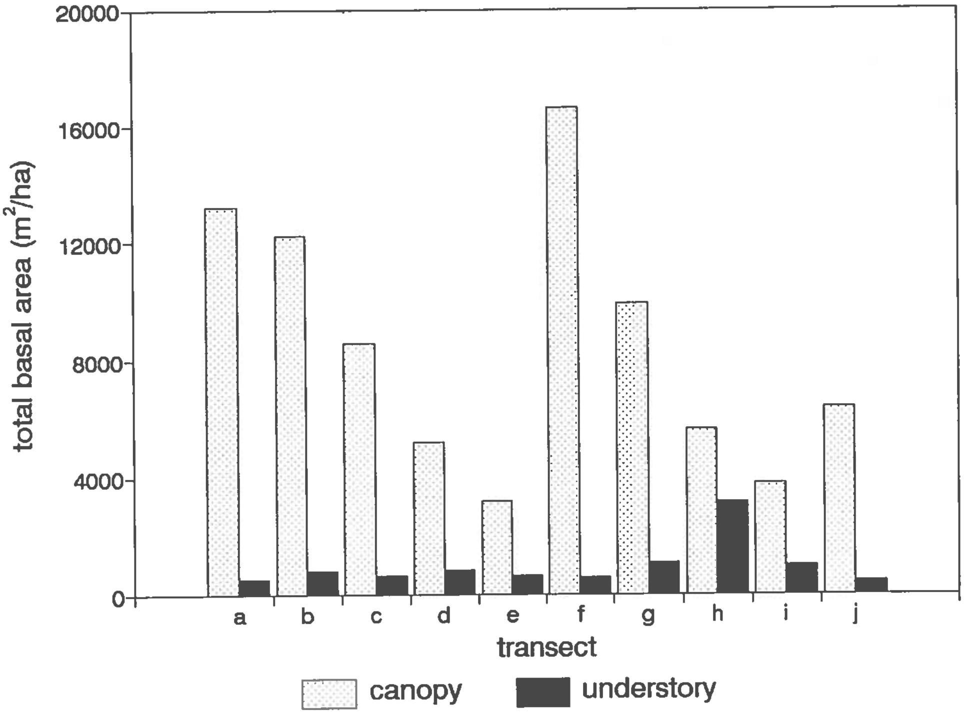

Figure 1. Basal area of canopy and understory trees at 10 transects arranged from north (a) to south (j).

Cynometra ramiflora L. had relatively low basal area. The irregularly distributed *Dendrocnide latifolia* (Gaud.) W.L. Chew dominated at only one transect. In the understory, *C. ramiflora* and the Marianas endemic *Guamia mariannae* (Saff.) Merr. predominated, although the irregularly distributed *Pouteria obovata* (R.Br.) Baehni also had a high average basal area (Table 2).

Canopy tree densities exhibited a divergent pattern from basal areas (Table 1). *Cynometra ramiflora* had the highest density, whereas *P. grandis* was comparatively uncommon. *Intsia bijuga* (Colebr.) O. Kuntze occurred commonly at the southernmost 5 transects, but was virtually absent in the northern portion of the study area. Stumps of logged *I. bijuga* trees suggested that its distribution was at least in part an artifact of logging. It was the only native species in the Marpi forest which appeared to have been logged. In the understory, *C. ramiflora* and *G. mariannae* even more strongly predominated in density than they had in basal area (Table 2).

The relative measure of forest prevalence, the importance value, showed that *P. grandis* and *C. ramiflora* were the principal canopy species (Table 1), and *C. ramiflora* and *G. mariannae* were the major understory species (Table 2). Because *P. grandis* was not abundant, its importance value was largely a reflection of its

