

Woody Vegetation in the Upland Region of Rarotonga, Cook Islands¹

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ABSTRACT: Rarotonga is the largest (64 km²) and by far the highest (652 m) of the Cook Islands. The native coastal and lowland vegetation of this high volcanic, tropical island has been either completely removed or heavily disturbed. Numerous exotic plant species have been introduced and many of these are now naturalized in the lower elevation habitats of the island. The results of this initial, quantitative study in the upland forests of Rarotonga indicate, however, that the plant life of the rugged interior is still largely dominated by native species. Over 92 percent of all the woody plants (dbh > 2.5 cm) sampled in the 19 upland forest transects are either indigenous or endemic to Rarotonga. Native plants also accounted for more than 95 percent of the basal area covered by the woody vegetation in the upland study area. Three basic native plant associations have been recognized by dendrogram analysis: (1) the *Homalium montane* forest; (2) the *Fagraea-Fuchsia* ridge forest; and (3) the *Metrosideros* cloud forest. The first two associations develop under subtropical climatic conditions, while the cloud forest is adapted to warm temperate conditions. Some aspects of the biogeographical significance of this unique forest region and the ecological implications of human disturbance in the uplands are also discussed.

THE COOK ISLANDS INCLUDE fifteen small coral and volcanic islands with a total land area of approximately 238 km² scattered over about 2,176,000 km² of the South Pacific Ocean between 9° and 23° S latitude and 156° and 167° W longitude (see Figure 1). Rarotonga, located near the southern end of the archipelago at 21° 12' S latitude and 158° 46' W longitude, is the largest (64 km²) and by far the highest (652 m) of the Cook Islands (Figure 1). This island is the subaerial portion of an extinct shield volcano typical of the igneous formations commonly found in the deep Pacific Ocean Basin.

In his annotated bibliographic study of botanical research carried out in the Cook Islands, Sykes (1980) briefly described the vegetation of the Cook Islands and presented an exhaustive survey of the references to the terrestrial plant life in the archipelago. He notes

that both vegetation and floristic research in the island group have been quite limited. Rarotonga is the only island in the Cook Archipelago with two published floras (Cheeseman 1903, Wilder 1931); but the most recent of these, over 50 years old, has a number of inaccuracies and needs considerable updating (Sykes 1980, W. Authur Whistler, pers. comm. 1984). In addition to Sykes' literature review, the only recent botanical publications dealing with Rarotonga include a brief floristic discussion emphasizing phytogeography (Philipson 1971), a taxonomic account of the ferns and fern allies found in the Southern Cook Islands (Brownlie and Philipson 1971), and a list of the vascular flora on the reef islands of Rarotonga (Fosberg 1972).

In an unpublished, descriptive report based on field work carried out in 1974 and 1975, Sykes (1976, revised in 1983) divided the vegetation of Rarotonga into coastal, lowland, and upland zones. The coastal zone, which contains strand, scrub, and small *makatea* (raised limestone) components, still has some

¹ Manuscript accepted 15 August 1984.

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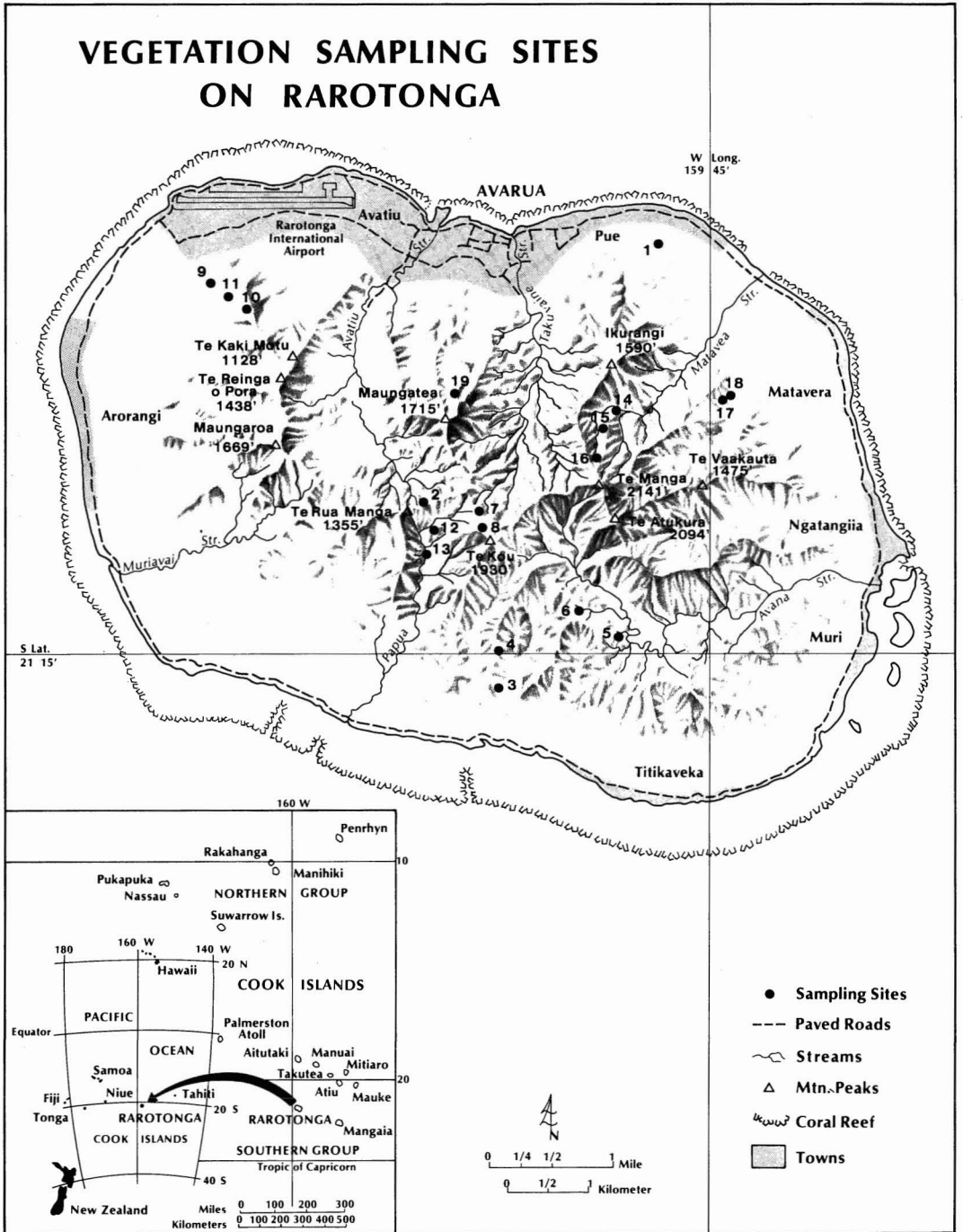


FIGURE 1. Map of the Cook Islands and vegetation sampling sites on Rarotonga.

