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Vegetation of Samoa and Tonga[1]

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ABSTRACT: Based on field studies and a previous review of the literature, 22 plant communities are recognized in the two adjacent South Pacific archipelagoes of Samoa and Tonga. Because of similarities of climate and flora, most of the communities are similar in the two archipelagoes; the major differences result from the coralline nature of most of Tonga and the volcanic nature of Samoa. The communities are briefly described, the dominant species are listed, and the variation between the two archipelagoes is noted.

The Tongan and Samoan archipelagoes are situated in the tropical South Pacific to the east of Fiji (Figure 1). Tonga, which lies at a latitude of 15–23° S and a longitude of 173–177° W, comprises about 150 islands with a total area of 697 km^2, but only about 36 of these islands are currently inhabited. The archipelago is basically a double chain of islands running in a north-northeast direction with small, high, volcanically active islands on the west, and lower, larger, raised coral islands on the east. The main limestone islands are Tongatapu (257 km^2 in area, 80 m elevation), 'Eua (87 km^2, 330 m), and Vava'u (90 km^2, 200 m). Numerous, small, raised-coralline islands known collectively as Ha'apai lie between Tongatapu and Vava'u. In the volcanic chain, the main islands of the southern part, going from south to north, are 'Ata, Tofua, Kao, Late, and Fonualei; of these, only Tofua is inhabited. Kao, which lies adjacent to Tofua, has the highest elevation in Tonga (1046 m). The northern part of the volcanic chain comprises three islands, Niuafo'ou, Niuatoputapu, and Tafahi, all of which are inhabited; these are actually closer to Samoa than they are to the nearest inhabited island of Tonga (Vava'u).

Samoa is an archipelago divided politically into Western Samoa, which is an independent country, and American Samoa, which is an unincorporated territory of the United States. It lies at a latitude of 13–15° S (11° when Swains Island is included) and a longitude of 168–173° W. The archipelago comprises nine inhabited islands, plus Swains Island and uninhabited Rose Atoll (ca. 200 km beyond the easternmost volcanic island, Ta'ū), and has a total area of ca. 3100 km^2. It is a single chain of volcanic islands running in a west-northwest direction. The four main islands, going from west to east, are Savai'i (1820 km^2 area, 1860 m elevation), 'Upolu (1110 km^2, 1100 m), Tutuila (124 km^2, 650 m), and Ta'ū (39 km^2, 930 m).

Because both Tonga and Samoa are situated between the Tropic of Capricorn and the equator, their climate is tropical. There is little seasonal or diurnal temperature variation, although the winters in Tonga, which is farther from the equator than Samoa, are sometimes relatively cool. There is no pronounced dry season and all areas except the Ha'apai Islands of Tonga receive at least 200 cm of annual precipitation. Occasional droughts, however, may occur, and hurricanes are a threat in the summer season (December to April).

The two archipelagoes differ, however, in geology and soils. Samoa is volcanic in origin and "oceanic" (i.e., it was formed from basalt rising from the ocean floor of the Pacific basin [from the Pacific Plate] beyond the continental islands to the west). The islands were born in isolation and have never had a connection to any other land area. The islands of Tonga, however, are mostly coralline and "continen-

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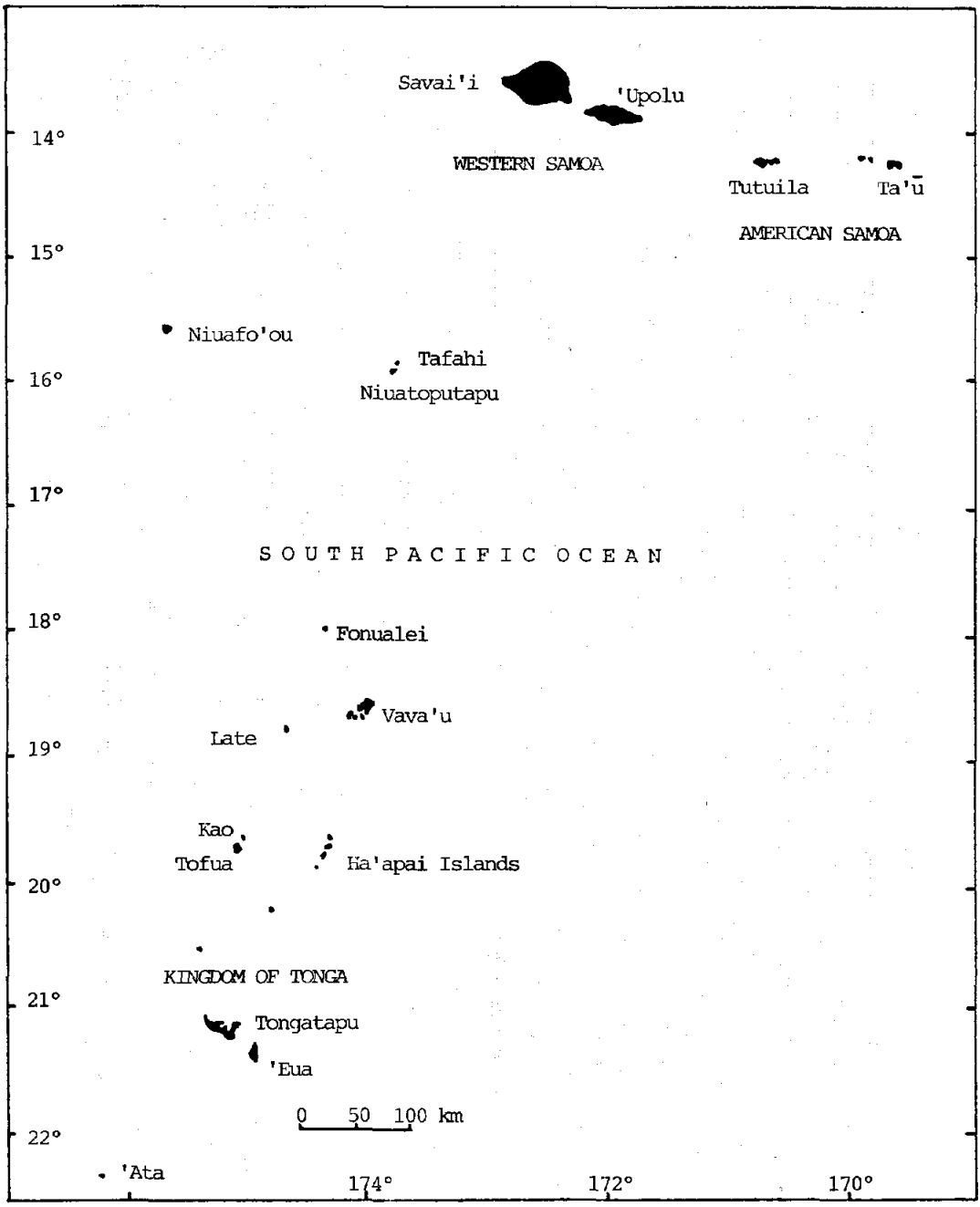

FIGURE 1. Map of Tonga and Samoa.

tal," and lie on the eastern edge of the Asia-Australia Plate. Uplifting of the edge of this plate has been caused by subduction of the Pacific Plate under it, which in turn has caused the volcanic activity on the western edge of the island chain (Crane 1979).