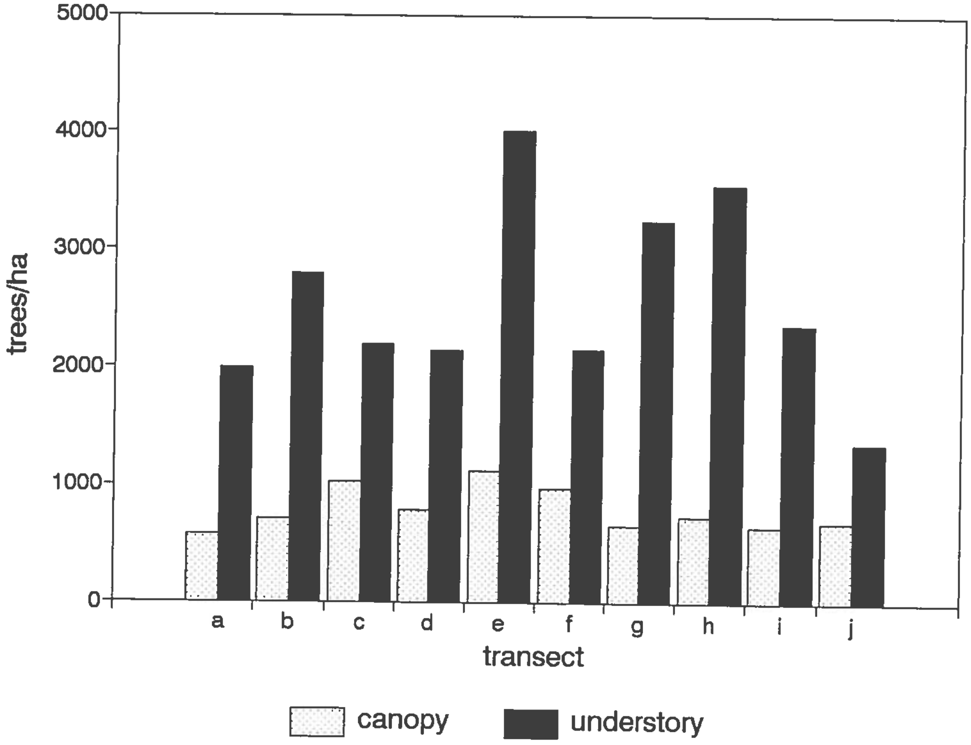

Figure 2. Density of canopy and understory trees at 10 transects arranged from north (a) to south (j).

basal area (Figure 3). Canopy heterogeneity in basal area (Figure 1) largely mirrored its uneven basal area distribution. In contrast to its canopy dominance, no understory *P. grandis* were encountered on transect points. Saplings and seedlings (sometimes appearing to be broken branches that had rooted) were observed, but infrequently. A minimum age for some of the larger *P. grandis* specimens was provided by World War II shrapnel embedded in their trunks, indicating an age >47 yr, and possibly >100 yr.

In both the canopy and understory, *C. ramiflora* showed an increase in basal area from north to south, but its basal area declined sharply near the southern end of the study area (Figure 4). However, the basal areas of the canopy and understory trees showed little relationship to each other ($r^2 = 0.5$, df = 8). Unlike *C. ramiflora*, which averaged highest in canopy compared to understory basal area (although not significantly; canopy: $\bar{x} = 464.4 \pm 509.5$; understory: $\bar{x} = 286.4 \pm 243.1$ m^2/ha; $t = 1.0$, df = 8, $P > 0.3$), *G. mariannae* had its highest basal area in the understory (canopy: $\bar{x} = 20.0 \pm 23.7$; understory: $\bar{x} = 175.9 \pm 101.3$ m^2/ha; $t = 5.3$, df = 8, $P < 0.001$). Again, little relationship existed between the basal area of canopy and understory *G. mariannae* ($r^2 = 0.4$, df =

Table 1. Mean occurrence (± SD) of canopy trees in the Marpi forest, arranged in descending order by importance values.

