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Vegetation of the Society Islands[1]

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ABSTRACT: The vegetation of the Society Islands, 16°–18° south of the equator, in the wet SE trade wind belt, is described. The flora is primarily of Indo-Malayan derivation with a few New Zealand, Australian, American, and Hawaiian elements. There is little doubt that the volcanic islands at the time of human arrival, perhaps 4000 yr ago, were forested from mountaintop to seashore. The original vegetation consisted of broad-leaved, usually hygrophilous, montane rainforest. There was an abundance of shrub and small tree species, and terrestrial ferns dominated the ground layer. The sequence of vegetation from forest on the coastal zone and in deep valley bottoms through montane rainforest, mossy or cloud forest, and mossy scrub-covered crests and peaks is distinguished. With the arrival of the Polynesians, nonindigenous plant species were introduced for food, medicine, and fiber, and "camp followers" arrived accidentally. Native species, especially in the lowland coastal zone, were replaced with coconut groves; taro marshes; and valley-bottom forests of mape, breadfruit, and bamboo. The advent of Europeans brought further, often disastrous, change as newly introduced goats and pigs and logging and clearing opened up originally closed formations. Exotic species such as mango and guava came to dominate the vegetation in some places. The flora of the five atolls and the barrier-reef islets is essentially that of strand habitats throughout the Indo-Pacific and is impoverished. There was a mixed broad-leaved forest of several common widespread strand species such as *Pisonia*, *Guettarda*, *Pandanus*, etc., and the halophytic *Tournefortia* and *Scaevola* toward the seaward periphery. The original vegetation has also been changed by human activity, replaced by coconut and breadfruit groves and, in wet places, by taro pits. The vegetation patterns of the individual islands are also described.

The subject of this symposium, Vegetation Ecology of the Pacific Islands, calls for more than a simple description of the vegetation of the islands. Vegetation ecology implies a consideration of environmental relations and their influence on the plant cover and, I suggest, includes the dimension of time. I will attempt to reconstruct the history of the island vegetation speculatively, to begin with, and successively follow changes in vegetation as they respond to environmental influences, including, especially, that of man.

THE SOCIETY ISLANDS

The Society Islands form an archipelago in the central Pacific, lying about two-thirds of the way between Peru and Australia, within the Tropics but somewhat south of the equator (16°–18° S, 148°–154° W). Ten of the 15 islands are so-called high islands, extinct basaltic volcanoes; from east to slightly north of west they are Mehetia, Tahiti, Moorea, Maiao, Huahine, Raiatea, Tahaa, and Maupiti. There are, in addition, five atolls: Tetiaroa, Tupai, Mopelia, Bellingshausen, and Scilly. All except Tetiaroa are scattered around the western and older end of the archipelago. These, as well as the satellites and motus associated with the high islands, are flat accumulations of coral debris and calcareous skeletons of

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reef-associated organisms, plant and animal, loose or locally cemented into hard reef-limestone that lies on the flat surfaces of reefs that have grown up to, or eroded down to, approximately present sea level. These reefs, being largely made up of calcareous plants, may be regarded as marine vegetation (Setchell 1928), but will not be further discussed here, except as substrata for terrestrial vegetation.

Geology

All of the Society Islands are ancient volcanoes that arose from the sea floor, presumably reached much greater than their present elevations, and have been subject to erosion and subsidence over geologically long periods of time. Below present sea level they presumably consist of "pillow lava," originally extruded under water. Above original sea levels, there are layer upon layer of flow-basalt or basaltic ash, pumice, and scoria, with palagonite representing periods of submergence. The upper submarine slopes and summits are capped with massive layers of reef-limestone, bench-like around high islands, complete caps on atolls. Thus the substrate for Society Island vegetation is either basalt, often deeply weathered into soils, or limestone, slightly or locally more deeply weathered.

Climate

The Society Islands lie in the southeast trade wind belt, with moderate maritime tropical temperatures and normally moderate rainfall at sea level, but with precipitation increasing rapidly orographically on windward sides of high islands. The leeward sides, at least lower down, are likely to be drier, because of rain-shadow effects. At high elevations rainfall may be excessive. No parts of this archipelago can be considered arid or even semiarid. Hurricanes occur infrequently but erratically, and with great force.

Hydrology

Because the high islands, except possibly Mehetia, are very old and weathered, surface permeability is moderate to locally slight or none, and surface run-off is high. Perennial streams are present in practically all valleys and ravines. Spectacular waterfalls are frequent. The porous basalt is filled by a Hertzberg lens of fresh water floating on denser seawater. The atolls and motus, freely permeable, contain a much thinner lens of fresh water, so long as the rainfall is sufficient to make up for the amount lost by evapotranspiration and lateral diffusion.

Floristics

The relationships of the Society Islands flora are principally with the Indo-Malayan region to the west, but with a few New Zealand and Australian elements, a very few American (at low elevations) types, one or two Hawaiian and some "Old Pacific" representatives, and the usual pantropical strand and lowland elements.

The flora is poorly known, considering that Pacific Island botany began in Tahiti and that much collecting has been done there. Much poor work has made present knowledge unreliable. No serious modern general updating has appeared in print.

The Society Islands are clearly oceanic and were never connected or close to any continental land or large islands. The indigenous flora is, therefore, totally derived from propagules carried or drifted across great distances of seawater. The vegetation has developed from the progeny of these relatively few waifs, gradually increasing in complexity as new arrivals were added and as successful colonists evolved and underwent adaptive radiation filling vacant niches.

VEGETATION

Our ideas of the early history and development of island vegetation are a matter of speculation, based largely on observation of vegetation established on young and volcanically active islands elsewhere. Colonization by plants on new lava and ash surfaces remote from areas of already developed vegetation is such a slow process that no human could ever observe a significant part of such

development. Hence any account of early development of island vegetation is largely inferential, based on assumed similarity to that observed on young volcanic surfaces in many different stages on islands elsewhere.

We may imagine a new island, emerged from the waves only a few years, or a few thousands of years, with a topographically uniform, rough but not rugged lava surface. Its principal ecological differences were along clines or gradients from wet windward to dry leeward sides, and altitudinal clines in temperature, condensation, and rainfall. There were important differences between pahoehoe (smooth or ropy) and aa (rough or blocky) lava surfaces, and ash, pumice, or scoria. An outstanding feature, from a viewpoint of evolution and vegetation development, would have been its "openness," permitting any colonists, locally produced or immigrant, plant or animal, and their progeny to persist and reproduce if genetically capable of tolerating these harsh environments. Variants with such capability would have a chance to establish themselves at first with little or no competition and perhaps minimal predation.

The early vegetation on such a new island would have been entirely made up of pioneer species, mostly preadapted for water, wind, or bird dispersal, halophytes or xerophytes, and capable of germination and establishment on undecomposed rock or ash. The widespread *Casuarina equisetifolia* is such a plant, and the only plant that I saw on the cinder slopes on my first visit to Anak Krakatau, in 1960, while the volcano was still erupting explosively. That is not to say, however, that *Casuarina* was an early colonist in the Society Islands. What little evidence there is suggests that there it may have been a relatively late arrival.

There is, of course, no information as to the pioneer plants that actually made up the cover on the bleak slopes of the newly born Society Islands, but the probabilities favor cryptogams, spore-formers, just on the basis of dispersability. Nor is there reason to think of dispersal agents other than those present today: wind, water, and birds. The original habitats were relatively simple. Complexity developed with more colonizations as the vegetation became more and more closed, animal populations increased, and weathering, soil formation, and erosion occurred.

This is, of course, a description of old-fashioned Clementsian succession, but on a vastly long time scale and modulated by the extensive water barriers that screened out most potential colonists. It enormously lessened the frequency of successful colonizations, at the same time increasing the time available for the successfully established colonists to increase their populations with little competition.

These speculations apply to any new islands, as well as the Society Archipelago. Until palynological investigations are carried out, to yield some "hard" information on the early history of the Society Islands vegetation, all we have is inference based on observations elsewhere and indirect evidence from present floras, vegetational phenomena, and physical environment. Colonizations, doubtless mostly from the continental and large island areas to the west, certainly took place, with subsequent evolution, adaptive radiation, extinction, and consequent development, through the ages, of vegetation, to the state that existed at the time of arrival of the Polynesians.

Vegetation before Human Arrival

There is little doubt that these islands, with the possible exception of parts of Mehetia, at the time of human arrival, possibly 4000 yr ago, were forested down to the seashores, except for cliffs and exposed peaks and crests, and just possibly the fernlands and grasslands.