Nearly the entire surface of Samoa is covered with soil derived from basalt (Wright 1963), but in Tonga this can be said only of the western chain of islands. The most recent volcanic activity in Samoa occurred on the island of Savai'i (ending in 1911), and in Tonga on several islands, most notably Niuafo'ou (which last erupted in 1946) and Tofua (which is still steaming). Most of Tonga has a coralline surface, although much of this is now covered with a layer of volcanic ash from an ancient volcanic eruption to the west of the main islands (Crane 1979). The exposed edges of the uplifted coralline deposits that are characteristic of Tonga are not found in Samoa, and consequently some plants adapted to this habitat are absent from there.

Both Tonga and Samoa are floristically part of the "Fijian Region" that extends from the Santa Cruz Islands and Vanuatu to Niue (Takhtajan 1969). Lying in the eastern portion of this region, the two archipelagoes have smaller native floras than the Melanesian islands to the west, which lie closer to the Indo-Malaysian source region.

Several floristic studies of Tonga have been published (Hemsley 1894, Burkill 1901, Yuncker 1959, Sykes 1978, 1981), and large collections by M. Hotta, G. Buelow, W. R. Sykes, and W. A. Whistler have added many unpublished records. Several floristic studies of Samoa have also been published (Reinecke 1896, 1898, Setchell 1924, Christophersen 1935, 1938, Christensen 1943, Yuncker 1945, Whistler 1983*b*), and these have been augmented by a large collection by W. A. Whistler between 1972 and 1991. Based on a compilation of these sources and specimens, the numbers in Table 1 were obtained.

The floras of Tonga and Samoa are very similar to each other; over 70% of the native Tongan flowering plants are also found in Samoa. A comparison of the two floras (Table 1) shows that Samoa has four times the area and nearly twice the elevation of Tonga, but

TABLE 1

COMPARISON OF THE NATIVE FLORA AND GEOGRAPHY OF TONGA AND SAMOA

	TONGA	SAMOA
Area	797 km^2	3,100 km^2
Highest elevation	1,046 m	1,860 m
Angiosperm families	83	95
Angiosperm genera	248	300
Angiosperm species	340	ca. 550
Gymnosperm species	2	0
Pteridophyte species	77	215
Endemism	3%	ca. 30%

the number of families and genera in the two archipelagoes are not very different. The number of species and level of endemism, however, are much higher in Samoa.

Although the geology of the two archipelagoes is quite different, the similarity of climate and flora make the vegetation of the two archipelagoes similar enough to be treated together, and this has been done in this paper.

Like the rest of Polynesia, the two archipelagoes, which have been inhabited for over 3000 yr, have been extensively modified by human activity. This disturbance has led to the loss of much of the native vegetation that once covered the islands. The loss was greatest on the lowest, smallest, most fertile islands. Tongatapu, which is very flat and fertile, is now almost entirely devoid of native vegetation, except for a narrow strand of littoral forest along some of the coasts and areas of mangrove on the north side. Vava'u is also relatively flat and low, and its native vegetation is now restricted mostly to the cliff areas on the northern coast. 'Eua, however, is somewhat less disturbed, primarily because the eastern portion is higher and more rugged and population pressure is less. The volcanic islands are even less disturbed by human activity, particularly the uninhabited ones, but they are small in area and their vegetation (and flora) is more similar to that of Samoa than it is to the rest of Tonga.

Samoa, with a larger area and higher elevation, is somewhat less disturbed, although probably over half of its native vegetation has been severely altered by human activity and natural catastrophies. Much of this has hap-

pened in the last few decades, as an increasing population, an unregulated forestry industry, and two destructive hurricanes have taken their toll. The best remaining areas of undisturbed vegetation in Samoa are in the highlands of Savai'i. However, the vegetation of Western Samoa has not been evaluated since the devastating hurricane of February 1990.

To make some kind of sense out of the patterns of plant distribution, the vegetation is divided here into 22 communities, as shown in Table 2. These 22 are classed into six broader categories: littoral vegetation, wetland vegetation, rainforest vegetation, upland scrub vegetation, volcanic vegetation, and disturbed vegetation.

TABLE 2

VEGETATION TYPES IN SAMOA AND TONGA

	SAMOA	TONGA
Littoral vegetation		
1. Herbaceous strand	+	+
2. Littoral shrubland	+	+
a. *Makatea*	−	+
3. Pandanus scrub	+	+
4. Littoral forest	+	+
a. Mixed species	+	+
b. *Barringtonia*	+	−
c. *Calophyllum*	+	−
d. *Pisonia*	+	+
e. *Hernandia*	+	−
f. *Terminalia*	+	+
g. *Excoecaria*	−	+
Wetland vegetation		
5. Coastal marsh	+	+
6. Montane marsh	+	−
7. Montane bog	+	−
8. Mangrove scrub	+	+
9. Mangrove forest	+	+
10. Swamp forest	+	−
a. Coastal	+	−
b. *Pandanus*	+	−
c. Mixed species	+	−
Rainforest vegetation		
11. Coastal forest	+	+
12. Lowland forest	+	+
a. *Dysoxylum*	+	−
b. *Pometia*	+	−
c. *Syzygium*	+	−
d. *Planchonella*	+	−
e. *Calophyllum*	−	+
f. *Myristica*	−	+
g. *Maniltoa*	−	+
13. Montane forest	+	+
14. Cloud forest	+	−*
Upland scrub vegetation		
15. Summit scrub	+	+
16. Montane scrub	+	−
Volcanic vegetation		
17. Lowland volcanic scrub	+	+
18. Upland volcanic scrub	+	−
Disturbed vegetation		
19. Managed land	+	+
20. Secondary scrub	+	+
21. Secondary forest	+	+
22. Fernland	+	+

*This may occur on the summit of Kao, but little has been published about the vegetation on this island.

Littoral Vegetation

The littoral vegetation category comprises four communities: herbaceous strand, littoral shrubland, *Pandanus* scrub, and littoral forest. Several factors tend to blur the distinctiveness of these communities: (1) the communities are usually narrow zones of vegetation; (2) one or more are frequently missing from coasts; and (3) boundaries between the communities are sometimes indistinct. For this reason, they are sometimes lumped into one strand community. Here, however, they will be treated as four discrete entities.

1. HERBACEOUS STRAND COMMUNITY. This is the low, herbaceous vegetation growing on the shore, typically between the high-tide mark and the other types of littoral vegetation, especially littoral shrubland. Virtually all of the species present are heliophytes, and they are rarely found inland in the shade of the forest. Two subtypes are sometimes recognized on the basis of the substrate of the vegetation—sand or rock.

On sandy beaches, the herbaceous vegetation, sometimes referred to as "sand strand" (Whistler 1980), is dominated by vines such as *Ipomoea pes-caprae*, *Vigna marina*, *Canavalia rosea*, and *Canavalia sericea*. The first two are common in both archipelagoes, but *Canavalia sericea*, which is common in Tonga, is reported from only one small locality in Samoa ('Olosega Island, American Samoa), and *Canavalia rosea*, which is common in Samoa, is uncommon in the southern Tongan Islands.