Species	Basal area (m²/ha)	Trees/ha	Importance value
Pisonia grandis (Pg)[a]	5747.4 ± 4901.4	65.2 ± 45.4	73.5 ± 40.1
Cynometra ramiflora (Cr)	464.4 ± 509.5	214.9 ± 110.0	57.4 ± 28.6
Intsia bijuga (Ib)	302.1 ± 365.4	65.2 ± 82.0	21.4 ± 25.5
Dendrocnide latifolia (Dl)	509.2 ± 982.7	32.6 ± 64.0	16.6 ± 29.5
Premna obtusifolia (Pr)	179.7 ± 230.1	44.1 ± 41.5	15.6 ± 17.5
Ficus tinctoria (Ft)	153.0 ± 171.5	40.3 ± 39.9	14.2 ± 12.9
Melanolepsis multiglandulosa (Mm)	91.0 ± 100.3	36.5 ± 33.2	11.9 ± 10.5
Ficus prolixa (Fp)	163.2 ± 158.9	21.1 ± 14.2	9.5 ± 7.1
Erythrina variegata (Ev)	274.6 ± 396.9	23.0 ± 31.1	9.0 ± 11.4
Guamia mariannae (Gm)	20.0 ± 23.7	28.8 ± 31.7	9.0 ± 9.5
Pouteria obovata (Po)	88.6 ± 88.1	26.9 ± 22.5	8.5 ± 6.2
Aglaia mariannaensis (Ag)	49.3 ± 66.1	24.9 ± 32.7	8.0 ± 9.6
Carica papaya (Cp)	37.6 ± 41.1	26.9 ± 22.5	7.4 ± 6.9
Ochrosia mariannensis (Om)	40.5 ± 46.0	24.9 ± 35.1	7.3 ± 8.4
Neisosperma oppositifolia (No)	78.7 ± 131.8	17.3 ± 24.7	6.3 ± 9.2
Leucaena leucocephala (Ll)	25.1 ± 38.1	17.3 ± 19.1	5.1 ± 5.4
Albizia lebbeck (Al)	64.2 ± 192.6	17.3 ± 54.6	4.6 ± 13.8
Pandanus dubius (Pd)	12.6 ± 26.3	7.7 ± 18.5	2.3 ± 5.0
Psychotria mariana (Ps)	3.1 ± 6.4	7.7 ± 18.5	2.2 ± 5.1
Morinda citrifolia (Mc)	8.8 ± 22.1	5.8 ± 13.0	1.9 ± 4.0
Pandanus tectorius (Pt)	13.3 ± 28.4	5.8 ± 13.0	1.6 ± 3.2
Artocarpus altilis (Aa)	66.7 ± 200.1	1.9 ± 6.1	1.6 ± 4.9
Artocarpus mariannensis (Am)	34.7 ± 104.2	1.9 ± 6.1	1.5 ± 4.6
Acacia confusa (Ac)	53.0 ± 158.9	3.8 ± 12.1	1.5 ± 4.6
Drypetes dolichocarpa (Dd)	2.4 ± 7.2	1.9 ± 6.1	0.7 ± 2.0
Cordia subcordata (Cs)	1.7 ± 5.1	1.9 ± 6.1	0.6 ± 1.9
Aidia cochinchinensis (Ai)	0.8 ± 2.5	1.9 ± 6.1	0.6 ± 1.7

[a] Abbreviations of species names in parentheses are used in Figure 6.

8), and the distribution of basal areas in the study area showed no consistent pattern (Figure 5).

The ratio of importance values for canopy and understory trees (Figure 6) showed that 2 common species, *P. grandis* and *I. bijuga*, were detected only in the canopy. *Pisonia grandis* flowers only rarely (although it flowered heavily in Feb.-Mar. 1991), and propagates vegetatively from broken branches (Stone 1970). Furthermore, *I. bijuga* also appears to flower infrequently on Saipan, although some fruits and seedlings were found during the study. The rarity of these species in the understory may indicate that reproduction occurs primarily after disturbance, such as after typhoons, or after some other unusual circumstance. The rarity in the understory of *D. latifolia*, which appears to flower and fruit regularly, suggests that this and other regularly fruiting canopy species with importance value ratios approaching 1 may have seeds that germinate poorly in shade, and so may also profit from disturbance or other unusual circumstances.

Table 2. Mean occurrence (± SD) of understory trees in the Marpi forest, arranged in descending order by importance values.

Species	Basal area (m²/ha)	Trees/ha	Importance value
Cynometra ramiflora	286.4 ± 243.1	764.5 ± 398.3	83.9 ± 44.9
Guamia mariannae	175.9 ± 101.3	668.2 ± 395.7	76.9 ± 39.0
Aidia cochinchinensis	33.9 ± 36.4	156.5 ± 70.7	19.5 ± 6.2
Pouteria obovata	189.8 ± 511.7	114.4 ± 156.6	17.7 ± 21.4
Eugenia palumbis (Ep)[a]	13.9 ± 18.0	162.5 ± 130.2	16.3 ± 9.2
Pandanus dubius	46.9 ± 92.1	78.3 ± 160.6	13.4 ± 25.2
Ochrosia mariannensis	44.4 ± 53.4	60.2 ± 56.8	11.6 ± 12.2
Aglaia mariannensis	28.5 ± 47.9	90.3 ± 110.8	11.4 ± 13.5
Ficus tinctoria	33.7 ± 60.3	66.2 ± 44.4	9.0 ± 6.7
Morinda citrifolia	43.5 ± 98.6	36.1 ± 58.2	8.5 ± 15.5
Carica papaya	13.0 ± 15.4	36.1 ± 31.1	5.8 ± 4.9
Psychotria mariana	11.4 ± 12.7	42.1 ± 29.1	5.7 ± 3.7
Premna obtusifolia	12.9 ± 28.6	30.1 ± 51.2	3.9 ± 6.3
Maytenus thompsonii (Mt)	7.4 ± 12.4	30.1 ± 51.1	3.9 ± 6.4
Albizia lebbeck	5.5 ± 16.4	12.0 ± 38.1	2.4 ± 7.3
Neisosperma oppositifolia	4.4 ± 10.1	12.0 ± 25.4	2.1 ± 4.4
Ficus prolixia	8.8 ± 26.5	6.0 ± 19.0	2.0 ± 6.1
Erythrina variegata	2.8 ± 8.4	12.0 ± 38.1	1.8 ± 5.4
Melanolepsis multiglandulosa	2.9 ± 6.0	12.0 ± 25.4	1.8 ± 3.6
Pandanus tectorius	3.5 ± 10.6	6.0 ± 19.0	1.1 ± 3.4
Dendrocnide latifolia	2.6 ± 7.7	6.0 ± 19.0	0.7 ± 2.2
Leucaena leucocephala	0.2 ± 0.5	6.0 ± 19.0	0.6 ± 1.9