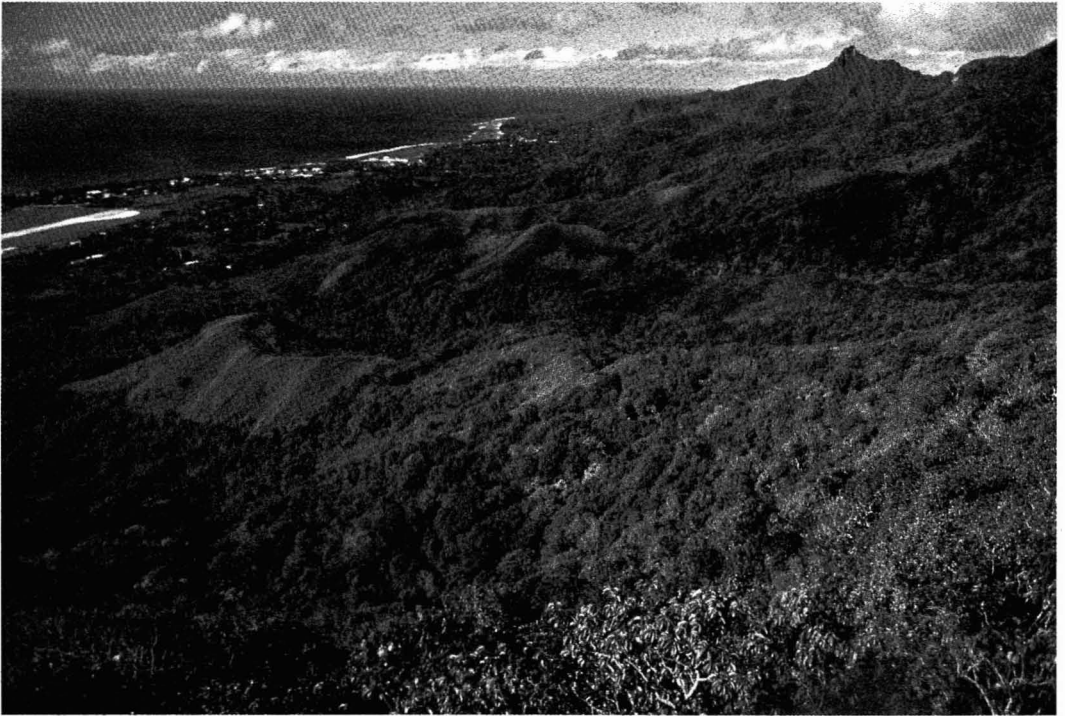


FIGURE 2. The northern coast, lowlands, and lower uplands of Rarotonga.

areas (e.g., the Muri Sand) where native vegetation can be found. However, the majority of this zone has been greatly modified by human disturbance. The native plants that can still be found in this zone, such as *Ipomoea pes-caprae*, *Vigna marina*, *Scaevola taccada*, *Barringtonia asiatica*, *Hernandia nymphaeifolia*, and *Pisonia grandis*, are almost all organisms commonly found in the coastal areas of tropical South Pacific islands.

The lowland vegetation zone of Rarotonga comprises the low lying, generally level area located between the coastal coral sands and the steep hills a few hundred meters inland. This zone also includes the lower, moderately inclined, hilly areas near the coast and the valley bottoms which, in some places, penetrate far into the interior of the island (Figure 2). Although this zone contains the most fertile soils on Rarotonga, almost all of the original lowland plant life of Rarotonga has been replaced by exotic associations of cultivated and/or weedy plants (Figure 3).

Numerous introduced species have become naturalized along the coast or in the lowlands. Some of these nonnative plants were brought in during the prehistoric Polynesian period, but many more were introduced after the initial European contact in the early part of the 19th century.

Weedy plants that have become abundant in some parts of the lower habitats of Rarotonga include herbaceous species such as *Bidens pilosa*, *Elephantopus mollis*, *Euphorbia hirta*, *Mimosa pudica*, *Sida rhombifolia*, *Mikania micrantha*, *Momordica charantia*, *Panicum maximum*, *Chrysopogon aciculatus*, *Cenchrus echinatus*, *Sorghum bicolor*, and *Stenotaphrum secundatum*. Exotic woody species that are commonly naturalized in some coastal or lowland habitats include *Leucaena leucocephala*, *Lantana camara*, *Aleurites moluccana*, *Inocarpus fagifer*, *Mangifera indica*, *Cecropia palmata*, *Inga edulis*, *Syzygium* sp., *Psidium guajava*, and more recently *Ardisia humilis*. It should also be noted

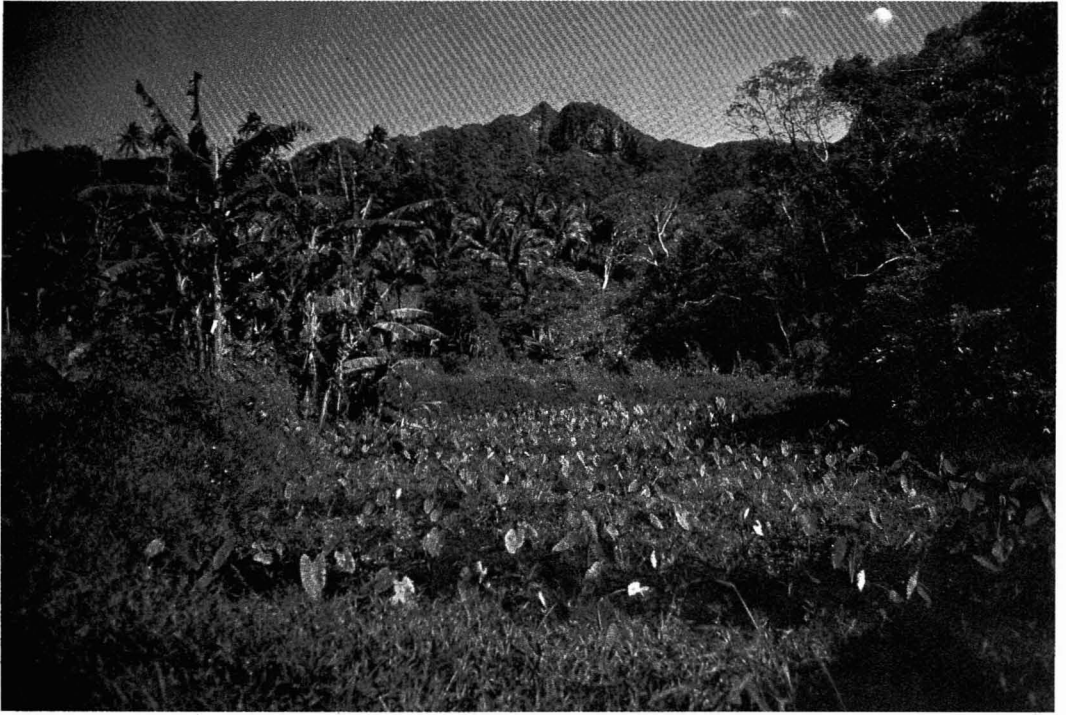


FIGURE 3. Cultivated pondfields and plantations in lower Takuvaive Valley, with Ikurangi Peak in the far background.

that *Hibiscus tiliaceus*, an aggressive, woody species which is commonly found along some coastal areas, in abandoned plantations and taro (*Colocasia esculenta*) pondfields, on stream banks (Figure 4), and even in some of the more recently disturbed lower forest slopes, is here considered to be an early Polynesian introduction in the Cook Islands (cf. Fosberg 1975).

Unlike the vegetation in the coastal and lowland zones on Rarotonga that is predominately exotic, the plant life found in the rugged uplands is overwhelmingly made up of native species (Cheeseman 1903, Philipson 1971, Sykes 1980). This upland zone includes all of the interior area above about 50 m to 200 m (Figure 5). It can be separated into subtropical and warm temperate subzones which have distributions that vary widely according to the altitude and aspect of the narrow ridges, steep slopes, and deep valleys. Thus, for example, the subtropical and warm temperate subzones

both start at lower elevations on the windward side of the island.