Where the littoral vines are less abundant, grasses and sedges may dominate. The most

common grass species are *Thuarea involuta*, *Lepurus repens*, *Stenotaphrum micranthum*, and *Sporobolus virginicus*, and the most common sedge is *Cyperus stoloniferus*. All of these, except *Sporobolus*, which is absent from Samoa, are found in both archipelagoes. Herbs or low shrubs, such as *Triumfetta procumbens* and *Chamaesyce atoto*, sometimes also occur here.

On rocky beaches, the vegetation, sometimes referred to as "rock strand" (Whistler 1980), is dominated by the sedge *Fimbristylis cymosa* and the grass *Lepturus repens*, which are common in both archipelagoes. The same vines that occur in sandy habitats, particularly *Ipomoea pes-caprae*, are found here, but they are less common than grasses and sedges, which are better able to survive in the rock cracks. Other species common on rocky substrates of both archipelagoes include *Acrostichum aureum* (a fern) and *Hedyotis foetida*. Intermediate between these two types are coral-rubble beaches, which, if vegetated, tend to be dominated by vines.

2. LITTORAL SHRUBLAND COMMUNITY. This is the shrubby vegetation occurring on rocky or sandy seashores; it is typically dominated by the shrubs *Wollastonia biflora* and/or *Scaevola taccada* in both Tonga and Samoa and was described in some detail by Whistler (1980). It usually occupies a zone between the herbaceous strand and littoral forest or *Pandanus* scrub, but is sometimes absent or its boundaries with the other littoral communities are indistinct. Other species typical of this community include *Ficus scabra*, *Clerodendrum inerme*, *Premna serratifolia*, and *Colubrina asiatica*, which are common to both archipelagoes.

A subtype of littoral shrubland grows on coastal coralline *makatea* rock (the same name as the Tuamotuan island of Makatea that is composed of it) that is often highly eroded into a jagged surface. This type of rock is absent from Samoa, but is common in Tonga, where the vegetation is dominated by *Pemphis acidula*, a low-growing shrub (Figure 2). *Pemphis* is rare in Samoa, where it has been reported only from the southeastern corner of Savai'i. Another characteristic species of the Tongan *makatea* is a small shrub, *Bikkia tetrandra*, which is absent from Samoa.

3. *Pandanus* SCRUB COMMUNITY. This is the vegetation dominated by the screwpine *Pan-*

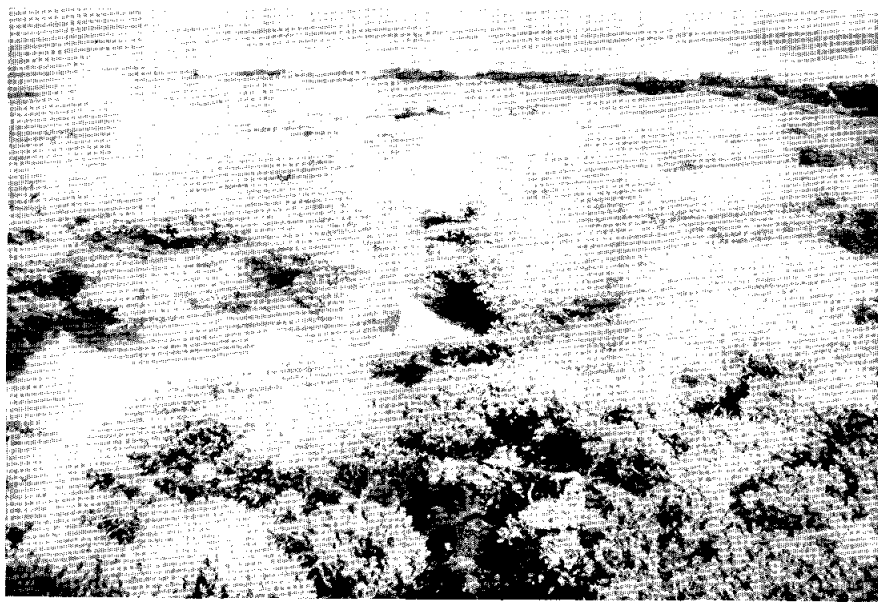

FIGURE 2. *Makatea* vegetation on 'Eua dominated by *Pemphis acidula*.

FIGURE 3. *Pandanus* scrub on the southern Savai'i coast.

danus tectorius that forms thickets in patches or in a narrow zone on the seaward side of the littoral forest. It is particularly characteristic of the east coast of Ta'ū and portions of the southern, cliff-bound coasts of 'Upolu and Savai'i (Figure 3), but is less common in Tonga, although *Pandanus* is frequent there as a subcanopy tree in littoral forest. In some places, it may form monodominant scrub forests that exclude nearly all other species (Whistler 1980); examples of this occur on the eastern side of 'Aunu'u (American Samoa) and along the southeastern tip of Ta'ū.

4. LITTORAL FOREST COMMUNITY. This is the forest occurring in a narrow zone on rocky or sandy shores, between the lowland or coastal forest on its inland side and other types of littoral vegetation on its seaward side. Sometimes, however, the other littoral communities may be absent, particularly where the forest is growing on a coral-rubble beach. This is the most extensive of the littoral communities and was described in some detail in Samoa by Whistler (1980, 1983*a*).

Littoral forest trees are typically dispersed by bouyant, saltwater-resistant seeds or fruits (with *Pisonia grandis*, which has sticky fruits that adhere to bird feathers, being a major exception). The trees are resistant to the brackish groundwater and salty sea winds, which are major factors that exclude inland trees from coastal areas. Most littoral trees rarely occur very far inland, possibly because of their limited dispersal mechanisms and because of competition from lowland and coastal forest trees. The forest floor often has only a sparse ground cover, since littoral shrubs and herbs are usually heliophytes and cannot survive in the shade of the forest.

Littoral forests are often dominated by a single tree species such as *Barringtonia asiatica*, *Calophyllum inophyllum*, *Hernandia nymphaeifolia*, *Terminalia catappa*, or *Pisonia grandis*. All of these trees are present in both archipelagoes, but *Barringtonia* and *Calophyllum*, which form distinct, monodominant forests in Samoa, have not been reported to do so in Tonga. Another species, *Excoecaria agallocha*, often forms monodominant forests on the limestone coasts of Tonga (Figure 4), but the tree is absent from Samoa. Other littoral trees that occur in the forests of both archipelagoes include *Guettar-*

FIGURE 4. *Excoecaria* littoral forest, 'Eua.

da speciosa, *Neisosperma oppositifolium*, *Tournefortia argentea*, *Cocos nucifera*, *Cordia subcordata*, *Thespesia populnea*, *Acacia simplex* (restricted in Samoa mostly to the western end of Savai'i), and *Cerbera* spp. (*C. manghas* in Samoa, *C. odollam* in Tonga). Another tree, *Casuarina equisetifolia*, which is believed to be a Polynesian introduction, is naturalized in Tonga (Sykes 1981) but not Samoa.

Wetland Vegetation

The second vegetation category comprises six wetland communities distinguished from each other by floristic, physiognomic, and geographical differences. The first three of these communities, coastal marsh, montane marsh, and montane bog, are dominated by herbaceous species; the last three, mangrove scrub, mangrove forest, and swamp forest, are dominated by woody species. The herbaceous wetland communities are much better developed in Samoa than they are in Tonga, and only the first one, coastal marsh, is found in the latter archipelago.