The coastal strips and deep valley bottoms may have had some "tall rainforest" such as exists farther west, but this is conjectural, as these habitats were fully occupied by humans when the Europeans arrived. The rainforest may have extended up some of the gentler mountain slopes, where there would have been a gradual transition to the principal vegetation formation of the islands, the broad-leaved, usually hygrophilous, locally subsclerophyll, montane rainforest. This is a rather low forest of many tree and shrub species and an abundance of ferns. Its stature

and floristic composition would have varied (and still does) from place to place and from habitat to habitat. Its stratification was probably obscure, with an abundance of shrub and small tree species. Clear dominance was rare, but *Weinmannia* was (and is) the most abundant tree on many ridges. In gulches such trees as *Neonauclea*, *Alphitonia*, *Alstonia*, *Cyathea*, *Metrosideros*, *Homalanthus*, and *Pandanus* reached a considerable stature. *Freycinetia* formed dense tangles of coarse semi-lianas, especially on some steep slopes. Tree ferns, *Cyathea* spp., some very tall, were locally common. A plethora of smaller tree or large shrub species formed a dense intermediate growth. These included *Canthium*, *Wikstroemia*, *Cyrtandra*, *Piper*, *Myrsine*, *Geniostoma*, *Alyxia*, *Psychotria*, *Coprosma*, *Pittosporum*, *Glochidion*, *Meryta*, *Sclerotheca*, *Fitchia*, *Metrosideros*, *Polyscias*, *Fuchsia*, and, perhaps more rarely, *Lepinia*, *Erythrina*, and *Scaevola*. Epiphytic ferns and orchids were common. Terrestrial ferns dominated the ground layer, some of them, such as *Angiopteris*, *Marattia*, *Diplazium*, and *Asplenium nidus* reaching great size; and *Gleichenia* formed tangles in small openings. This formation still exists over large areas of the steep slopes and ridges of the present islands, especially Tahiti. At higher elevations, where there was, then as now, an almost continuous cloud or fog, montane rainforest changed to cloud forest or mossy forest, of lower stature, somewhat similar in composition, but more sclerophyllous. Its outstanding characteristic was (and is) the incredible abundance, both on the ground and on tree trunks and branches, and even on leaves, of bryophytes—hepatics and mosses, as well as some lichens. Ferns and orchids were also common epiphytes. Such shrubs as *Vaccinium*, *Ascarina*, and *Styphelia* as well as dwarf forms of *Metrosideros* and *Myrsine* were common. This cloud forest still exists, mostly unchanged, in suitable habitats.

Polynesian Period

With the arrival of humans, we have an event of solid factual, incontrovertible information, though we cannot yet say with certainty just when this took place.

Human actions or activities had various effects on the ecosystems found on the islands, and these produced changes in the vegetation. Some changes can be reconstructed with reasonable confidence. Nonindigenous plant species, useful to the people as food, medicines, fibers, and "camp followers" or weeds, were brought by the Polynesians, mostly, but not always, from their former homes in the west. These replaced native species in some situations, augmented some vegetation types, and formed some new associations, among them coconut groves, taro marshes, valley-bottom forests of mape (*Inocarpus*), breadfruit (*Artocarpus*), vi (*Spondias*), bamboo (*Phyllostachys*), and possibly hau or purau (*Hibiscus*) and fara (*Pandanus*). Undergrowth in these forests included such nonindigenous shrubs as kava (*Piper*), aute (*Broussonetia*), and tiare (*Gardenia*). Giant herbs, such as fehi and other bananas (*Musa*), and ape (*Alocasia*) were (and are) conspicuous in these inhabited valleys. Because the Polynesians were (and are) a horticultural people, dooryard ornamentals locally added to the plant cover. The weedy herbaceous vegetation at that time certainly included some aliens from the west, as the Forsters found at least ten of these in 1773–1774. Sweet potatoes (*Ipomoea*) and possibly bottle gourds (*Lagenaria*) were brought from the east, and formed a part of this anthropogenous vegetation.

As the populations increased, more of the native vegetation gave way to the alien. Much or all of the lowland strip of flat ground was occupied by altered native or completely exotic vegetation. Fehi bananas, at least, were established on the lower slopes of the wet valleys in the interior. We may assume that the Polynesians profoundly altered the coastal strips of the islands and the motus, where most of them lived, and the valley bottoms and some lower slopes, where their food was grown. In all probability, disturbed lower slopes, if not utilized, were occupied by tangled purau (*Hibiscus tiliaceus*), as at present.

Information on useful plants and cultiva-

tion is to be found in the journals of the earliest European visitors, but there is little on vegetation, or on the unutilized parts of the islands. Mangroves were apparently lacking, though suitable habitats were there. Only a single enigmatic reference to *Rhizophora* there occurs in J. R. Forster's journal.

Banks and Solander, naturalists with Cook on his first voyage, the Forsters on his second, David Nelson on the third, and Commerson, with Bougainville, avidly collected specimens of plants. We have good records of species, many of which are now missing or scarce in these habitats. But there is very little information from that period on the vegetation (i.e., the plant cover), the most obvious aspect of the landscape.

Most problematical are the history, nature, and origin of the large areas of "fern lands" or fern savanna and grass savanna. These certainly predate European contact, as Banks and Solander collected *Miscanthus floridulus*, the dominant grass in the savannas, not usually found elsewhere. The fern lands occupy lower slopes, up to about 500 m, in many places, on leached red soils (latosols in older terminology). The vegetation is an almost pure tangle of the fern *Gleichenia linearis*, with *Lycopodium cernuum* and scattered shrubs of *Metrosideros collina*, *Wikstroemia coriacea*, *Dodonaea viscosa*, *Decaspermum fruticosum*, and *Melastoma*, none endemic or peculiar to this vegetation type. On some drier leeward slopes *Gleichenia* is replaced by *Miscanthus floridulus*, a widespread savanna grass or "sword grass," found across the Pacific from the Northern Marianas to New Caledonia and eastward to the Marquesas and Mangareva in suitable, usually degraded, habitats. The relation of humans to the spread and distribution of this coarse grass is obscure and controversial. It is obviously encouraged by fire and is deliberately burned in many places. In the high active volcanoes of the Northern Marianas, *Miscanthus floridulus* dominates certain habitats, some natural, some influenced by humans, where fire is a normal or frequent factor. Such volcanic situations may possibly be the natural home of this species before human contact.

Gleichenia linearis is even more widespread, pantropical, in fact, dominant locally in many parts of Polynesia, and often sharing habitats with *Miscanthus*. It also survives fire, except for the most severe, because its underground rhizomes are deep enough to be protected and resistant to moderate heat.

It is tempting to consider these "landes," as the French term them, as the result of repeated burning during the human period. This idea is supported by the paucity of the flora found in the vegetation sites. No endemics occur there: if they were an ancient phenomenon, one would expect at least a few endemic species to have evolved. It is hoped that the nature and origin of this interesting vegetation phenomenon may be clarified before the French foresters have converted all the significant examples of it to pine plantations.

The pre-European vegetation remaining to be discussed is that of the coral islands or "motus" (low coral islands on the barrier reef) comprising the five Society Islands atolls and the barrier-reef islets associated with the high islands. The only high island of the group that lacks such satellites is young Mehetia. We know so little about Maiao that it may also be an exception, but it seems safe to assume that the flat part of it is of reef origin.

The substratum of these flat lands, mostly not more than 2–3 m above sea level, except for a few storm-ridges and sand dunes, is entirely of limestone. Locally it may be consolidated, but it is mostly of loose lime-sand, rubble, and gravel. The upper horizons (layers), where not disturbed by storms, were dark from humus in the places originally covered by forests of *Pisonia grandis*, with some calcium phosphate from droppings from fish-eating seabirds. Some mineral elements, essential for plant growth, were almost totally lacking. This deficiency doubtless contributed to limiting the floras of these calcareous habitats to relatively few species.

The flora of the motus was, and is, impoverished. The vegetation is essentially that of strand habitats throughout the Indo-Pacific, but in the Society Islands it is poorer than it is to the west. No one knows if it was richer before the Polynesians arrived, but the islands, flat and readily accessible, must have early been occupied by people. Undoubtedly some of the vegetation was replaced by coconut and breadfruit groves, and, in low wet

places, by taro pits. Most other crop plants, unless planted in the taro pits, would probably have done poorly because of salt spray. There is little doubt that much of the stony seaward storm-ridge zone and narrow sand-spit land, neither very productive, were left in natural vegetation. On windward sides the storm-ridge would have served as a windbreak protecting the planted land from salt spray.