These upland vegetation subzones of Rarotonga are botanically unique and of special scientific interest for two reasons: (1) as noted above and supported in the present study, these subzones are still almost entirely covered by native species; and (2) since the summit of Mangaia, the second highest island in the Cook group, is only 168 m (550 ft) above sea level, the native vegetation above about 200 m on Rarotonga is not, or in many cases may never have been, found anywhere else in the Cook Islands. Consequently, the native upland forests of Rarotonga can only be compared with similar native subtropical and warm temperate ecosystems found on other high volcanic islands in: (1) the Society, Marquesas, and Austral islands located hundreds of kilometers to the east; (2) the Samoan, Tongan, and Fijian islands located hundreds of kilometers to the west; or (3) in



FIGURE 4. *Hibiscus tiliaceus* and native ferns on the banks of Papua Stream.

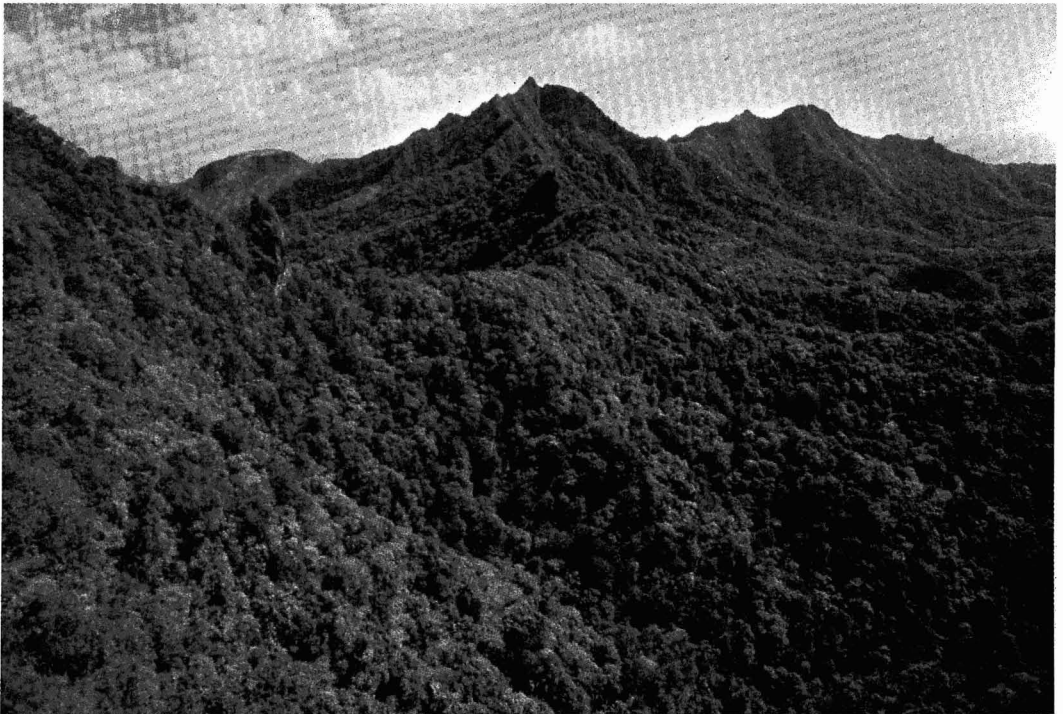


FIGURE 5. The uplands in the interior of Rarotonga, with Maungaroa (509 m) the highest peak in this east-facing view.

the Kermadec Islands and part of the North Island of New Zealand farther to the southwest.

In spite of the unique environmental situation and nearly original condition of the native upland forests of Rarotonga, there have been no previous detailed ecological studies of this region (Sykes 1980). The nearly pristine ecology, exceptional phytogeography, and lack of any prior quantitative vegetation research in the central part of the island have prompted this study of the woody vegetation in the subtropical and warm temperate uplands of Rarotonga. The major aims of this research are to determine what kinds of woody plant associations occur in these uplands, to measure the relative dominance and frequency of the individual species found in these vegetation types, and to quantify the extent to which introduced species have invaded this unusual region in the Cook Islands.

STUDY AREA

Since the last volcanic eruption on Rarotonga more than two million years ago in the Pliocene epoch (Tarling 1967), mass wasting and stream erosion have cut deeply into the terrestrial part of the volcano, leaving no remnants of the gently sloping, subaerial surface of the original shield (Wood and Hay 1970). The mountainous interior of the island is therefore now characterized by towering peaks and razor-backed ridges punctuated by several crags, pillars, and needles in the higher areas. Many of the knife-edged ridges owe their existence to the erosionally resistant, basaltic dikes which invaded the lava flows and pyroclastics constituting the great bulk of the volcano.

A thin layer of soil supporting dense forest vegetation covers the very steep slopes that are typical of the rugged interior of Rarotonga. The steep slopes lead down from the peaks and narrow ridges to small valleys that radiate out from the central part of the island. The densely forested upland region of the island is surrounded by a narrow coastal lowland area composed of raised coral and alluvial de-

posits. These are bordered by a small fringing reef that encloses a narrow lagoon.

Although Rarotonga lies in the path of the generally mild, prevailing southeast trade-winds, it is periodically affected by severe tropical storm or cyclone conditions during the warmer, more humid hurricane season that usually lasts from November to April. In the lowlands of the island, the mean monthly temperature ranges from 22° C in July to 26° C in January, a difference of only 4° C (Kennedy 1974). The average annual rainfall in the coastal lowlands is 2110 mm. A large percentage of the yearly precipitation usually occurs during the summer months of the Southern Hemisphere (especially December–March) when the tradewinds are more variable and the island may experience squalls and northerly winds (Stoddart 1975).

There is a lack of published climatic data for the mountainous, central region of Rarotonga. However, on the basis of field observations, some reasonable assumptions can be made. The upland interior of the island certainly experiences lower temperatures and more cloudiness than the lowlands. Throughout the year, precipitation is also probably greater in the uplands; and in the relatively small land areas above the lifting condensation level where fog is common, drip must make a considerable contribution to the available moisture. Strong winds are also typical of the uplands, especially on the exposed peaks and ridges. However, because of the cooler, cloudier conditions in the higher interior of the island, evapotranspiration, as well as insolation, are probably lower in the uplands. Therefore, inland from the coastal lowlands, climatic conditions on Rarotonga change from tropical to subtropical and eventually become warm temperate as elevation increases to the summit areas over 600 m high.

METHODS

The woody vegetation in the uplands of Rarotonga was studied during the period from 19 July to 8 August 1983. The point-centered quarter method of transect sampling (Mueller-Dombois and Ellenberg 1974) was

used because of the extreme steepness of the slopes and very narrow widths of most ridges in the region. Nineteen transect sites (see Figure 1) were chosen in a stratified random manner so as to allow for variations in elevation, available moisture, aspect, topography, and distance from areas altered by human disturbance. Ten points were established at 10 intervals along all 100-m transect lines. Around each point, four quarters were recognized. In each quarter, the distance to the nearest woody plant with a basal diameter greater than 2.5 cm was measured so that tree and shrub densities could be determined. Plants were then identified to ascertain absolute species frequencies (number of points with species present) and basal diameters were measured to determine average relative dominance (basal stem area of species divided by the total basal area of all woody species present). In addition, heights of individual trees were estimated and geographical origins of the species (native or introduced) were noted. With 10 points in each transect, a sample size of 40 trees per transect and a total of 760 trees for all 19 transects combined were observed. Results are presented in Tables 1 and 2.