5. COASTAL MARSH COMMUNITY. This is the herbaceous wetland vegetation occurring in coastal areas; in Samoa, most coastal marshes are in low-lying coastal basins that are separated from the sea by a sand barrier and lack a stream outlet. A major exception to this is the marsh inside the tuff-cone crater of 'Aunu'u (Whistler 1980) in American Samoa. In Tonga, the best coastal marsh, Ngofe marsh on Vava'u (Figure 5), is some distance inland. The absence of a stream connection to the sea may prevent mangrove species from invading coastal marshes, which otherwise appear well suited to mangrove scrub or mangrove forest. Coastal marshes are much better represented in Samoa than in Tonga.

The characteristic coastal marsh species are *Eleocharis dulcis* (a leafless sedge) and *Cyclosorus interruptus* (a fern), which together may form almost pure stands in Samoa; *Cyclosorus*, however, is not reported from Tonga (where *Eleocharis* may dominate by itself). Another species sometimes common in coastal marshes is *Acrostichum aureum*, a large, clump-forming fern. In the marsh inside 'Aunu'u Crater, *Acrostichum* surrounded the center pond and covered the lower (eastern) portion of the marsh; the rest was a mixture of *Eleocharis* and *Cyclosorus*. However, this vegetation was devastated by the 1990 hurricane. Two other species, *Polygonum* cf. *glabrum* and *Lepironia articulata* (a sedge), are found in Tongan marshes, but are absent from Samoa.

When coastal marshes are disturbed, as they are for growing taro, weedy species, such as *Ludwigia octovalvis*, *Paspalum conjugatum*, and *Rhynchospora corymbosa*, dominate. A native, prostrate herb, *Limnophila fragrans*, is sometimes found in disturbed coastal marshes in Samoa but is now rare.

Another type of coastal marsh occurs in both Samoa and Tonga in flat, coastal areas and estuary margins. It is typically dominated by a grass, *Paspalum vaginatum*, which apparently was a very early, unintentional, European introduction to Polynesia. Good examples

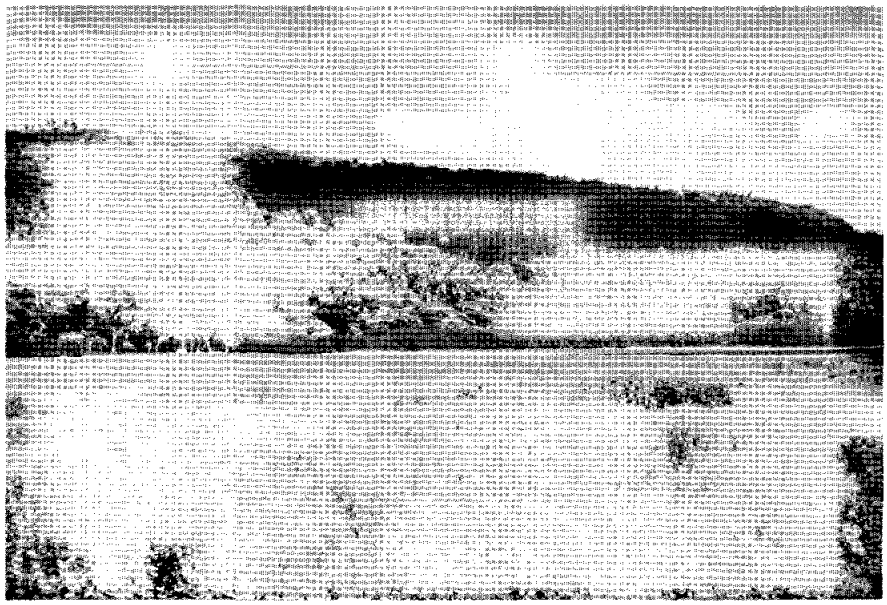

FIGURE 5. Ngofe coastal marsh, Vava'u.

of this are found around Nuku'alofa on Tongatapu and Apia on 'Upolu.

6. MONTANE MARSH COMMUNITY. The separation of coastal marsh and montane marsh is somewhat artificial, since both may be dominated by the same species, *Eleocharis dulcis*. However, the other two species typical of coastal marshes, *Cyclosorus* and *Acrostichum*, are rare or absent in montane marshes. Also, there is a different type of vegetation dynamics occurring in the montane marshes. Many of them occur only as a fringe around crater lakes (Figure 6) at 500–1000 m elevation, as noted by Ollier et al. (1979).

Montane marshes are found in Samoa, particularly on 'Upolu, but because of insufficient elevation and unsuitable topography, they are absent from Tonga. In some craters on 'Upolu, the ground is less waterlogged, and the dominant species are *Rhynchospora corymbosa* (as in the crater on the eastern flank of Mt. Fiamoe), *Paspalum orbiculare*, or *Erianthus maximus* (as in Mt. Sina'ele); the latter species is otherwise rare in Samoa. It is not known how these three types of vegetation, *Pandanus* swamp forest, montane marsh, and the variation on less waterlogged soil that may be called montane meadow, are related to each other successionally, and this is a subject in need of further study.

7. MONTANE BOG COMMUNITY. The last of the three herbaceous wetland communities, montane bog, comprises the herbaceous wetland vegetation dominated by the genus *Carex* in the uplands of Savai'i. This community was first noted by Whistler (1978), who called it montane meadow, but the name montane bog seems more appropriate. It is known to occur only in the poorly explored uplands in the vicinity of Mt. Silisili at over 1500 m elevation.

The major difference between these bogs and the lowland and montane marshes is their species composition; montane bogs are dominated by two indigenous sedges, *Carex graeffeana* and *Carex maculata*. The former species occurs in the uplands of Savai'i, reportedly only from above 1300 m; the latter is found on both 'Upolu (from a single, century-old record) and Savai'i, reportedly above 1500 m (but at ca. 700 m on 'Upolu). This vegetation appears to be very similar to the "*Carex* sedgeland" reported from Hawai'i (Wagner et al. 1990).

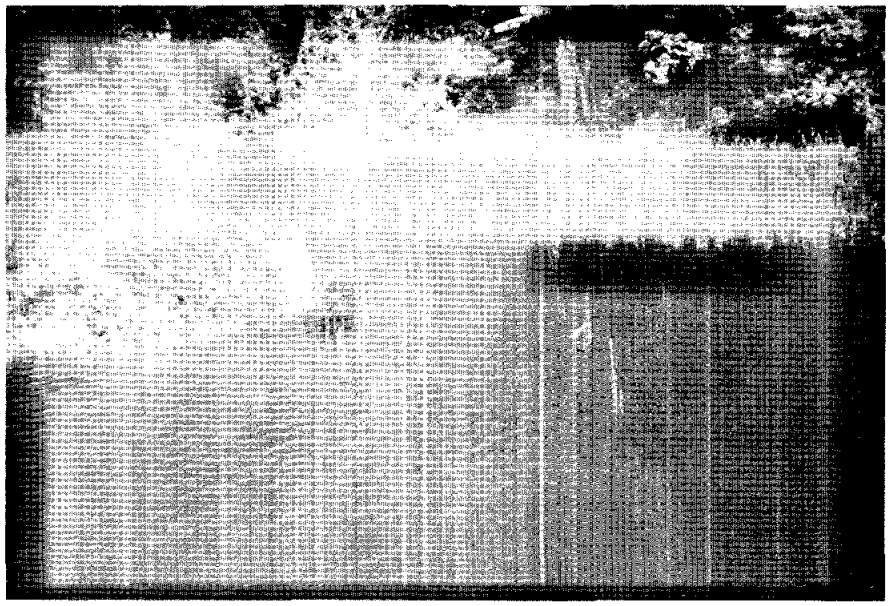

FIGURE 6. Montane marsh growing around a montane lake, Lepu'e, 'Upolu.