[a] Abbreviations of species names in parentheses are used in Figure 6.

Support for the notion of disturbance-related reproduction by certain tree species was obtained after a September, 1991 typhoon, when the forest floor at Marpi was littered with numerous branches of *P. grandis* and *D. latifolia.* Many branches from both species rooted, sprouted leaves, and flowered during Oct.–Nov. Other native tree species, including *I. bijuga,* were not observed to vegetatively propagate, however. *Intsia bijuga* may maintain itself in the forest by some other mechanism, such as fruiting after a period of unusual weather.

In contrast to these species, heavily fruiting, common canopy species like *Ficus tinctoria* G. Forst. v. *neo-ebudarum* (Summerh.) Fosb. and *C. ramiflora* reproduced readily in shade as demonstrated by their importance value ratios approaching or <0. In fact, seedling *C. ramiflora* were one of the most abundant components of the forest herbaceous layer in the wet season (June–Nov.). Although these suffer high mortality in the dry season, clearly enough survive to produce recruitment into the understory. Such species likely increase in abundance during periods of low forest disturbance.

Of those species predominating in the understory (Figure 6), *G. mariannae, Aidia cochinchinesis* Lour., *Eugenia palumbis* Merr., and *Maytenus thompsonii* (Merr.) Fosb. are small trees that rarely grow large enough to invade the canopy (Stone 1970, Raulerson and Rinehart 1991). Other more robust, commonly fruit-

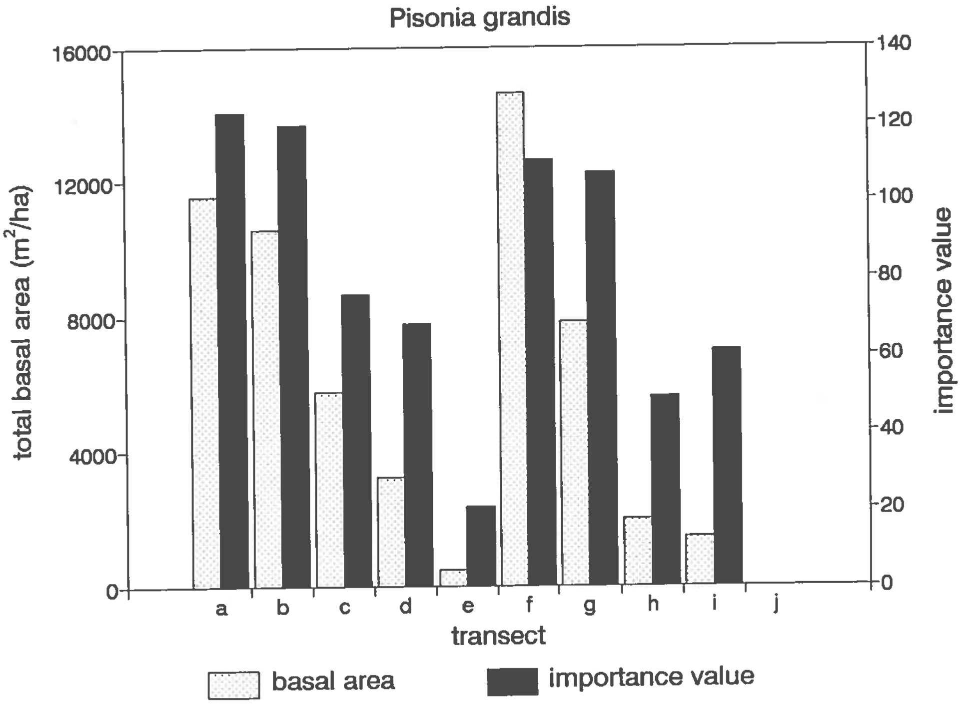

Figure 3. Basal area and importance value of *Pisonia grandis* at 10 transects arranged from north (a) to south (j).

ing species, such as *P. obovata, Ochrosia mariannensis* A. DC., and *Aglaia mariannensis* Merr. may, based on their negative importance value ratio, increase in the forest canopy under conditions of low disturbance.