What we know of Pacific coral island vegetation, excluding arid equatorial islands and isolated peripheral atolls, such as Wake and Ducie, with very small floras, fits a general pattern. Basically there is a "mixed broadleaf forest" of a small number of common widespread strand species. Principal tree species are *Pisonia grandis*, *Guettarda speciosa*, *Pandanus tectorius*, *Premna serratifolia*, *Cordia subcordata*, *Neisosperma oppositifolia*, *Cerbera manghas*, and *Morinda citrifolia*. Other trees are occasional, and several shrubs such as *Allophylus timoriensis*, *Scaevola sericea*, and *Timonius polygama* are common. In this forest are large trees of *Tournefortia argentea*, but no reproduction. Seedlings and young trees of *Tournefortia* are abundant around the periphery. The interior of an islet tends to be rather mesophytic, the condition approaching the lagoon shore, where there are likely to be conspicuous trees of *Calophyllum inophyllum* and *Cordia subcordata*, with occasional *Barringtonia asiatica*. There is a strong tendency, unusual in the tropics, for formation of pure, single-species stands of almost any of the trees or shrubs. Toward the seaward periphery, especially on windward shores, on stony storm-ridges, halophytic *Tournefortia* and *Scaevola*, both here with very thick fleshy leaves, form a dense scrub forest and scrub, sloping to beach level. Here may be a herbaceous fringe of *Ipomoea pes-caprae*, *Lepturus repens*, and *Fimbristylis cymosa*. On sandy beachtops and ridges are stands of *Suriana maritima*. Where there are exposures of consolidated limestone there may be scrub or scrub forest of stiff, brittle, microphyllous *Pemphis acidula*.

The European Period

The first European explorers to visit the Society Islands—Wallis, Cook, and Bougainville—found in Tahiti a world that, although changed from its primitive condition of near-equilibrium, was in a state where the human population was apparently sufficiently self-regulated that its influence on its environment was not such as to cause conspicuous degradation. During a period of possibly 2000 yr, or even more, the Polynesian population and culture had come sufficiently to terms with its environment that it supported them at a comfortable "standard of living," and the vegetation component of the environment was reasonably stable.

The advent of the Europeans, and what followed as they came to stay, was a disaster to the Polynesians and to most native lowland organisms. The introduction of a cash economy, and of foreign plants and animals, regarded as desirable by the newcomers, and the unintentional introduction of their "camp followers," such as rats, mosquitoes, fleas, and weeds, wrought major changes in the ecosystems and human culture.

Initially the coming of the Europeans affected mainly the coastal lowlands and lower valleys. Much of the available flat or gently sloping land was converted to coconut plantations to produce a cash crop, copra (dried coconut meat [endosperm]), which was in demand and traded for European goods and liquor. Local foods (taro, breadfruit, coconuts, fehi and other bananas, mape, yams, pia [*Tacca*], sweet potatoes, vi, and, later, cassava) remained principal items of the Polynesian diet, along with local animal foods, principally fish and occasionally pork.

On oceanic islands, such as the Society group, no endemic species have developed even such obvious defensive means as spines, poisonous alkaloids, bitter principles, or strongly unpleasant odors. The only apparent exceptions are those, such as the prickly *Erythrina sandwicensis*, whose ancesters brought their existing defensive adaptation with them.

On reasonably moist islands, such as the Societies, the original plant species are well adapted to the island environments. Where they formed closed vegetation, colonization by exotic plants was not usually successful, until a perturbation, such as invasion by introduced grazing animals or logging or

clearing by humans, opened up the closed formation. Only an unusual species that could become established and thrive in dense shade was a threat to the closed native vegetation, which suffered little damage so long as nothing occurred to open it up and permit the establishment of weedy sun-loving species. Such opening-up was most effectively done by large four-footed herbivores (and humans). Hence the vegetation that evolved there was exceptionally vulnerable when the European voyagers released goats on islands to provide food for possible future shipwrecked sailors.

In the Society Islands goats, though present, apparently did not thrive well on the wet windward sides. On the drier, more open leeward sides they were more successful, but were hunted by the local people, which afforded some measure of control. Humans were more effective in opening up the windward sides. Aboriginal settlers planted the fehi (*Musa troglodytarum*) and probably also the vi (*Spondias dulcis*) on lower mountain slopes and in valleys, and in valleys and on the lowest slopes, certainly, the mape. When the sweet orange (*Citrus sinensis*) was brought in, reputedly by Captain Cook, it was carried into the mountains, where it found a favorable habitat on disturbed lower slopes. Its excellent fruit was extensively harvested, the harvesters creating more disturbance. An attractive ornamental, *Tecoma stans*, was somehow introduced and found in these same disturbed areas an ideal home. By 1934 I found it abundant, along with oranges and fehi, in some of the deep northern valleys of Tahiti.

With time, goats and pigs, as well as humans, continued to open up the native vegetation, allowing such exotic species as mango, guava, strawberry guava, citrus, and coffee to invade and, in places, to dominate the vegetation. More and more exotics came in, brought as ornamentals, curiosities, or forestry plantings. *Tecoma*, *Cecropia*, *Spathodea*, *Leucaena*, *Albizia*, *Cryptomeria*, *Pinus*, and, lately, worst of all, *Miconia calvescens*, a South American member of the family Melastomataceae, multiplied explosively. *Albizia* and conifer species were planted extensively at the expense of the native (and aboriginally introduced) vegetation, changing its character completely. *Miconia*, its small berrylike fruits eaten and the seeds carried and dropped by birds, now invades even the upland montane rainforest. It reproduces even in its own dense shade and shades out all other plants except mature tall trees. This bodes ill for the largest and finest example of montane rainforest still remaining intact on oceanic Pacific Islands.

VEGETATION AND GEOGRAPHY OF INDIVIDUAL ISLANDS

Reliable descriptions of the vegetation of the individual Society Islands are almost nonexistent. Brief introductions to a few floristic lists and our own rather brief descriptions of Tetiaroa, Mopelia, Tupai, and Maupiti (Fosberg and Sachet 1987) are about all that are available.

The only vegetation maps of these islands are those by Papy (1954–1955), which use Gaussen's (Toulouse) system and color scheme. The part on the interior of Tahiti was based on information inadequate for this system and is unsatisfactory. The maps are useful, but the scale is small for our purposes.

Mehetia

Mehetia (17° 53′ S, 148° 05′ W), the easternmost of the Society Archipelago, is a small island, about 7 km^2, steep-sided, and 487 m high. It seems to be the youngest of the Society group of volcanoes, and recent enough to still have a small crater in its summit. There is little information on its natural features. Wave erosion has cut the shore back so that there is a narrow (5–10 m) wave-cut bench and a low vertical cliff, 10–30 m high, with many small stacks and blocks off the outer edge of the bench. Around the south half is a shelf or terrace extending back from the cliff and forming a surface that seems to correspond in slope to the bedding of the volcanic material. It slopes gently upward until it reaches the foot of the steep part of the volcanic cone. The three sides of the northern half slope steeply up from the top of the wave-cut cliff to the summit. One of these

sides was, in 1934, of loose rock talus without vegetation. The lower two-thirds of the remaining steep slopes are covered with dense forest of a number of tree species, including at least *Hibiscus tiliaceus*, *Pisonia*, *Casuarina equisetifolia*, and *Ficus*. Above this, to the summit, is a coarse grassland of *Miscanthus floridulus*. The total flora of the island may be less than 100 species.

Tahiti

Tahiti (17° 38′ 30″ S, 149° 30′ W) is the largest and by far the highest of the Society group. It is in reality two islands connected by a low isthmus. Its highest peak, Orofena (2272 m), is the highest point in Polynesia outside Hawaii (and New Zealand). The original basalt domes are deeply and spectacularly dissected, and steep slopes are the rule except for some terracelike remnants of original flow slopes on the lower flanks between the deep valleys or gulches. These valleys often have spectacular waterfalls near their heads. Fautaua Falls is an outstanding example.

The orientation of the two connected parts is more or less in the direction of the southeast trade winds, with the smaller and lower of the two volcanoes toward the wind. The whole island, because of this orientation, is rather wet, with lower rainfall in the northern parts, and somewhat of a lee, but not a dry slope or real rain shadow, on the west side. The elevations induce a high orographic rainfall. No rainfall measurements are available for the central peaks, but, judging from the vegetation and from personal experience of 10 days on the slopes of Orofena in the supposed dry season in 1934, these high peaks and the valley heads between them must form one of the wettest areas on earth.

CLOUD FOREST. Certainly everything known of the vegetation above 1000 m, and in some areas below this, is mossy forest or "cloud forest," continuously soaked with condensation or drenched with rain. Because of the high percentage of cloud cover, as well as the elevation, the temperature is uncomfortably cold, and the "warm moist" purple coloring of the high interior on Papy's (1954) map is most inappropriate.