8. MANGROVE SCRUB COMMUNITY. Mangrove scrub is found in coastal areas such as estuaries or on protected reef flats, and along the margins of mangrove forest. It is a monodominant community where the small to medium-sized tree *Rhizophora mangle* (also known as *R. samoensis*) forms open or closed thickets. Where it competes with the larger mangrove species, *Bruguiera gymnorrhiza*, it is eventually shaded out and disappears. The only other species commonly found in mangrove scrub are *Rhizophora stylosa* and *Lumnitzera littorea*, but neither of these occurs in Samoa. Large areas of mangrove scrub occur around the northern end of Tongatapu in Tonga, the southern side of Vava'u, the south-central part of Tutuila (Whistler 1976), and in the Apia area of 'Upolu.

9. MANGROVE FOREST COMMUNITY. Mangrove forest is another community dominated by a single species, *Bruguiera gymnorrhiza*, and was described in some detail by Whistler (1976, 1980) in American Samoa. These forests (or at least the species) are found in Tonga, but are larger and better defined in Samoa. They occur on reef-protected coasts, along bays and estuaries, and in inland coastal basins with a freshwater outlet to the ocean. They are usually inundated by saline or brackish water at high tide, and the forest floor is covered with knobby breathing roots that enable the trees to obtain oxygen in the muddy, anaerobic soil. The only plants that can survive on the forest floor under a closed canopy are seedlings of *Bruguiera*, but under openings in the canopy, the swamp fern *Acrostichum aureum* or *Rhizophora mangle* may form thickets.

Two other species sometimes occur in this community, *Xylocarpus moluccensis* and *X. granatum* (which is absent from Samoa). *Xylocarpus moluccensis* is becoming rare in Samoa and in Western Samoa is mostly restricted to a single, interesting forest (which it dominates) on the isolated southern Savai'i coast southeast of Sala'ilua. Both species are fairly common in Tonga.

10. SWAMP FOREST COMMUNITY. Swamp forest is the woody vegetation occupying areas with soil saturated with fresh water, typically in inland or even montane areas. This type of forest has not been reported from

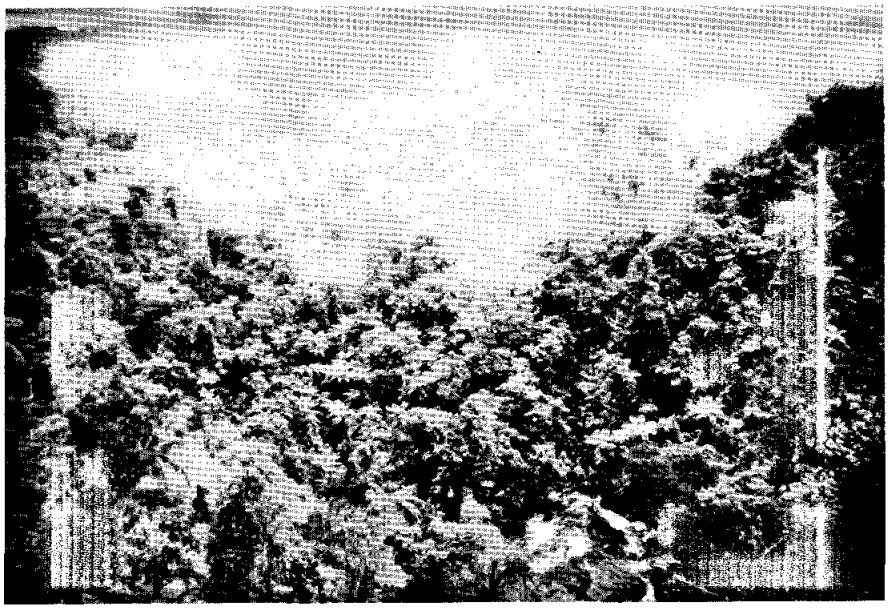

FIGURE 7. Afulilo swamp forest, 'Upolu.

Tonga, but occurs in inland basins and craters with poor drainage on 'Upolu and Savai'i (Wright 1963). Two types may be distinguished, one dominated by *Pandanus turritus*, an endemic screwpine, the other by a mixture of tree species. In one crater in eastern 'Upolu (Fogalepolo), the outer margin of the swamp was an almost pure stand of *Barringtonia samoensis*, and the center portion was dominated by *Pandanus* (Pearsall and Whistler 1991). Sedges and other herbaceous species are also abundant in swamp forests. In eastern 'Upolu, there are several large areas of swamp forest composed of a mixture of species (Figure 7), but these areas have not been studied and the best one was destroyed for a hydroelectric dam currently under construction.

Swamp forests also occur in coastal areas of Samoa. One type is dominated by *Inocarpus fagifer* and is reported from the southern coast of 'Upolu. Another is dominated by *Erythrina fusca* and is reported from the western end of 'Upolu. The latter tree apparently does not actually form forests; individual trees are scattered inside or along the margins of coastal marshes, and thus it is debatable whether this qualifies as a forest at all.

Rainforest Vegetation

The third category of vegetation includes four rainforest communities, but one of them, lowland forest, is divided here into several subtypes. Rainforest originally covered nearly the entire surface of both Samoa and Tonga (a notable exception being areas of recent volcanic activity). It is typically a tall forest with a canopy up to 30 m in height in some places and has a great diversity of species, including epiphytes, terrestrial herbs, and lianas. In Samoa, for example, nearly 100 native orchid species and ca. 215 species of ferns have been recorded, and most of these occur in the rainforest. The woody plants can be divided into canopy trees, subcanopy trees, understory trees, and shrubs, but distinct layers are not usually recognizable.

The four types of rainforest recognized here, coastal forest, lowland forest, montane forest, and cloud forest, are distinguished most readily by differences in species composition. These differences are related to prox-

FIGURE 8. Windswept coastal forest on 'Eua.

imity to the coast and to elevation, which in turn affect temperature and rainfall, the major determinants, along with edaphic factors, of species distributions.

11. COASTAL FOREST COMMUNITY. The name coastal forest may be a little misleading since littoral forest is sometimes labeled this way. However, the coastal forest community recognized here is the medium-stature forest occurring inland from littoral forest rather than directly on the seashore, typically on steep slopes or on tuff-cone craters. It is best developed on offshore islands such as the Aleipata Islands (Whistler 1983*a*) off the eastern end of 'Upolu, Apolima Island situated in the strait between Savai'i and 'Upolu, Nu'utele Islet off 'Ofu in American Samoa (Whistler 1980), and Niuatoputapu Island in Tonga.