A cluster analysis of the transect data based on species presence/absence and relative dominance was also performed to determine whether plant associations recognized in the field could be supported by objective techniques. The dendrogram technique described by Mueller-Dombois and Bridges (1975) was used to analyze the distributional patterns in the study area. The dendrogram computer program used was COMM (Kent W. Bridges, pers. comm. 1983).

Plant specimens, including all those recorded in the transects, were collected and deposited in the herbarium of the Botany Division, Department of Scientific and Industrial Research (DSIR), Christchurch, New Zealand (CHR).

RESULTS AND DISCUSSION

The final dendrogram based on the cluster analysis calculations of presence/absence and

relative dominance data is shown in Figure 6. The 19 transect study sites are arranged in a linear sequence along the bottom of the figure, and the percent similarity of the paired plots is indicated on the vertical axis. In order to identify ecologically meaningful clusters, a single cutoff line was drawn so that no transect sites were left unclustered. In the computer-derived classification, this condition was satisfied at a within-group similarity of 27 percent identifying three major clusters: A, B, and C (see Figure 6). These three similarity clusters recognize the natural groupings of the vegetation into the habitat categories described below.

Homalium Montane-slope Forest

Cluster A groups 10 transects (nos. 1, 18, 10, 17, 11, 13, 15, 13, 4, and 2) located on the generally steep slopes between about 30 m and 350 m elevation (Figure 7). This habitat type is usually dominated by a moderately tall (10–15 m) closed canopy forest. *Homalium acuminatum*, an endemic tree species with mean and maximum heights of 9.7 m and 15.5 m (sample size = 137), is by far the most common woody species on these slopes. It had a frequency of 81 percent and a relative dominance of 72 percent in the cluster A transects. The plant association represented by the study sites in cluster A is thus referred to here as the *Homalium montane-slope forest* (see Table 1).

Other relatively common native woody species found in this shady, lower mountain, forest association include: *Canthium barbatum*, a small indigenous tree with a frequency of 27 percent and a relative dominance of 2 percent; *Elaeocarpus rarotongensis*, a medium-sized, indigenous tree with a frequency of 19 percent and a mean relative dominance of 5 percent; and *Ixora bracteata*, a small endemic tree with a frequency of 17 percent and a relative dominance of less than 0.5 percent.

Entada phaseoloides, a large, indigenous woody vine, and *Fitchia speciosa*, a small endemic tree with prop roots, are both also commonly found in some parts of this slope forest habitat. The *Fitchia* species (Figure 8),

TABLE 1

DIFFERENTIATED TABLE OF THE RELATIVE DOMINANCE (%) OF WOODY SPECIES FOUND IN FOREST TRANSECTS IN THE UPLANDS OF RAROTONGA

ORIGIN*	SPECIES	TRANS. NOS.	<i>Homalium</i> MONTANE- SLOPE FOREST										<i>Fagraea-Fitchia</i> RIDGE FOREST						<i>Metrosideros</i> CLOUD FOREST		
			1	18	10	17	11	14	15	13	4	2	3	5	9	19	12	16	6	8	7
E	<i>Homalium acuminatum</i> Cheesem.		69	69	93	94	80	70	74	59	41	27	17	15	11	13	8	—	33	—	—
E	<i>Elaeocarpus rarotongensis</i> Cheesem.		—	3	1	1	12	1	1	1	17	13	—	—	1	1	—	1	—	+	5
I	<i>Canthium barbatum</i> (Forst. f.) Seem.		3	4	+	3	+	1	+	+	9	—	2	1	+	1	3	+	5	—	—
I	<i>Bischofia javanica</i> Bl.		—	—	—	—	7	2	+	1	—	—	—	—	—	—	—	—	—	—	—
E	<i>Weinmannia rarotongensis</i> Hemsl.		—	—	—	—	—	—	—	5	4	56	—	—	—	1	4	4	—	2	3
E	<i>Ixora bracteata</i> Cheesem.		—	+	+	1	—	—	2	—	—	+	—	—	—	—	—	1	—	—	—
I	<i>Macaranga harveyana</i> M. A.		—	—	—	+	—	27	8	—	—	—	—	—	—	—	—	—	—	—	—
I	<i>Planchonella grayana</i> St. John		—	—	—	—	—	—	10	—	—	—	—	—	—	—	—	—	—	—	—
I	<i>Terminalia glabrata</i> Forst. f.		—	—	—	—	—	—	—	—	25	—	—	—	—	—	—	—	—	—	—
I	<i>Entada phaseoloides</i> (L.) Merr.		—	+	—	—	+	1	1	—	—	—	—	—	—	—	—	—	—	—	—
E	<i>Xylosma gracile</i> Hemsl.		—	+	+	—	—	—	3	—	—	—	—	—	+	1	—	+	—	—	—
E	<i>Meryta pauciflora</i> Hemsl.		—	2	—	—	—	—	1	—	—	+	—	1	+	—	—	+	—	—	—
A	<i>Hibiscus tiliaceus</i> L.		16	7	1	—	—	—	—	—	1	—	+	—	4	—	—	—	—	—	—
A	<i>Inocarpus fagifer</i> (Park.) Fosb.		8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
A	<i>Aleurites moluccana</i> (L.) Willd.		3	—	2	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
A	<i>Cordyline terminalis</i> (L.) Kunth		—	+	+	+	—	—	—	—	—	—	—	—	—	—	—	—	+	—	+
A	<i>Morinda citrifolia</i> L.		+	—	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
I	<i>Pandanus tectorius</i> Park.		—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
R	<i>Ardisia humilis</i> Vahl.		+	—	—	—	+	—	—	—	—	—	1	—	+	—	—	—	—	—	—
R	<i>Psidium cattleianum</i> Sab.		—	—	—	—	—	—	+	—	—	—	—	—	—	—	—	—	—	—	—
R	<i>Psidium guajava</i> L.		—	—	—	—	—	—	—	—	—	—	+	—	—	—	—	—	—	—	—
A	<i>Cocos uncifera</i> L.		—	—	—	—	—	—	—	—	—	—	25	—	—	—	—	—	—	—	—
A	<i>Casuarina equisetifolia</i> L.		—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—
R	<i>Cecropia palmata</i> Willd.		—	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—	—	—	—
?	unidentified sp.		—	+	—	—	—	—	—	2	—	—	—	—	1	—	+	—	1	—	—
I	<i>Fagraea berteriana</i> A. Gray		—	12	—	—	—	—	—	—	17	—	50	79	81	75	71	82	—	—	12
E	<i>Fitchia speciosa</i> Cheesem.		—	—	—	—	—	—	+	6	8	2	2	2	1	2	4	5	9	1	11
E	<i>Alyxia elliptica</i> Cheesem.		—	1	—	1	—	—	—	—	—	1	—	+	+	+	2	—	8	—	—
E	<i>Coprosma laevigata</i> Cheesem.		—	—	—	—	—	—	—	—	—	+	—	—	—	—	4	2	—	—	+
E	<i>Wikstroemia sericea</i> Chr.		—	—	—	—	—	—	—	—	3	—	—	+	—	—	—	—	—	—	—
E	<i>Geniostoma rarotongensis</i> Fosb. & Sacket		—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—
I	<i>Alstonia costata</i> R. Br.		—	—	—	—	—	—	—	—	—	+	—	—	—	—	—	—	—	—	—
I	<i>Mussaenda raiaateensis</i> J. W. Moore		—	—	—	—	—	—	—	—	—	—	1	—	+	—	—	—	—	—	+
I	<i>Metrosideros collina</i> (Forst.) A. Gray		—	—	—	—	—	—	—	—	—	—	—	—	—	6	—	2	44	81	13
E	<i>Myrsine cheesemanii</i> (Mez) Fosb. & Sacket		—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	1	—	—	—
I	<i>Ascarina diffusa</i> A. C. Sm.		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	16	46
E	<i>Pittosporum rarotongense</i> Hemsl.		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	9
I	<i>Leucosyke corymbulosa</i> (Wedd.) Wedd.		—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—	—	—