These are only preliminary data on recruitment dynamics in limestone forest; for a thorough assessment, data on such parameters as seed viability, dispersal, survivorship, and importance of vegetative propagation are needed. However, the data provide initial insights into the mechanisms of forest maintenance in this system. A model may be proposed for limestone forest dynamics: forest species composition is regulated by the frequency and intensity of external (i.e. typhoon) disturbance. A suite of vegetatively reproducing species that also flower after mechanical injury are maintained in the system by disturbance, and a suite of mostly sexually reproducing, shade tolerant species are maintained during times and in areas of limited disturbance.

The introduced *Leucaena leucocephala* (L.) de Wit and *Acacia confusa* E. Merr. occurred predominantly in the canopy (Figure 6), and therefore appeared to have little reproductive success in this forest. However, *Carica papaya* L. (introduced) was regular in the understory. Notably, of these introduced species, only the fleshy-fruited *C. papaya* is fed upon and probably dispersed by birds. *Albizia lebbeck* (L.) Benth. (introduced) was limited to 1 transect, and was there-

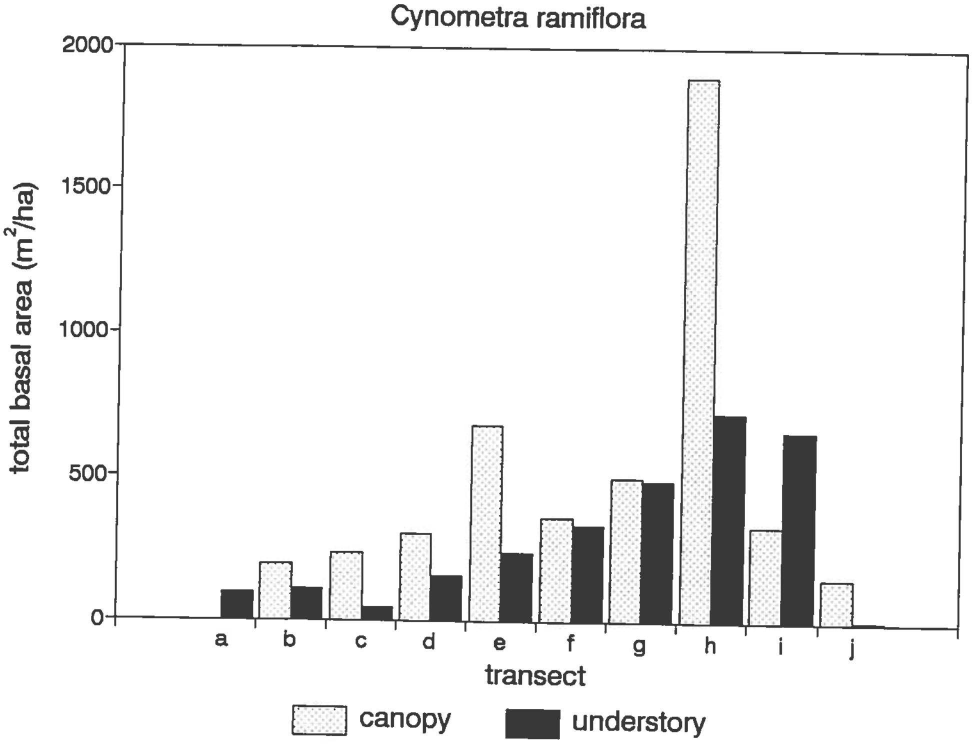

Figure 4. Basal area of canopy and understory *Cynometra ramiflora* at 10 transects arranged from north (a) to south (j).

fore too uncommon for any definitive statement to be made concerning its reproduction.

Recently introduced species (not including prehistorically introduced species like *Artocarpus altilis*), although now of limited significance in the limestone forest based on their importance values (Tables 1, 2), require further study to determine their potential role in future forest composition. Based on importance values, they presently comprise 6.4 ± 7.5% of the canopy and 2.9 ± 3.5% of the understory. Like the similarly high percent native cover found by Merlin (1991) for the native woody vegetation of Mangaia, Cook Islands, this finding suggests that native forest is resistant to invasion by alien species. Only the transect at the northern end of the study area had relatively high cover by introduced species (26.3% of the canopy importance values). The vicinity of this transect, near the Japanese Last Command Post of World War II, was heavily bombed during the American invasion of Saipan. A circular patch of *L. leucocephala* on the cliffs above the Last Command Post, an area never cultivated, is a likely consequence of a very large explosion.