The dominant and characteristic trees of coastal forest are *Syzygium clusiifolium*, *Syzygium dealatum*, *Diospyros elliptica*, and *Diospyros samoensis*. These and other coastal forest trees typically have colorful, bird-dispersed fruits, unlike trees characteristic of littoral forest. Coastal forest sometimes intergrades with littoral forest, and in some places large littoral forest trees, such as *Pisonia grandis*, may be mixed with the *Syzygium* and *Diospyros* trees.

A variation of coastal forest is found on the east-coast cliffs of 'Eua (Figure 8), where the vegetation is dominated by a number of wind-pruned woody species, including some of the four coastal forest trees listed above, but also with some species endemic to that island.

12. LOWLAND FOREST COMMUNITY. The lowland forest is the most extensive and most complex type of rainforest in the two archipelagoes, and because of edaphic factors, variation in climate (Tonga is less tropical than Samoa), and floristic differences, the dominant species in the subtypes recognized here differ in the two archipelagoes. Four subtypes of lowland forest are distinguished in Samoa, and three in Tonga (all from 'Eua).

The first subtype of lowland rainforest, *Dysoxylum* lowland forest, is dominated by *Dysoxylum samoense* and *Dysoxylum maota*, which in some places may together or singly attain over 80% relative dominance (Whistler 1980, 1983*a*). It occurs in alluvial valleys

(particularly on the northern coast of Tutuila), on steep lowland cliffs away from the immediate coast, and on narrow coastal lowlands covered with talus and coral-rubble deposits (as on the eastern coast of Ta'ū). The two *Dysoxylum* species are also common in other types of lowland forest and even in disturbed forest, but they rarely achieve dominance there. *Dysoxylum* lowland forest apparently does not occur in Tonga, where the two characteristic species are absent (except on the three northern Tongan islands, where *D. maota* occurs).

The second subtype, *Pometia* lowland forest, is dominated by a single species, *Pometia pinnata*, which is the most important timber tree in Samoa (Ollier et al. 1979). It once occupied large areas of the lowlands of Savai'i and to a lesser extent 'Upolu and Tutuila, principally on areas of rocky soil below about 450 m elevation. This is perhaps the tallest of the rainforests, since *Pometia* is one of the most massive trees in Samoa. Several areas of this forest still occur along the southern coasts of Savai'i and 'Upolu, but these were badly damaged by the hurricane of 1990. Although *Pometia* is also found in Tonga, it is apparently a Polynesian ancient introduction there and grows only in villages and plantations, where it is cultivated for its edible, litchi-like fruit.

The third subtype, *Syzygium* lowland forest, is also restricted to Samoa. It is typically dominated by *Syzygium inophylloides* (a species rare in Tonga), but associated with it are a number of other canopy species, such as *Calophyllum neo-ebudicum*, *Canarium vitiense*, *Myristica hypargyraea*, and *Planchonella garberi*, which may in places attain dominance (Olsen 1978). This forest is typically found on the highly weathered volcanic substrate derived from the ancient Fagaloa Volcanics (Wright 1963) on lowland ridges and steep interior slopes where perhaps the soil is drier than on the flatlands. Olsen (1978) recognized a separate forest type dominated by *Calophyllum neo-ebudicum*, but this type seems to be insufficiently distinct in Samoa to separate it from *Syzygium* lowland forest.

The fourth subtype, *Planchonella* lowland forest, is typically dominated by *Planchonella torricellensis* and once covered much of the lowlands of 'Upolu and, to a lesser extent, Savai'i, on areas of moderately weathered volcanic substrate (Olsen 1978). Other common canopy and subcanopy species in this community are *Dysoxylum samoense*, *Dysoxylum maota*, *Canarium vitiense*, *Calophyllum neo-ebudicum*, *Terminalia richii*, and *Myristica fatua*. Like the three subtypes noted above, this vegetation does not occur in Tonga; the dominant species, *Planchonella torricellensis*, in fact, only occurs in the northern islands there.

The following three subtypes of lowland forest are found in Tonga but not in Samoa. The best remaining lowland forests in Tonga are on 'Eua, where all three subtypes were first noted. The first of these, *Calophyllum* lowland forest, is dominated by *Calophyllum neo-ebudicum*, with *Garcinia myrtifolia* being the most common subcanopy tree. Drake et al. (1990) noted this as two communities, "*Calophyllum* mixed forest" and "*Calophyllum–Garcinia* forest," and Straatmans (1964) referred to something similar on 'Eua as "*Calophyllum–Elattostachys* association." This tall-stature forest occurs on limestone or on weathered volcanic soil that is generally poor in nutrients, and comprises most of the remaining native forest on the upper terraces of the island. In samples made in this forest on 'Eua, *Calophyllum* was determined to be common in all dbh (diameter at breast height) size classes (unpublished data), which indicates that the forest is a climax community. In overall species composition, this forest is somewhat similar to the *Syzygium* lowland forest noted above as occurring in Samoa, but the underlying substrates (volcanic versus limestone) and the associated species differentiate the two.

The second subtype found in Tonga, *Myristica* forest, is completely dominated by *Myristica hypargyraea* (Figure 9). Population analyses of this forest indicate that the tree is common in all dbh size classes (unpublished data), and the forest is a climax community on the lower terraces all around the island, except in the northwest quarter. It was not recognized by Straatmans (1964), but was

FIGURE 9. *Myristica* lowland forest, 'Eua.

described by Drake et al. (1990) as "*Myristica* coastal forest." The same species occurs in Samoa, but there it rarely achieves dominance and is a subcanopy species of inland ridges, particularly in *Syzygium* lowland forest.

The third subtype is *Maniltoa* lowland forest, which covers the lower terraces on the northwest quarter of 'Eua. The dominant species is *Maniltoa grandiflora*, associated with *Pleiogynium timoriense*, *Vavaea amicorum*, and *Xylosma simulans* (all of which are absent from Samoa), and lesser amounts of *Sapindus vitiensis*, *Chionanthus vitiense*, *Diospyros samoensis*, and *Aleurites moluccana*. It was first recognized by Drake et al. (1990), who called it "*Maniltoa–Pleiogynium* coastal forest."

13. MONTANE FOREST COMMUNITY. This is the rainforest that occurs at high elevations (above 550 m or so) and is typically dominated by *Dysoxylum huntii* (Ollier et al. 1979). The other two species of *Dysoxylum*, *D. maota* and *D. samoense*, which are so common in lowland forests, disappear at about this elevation. A number of other tree species occur in this forest, such as *Syzygium samoense*, *Syzygium* spp., *Weinmannia* spp., *Fagraea berteroana*, *Bischofia javanica*, *Hernandia moerenhoutiana*, *Trichospermum richii*, *Spiraeanthemum samoense*, *Astronidium* spp., and *Reynoldsia* spp., but none approaches the dominance of *Dysoxylum*.

The montane forest is very wet and somewhat cooler than the lowland forest. As elevation increases along gentle slopes, there is a gradual transition from *Planchonella* lowland forest to montane forest, and the boundaries between the two are difficult to draw. On ridges, montane forest replaces *Syzygium* lowland forest at higher elevations.