TABLE 2

ABSOLUTE DENSITY, TOTAL BASAL AREA, AND AVERAGE HEIGHT OF WOODY SPECIES IN 19 UPLAND SAMPLE TRANSECTS ON RAROTONGA*

TRANSECT	ABSOLUTE DENSITY OF TRESS/100m ²	TOTAL BASAL AREA/100m ²	AVERAGE HEIGHT
<i>Homalium</i> Montane-Slope Forest			
1	33.78	1.39m ²	6.21m
18	49.50	2.35m ²	7.52m
10	41.66	1.64m ²	6.27m
17	34.24	2.08m ²	6.39m
11	59.17	5.23m ²	8.07m
14	53.76	4.50m ²	10.19m
15	52.63	4.15m ²	6.99m
13	54.05	2.20m ²	7.54m
4	68.99	1.68m ²	5.38m
2	62.11	4.14m ²	7.28m
<i>Fagraea-Fitchia</i> Ridge Forest			
3	30.40	1.28m ²	4.37m
5	64.10	4.05m ²	4.49m
9	64.94	5.87m ²	4.63m
19	99.20	7.60m ²	3.76m
12	175.44	5.58m ²	3.75m
16	116.27	5.41m ²	3.38m
<i>Metrosideros</i> Cloud Forest			
6	113.64	1.74m ²	3.54m
8	17.50	2.92m ²	5.02m
7	63.30	1.02m ²	4.12m

*Absolute density and total basal area/100m² figures were calculated according to the point-centered quarter method described in Mueller-Dombois and Ellenberg 1974.

an interesting member of Asteraceae (or Compositae), produces probably the largest achenes in the sunflower family. According to Carlquist (1974), it belongs to a genus unique to Tahiti (*F. tahitensis* and *F. nutans*), Raiatea (*F. cuneata*), Tahaa (*F. cuneata* subsp. *tahaensis*), Bora Bora (*F. cordata*), Mangareva (*F. mangarevensis*), Rapa (*F. rapensis*), and Rarotonga, where it has achieved its most extreme penetration into the Pacific from a presumed ancestral homeland in South America.

My observations in the uplands of Rarotonga do not, however, support Carlquist's description of *Fitchia speciosa* as "a relatively tall tree of deep forest." Although it had a frequency of 31 percent in the *Homalium* montane-slope forest study sites on Rarotonga, *Fitchia* was only found within what appeared to be recently disturbed areas of this

forest type (Figure 9). It is probably a pioneer woody species in the montane-slope forest, where it reaches a maximum height of only about 8m and is eventually shaded out by emerging canopy trees such as *Homalium*, *Elaeocarpus*, or in occasional cases by *Bischofia javanica*, *Weinmannia rarotongensis*, *Macaranga harveyana*, *Planchonella grayana*, or *Terminalia glabrata*. For example, in transect 13, on a shady slope in Vaimanga Valley between 145 m and 185 m, many fully grown (6–7 m), but often dead or dying, individuals of *Fitchia* were found under a taller canopy (10–15 m) of *Homalium* trees.

Cheeseman (1903) refers to the distribution of *Hibiscus tiliaceus* and *Aleurites moluccana*, two species which were probably brought in by Polynesians during the prehistoric period, as being common in the valleys and ascending the uplands "to a height of at least 800 ft" (c. 245 m). Cheeseman also claimed that these species usually made up "the major portion of the forest." These two species are indeed very common in areas disturbed by humans and along streams (especially *H. tiliaceus*, which some believe is indigenous to Rarotonga). However, in the cluster A study sites, I observed only a frequency of 11 percent for each of these species; they were found mainly in those areas adjacent to or near formerly cultivated land in the lower hilly slopes of Rarotonga.

The extreme dominance of the endemic *Homalium acuminatum* on the steep slopes, which typify the montane-slope forest environments below about 400 m, may be explained by the relationships between the flowering habits of the genus and the patterns of natural disturbance on Rarotonga. Landslides, triggered by the intense rainfall associated with severe storms such as hurricanes or well-developed cold fronts, appear to be common on the steeply sloped uplands. This assumption is supported by numerous observations of old scars, produced by rapid mass wasting, which have been recolonized by later forest (cf. Wood and Hay 1970). Although the phenology of *H. acuminatum* is poorly known (William R. Sykes, pers. comm. 1983; I observed only one individual flowering during my field work), Corner (1940) has pointed