The cloud forest of most of the high mountains of Tahiti is probably as nearly an undisturbed example of Polynesian vegetation as still exists. This mossy, epiphyte-laden forest is dense, of low stature, and without clear stratification. Its actual stature varies with slope, soil depth, and exposure from a meter or so on exposed crests and precipices to a few meters on steep slopes and as much as 15 or even 20 m or more in deep ravines and bottoms of high valleys. Leaves tend to be small and mostly, but not all, simple, often firm or even coriaceous. Forest on ridges above 1000 m tends to be dominated by *Weinmannia parviflora*, that on slopes of high valleys is, in many areas at least, dominated by *Alstonia costata*. Tree ferns (*Cyathea*) tend to be abundant and give the vegetation a spectacular character, almost unreal as seen in the swirling clouds that so often enshroud them. The ground as well as the trunks and branches of trees are covered by masses of bryophytes and ferns. Such genera as *Myrsine*, *Fuchsia*, *Sclerotheca*, *Cyrtandra*, *Ascarina*, *Metrosideros*, *Meryta*, *Reynoldsia*, *Coprosma*, *Psychotria*, and the spectacular *Fitchia* occur prominently. Composition varies from place to place, but the ecological basis for this variation is not at all understood.

MONTANE RAINFOREST. Below the mossy forest, and especially on the drier western middle to lower slopes, is a montane rainforest, not so wet and less laden with epiphytes, but with many of the same tree genera as in the cloud forest. *Freycinetia* and *Pandanus* are common, the former forming tangled masses. *Metrosideros* is locally dominant. *Fagraea*, *Canthium*, *Crossostylis*, *Wikstroemia*, *Dodonaea*, *Alyxia*, and many large ferns of various genera are common. This forest is now rather restricted in its distribution, replaced by fern and *Miscanthus* savannas, but was doubtless in times before human contact, and likely in pre-European times, the most extensive major formation in Tahiti. The extent to which the forest has been removed or replaced makes it unlikely that much in the way of correlation with soil and

slope will ever be possible. Changes by leaching in the actual substratum on the lower secondarily fern-covered slopes has probably been so profound as to be irreversible. What remains of the forest is now being replaced by stands of *Psidium cattleianum*, *Psidium guajava*, and, most recently, *Miconia calvescens*, or, in places, *Tecoma stans*—with undergrowth of *Lantana camara* and *Rubus rosaefolius*. The sweet orange (*Citrus sinensis*) and the mountain banana (fehi) are found in these forests, but apparently not nearly so abundantly as formerly. In 1934 large quantities of fehi and oranges were carried down daily from the mountain forests through such valleys as Punaruu, Papenoo, Fautaua, and others. This strenuous occupation still exists but has declined as foods tend to be imported, and as plant disease and change in vegetation have reduced the supply of wild fruits.

VALLEY VEGETATION. Tahiti has many long, deep valleys with steep sides and flat, boulder- and gravel-filled bottoms, with streams characteristically meandering from side to side and covering these floodplains when heavy rains occur in the high headwaters. The characteristic vegetation of these deep valleys, except some of the narrowest, is mape forest, with dense patches of tall bamboo (*Schizostachyum glaucifolium*). The mape is a large tree with dense, dark green crowns and massive, spectacularly buttressed trunks. The large seeds, so-called "Tahitian chestnuts," were and are an important food source for the Tahitians, and the prevalence of these forests on valley floors and lower slopes is likely the result of scattering, or perhaps planting, seeds to increase the food supply. In many of the valleys, coffee (*Coffea arabica*), descended and abundantly naturalized from old commercial plantings, forms a dense understory. Its seeds germinate abundantly in its own dense shade, and the seedlings form a close-set undergrowth a meter or two tall. *Hibiscus tiliaceus*, which forms dense tangled thickets most difficult to traverse except on established paths to the mape trees, is a common component of this valley forest, especially on the lower slopes.

In relatively recent times this forest has been extensively invaded by a number of exotic tree species, especially the African tulip (*Spathodea campanulata*), *Cecropia palmata*, and now, *Miconia calvescens*. Mango (*Mangifera indica*), *Aleurites moluccana*, breadfruit, and coconut are also common components of these forests. Clearings for shifting cultivation of taro, bananas, papayas, and pineapples are common, especially in the lower reaches of the valleys.

SAVANNAS. At the present time, though for how long in the past is not clear, the greater part of the slopes below 500–600 m, and in places even higher, are covered by savanna of *Gleichenia linearis* and, on the west side of the island, grasslands of *Miscanthus floridulus*, and mixtures of the two. The *Gleichenia* slopes are a bright light green; the *Miscanthus* presents a more drab appearance, especially in the drier season, May through September. Scattered in these savannas are small trees and shrubs, especially *Metrosideros*, *Dodonaea*, *Melastoma*, and *Wikstroemia*, and in some places, *Casuarina*. Planted by the forest department are *Albizia falcataria*, a fast-growing tree with dense, fine, feathery dark green foliage; the redwoodlike *Cryptomeria iaponica*; and in recent years, almost exclusively pine (*Pinus caribaea* var. *hondurensis*). Underlying these savannas is generally a deeply weathered and leached bright red soil. This erodes badly when disturbed by bulldozing or burning. The vegetation of both types of savanna seems to recover rapidly after fire, as the underground parts of the principal species are fire-resistant. Weeds, especially *Elephantopus mollis* and *Melinis minutiflora* (molasses grass), colonize disturbed places rapidly. *Stachytarpheta urticaefolia* is also abundant locally in such situations. The savanna slopes are in places invaded and even dominated by *Psidium guajava* (guava) and *Lantana camara*, and dotted here and there by dark green mango trees.

RAVINE FOREST. Ravines in these slopes are occupied by "ravine forests," mixtures of mostly exotic species such as mango, *Hibiscus tiliaceus* (possibly native), *Spathodea campanulata*, guava, and, at higher elevations, *Psidium cattleianum*. Clumps of bamboo and

breadfruit trees, probably planted by humans, may also share this habitat. Bananas, both fehi and common *Musa sapientum*, are also planted here by proprietors of these mountain lands. The nature of these ravine forests would repay further study, as they have not attracted botanists interested in the Tahitian flora.

CLIFF AND STEEP SLOPE VEGETATION. A conspicuous vegetation type about which almost nothing is known, for obvious reasons, is that of the cliffs and very steep valley walls. It is thin, only locally arborescent, and appears from a distance to be largely herbaceous or shrubby. A rather low-elevation vertical face in Orofero Valley is dominated by a vinelike, pendent form of *Metrosideros*, possibly an undescribed species, as scandent *Metrosideros* are otherwise known only from New Zealand. Specimens of this, while available, have not, as yet, been studied.

RIDGE-CREST SCRUB. The high crests of ridges and peaks have dwarfed shrubby vegetation, with much moss and ferns, *Garnotia*, and, at least on Orofena (highest peak), the tufted miniature sedge, *Oreobolus*.

FERN ABUNDANCE. What has not been brought out in the above descriptions is the prevalence of ferns in almost all Tahitian natural or seminatural vegetation types. Even in totally altered but unmanipulated vegetation, indigenous ferns have been able to establish themselves and are a conspicuous part of the plant cover. One presumably introduced fern, *Pityrogramma calomelanos*, is a conspicuous element of the trail-side vegetation and that of very much disturbed lower elevation sites generally. The notably white undersides of its otherwise dark green fronds make it easy to identify. Otherwise, even the pioneer ferns of disturbed places are apparently native.

Terrestrial ground cover and epiphytic vegetation in most situations except cultivated or pasture land and marshes is largely of ferns. Even coastal brackish swamps and marshes exhibit large stands of clumps of the large leathery *Acrostichum aureum*. The montane and cloud forests have, in addition to many species of ordinary terrestrial and epiphytic ferns, giant *Angiopteris*, *Marattia*, and *Cyathea* tree ferns as major components. Tangled, vinelike *Lygodium* is almost universal in forests and thickets at lower and mid-elevations.

LOWLAND AND STRAND VEGETATION. The strand and flat coastal zones remain to be noted. The flat lands are almost completely occupied by dwellings, their accompanying gardens and ornamental plantings, plus a few pastures and occasional thickets of, as yet, "undeveloped" land. Here, as rich a representation of the "pan-tropical flora" as is likely to be seen anywhere is displayed. A drive around Tahiti is like a kaleidoscope of flowering trees and shrubs, and colorful foliage plants. The coconut, from pre-European times, has dominated the landscape of this zone. It is no longer to be considered, in Tahiti, a commercial plantation tree, but as an ornamental and a dooryard food plant it is certainly the most obvious plant in the Tahiti lowland landscape. The "almost mangrove" swamp vegetation noted earlier occurs here and there, but has mostly been planted to coconuts or filled for houses and gardens.