In addition to those located during sampling, I found the following tree species in the Marpi study area: *Annona reticulata* L. (introduced; scattered in-

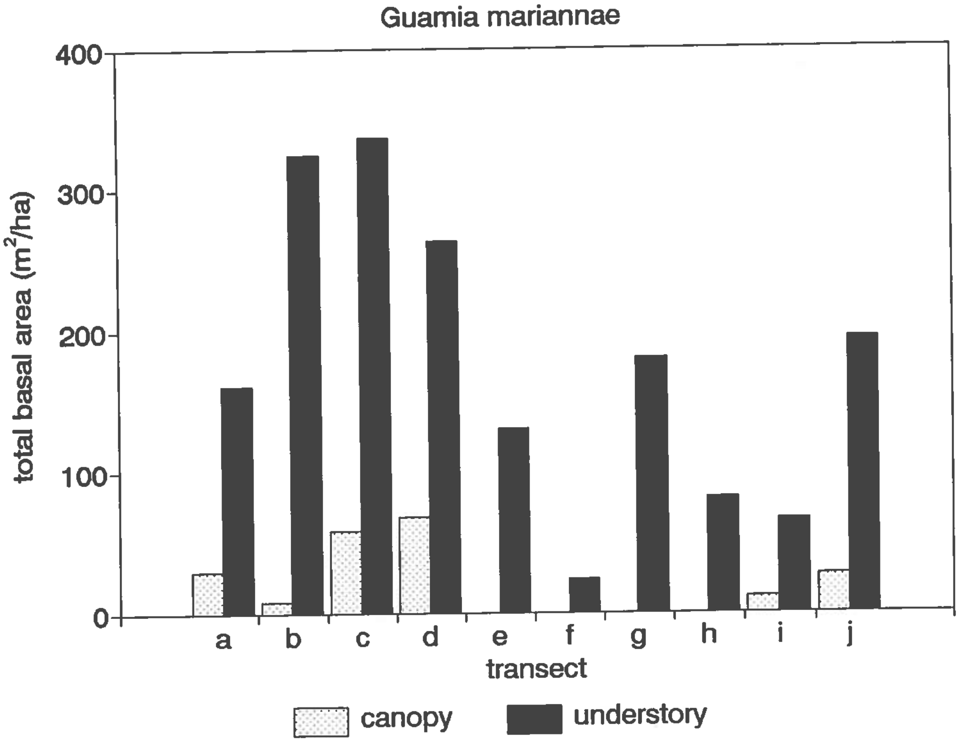

Figure 5. Basal area of canopy and understory *Guamia mariannae* at 10 transects arranged from north (a) to south (j))

dividuals), *Cerbera dilatata* Markg. (native; scattered individuals), *Casuarina equisetifolia* L. (native; scattered individuals), *Excoecaria agallocha* L. v. *orthostichalis* Muell.-Arg. (native; scattered individuals), *Hernandia sonora* L. (native; several at slope base), *Barringtonia asiatica* (L.) Kurz (native; in intermittent stream valleys), *Hibiscus tiliaceus* L. (native; in intermittent stream valley), *Guettarda speciosa* L. (native; scattered individuals), *Polyscias grandiflora* Volkens (native; scattered individuals), *Muntingia calabura* L. (introduced; forest edge), *Delonix regia* (Bojer) Raf. (introduced; single tree at high elevation), *Trema orientalis* (L.) Blume v. *argentea* (Planch.) Laut. (native; forest edge), *Callicarpa candicans* (Burm.) Hochr. (native; forest edge), *Streblus pendulinus* (Endl.) F. von Muell. (native; southern end of study area only), *Allophylus timorensis* (DC.) Blume (native; scattered individuals), *Bauhinia monandra* Kurz (introduced; single clump of individuals), and *Pipturus argenteus* (Forst. *f.*) Wedd. (native; forest edge and openings).