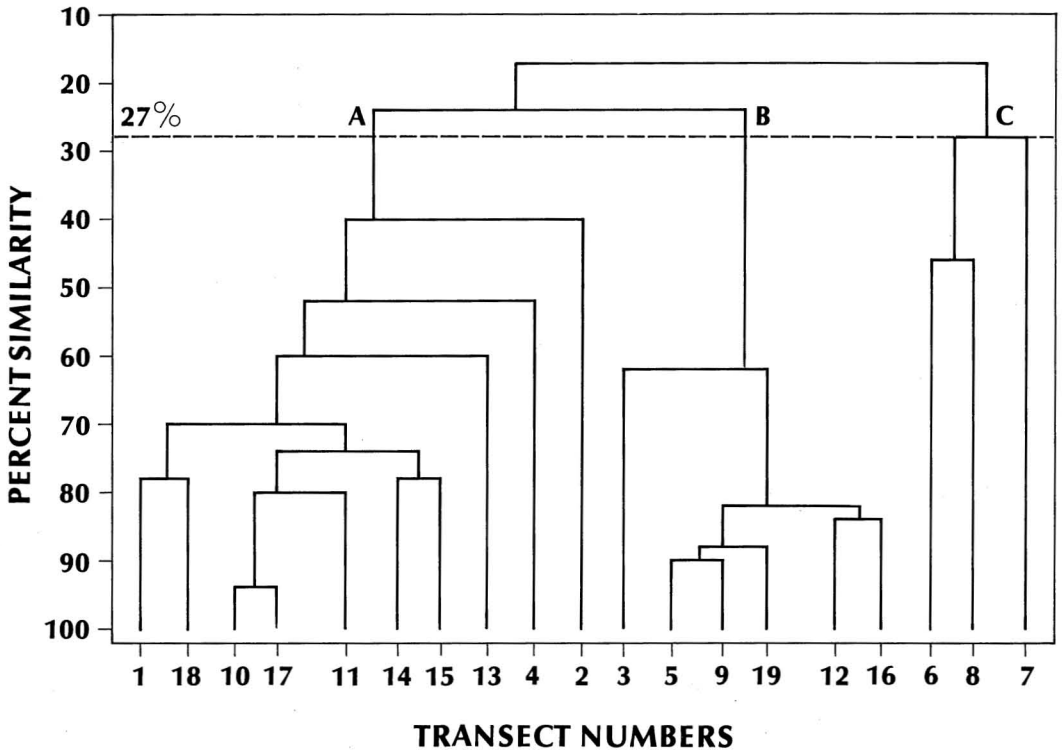


FIGURE 6. Dendrogram based on similarity matrix of species presence/absence and relative dominance for transect data from uplands of Rarotonga. A 27 percent cut-off line separates the following clusters: A = *Homalium* montane-slope forest; B = *Fagraea-Fitchia* ridge forest; and C = *Metrosideros* cloud forest. The transect study sites include: 1. Punataia Valley slope (30–75 m); 2. Avatiu Valley slope (335–350 m); 3. Totokoitu Valley ridge (45–90 m); 4. Totokoitu Valley slope (150–170 m); 5. Avana Valley ridge (75–150 m); 6. Avana Valley ridge (240–280 m); 7. slope below Te Kou (440–490 m); 8. below Te Kou summit (565 m); 9. Pokoinu Valley ridge (75–125 m); 10. Pokoinu Valley slope (195–270 m); 11. Pokoinu Valley slope (110–125 m); 12. Vaimanga Valley ridge (245–280 m); 13. Vaimanga Valley slope (145–185 m); 14. Tupapa Valley slope (145–185 m); 15. Tupapa Valley slope (305–335 m); 16. ridge below Te Manga summit (425–485 m); 17. Matavera Valley slope (45–90 m); 18. Matavera Valley slope (50–95 m); 19. ridge below Maungatea (395–470 m).

out that in Malaysia, *H. grandiflorum* flowers only once every 10 to 15 years. Perhaps the phenology of this and other *Homalium* species is dependent upon some stress signal from the environment. For example, *H. paniculatum*, a very common tree in the moderately wet uplands of Mauritius, flowers gregariously shortly after severe hurricanes: “In May 1931, 2 months after the hurricane of that year, this species, with its long white silky panicles, was a conspicuous feature of upland river reserves and indigenous thickets” (Vaughan and Wiehe 1937). During hurricanes, such as the one noted above, torrential rainfall frequently causes landslides on the steep mountain slopes

of heavily dissected oceanic volcanoes such as Mauritius and Rarotonga. Therefore, those trees that produce seeds relatively soon after the open areas are created, as with at least some species of *Homalium*, will have an advantage in the subsequent plant succession.

Based on his observations at the end of the last century, Cheeseman pointed out that the reddish, durable wood of *Homalium acuminatum* (*moto*) was used in canoe construction and was a common tree which could still be found throughout the island, “from sea-level to quite 1000 ft.” Sykes (1976) more recently observed *H. acuminatum* as one of a few native trees still occasionally found around



FIGURE 7. Montane forest of Avatiu Valley.



FIGURE 8. Inflorescence of *Fitchia speciosa*, a very common endemic woody species in the native upland forests of Rarotonga.



FIGURE 9. Broad-leaved *Fitchia speciosa* growing in an opening of a *Homalium* montane-slope forest at c. 150 m in Totokoitu Valley.

plantations in the “inland lowland forest” region, where, he suggested, it was most likely the “most common dominant” before human disturbance. In a 10 m × 10 m plot located next to a citrus plantation that I sampled 25 m above sea level near Nikao, all the woody plants (dbh > 2.5 cm) were introduced, except for five individuals of *H. acuminatum* and one of *Canthium barbatum*. In this same small quadrat, I also observed a number of seedlings of *H. acuminatum*, further evidence of its ability to thrive in disturbed areas.

Fagraea-Fitchia Ridge Forest

Cluster B groups six transects (nos. 3, 5, 9, 19, 12, and 16) located on the narrow, exposed ridges below about 500 m (Figure 10). These windswept environments have very shallow, rocky soil and are usually covered by a dense forest of large shrubs or small trees dominated by two species, *Fagraea berteriana* and *Fitchia*

speciosa. The plant community represented by the cluster B study sites is thus referred to here as the *Fagraea-Fitchia* ridge forest.

Although *Fagraea* heavily dominated all six study sites in the ridge forest association with a relative dominance of 73 percent, its frequency was only 32 percent in the Cluster B group. Nevertheless, it is certainly the largest tree in these highly stressed environments below 400 m, with mean and maximum heights of 6.4 m and 13.7 m (sample size = 19). Furthermore, its sprawling habit appears to help retard mass wasting on the ridges.

The abundant knife-edged ridges of the upland interior of Rarotonga usually have a substrate composed of broken rock held together by tree roots. It might seem that such conditions would be most susceptible to rapid erosion; however, the stability of this exposed type of environment is enhanced by the free-draining fractured surfaces of the ridges and the protection provided by the extensive,



FIGURE 10. Narrow ridge leading down from the interior uplands to the southern coast of Rarotonga.

sturdy root systems of the most dominant species, *Fagraea berteriana*. Large trees of this species have a considerable amount of surface root growth which sprawls out over the rugged ground. This growth covers and holds together a large area of the ridge crest and the upper slopes near the crest.

Almost all of the individuals of *Fagraea* that I observed were large, mature trees, some with lower trunks as wide as 2 m in diameter. This may be explained by the effects of extreme storms in the recent past. According to Marshall (1930), after the hurricane affecting Rarotonga in March 1926, the steep slopes of the upland interior showed much evidence of sliding soil, rock, and vegetation, while most of the ridge crests remained intact.

According to Cheeseman, in the late 19th century, *Fagraea* was commonly found in the interior of the island and was even occasionally "planted for ornament near the native

villages." He noted that the tree was still being used to provide fragrant flowers for wreaths and he referred to its durable wood, which was said to have been used for all kinds of sculpture, especially the "elaborately carved handles of the ceremonial axes reserved for the use of the chiefs." Although it has long been used by the people of Rarotonga, *Fagraea* was almost certainly not cultivated since few, if any, native plants were consciously propagated in the Cook Islands, or for that matter elsewhere in Polynesia. It is more reasonable to assume that what Cheeseman thought were "planted" trees of *Fagraea* near native settlements were actually individuals which had naturally invaded clearings or abandoned plantations, and that the native people had selectively chosen not to cut down these valuable trees. Today, *Fagraea* is still found near some plantations or other disturbed areas in the lowlands, as well as in ridge forests of the uplands.

Fitchia speciosa is much smaller than *Fagraea berteriana*, with a mean height of 3.6 m and only a few individuals taller than 6 m in the ridge forest of Rarotonga (sample size = 89). In addition, the relative dominance of *Fitchia* (3 percent) in the ridge forest is extremely low compared to that of *Fagraea* (73 percent). However, with its sturdy prop-roots, this endemic woody species, like the larger *Fagraea*, also plays a significant role in stabilizing the blocky, open-structured substrates of the ridges, especially since it is very abundant (absolute frequency of 78 percent in the cluster B sites). Therefore, *Fagraea* and *Fitchia* are both here considered to be the two most important species in the frequently disturbed, knife-edged ridges of Rarotonga.