The strand vegetation may earlier have been well developed, but most of its habitat is now occupied by dwellings, swimming beaches, marinas, and other human artifacts. *Pandanus*, *Hibiscus tiliaceus*, *Cordia subcordata*, *Thespesia populnea*, *Scaevola sericea*, *Paspalum distichum*, *Barringtonia asiatica*, and other strand plants may be seen frequently along the shore, but little real strand vegetation remains, at least in readily accessible areas.

Moorea

Moorea (17° 34′ 15″ S, 150° 00′ 30″ W), the island in the Society group nearest Tahiti, is one of the most spectacularly rugged islands in the world, dominated by ridges with many bare vertical slopes around deep valleys and high, almost spirelike peaks towering above the rest of the landscape. The scenery, viewed from such vantage points as la Belvedere, at the head of Opunohu Valley, is breathtaking. At the base of the volcanic cliffs and basal debris slopes is a flat coastal strip of varying

width, lacking in some short stretches of coast. Several deep fjordlike bays, notably Cook Bay and Opunohu Bay, on the north side, penetrate well into the interior.

The vegetation, except for some slopes and ridges with grass or fern savannas, slopes and cliffs too steep for tree growth, and cultivated lowlands, is principally broad-leaved evergreen forest and scrub of various sorts. Most of the lowland vegetation has been profoundly altered by man.

VALLEY VEGETATION. Valley bottoms and lower slopes, where not under cultivation, are occupied by mape forests. *Hibiscus tiliaceus* is an important component, with some bamboo, and in some of the valleys introduced *Coffea arabica* forms a dense understory 4–6 m tall with a crowded mass of slender saplings 1–2 m tall between the older trees. *Coffea* seeds germinate abundantly in the dense shade of these stands. *Ixora moorensis* and *Canthium barbatum* are frequent in areas where *Coffea* is not abundant. Ferns, both terrestrial and epiphytic, are plentiful and varied. The largest of these, *Angiopteris evecta*, with huge barrel-like erect rhizomes or corms, covered by fleshy stipules, and gigantic fronds, spreading to ascending, 4–5 m long, is generally common here and forms on some slopes an almost pure understory under the mape. The sides of these valleys are occupied by dense, tangled stands of *Hibiscus tiliaceus*, with *Aleurites moluccana*, *Rhus taitensis*, etc. On talus slopes, consisting of large boulders at the foot of the sheer cliffs at the heads of the valleys, are indigenous plants, such as *Pisonia umbellifera*, *Boehmeria virgata*, *Aleurites moluccana*, *Panadanus* sp., *Freycinetia impavida*, *Hernandia* sp., *Canthium barbatum*, *Macaranga* sp., *Weinmannia parviflora*, *Glochidion* sp., *Neonauclea forsteri*, *Ixora moorensis*, *Tarenna sambucina*, and, very locally, the rare and remarkable *Lepinia taitensis* (Apocynaceae) with improbable "hanging basket–like" fruits. This vegetation also, in places, extends down spur ridges from the bases of the cliffs. Epiphytes are abundant. All forests on the island are likely to be tangled with *Merremia peltata*, an extensive liana, with white morning-glory flowers.

STEEP SLOPES, RIDGES, CRESTS, AND PEAKS. Nothing is known of the vegetation of the steep slopes and crests above the cliffs. Serious mountaineering would be necessary for even a cursory examination of the really high parts of this island, between 600 and 900 m, culminating in Mt. Tohiea, 1207 m.

OPEN SLOPES AND RIDGES. Open slopes and ridges are less conspicuous than those of some of the neighboring islands, but bear a notable part of the vegetation. On the apparently wetter south and southwest slopes, *Gleichenia linearis* is locally dominant, but the areas of fern land are not large, and they tend to be crowded by the *Hibiscus*. The drier northeast slopes and ridges tend to be grassy, with *Miscanthus* at higher elevations and *Melinis minutiflora*, introduced for forage, on the lower areas. Much of what seems from a distance to be open slopes is a prickly scrub of *Lantana camara*, mixed in more favorable spots with *Psidium guajava*, which is also frequent in the more wooded areas. The ravines on the savanna slopes are filled with *Hibiscus* and *Psidium*, covered by *Merremia*. The steep crests of the ridges in these areas are bare and eroded in their lower parts. An interesting feature is the presence of a number of prominent rocky knobs overlooking the sea. Several of these have small bits of *Casuarina* forest on their summits. The others are bare.

COASTAL AND STRAND VEGETATION. The lowest slopes and the coastal flats all around the island are planted to coconuts, interrupted frequently by villages and isolated dwellings, patches of *Hibiscus* forest, and, locally, especially on the northeast corner around the airport, by *Typha* marshes. Some flat areas have been cleared, or partially so, for pasture and are dominated by *Paspalum* of several species, frequently *P. conjugatum*. Most coconut plantations have a grassy ground cover, with many exotic weeds, such as *Elephantopus mollis*, *Stachytarpheta urticaefolia*, and *Pseudelephantopus spicatus*. Roadsides and some lowest slopes are covered by a bright green mat of the recently introduced *Wedelia trilobata*. Some coconut plantations on very low-lying flats near the sea have no ground veg-

etation at all or occasional clumps of the large leathery salt-tolerant fern *Acrostichum aureum*. The ordinary dwellings are surrounded by "tree gardens" of breadfruit, mango, avocado, bananas, taro, and *Manihot* (cassava).

The homes of more wealthy people are landscaped with colorful and luxuriant tropical ornamentals, exotics from all warmer parts of the world. Orchid gardens are frequent. Flowering trees and shrubs such as *Plumeria*, *Bougainvillea*, and numerous varieties of *Hibiscus* are favored.

The strand proper, in addition to a rather depauperate ordinary strand vegetation, has trees of *Hibiscus tiliaceus*, *Thespesia populnea*, *Casuarina equisetifolia*, and, back of these, *Terminalia catappa*, *Pandanus tectorius*, and occasional *Barringtonia asiatica*. Along the west coast, *Rhiziphora mucronata* var. *stylosa*, introduced about 45 yr ago, has thoroughly established itself in very shallow water and forms, here and there, small mangrove swamps.

Maiao (Tupaemanu, Tapuaemanu)

Maiao (17° 34′ 41″ S, 150° 33′ W) is a small (10 km^2), rather low (147 m) volcanic island with low coral flats and a barrier reef with seven islets enclosing a lagoon. The flats are planted to coconuts except for swampy areas. Uplands are largely fern land. Almost no information is available on the vegetation and flora.

Huahine

Huahine (16° 42′ 30″ S, 159° 01′ 15″ W) is another high island—really two islands, Huahine Nui and Huahine Iti, lying close to and almost touching each other, northwest of Moorea. Its topography, though locally high and rugged, is not nearly as extreme as that of Moorea; its highest peak reaches an elevation of 456 m. It has much more extensive lower slopes than Tahiti and Moorea and is partly surrounded by flat islets (motus) similar to those making up an atoll. One of these, Motu Oavarewi, is at its western end, broadly joined to the main western island, Huahine Nui. The motus differ from most parts of the large islands in that they are entirely of coral limestone and very flat. At present they are mostly covered by coconut plantations, which are being cleared for watermelon cultivation.

With the exception of modified indigenous vegetation on the seaward sides of the motus, the forest on the lower ca. 200 m has been so completely altered that almost no indigenous plants remain, except *Gleichenia linearis*, *Miscanthus floridulus*, and *Hibiscus tiliaceus*, if it can be considered indigenous. *Miscanthus*, a coarse grass, dominates the drier ridges and some steep rock slopes. *Gleichenia* covers wetter ridges and lower slopes and hills of a deeply weathered, sterile, bright red soil. Other than these savannas and fern lands, the basic vegetation in uncultivated land is a tangled forest of *Hibiscus tiliaceus* with various admixtures of *Inga ynga*, *Psidium guajava*, *Casuarina equisetifolia*, *Cocos nucifera*, *Pandanus tectorius*, *Adenanthera pavonina*, *Mangifera indica*, and *Inocarpus fagifer*. *Merremia peltata* forms tough, twining, large-leaved tangles here, as it does in most places from sea level to as high in the mountains as there are data. The narrower valley bottoms are occupied by dense stands of huge, ancient-looking buttressed mape trees.

The gentler lower slopes, flat coastal strip, and the wider valley bottoms are mostly under cultivation. Coconut groves and plantations are prominent, but many are not well maintained and are choked with miscellaneous undergrowth of various exotic shrubs and vines. Some "slash-and-burn" agriculture is practiced, the plantings being mostly dryland taro (*Colocasia* and *Xanthosoma*) and bananas. A few vanilla plantings, with the vines twining on tall *Polyscias quilfoylei* saplings, may still be seen, persisting from the "vanilla boom" of 50–60 yr ago.