A small patch of this forest (but without the characteristic *Dysoxylum huntii*, which is endemic to Samoa) occurs on the summit of Tafahi Island in Tonga (Figure 10), but this is shrinking in size because of forest clearing for cultivation of kava. The rest of Tonga is at too low an elevation for montane forest, or is covered by a recent volcanic substrate.

14. CLOUD FOREST COMMUNITY. This is the medium-stature forest that occurs at the highest elevations of Savai'i (above ca. 1200 m) and is characterized by dominance of *Reynoldsia pleiosperma*, an endemic tree that starts life as a strangler. One of the most noticable characteristics of cloud forest is the thick accumulation of mosses and other epiphytes on the tree trunks. Droughts are virtually unknown. During much of the daytime the forest is enveloped in clouds, and everything is dripping wet. Other common tree species include *Spiraeanthemum samoense*, *Dysoxylum huntii*, *Coprosma* spp., *Pittosporum samoense*, *Ascarina diffusa*, *Streblus anthropophagorum*, *Omalanthus acuminatus*, *Claoxylon echinospermum*, *Xylosma samoense*, *Cyrtandra* spp., *Psychotria* spp., *Ficus godeffroyi*, *Rapanea longipes*, and *Weinmannia* spp.

Because cloud forest occurs at high elevations far away from villages, there has been little opportunity for Samoans to utilize, or even visit it, and consequently, it is the best

FIGURE 10. Montane forest at the summit of Tafahi, Tonga.

preserved of all types of rainforest remaining in Samoa. It is also the least understood of the rainforest types, and only a small portion of it has been studied (Whistler 1978).

Upland Scrub Vegetation

This comprises two communities that are characterized by their scrubby stature and the dominance of ferns and lianas. They occur at elevations where rainforest would be expected, but because of climatic or edaphic factors a scrubby rather than a forest vegetation is present.

15. SUMMIT SCRUB COMMUNITY. This is the low, scrubby vegetation that covers a large part of the summit region of Ta'ū in American Samoa. With high rainfall and little disturbance from man, this area would be expected to support a montane forest. However, at least partly because of two recent hurricanes (1987 and 1990), the summit (at least its eastern side) is entirely covered by a scrub vegetation dominated by *Freycinetia storckii*, terrestrial ferns (especially *Dicksonia brackenridgei* and *Blechnum vulcanicum*), tree ferns (*Cyathea* spp.), and shrubs (especially *Cyrtandra* spp.).

Dicranopteris linearis (false staghorn fern) is absent from summit scrub (and from the island), which floristically distinguishes summit scrub from the montane scrub described below. *Clidemia hirta* (Koster's curse), an aggressive weed that was not reported from the island during a study of the area in 1976 (Whistler 1980), is also common. The trees present are scattered and are greatly outnumbered by dead snags (Figure 11). Perhaps the small size of the island contributes to hurricane damage, because at similar elevations on much-larger Savai'i and 'Upolu a high-canopy montane forest prevails (at least it did before the 1990 hurricane).

A similar type of vegetation that is perhaps best included in this community is the scrubby vegetation occurring on the eastern side of the summit of Tafahi Island in northern Tonga, where a steep slope (Figure 12) is dominated by shrubs, ferns, and grasses. This scrubby vegetation is similar to summit scrub in that its origin appears to be related to climatic rather than edaphic factors. It is also similar to the montane scrub because of the presence of *Dicranopteris linearis*. The dominant species are shrubs such as *Geniostoma rupestre*, *Maoutia australis*, and *Cyrtandra samoensis*, ferns such as *Dicranopteris*, and grasses such as *Paspalum orbiculare* and *Imperata conferta*.

16. MONTANE SCRUB COMMUNITY. This is the scrubby vegetation that occurs on Tutuila on the summits of "trachyte plugs," old volcanic cores that have a highly weathered soil (Whistler 1980). The trees are scattered amidst a tangle of ferns, shrubs, and climbers. The characteristic tree species are *Pandanus reineckei* (an endemic screwpine), *Rapanea myricifolia*, *Spiraeanthemum samoense*, *Metrosideros collina*, *Astronidium* sp., *Alstonia pacifica*, and *Syzygium brevifolium*, but climb-

FIGURE 11. Summit scrub on Lata Mountain, Ta'ū, at 900 m.

FIGURE 12. Summit scrub on Tafahi Island at 500 m.

ers such as *Freycinetia* spp. and ferns such as *Dicranopteris linearis*, *Dipteris conjugata* (which in Samoa is known only from this community on Tutuila), *Davallia epiphylla*, and *Nephrolepis biserrata* are also common.

Montane scrub is most similar to the fernland vegetation described below, particularly because of the presence of *Dicranopteris linearis*; however, fernlands are anthropogenic rather than natural in origin (Wright 1963). A vegetation similar to montane scrub apparently occurs on the summit of Ra'iatea in the Society Islands.

Volcanic Vegetation

The fourth category of Samoan and Tongan vegetation, volcanic scrub, comprises two types of vegetation: lowland volcanic scrub and upland volcanic scrub. Recognizing two volcanic vegetation types points out a major difficulty in the delimitation of plant communities. In Samoa, the 1902–1911 Savai'i flows do not present a problem, because the earlier ones are all above 1150 m and are distinctly different from the lower flows that are all below 700 m. But the 1760 flow starts at 1580 m and extends down to the coast. At low elevations, this continuous flow is dominated by one combination of species, but at the summit the species are undoubtedly different. However, even though it may be very difficult to draw a boundary between the two communities, it is useful to maintain the two because of the floristic differences.

17. LOWLAND VOLCANIC SCRUB COMMUNITY. Lowland volcanic scrub occurs on Savai'i and on several of the small, volcanically active islands in Tonga. It is present in two places on Savai'i, one from the site of a 1905–1911 series of eruptions that reached the coast between Sale'aula and Samalae'ulu on the northeastern coast, and the other from the site of a series of flows (ca. 1760) that reached the coast below A'opo on the northwestern coast. At the lower elevations, the open vegetation is restricted mostly to cracks in the pahoehoe lava and to kipukas, the small islands of vegetation that lava flows failed to cover. The dominant trees are *Fagraea berteroana*, *Glochidion ramiflorum*, and *Morinda citrifolia*. Two native ferns are also common, *Davallia solida* and *Nephrolepis hirsutula*. The 1760 A'opo flow is dominated by *Fagraea berteroana*, *Arytera brackenridgei*, and *Glochidion ramiflorum* at 200 m elevation (unpublished data), although Uhe (1974*b*) did not record *Arytera* as being present. If undisturbed long enough, this scrub will probably develop into *Pometia* lowland forest, which is common over much of Savai'i.

At the top of the 1905–1911 flow at Matavanu (700 m elevation), the dominant trees are *Metrosideros collina*, *Weinmannia samoensis*, *Fagraea berteroana*, and *Glochidion ramiflorum*. The latter two are dominants at lower elevations, but the *Metrosideros* and *Weinmannia* are found only at higher elevations in Samoa (unpublished data).