Although *Homalium acuminatum* is not nearly as common in the ridge forest as it is in the montane-slope forest, it was observed to be an important tree in the cluster B study sites where its relative dominance was 11 percent and its frequency was 37 percent. As expected, because of relatively poor edaphic conditions, *H. acuminatum* does not grow as tall in the ridge forest as it does in the montane-slope forest where it is by far the dominant species. The mean height for 34 individuals of *H. acuminatum* observed in the cluster B sites

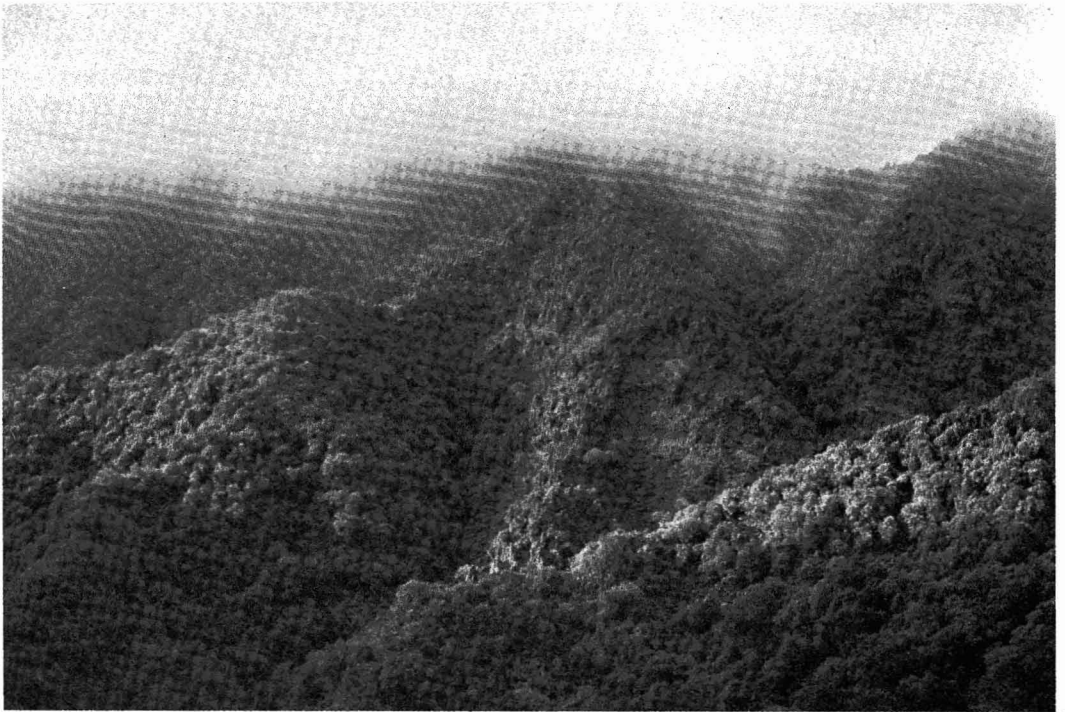


FIGURE 11. Clouds intercepting the high ridge that separates Takuvaine and Tupapa Valleys.

was 4.8 m, or less than half its mean in the montane-slope forest. In fact, only two trees observed in the ridge forest habitat had estimated heights greater than 6 m.

Other woody species found in the narrow ridge forest vegetation were much less significant in terms of either their average relative dominance or absolute frequencies. *Canthium barbatum* and *Alyxia elliptica*, two relatively small native woody species, each had dominance measurements under 1.5 percent and frequencies of 23 and 20 percent, respectively. *Metrosideros collina*, *Hibiscus tiliaceus*, *Coprosma laevigata*, and *Meryta pauciflora* are not rare in the ridge forest, but all of these species were observed to have less than 10 percent frequency or 2 percent dominance in the cluster B study sites (see Table 1).

Metrosideros Cloud Forest

Cluster C groups only three transects, one (no. 6) sampled on a windward ridge between

240 m and 280 m elevation in Avana Valley, and two others (nos. 7 and 8) located in the higher elevations above the lifting condensation level between 440 m and 490 m (no. 7) and at 565 m (no. 8) where fog is common (Figure 11). Although the number of sites in cluster C is very small, this grouping does seem to support the qualitative description of the upland warm temperate forest outlined by Sykes (1976) in his unpublished report to the Department of Scientific and Industrial Research in New Zealand.

Thus, in the areas of higher rainfall, lower insolation, and stronger, cooler tradewinds, the forest vegetation is normally less than 8 m in height and is dominated by *Metrosideros collina*. Although these climatic conditions are generally restricted to areas above 350 m on Rarotonga, they are also found on some exposed, windward ridges down to elevations as low as 200 m—for example, in the subtropical environment on the windward ridge in Avana Valley (site no. 6).



FIGURE 12. *Metrosideros collina* supporting a multitude of epiphytes and lianas in the cloud forest near the summit of Te Kou.

Metrosideros was the dominant species with a relative dominance of 44 percent, while *Fagraea berteriana*, the dominant species in all other lower ridge forest study sites, was absent. Near the summit region of Te Kou in the highest area sample (site no. 8), *Metrosideros* had a relative dominance of 81 percent. On the other hand, in some of the higher, wetter, warm temperate environments, *Ascarina diffusa* is the dominant species, as in the transect study site below the peak of Te Kou (site no. 7) where it had a relative dominance of 46 percent.

Exposure to significantly stronger winds in the cloud forest often results in associations of gnarled scrub vegetation. In the very highest cloud forest areas, fog drip also plays an important role in the distribution of some species. Because of the greater availability of moisture in these summit regions, *Metrosideros* and *Ascarina* trees are usually festooned with epiphytic mosses and ferns (Figure 12).

Other woody species found in these warm

temperate cloud forest environments include *Fitchia speciosa*, *Elaeocarpus rarotongensis*, *Weinmannia rarotongensis*, and *Pittosporum rarotongense*, and to a lesser degree, *Coprosma laevigata*, *Xylosma gracile*, *Geniostoma rarotongensis*, *Morinda forsteri*, and the small shrub, *Vaccinium cereum*. The large liana *Freycinetia wilderi* is also quite common in the cloud forest, either wrapped around the *Metrosideros* trees and some other woody species, or sprawled out in what are apparently disturbed places in the higher elevations.

Dicranopteria *Ferlands*

As noted earlier, long-term human disturbance in the lower elevations of Rarotonga has resulted in the almost complete removal of native vegetation, especially in the lowland environments away from the immediate coast. There are also a number of areas on the lower hills and ridges where it is assumed that soil

and woody plants are now largely absent because of human activities. The vegetation in these areas is now strongly dominated by a single herbaceous species, the indigenous false staghorn fern, *Dicranopteris linearis*. These "fernland" areas probably have been produced by repeated burning which most likely began in pre-European times and has continued into recent years (see Cumberland 1949, Sykes 1976). Over the years, fires started by humans may have destroyed some areas of the native forest, exposed the soil to severe erosion, and provided open environments where pioneer species such as the native *Dicranopteris* fern and a number of herbaceous weeds (mainly introduced composites and grasses) have become established (see Figure 2).

There are also a number of woody species found infrequently in the fernlands. These are mostly introduced species including stunted individuals of *Psidium guajava*, *Ardisia humilis*, *Hibiscus tiliaceus*, and *Lantana camara*. Some native woody species also occasionally invade the fernlands, including *Weinmannia rarotongensis*, *Melastoma denticulatum*, *Fitchia speciosa*, *Metrosideros collina*, and *Mussaenda raiateensis*.

Although the *Dicranopteris* fernlands are generally restricted to elevations below about 250 m, they can be found in a few places up to approximately 550 m. Since the continued existence of the fernlands is dependent upon periodic fires, it can only be hoped that further burning will be curtailed and that these apparently degraded areas will not be extended.

STATUS OF THE NATIVE UPLAND FOREST

At the end of the last century, Cheeseman observed that the upland vegetation of Rarotonga was almost completely composed of native species. Seventy years later, Philipson (1971) referred to the central areas of Rarotonga as having experienced little human impact and described the forest cover in these uplands as appearing "to be in a completely primitive condition." More recently, Sykes (1976) noted that the plants of foreign origin still had not become widely naturalized in the interior of the island.