TREE GARDENS AND OTHER CULTIVATIONS. By far the most prominent culture is what may be called "tree gardens." A dominant overstory of coconut, breadfruit, mango, *Inga*, and others shades a ground layer of taro, cassava, bananas, papayas, yams, and other shade-tolerant vegetables and fruits. Dwell-

ings are scattered in these gardens, and ornamental plants are prominent and showy.

Former swamps and marshes are mostly now occupied by wetland taro culture, a most productive food source. Large areas of flat coral soil on the motus have been cleared and are devoted to melon raising—watermelon and cantaloupe. Production of these in the sterile lime soil is made possible by importation of dark topsoil from the adjacent higher slopes and valleys to make small mounds or filled depressions for the melon plants. Chemical fertilizers and herbicides are used in quantity. Protection from salt spray is provided by a strip of strand forest and coconuts between the melon fields and the seaward beaches.

STRAND VEGETATION. The strand vegetation of the motus and some areas of exposed high-island coast is composed of such wide-ranging coastal species as *Hibiscus tiliaceus*, *Thespesia populnea*, *Casuarina equisetifolia*, *Pandanus tectorius*, *Premna serratifolia*, *Guettarda speciosa*, *Tournefortia argentea*, *Scaevola sericea*, *Cordia subcordata*, *Pisonia grandis*, and herbs and vines such as *Lepturus repens*, *Thuarea involuta*, *Canavalia sericea*, *Ipomoea macrantha*, *Cassytha filiformis*, *Euphorbia* sp., and many exotic weeds. Now, of course, most of this has been cleared and planted to coconuts and, more recently, as noted above, to melon culture. Sweet potatoes (*Ipomoea batatas*) are planted here occasionally, but more commonly in clearings in the coastal areas of the main islands.

VALLEY AND SLOPE VEGETATION. The *Inocarpus–Hibiscus* vegetation of the valleys and slopes above most of the cultivation tends to have a thick undergrowth of small trees and abundant seedlings and saplings of *Coffea arabica*. The giant fern *Angiopteris*, with prominent lacerate stipules, is common on these slopes and especially in ravines. In places it forms a complete understory in open *Hibiscus* forests on moderately steep slopes, the spacing being fairly open, but the enormous, 5-m-long, ascending fronds interlace toward their ends. A grass (*Centosteca lappacea*) and fern (*Thelypteris* spp.) ground cover is general in this and other vegetation types at such elevations (100–300 m).

Just above the *Angiopteris–Hibiscus* type is a zone of an enormous *Pandanus* species (not seen fertile), with stilt roots 5 m or longer. With this, such native trees as *Neonauclea forsteri*, *Canthium barbatum*, *Ixora st. johnii*, *Fagraea berteroana*, *Crossostylis biflora*, occasional *Xylosma suaveolens*, and the inevitable *Hibiscus tiliaceus*, vines such as *Freycinetia impavida* and *Merremia peltata*, and many ferns are found, including, of course, *Angiopteris* and *Gleichenia*. This forest has a few epiphytes and some moss on trunks and branches.

Where the ridges and slopes become steep, between 400 and 500 m, the moss and epiphytic ferns and orchids become more abundant. The above-listed trees are still dominant. *Freycinetia* becomes so prominent and tangled as to make penetration difficult. A second species of *Angiopteris* (*A. lasegueana*?), with notably glaucous stipes, a species of *Psychotria*, one of *Cyrtandra*, one each of *Premna*, *Alyxia*, *Canthium*, and *Decasparmum fruticosum*, as well as an abundance of large terrestrial ferns, form a dense undergrowth.

Little is known of the vegetation on slopes and ridges above 400 m, as almost no botanists have reached these elevations.

Raiatea

Raiatea (16° 40′ S, 154° 40′ W), about 80 km west of Huahine, is the second largest of the Society Islands, more or less arrowhead-shaped, about 18 km long, 194 km^2 in area, with three principal mountain masses connected by saddlelike ridges. The central mass culminates in Tefatoaiti, 1017 m. The northern mountain mass, the famous Temehani Plateau, is much lower, at its highest peak, Tepahu, 821 m. The topography is generally rugged, with many deep valleys and sharp ridges, leaving relatively little level ground in valley floors and on the much-interrupted coastal strip. The east coast is cut by many ridges and a number of deep bays.

SAVANNA. Although there is considerable forest, a general view of the island suggests

proportionally more open savanna land than on any of the other islands of the archipelago. Much or most of this is *Gleichenia* fern land, bright green, with darker patches and dots of trees. The lower slopes and ridges on the north end and northwest side are drier, browner, and mainly dominated by aiho or sword grass (*Miscanthus*), a tall coarse bunch grass. *Melinis* (molasses grass) is also common, forming gray-green patches where not shaded out by the taller *Miscanthus*. The lower ends of these dry ridges are badly eroded, especially in the Uturoa area. At higher elevations and generally, farther south, the open areas are covered by a deep tangled mat of *Gleichenia linearis*, as much as 2 m deep in some favorable spots, and are traversed on foot only very laboriously.

BROAD-LEAF EVERGREEN FOREST. Other than in these open savannas, the high-elevation Temehani Plateau with its special vegetation, described below, and coastal pastures and marshes, the predominant vegetation is of various sorts of broad-leaved evergreen forest.

As on the other high islands of the group, the deep valley floors are mostly occupied by mape forest. Mape trees here are large, even to 25 m or more tall, their trunks irregularly fluted and conspicuously buttressed. Other trees include *Hibiscus tiliaceus*, bamboo (*Schizostachyum glaucifolium*), breadfruit, *Cananga odorata*, and the introduced and rapidly spreading *Cecropia palmata*. *Coffea arabica*, spreading from earlier cultivation, in places forms a dense undergrowth. Epiphytic bryophytes, ferns, and a few orchids are common. Terrestrial ferns are abundant, the largest, *Angiopteris evecta*, forming a conspicuous feature of the undergrowth. In Faaroa, one of the largest valleys, with areas of relatively gentle slopes and rolling ground, mape is present but not abundant, and the forest is largely dominated by the Asiatic *Syzygium cuminii*, the jambolan or Java plum. With it are *Hibiscus*, *Artocarpus*, and *Cecropia*. One of the guavas, *Psidium guineense*, is common. A weak bramble, *Rubus rosaefolius*, has become established, especially along roads and paths, forming low tangles.

Toward the head of this valley and perhaps others are extensive brakes of *Schizostachyum glaucifolium*, the tall indigenous bamboo, the culms reaching 10–15 m in height and spaced from a few centimeters to a meter or so apart.

On the saddle ridges separating the valleys, the forest has more native elements, such as *Alstonia costata*, *Commersonia bartramia*, *Alphitonia zizyphoides*, *Hernandia* cf. *moerenhoutiana*, *Cerbera manghas*, *Canthium barbatum*, *Decaspermum fruticosum*, and *Melastoma malabathricum* var. There are many epiphytes, and vines such as *Merremia peltata*, *Lygodium reticulatum*, and *Gleichenia linearis*. The *Gleichenia* forms dense tangles in somewhat open places.

On ridges and slopes between 300 and 500 m are areas of forest that appear to be rather natural and perhaps predominantly of indigenous species. These have not been studied, though they may be close to the makeup of the original mid-elevation montane rainforests. One would expect the epiphytic flora and the abundance of pteridophytes prominent at lower elevations, in more disturbed and altered situations, to be even better developed in these mid-elevation forests.

TEMEHANI PLATEAU. The most striking vegetational feature on Raiatea is the complex of scrub forest, scrub, dwarf scrub, and "bog" on and around the Temehani Plateau, the northern of the high mountain masses on the island. This vegetation may also occur on the other parts of the island above 500 m, but there is little information about these areas.

On the way up to Temehani Rahi from Pufau, the first several hundred meters are through *Hibiscus* forest and fern land, which is being actively planted to *Pinus caribaea*. Above 250 m there is a scrub forest and scrub of largely native species, except the abundant *Rhodomyrtus*, apparently introduced here. At the end of the jeep road, at the head of Pufau stream, there is a mixed scrub of native species, mostly somewhat dwarfed tree species, including *Alstonia costata*, *Metrosideros collina*, *Decaspermum fruticosum*, *Weinmannia*, *Myrsine*, *Crossostylis*, *Alyxia*, *Glochidion*, *Astronia*, and *Pandanus*. *Machaerina* and *Gahnia* are conspicuous sedges. Along the ridge upward, the stature of the scrub de-

creases and some additional species come in. Some of the common scrub forest elements even in dwarfed form seem to be replaced on the plateau, at about 600 m, by notably dwarfed forms, possibly of the same species, possibly distinct species or varieties.