Besides these species, vegetative specimens identified tentatively as *Psychotria hombroniana* (Baill.) Fosb. (native; scattered individuals) were encountered. On the study transects, one possible *P. hombroniana* specimen was combined

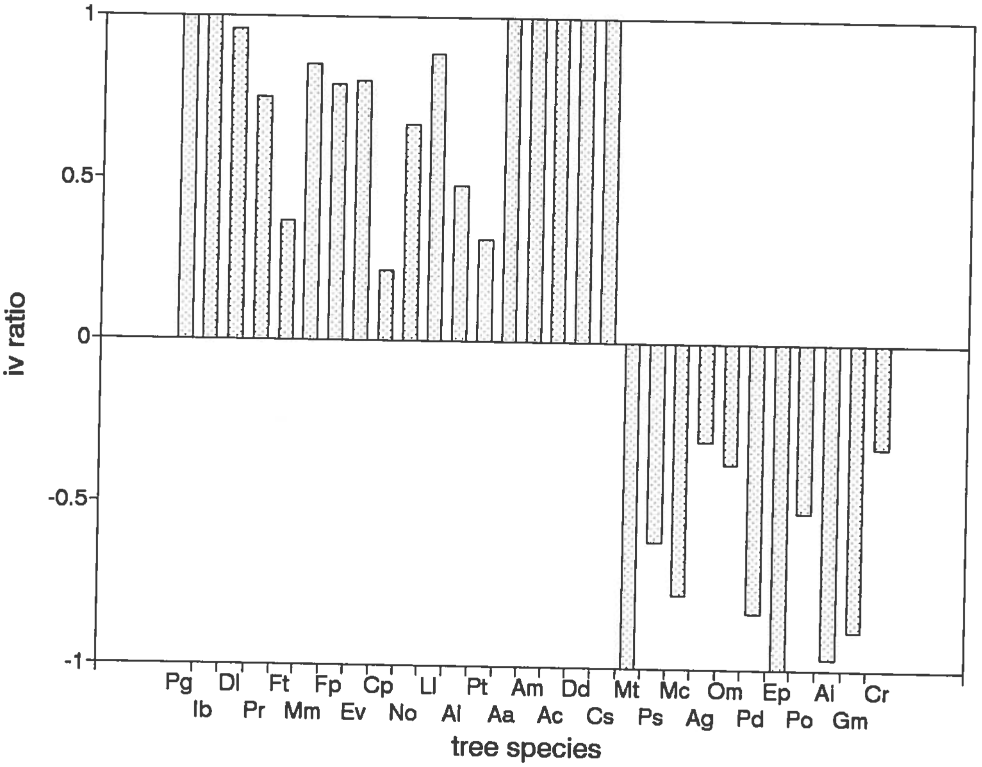

Figure 6. Ratio of canopy and understory importance values for tree species in the Marpi limestone forest. Species predominating in the canopy (values > 0) are arranged from greatest (left) to lowest (right) canopy importance value. Species predominating in the understory are arranged from greatest (right) to lowest (left) understory importance value. Hence, species at the graph edges are relatively important forest constituents, whereas species toward the graph center are relatively unimportant. See Table 1, 2 for abbreviations of species names.

with *P. mariana* Bartl. *ex.* DC. in analyses. Furthermore, because no flowering or fruiting was observed during the sampling period, I did not distinguish between *Eugenia reinwardtiana* (Bl.) DC. and *E. palumbis.* Most individuals, as verified during their July flowering appeared to be *E. palumbis*, and are reported as such in the figures, tables, and text.

Qualitative comparison of the Marpi forest with other limestone forests indicated a general similarity in appearance with low to mid-elevation forest elsewhere on Saipan and Tinian. Species proportions varied between sites, but a similar species assemblage was found throughout. The existing forest characteristics are likely in part a byproduct of human and feral animal activity (particularly in terms of species distributions and relative abundance), but the uniformity of its appearance even between islands suggested that the present limestone forest system retains some of its natural features.

In contrast to these forests, remnant limestone forest at the highest elevations of Mt. Tapotchau, Saipan, and the high elevation plateau forest of Rota exhibited strong differences in appearance. These fog-prone areas are cooler and wetter (Fosberg 1960, Young 1989) than the lower elevation forests, and had high densities of epiphytic lichens, mosses, ferns, and orchids. The forest floor was also typically moss-covered, and tree species such as *Pandanus* spp., *Pisonia umbellifera* (Forst.) Seemann, and *Claoxylon marianum* Muell.-Arg. were characteristic. On Rota, *Guettarda speciosa, Hernandia labrynthica, Fagraea galilai* Gilg & Benedict, *Macaranga thompsonii* E. Merr., *Cycas circinalis* L., and *Elaeocarpus joga* Merr. joined these as common tree species. The latter 3 species are rare on Saipan, and I have not found *F. galilai* on Saipan.