Observations reported in this study (see below) do support previous descriptions of the integrity of the native upland vegetation on Rarotonga. However, the area predominantly covered by native vegetation in the uplands may have been reduced during this century, especially in places near settlements or plantations. For example, "old residents" of Rarotonga told Philipson (1971) that "many striking native plants, specially *Fitchia* and the tree ferns, were now much less conspicuous on the coastal hills than a generation ago." Perhaps the area covered by the *Dicranopteris* fernlands has grown at the expense of native forest during this century?

It should also be pointed out that there are a relatively small number of introduced woody species that are naturalized in the predominantly native forest areas. These include *Aleurites moluccana*, observed in some areas up to about 400 m, *Cordyline terminalis*, commonly seen on shady slopes up to about 450 m, and *Hibiscus tiliaceus*, which is especially abundant along the many streams in the interior of the island. All three of these species were probably introduced during the pre-European period and are now thoroughly naturalized in some parts of the upland forests.

There are also a few exotic woody species that have become naturalized in the upland forests during historic or more recent times. In the lower elevations of the uplands, these species include *Psidium guajava*, *Syzygium* sp., *Solanum mauritianum*, *Lantana camara*, and *Ardisia humilis*. In addition, *Spathodea campanulata*, *Psidium cattleianum*, and *Cecropia palmata* are recently introduced species that can also be found in or near disturbed areas in the higher elevations of the interior. *Cecropia palmata* (Figure 13), which was not observed by Cheeseman in the late 19th century, was recorded as uncommon by Wilder in 1931. This large, rapidly growing, pioneer species from the New World Tropics is now found in many disturbed parts of Rarotonga from the inland lowlands to the higher regions in the forest. Although it is still not abundant, *C. palmata* is probably the most widely distributed of the more recently introduced woody species in the uplands. A number of



FIGURE 13. *Cecropia palmata* (shown here growing in a lowland clearing) was introduced during this century and is now found in many disturbed areas in the uplands and lowlands of Rarotonga.

herbaceous weeds of foreign origin can also be found in some open areas of the uplands where humans have caused changes in the vegetation. Among the more important of these are *Elephantopus mollis*, *Mikania micrantha*, and *Paspalum conjugatum*.

Even though a number of exotic species have become naturalized in some areas of the native forests, the introduced plants in the uplands are still greatly outnumbered by the native plants. Over 92 percent of the woody plants (703 of 760 individuals, dbh > 2.5 cm) sampled in my 19 transect study sites were either indigenous or endemic, while less than 8 percent (57 of 760 individuals) have been classified as pre-European (aboriginal) or recent (historic) introductions (see Table 1). The combined measurements of the transect data also indicate that the basal stem area covered

by woody species is strongly dominated by native plants. The total relative dominance of the native species for all study sites was 95.6 percent, while the dominance of the exotic species was only 4.4 percent. Furthermore, in the highest areas above about 450 m, the dominance of the native species exceeded 99 percent. Finally, casual observations of the herbaceous vegetation in the upland forests suggest that this life form type in the upland vegetation is also strongly dominated by native species.

The persistence of the native vegetation in the uplands of Rarotonga can be best explained by the relative lack of human disturbance in the interior region of the island. This conjecture is supported by recent research in the Hawaiian Islands which has helped generate some hypotheses regarding the continued existence of native species in terrestrial island ecosystems (Mueller-Dombois, Bridges, and Carson 1981). One of the most important of these assumptions suggests that species native to islands are as ecologically fit as those that are introduced. For example, it has been shown that exotic organisms do not readily penetrate into mature native forest vegetation unless there is a certain degree of sustained disturbance created by burning, cultivation, introduced grazing mammals, or other forms of direct or indirect human interference. Although the implications of this hypothesis for scientifically sound and successful resource management of island ecosystems are great, there has been little quantified research in other tropical Pacific Islands, except for the extensive investigations in Hawaii, to support this view.

As previously noted, there are some areas in the native upland forests that have been invaded by exotic species. However, these areas are almost always in environments intentionally or unintentionally disturbed by humans. Except for the *Dicranopteris* fernlands, humans have disturbed little of the native upland vegetation. Indeed, people apparently have never spent much time in the uplands. According to Cheeseman, the people of Rarotonga did occasionally go up the valleys into the interior of the island to collect the fruit of the introduced mountain plantain,

Musa fehi (especially between about 150 m and 250 m), and periodically climbed the lower hills to gather the abundant "honey" secreted from the flowers of the endemic composite, *Fitchia speciosa*. However, Cheeseman noted that aside from these intermittent foraging excursions, the natives and Europeans rarely went any further up into the interior because of the extremely steep slopes and the "dense jungle-like forest that everywhere covers the surface." Cheeseman (1903) therefore claimed that, except for some lower slopes, the vegetation of the uplands is "in its primitive state" and had "never been interfered with by man." Sykes (1976) suggested that the upland vegetation of Rarotonga above about 150 m is still in "an original or nearly original" condition because cultivation was impractical on the steep, relatively inaccessible, slopes of the interior. On the other hand, Sykes (pers. comm. 1984) has suggested that the Polynesian people before the present century commonly climbed into the uplands to collect plantains and probably also to hunt native birds, since many people previously lived further away from the coast and would not have had to struggle through the dense growth of *Hibiscus tiliaceus* and *Angiopteris* ferns now abundant in abandoned cropland along or near the streams (see Figure 4).

Certainly the lack of easy access, steepness of slope, and greater rainfall in the uplands have helped protect the native forest vegetation in the rugged interior of Rarotonga from prolonged, direct human disturbance. In addition, and perhaps more importantly, I believe that the native plant life in the uplands has not been greatly disturbed because of the absence of hoofed mammals. Introduced animals of this type are known to have a disastrous effect on native vegetation in other insular ecosystems (e.g., in Hawaii; see Mueller-Dombois, Bridges, and Carson 1981). There probably never have been any truly wild or feral populations of pigs, goats, cattle, deer or other potentially disruptive hoofed animals in the uplands of Rarotonga. The native vegetation in the rugged interior of the island therefore has not suffered from the deleterious effects of mammalian grazing, trampling, scarification, or seed dispersal of exotic weeds.

Given the nearly pristine plant communities, exceptional phytogeography, and past history of introduced animal damage to native plants that has been recorded in other island ecosystems, the future release and naturalization of hoofed mammals, or other kinds of exotic animals, in the interior of Rarotonga would almost surely produce a drastic loss of the natural heritage of Rarotonga, the Cook Islands, and the tropical Pacific in general.

ACKNOWLEDGMENTS

I would like to express my appreciation to W. Arthur Whistler, Pacific Tropical Botanical Garden, Kauai, Hawaii, for his considerable advice pertaining to the vegetation of the South Pacific. I would also like to thank William R. Sykes, Botany Division of the Department of Scientific and Industrial Research, Christchurch, New Zealand, for graciously sharing his unpublished vegetation reports and identifying my collection of plant specimens from Rarotonga. In addition, I am indebted to Kent W. Bridges, Botany Department, University of Hawaii at Manoa, for his computer guidance, Rebecca Brown for her assistance with the graphics, and the staff of the DSIR Research Station at Totokoitu, Rarotonga, for their cooperation in the field. Finally, I would like to acknowledge the inspiration I have received from James O. Juvik, Geography Department, University of Hawaii at Hilo, who prodded me into action.

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