The plateau is a gently sloping surface, undulating between about 600 and 650 m, with hills and crests to 700 m or more. The soil is a thin peat or mor, lying on a weathered rock surface, desiccated when I examined it, but obviously saturated at most times. The shallowness of this soil may be the cause of the general low stature of the woody vegetation, which varies between a few centimeters and 2–3 m, but except for patches of *Pandanus raiateensis* is usually less than 1 m, mostly about 0.5 m. Genera making up this low scrub are *Decaspermum*, *Alyxia*, *Weinmannia*, *Canthium*, *Wikstroemia*, *Alstonia*, *Astronia*, *Glochidion*, *Styphelia*, *Bidens*, *Xylosma*, *Metrosideros*, *Garnotia*, *Machaerina*, *Gahnia*, *Sphenomeris*, *Lycopodium*, and *Cassytha* plus undoubtedly others not noted or collected. In substantial areas the scrub becomes thin and *Gahnia* sp. cf. *schoenoides*, a conspicuously tufted species with black panicles reaching 0.4–0.8 m, becomes dominant. The clumps are fairly openly spaced, and dwarf shrubs, especially *Decaspermum lanceolatum*, occur between them. In slightly protected areas, the same component of shrubs becomes taller. *Pandanus temehaniensis*, a relatively dwarf species of the *P. tectorius* affinity, but amply distinct, occurs scattered in the scrub. It is a species with curious horizontal branching, smooth thick stems from 2 to 3 m tall, and a short, straight stiff peduncle. Up the slope toward the edge of the precipice the *Pandanus* plants and clumps become more abundant until finally they form an irregularly closed stand, which shelters a number of species that are either absent from or much more dwarfed in the low scrub of the open plateau.

The remarkable endemic lobelioid *Apetahia temehaniensis* is said to formerly have been abundant in the scrub on this plateau, but to have been pulled out so ruthlessly to serve as decorations for feast days that it is now gone completely from the plateau and only survives on the surrounding wet cliffs, where it is rare. It may possibly still exist on one or two of the other high mountains on Raiatea, but no specimens have been brought in to substantiate this rumor. Large patches of bare rock on the plateau are said to be where the *Apetahia* were pulled up, loosening the fragile soil cover. This dwarf vegetation type is apparently unique to the Temehani Plateau and surrounding slopes above 500 m. It is fairly extensive there, however, judging from examination with binoculars. It has been explored rather well floristically and many species have been described, but little has been published on its vegetation characteristics.

The lower slopes are largely covered by tangled *Hibiscus* thickets. Mango trees, dense rounded emergents, are present here and there in the *Hibiscus* cover. *Psidium* of two, and locally three, introduced species, is a component in most places, especially in the ravine forest on savanna slopes. The *Hibiscus* reaches the coconut plantations on the flats and lowest slopes, and, in a few places, the shore.

Almost the whole coastal strip is occupied by houses, gardens, and plantations. Mango, breadfruit, *Inga*, *Tamarindus*, *Samanea*, *Terminalia catappa*, and various ornamentals cover this area, hiding the houses and giving the appearance of a forest. Areas of pasture and taro gardens are common. Some areas of *Typha* marsh exist, especially north of Uturoa. Many of the coconut plantations on flat low coastal areas have no ground vegetation whatever, except occasional planted *Gardenia taitensis*. A peculiar bright green form of *Hibiscus tiliaceus* with straight trunk, hard wood, and a compact round crown, which occasionally produces a fertile branch of the normal form, lines the roads in many places along the coast. The related *Hibiscus hastatus*, with variously lobed leaves, is also planted along roads.

The strand vegetation is poorly developed, consisting of *Paspalum distichum* flats, *Thespesia populnea*, *Cordia subcordata*, *Casuarina equisetifolia*, and *Hibiscus tiliaceus*, with several other strand shrubs and herbs. Back of the strand are occasional marshes with *Cyperus javanicus*, *Ludwigia octovalvis*, and a suffrutescent acanthaceous bush, as well

as other plants of wet situations. Shrubs of *Annona glabra*, doubtless introduced, occur here and there in strand and brackish marsh situations. *Pemphis acidula* bushes occur where there are coral limestone shorelines, natural or artificial. Finally, cliffs and knobs overlooking the lagoon may have thin *Casuarina* forest.

The fairly numerous coral islets or motus that surround Raiatea on its barrier reef are mostly covered by old coconut plantings, but were not investigated.

Raiatea was a center for the ancient Polynesian civilization. Maraes (stone temple platforms and enclosures) are common. The vegetation shows the results of long human influence, but the rough terrain has perhaps preserved more of the indigenous plants than on most islands of the group.

Tahaa

Tahaa (16° 35′ S, 151° 35′ 06″ W), within the same barrier reef as Raiatea but slightly to the north, is third in size of "les Iles Sous-le-Vent," 61 km^2, and 580 m in maximum elevation; the driest of the islands, judging by the vegetation; and (except for little Maupiti) the most altered by human activities. Apparently little or no vegetation that could be in any sense called original remains. No forest dominated by undoubted indigenous species was studied, though some small remnants may exist on high slopes.

SAVANNA. The salient feature is the predominance of *Miscanthus* grassland, rather than fern land in the open areas. *Gleichenia linearis* is present in some of the *Miscanthus* stands, but there are relatively few significantly large areas dominated by *Gleichenia*.

WOODY VEGETATION. Coconuts are planted throughout the lowlands and well up the slopes. The palms are, as they are on others of the high Society Islands, mostly old, and little replanting was observed. However, there seems to be more active harvesting of copra here than on the other islands.

Mape is common in the lowlands and especially in the valley bottoms, but forests dominated by this species are less common than on other islands. Breadfruit is common, and with coconuts, mape, *Inga*, papaya, bananas, and *Manihot* is the basis of the "tree gardens" that surround most dwellings outside the centers of the villages.

Hibiscus tiliaceus is by far the most abundant "tree." In its usual tangled form, it lines the shores and extends through the coconut plantations and well up many of the slopes to near the mountaintops. It dominates wooded upper slopes, most lower slopes other than grasslands, and unused lowlands. *Pandanus* is scattered in most of these slope forests, except at very high elevations. *Aleurites moluccana* is more common here than on other islands of the group. *Angiopteris* is present but in smaller numbers than on other islands. Notable are the small numbers of the "weed trees" found so abundantly in the islands closer to Tahiti. *Psidium guajava* and *Coffea arabica* form, with *Hibiscus*, a dense undergrowth in many of the forests. Mango is the most common large tree, other than *Cocos*. *Inga* is common but not abundant. *Spathodea* and *Tecoma* were, in 1982, present only in very small numbers of young trees. Only one small seedling of *Cecropia* was seen, near the Agriculture Station. Fortunately, *Miconia* does not seem to have reached Tahaa at all. *Syzygium cuminii* and *Adenanthera pavonina* are only occasionally seen in the areas visited.

FOREST REMNANTS. In patches of scrub and forest above 150–200 m several native trees, especially *Alphitonia zizyphoides*, *Commersonia bartramia*, *Metrosideros collina*, *Pandanus* cf. *tectorius*, and at least two species of *Glochidion*, begin to form a significant part of the vegetation. *Freycinetia* is occasional. *Canthium barbatum* is present in thickets and forest from near sea level to as high as any observations are available. *Merremia peltata*, an extensive twining liana, forms tangles in all areas of woody vegetation examined.

A few areas of forest that appeared from a distance to be largely native were seen in 1982 on high, rather steep slopes, but there was no chance of reaching them.

In the grasslands and fern lands, scattered native shrubs are common. They are mostly

Metrosideros collina, *Dodonaea viscosa*, *Decaspermum fruticosum*, *Melastoma malabathricum* var., and *Glochidion* sp. *Miscanthus* and *Gleichenia* seem, by means of resistant underground parts, to be able to recover promptly after fires in these savannas. *Lycopodium cernuum*, also common with them, seems completely killed by fire, but apparently replaces itself promptly, probably by spore germination.

FORESTRY. Efforts have been made for some time to establish forests on these impoverished savanna soils. *Albizia falcataria* was apparently the favored tree earlier, and dense patches of it are in some areas very conspicuous at middle elevations. According to some of the forestry people on other islands it was found that *Albizia* required better soils to do well, and *Pinus caribea* var. *hondurensis* is now widely planted. Indeed, substantial areas of saplings of this pine may be seen, planted in regular rows, in some savanna areas. Whether or not these pines will further acidify and impoverish these poor red soils has apparently not been considered. The pines, in their early stages at least, seem to survive and even to thrive. Whether the prospective pine forests can be protected against fires that occur on the savannas remains to be seen.

SUBSISTENCE FARMING. Most lowland reasonably flat areas on the island are devoted to subsistence farming or gardening. Tree gardens, mentioned above, and taro patches, mostly "dryland taro," are dominant features of the landscape. Thickets of mixed vegetation, especially *Hibiscus*, in the lowland areas are apparently bush fallow, cleared at intervals for taro, banana, or pineapple culture.