In contrast to this study, Moore (1973) found that limestone forest dominants at Pagat Point, Guam were *Mammea odorata* (Raf.) Kost. and *Eugenia reinwardtiana*. Similar *M. odorata*-dominated forests also may be in strand communities on Saipan. At Hilaan Beach, Guam Muniappan (1976) found *Aglaia marianennsis* and *Guamia mariannae* to be the dominant limestone forest species. In general, the more southerly, apparently less xerophytic limestone forests of Rota and Guam appear more diverse than those of Saipan, but whether this represents the original condition of the forests is uncertain.

The native limestone forest of the Marpi region may be characterized as having a canopy dominated by two widespread (Stone 1970) Indo-Pacific species, and an understory dominated by an endemic (Stone 1970) Marianas genus. Some species may be maintained in the system by disturbance, whereas others appear to recruit successfully into a closed forest canopy. In the absence of human and feral ungulate disturbance, and relative proportions of these species may be affected by the frequency and severity of typhoons and other natural disturbance. Despite centuries of human-related disruption, forest composition remains overwhelmingly native, suggesting that native forest is resistant to invasion by alien species.

Acknowledgments

I thank M. Lefor, L. Raulerson, D. Steadman, S. Villagomez and G. Wiles for their insights concerning this study. L. Raulerson verified my plant identifications, and V. Camacho and K. Krauska assisted with field work. I especially thank my wife, Barbara, for her support and encouragement on all my studies in the Pacific. This work was funded by the Commonwealth of the Northern Mariana Islands, Division of Fish and Wildlife, in conjunction with Pittman-Robertson Federal Aid to Wildlife.

References

Ash, J. 1987. Stunted cloud forest in Taveuni, Fiji. Pacific Sci. 41: 191–199.

Cottam, G. & J. T. Curtis. 1956. The use of distance measures in phytosociological sampling. Ecology 37: 451–460.

Engbring, J., F. L. Ramsey & V. J. Wildman. 1986. Micronesian forest bird survey, 1982: Saipan, Tinian, Agiguan, and Rota. U.S. Fish & Wildl. Serv. Rep.

Fosberg, F. R. 1960. The Vegetation of Micronesia. Bull. Amer. Mus. Nat. Hist. 119.

Fosberg, F. R., M. V. C. Falanruw & M.-H. Sachet. 1975. Vascular flora of the Northern Marianas. Smithsonian Contrib. Botany 22: 1–45.

Fosberg, F. R., M. V. C. Falanruw & M.-H. Sachet. 1980. Systematic studies of Micronesian plants. Smithsonian Contrib. Botany 45: 1–40.

Franklin, J. & D. W. Steadman. in press. The potential for conservation of Polynesian birds through habitat mapping and species translocation. Cons. Biol.

Gerrish, G. 1990. Relating carbon allocation patterns to tree senescence in *Metrosideros* forests. Ecology 71: 1176–1184.

Holmes, R. T. & S. K. Robinson. 1981. Tree species preference of foraging insectivorous birds in a northern hardwood forest. Oecologica 48: 31–35.

Maxwell, B. D. 1982. Floristic description of the native upland forests on Kosrae, eastern Caroline Islands. Micronesica 18: 109–120.

Merlin, M. D. 1991. Woody vegetation on the raised coral limestone of Mangaia, southern Cook Islands. Pacific Sci. 45: 131–151.

Moore, P. H. 1973. Composition of a limestone forest community on Guam. Micronesica 9: 45–58.

Mueller-Dombois, D. 1985. Ohia dieback in Hawaii: 1984 synthesis and evaluation. Pacific Sci. 39: 150–170.

Mueller-Dombois, D. & H. Ellenberg. 1974. Aims and Methods of Vegetation Ecology. Wiley, New York, New York.

Muniappan, S. 1976. The determination of plant communities along a complex environmental gradient at Hilaan Beach, Guam. Micronesica 12: 283–302.

Raulerson, L. & A. Rinehart. 1991. Trees and Shrubs of the Northern Mariana Islands. Dept. Coastal Resource Management, Commonwealth Northern Mariana Islands. 120 pp.

Stone, B. C. 1970. The flora of Guam. Micronesica 6: 1–659.

Woodroffe, C. D. 1985. Vegetation and flora of Nui Atoll, Tuvalu,. Atoll Res. Bull. 283.

Woodroffe, C. D. 1987. Pacific island mangroves: distribution and environmental settings. Pacific Science 41: 166–185.

Wiles, G. J., T. O. Lemke & N. H. Payne. 1989. Population estimates of fruit bats (*Pteropus mariannus*) in the Mariana Islands. Conserv. Biol. 3: 66–76.

Young, F. J. 1989. Soil Survey of the Islands of Aguijan, Rota, Saipan, and Tinian, Commonwealth of the Northern Mariana Islands. U.S. Soil Cons. Serv.