Lowland volcanic scrub on Niuafo'ou island in Tonga is dominated by many of the same species occurring in the Samoan lowland volcanic scrub. Uhe (1974*a*) recorded the most common species on a 1929 flow as *Morinda citrifolia*, *Glochidion ramiflorum*, *Pipturus argenteus*, and *Macaranga harveyana*, and the most common herbaceous species as *Nephrolepis hirsutula*, *Phymatosorus scolopendria*, *Davallia solida*, *Psilotum nudum*, and *Hoya australis*. However, on the high volcanic island of Late, *Casuarina equisetifolia* dominates from the shore up to near the summit of the island (Sykes 1981).

18. UPLAND VOLCANIC SCRUB COMMUNITY. Upland volcanic scrub is apparently found only on Savai'i (although one Tongan volcanic island, Kao, may have sufficient elevation for such a vegetation to develop). At 1500 m on a 1902 flow, the dominant species were *Vaccinium whitmeei*, *Spiraeanthemum samoense*, and *Coprosma strigulosa*, all of which are endemic to Samoa and restricted to high elevations (Whistler 1978). This volcanic area is not uniform, however; in one place, at least, there is an "ash plain" virtually devoid of shrubs and dominated by the grass *Imperata conferta* and lichens, and some of the adjacent cinder cones are devoid of vegetation other than lichens.

Disturbed Vegetation

The last category of vegetation comprises managed land, secondary scrub, secondary forest, and fernland. Because these are not usually natural (i.e, most are anthropogenic), or at least are not climax vegetation types, they are discussed only briefly here.

19. MANAGED LAND COMMUNITY. Managed land comprises roads, villages, airports, and plantations that are actively prevented from returning to natural vegetation. It is dominated by weedy species, of which nearly 275 have been recorded from the two archipelagoes (Whistler 1988).

20. SECONDARY SCRUB COMMUNITY. This is the scrubby vegetation that occurs on recently abandoned land. The first invaders are the herbaceous weeds, but if the land is left undisturbed for long enough, characteristic shrubs and small tree species soon take over. The plants that dominate here typically are fast growing and have effective modes of long-distance seed dispersal. Most of them are heliophytes that disappear in later successional stages— when secondary scrub is replaced by secondary forest and the forest floor becomes shaded.

The most characteristic trees are *Pipturus argenteus*, *Macaranga harveyana*, *Omalanthus nutans*, *Trema cannabina*, and *Hibiscus tiliaceus*. In the montane region of Savai'i and of 'Upolu, recently cleared areas are sometimes dominated by *Musa* × *paradisiaca* var. *seminifera*, a seeded banana that apparently is native to Samoa.

21. SECONDARY FOREST COMMUNITY. Secondary forest is the high forest dominated by shade-intolerant trees that typically become established in sunny conditions in disturbed areas. Its trees grow taller than those of secondary scrub and produce a shade that eventually eliminates the smaller species. Secondary forest covers large areas of both Tonga and Samoa, and in structure may appear very similar to primary rainforest.

Several species dominate secondary forest in both Tonga and Samoa, principally *Rhus taitensis*, *Alphitonia zizyphoides*, and *Elattostachys falcata* (Straatmans 1964, Whistler 1980). Although these trees may dominate, a look at dbh sizes shows that they (especially *Rhus*) are rare in the smaller size classes where other canopy trees are common, indicating that after a certain period of time, the secondary forest species will eventually disappear until the next disturbance.

On Tongatapu, there are two remaining small patches of high forest near the airport. A cursory study of them in 1990 indicated that the dominant species are, in order of relative dominance, *Elattostachys* (estimated 45%), *Rhus*, and *Alphitonia* (unpublished data); these forests were briefly described by Hotta in 1962 in an unpublished study of Tongan plants. This same species combination dominates secondary forest on 'Eua; Straatmans (1964) noted an *Alphitonia–Rhus* association with *Elattostachys* as a "minor component."

Other common mature secondary forest species include *Hibiscus tiliaceus*, *Bischofia javanica*, *Adenanthera pavonina*, *Cananga odorata*, *Kleinhovia hospita*, *Macaranga stipulosa* (a Samoan endemic), *Neonauclea forsteri*, *Dysoxylum* spp., and *Dendrocnide harveyi*. The latter species, a stinging-nettle tree, is dominant in some disturbed forests on 'Eua, but such dominance is not reported in Samoa.

Another tree that should be mentioned is *Funtumia elastica*, an African rubber tree that was introduced to Samoa. It has "parachute seeds" that spread long distances and germinate in sunny or shady conditions (Figure 13). It has become a dominant subcanopy and understory tree in the western half of 'Upolu and has been reported to form monodominant forests there (Pearsall and Whistler 1991).

22. FERNLAND COMMUNITY. The last disturbed vegetation community recognized here is called fernland. This is a subclimax community dominated by herbaceous species, typically ferns. In Samoan fernlands, which go by the local name *kula*, the ferns occur only on weathered volcanic ridges in two localities on 'Upolu and in a few tiny patches on Tutuila (Whistler 1980) and are dominated by

FIGURE 13. Seedlings of *Funtumia elastica* on 'Upolu.

Dicranopteris linearis, with smaller amounts of *Lycopodium cernuum* and *Miscanthus floridulus*, a reed.

This same combination of species is found on some fernlands located on 'Eua in Tonga (Figure 14), where they are locally called *toafa*. Other fernlands there, however, are dominated by different species, such as the fern *Sphaerostephanos unitus*. Fernlands are apparently maintained by capricious rather than purposeful burning, since the fernlands are not used for anything. On 'Eua, however, some of these are now being planted with Caribbean pine.

The Effects of Recent Hurricanes

The Samoan plant communities have been drastically altered since a destructive hurricane slammed into Savai'i and 'Upolu in February of 1990 and an earlier one (1987) devastated Ta'ū. The 1990 hurricane did extensive damage to native forests as well as to plantation forests (such as those planted in *Eucalyptus deglupta*), and very few forests on Savai'i and 'Upolu escaped devastation. Some of the worst effects were in three areas of

FIGURE 14. Fernland (*toafa*) on 'Eua.

FIGURE 15. Former *Pometia* lowland forest after a hurricane and fire, Tafua, Savai'i.

lowland forest at Falealupo, Tafua, and 'O le Pupū (Figure 15); coincidentally, all three of these forest areas are nature reserves (one established by the government, the other two by nongovernmental agencies). It will be a long time before the damage to the forest is healed, and it is uncertain what effect introduced, weedy trees like *Funtumia elastica* will have on the outcome. This is something that needs monitoring. Because of these hurricanes, particularly the one in 1990, the descriptions above of the communities in Western Samoa (that is, on the two largest islands, Savai'i and 'Upolu) are out of date and need revision in the future.

CONCLUSIONS

Although the soils of the two archipelagoes are quite different, they support similar vegetation types. Sixteen of the 22 communities recognized here are found in both Tonga and Samoa; Tonga, which is less diverse ecologically than Samoa, is lacking six of the 22. However, subtypes recognized (especially for lowland forest) differ somewhat floristically. Only 'Eua in Tonga and American Samoa in the Samoan archipelago have been studied so far, and much needs to be done on Western Samoa, the volcanic islands of Tonga, and Vava'u before the comparison between the two archipelagoes can be more comprehensive.

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