SHORE VEGETATION. The shore is lined principally by the planted sterile, erect *Hibiscus tiliaceus* var. *sterilis*, with some *Thespesia*, *Calophyllum*, and *Cordia subcordata*. Immediately back of this, usually on the landward side of the road, are coconut plantations, mostly with little or no ground vegetation except occasional patches of *Paspalum distichum*. The reason for this lack of ground cover is not clear, unless the occasional flooding by spring tides and subsequent evaporation leaves the ground too saline for most plants. Low areas have patches of *Acrostichum aureum*, a coarse, leathery, salt-tolerant fern, and scattered *Hibiscus tiliaceus* trees and thickets. Other low areas, devoid of trees, are occupied by *Typha domingensis*, forming marshes of tall "cattails" to 2 m or more tall. Still others have a dense sod of *Paspalum distichum*.

Borabora

Borabora (16° 22′ S, 151° 40′ W) is very steep and rugged, with an almost unclimable towering central volcanic plug 579 m high. Far toward the western end of the chain, it shows the geomorphological results of more erosion; greater subsidence, surrounded by a lagoon; and a reef with a ring of motus, several of them with some relief, others flat. The flatter parts of both main islands and motus are very disturbed, with coconut plantations and villages with economically useful as well as ornamental trees and shrubs. The lower slopes are dry and covered by thin guava scrub or scrub forest; in other parts, especially on the steeper slopes, there is tangled *Hibiscus tiliaceus* scrub forest with few native plants. Many areas, probably repeatedly burned, bear a tangled blanket of the fern *Gleichenia linearis* and a few scattered woody species, mostly native—*Metrosideros collina*, *Wickstroemia coriacea*, *Glochidion* sp.—and the introduced *Psidium guajava*, native of tropical America. These denuded lower slopes and ridges are badly eroded and, in some places, bare of vegetation.

Along the shores, the back beaches are lined with great *Cordia subcordata* trees and *Hibiscus tiliaceus*, both the ordinary diffusely branched, large-leaved variety and the variety *sterilis*, with an upright trunk and rounded crown, leaves smaller, bright green on both faces, margins tending to be serrulate, and generally without flowers and fruits. The common form has larger leaves, dark green above and gray or whitish hairy beneath, margins entire. This ordinary form makes tangled thickets back of the beaches and on steeper slopes above. The sterile variety is planted along the road around the island and in the villages.

The higher ridges and slopes are still wooded

and green, the forest presumably mostly native, but little information is available. Up to the foot of the cliffs, on any more favorable places with soil, cultivation of breadfruit, mape, and cassava prevails. The forests on less favorable sites at these elevations are principally *Hibiscus tiliaceus*, with some admixture of *Neonauclea*, *Pipturus*, and other somewhat tolerant native species. These forests have probably diminished since 1934 when the above notes were made. The extent of erosion has been observed to be greater, as seen from the air.

Maupiti

Maupiti (16° 6′ S, 152° 12′ W) is floristically, at present, impoverished, though this may not always have been the case. The proportion of exotic species is high, and they are abundant. That they have all replaced indigenous plants is a truism, but suggestive that the native flora must once have greatly exceeded the 237 native species now on record (Fosberg and Sachet 1987).

The flora of the volcanic parts of the island has probably suffered the greatest loss of both indigenous species and numbers of individuals. Jean Raynal, who collected here in 1973, is said to have devoted most of his effort to the higher areas. He got a number of species not found in 1985 as well as several more that are now scarce. Those now missing or scarce are the most mesophytic, reflecting the present denuded condition of the ridges and summits. The slopes and ravines, which once must have had a fairly mesophytic flora, at least on the windward side, are now almost entirely occupied by exotics, both woody and herbaceous. The coastal strip is, except for the strand, covered by exotic trees and shrubs, mostly either economic or ornamental.

The motus, though they have been completely converted to coconut plantations, have probably retained a greater proportion of their indigenous flora than the high island, though their original total flora may probably have been much smaller. Most of the atoll species are pioneers or salt-tolerant plants and, hence, better able to survive clearing and exposure. Even so, a few species that might be expected in large motus such as these were not seen. *Pisonia grandis*, for example, seems completely lacking. *Pemphis acidula* is very local and in an unusual habitat, on sand flats and edges of a brackish pond. Neither *Hedyotis romanzoffiensis* nor *Digitaria stenotaphrodes* was found.

Society Atolls

The five sea-level atolls in the Society Islands, Tetiaroa, Mopelia, Tupai, Bellingshausen, and Scilly, are essentially similar in their vegetation types, though extent and patterns of distribution differ (Sachet 1983*a*,*b*, Sachet and Fosberg 1983). All have largely been planted to coconuts. The plantations have a herbaceous, or herbaceous and woody, ground layer, and when allowed to go unharvested develop a dense growth of coconut seedlings that is eventually almost impenetrable. The composition and physiognomy of the ground layer varies, depending on the amount of care, weeding, or burning applied and on the texture of the coral gravel or sand substrate. Several species not known otherwise from the Society Islands are found here (e.g., *Hedyotis romanzoffiensis*, *Nervilia aragoana*, *Terminalia samoensis*, *Sida fallax*, and *Digitaria stenotaphrodes*).

Around the peripheries of the plantation areas occurs a zone of shrubs and small trees—largely *Scaevola sericea*, *Tournefortia araentea*, *Pandanus tectorius*, *Guettarda speciosa*, *Suriana maritima* (on sand), and *Pemphis acidula* (on lithified rock). On windward exposures this belt is windsheared to a slope down to the beach top. Beyond it, on the berm or top of the beach, an open to closed herbaceous vegetation may occur of *Lepturus repens*, *Fimbristylis cymosa*, *Vigna marina*, *Ipomoea pes-caprae*, and *Triumfetta procumbens*. *Cassytha* parasitizes most of the shrubs and herbs, clothing them with tangled, leafless, stringlike stems of orange or green. Consolidated rock shores may support pure stands of tough sub-fleshy-leaved *Pemphis acidula*.

Inland on some islets are more or less extensive wet depressions mostly dominated by *Mariscus iamaicensis*, a tough, sharp-leaved sedge, elsewhere called "saw grass."

This may reach 2 m in height. Around the edges may be a solid stand of the diminutive sedge *Eleocharis geniculata*. Locally *Cyperus javanicus* may be common.

Around former village sites may be large trees of *Calophyllum*, *Hernandia sonora*, *Pometia pinnata*, and *Terminalia catappa*. On the ground under the coconut trees is a layer of *Boerhavia tetrandra*, *Triumfetta procumbens*, *Lepturus repens*, *Thuarea involuta*, and various weeds.

The motus (islets on the barrier reefs around the high islands) are flat, of calcareous sand and gravel, essentially similar to the islets on the atoll reefs. Their vegetation, or what remains of it after a century and more of commercial coconut planting and, on some, human habitation, is essentially similar to that of the atoll islets. On seaward sides of windward islets, windbreaks of natural vegetation have in many cases been left to protect the plantations from excess salt spray.

CONCLUSIONS

The Society Islands, in the South Pacific, 16°–18° south of the equator, in the wet SE trade wind belt, comprise 10 volcanic islands and five coral atolls. Original vegetation was hygrophilic broad-leaf forest, with the exception of scrub and dwarf scrub on high peaks, crests, and boggy plateaus, sparse scrub on cliffs, and possibly small leeward areas of coarse grass. The forest on the coastal strip and in deep valley bottoms approached tall rainforest. Above this is montane rainforest, then mossy or cloud forest, and finally, mossy scrub-covered crests and peaks. The coral islands had an impoverished halophytic strand forest. The floristic composition was an attenuated Indo-Malayan flora with a small component of Pacific endemic groups with uncertain affinities.

Two or more thousand years of Polynesian occupation altered the lowland vegetation to an extent that its nature before human contact is conjectural. Aboriginally introduced *Cocos*, *Artocarpus*, *Inocarpus*, and *Spondias* replaced much of the topographically habitable lowland forest. Gentler lower slopes were terraced and converted to muddy taro patches, and partly to tangled *Hibiscus tiliaceus* thickets. Leeward slopes below 500 m were repeatedly burned until their forests were replaced by a blanket of *Gleichenia* with a few fire-resistant woody species forming a leached fern savanna, or locally in drier places, *Miscanthus* grassland.

With European conquest and occupation came a large exotic flora of aggressive pantropical species, cultivated and spontaneous, which drastically altered and largely replaced the vegetation, both spontaneous and planted, of the Polynesian period. This process continues, with foreign species even invading and replacing the lower and middle montane rainforest. Disturbance by goats accelerates this process, at least on leeward slopes.

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