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SECONDARY PLANT COVER ON UPLAND SLOPES MARQUESAS ISLANDS, FRENCH POLYNESIA

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ABSTRACT

This monograph sheds light on the status of secondary plant cover, heretofore little known, on slopes between sea level and about 750m in the Marquesas Islands, a remote tropical Polynesian archipelago of high islands of volcanic origin situated in the dry tradewind zone of the South Pacific. Plant cover types are described and assigned to xerotropical, transitional and pluviotropical floristic zones determined in part by comparison with similar zones previously devised for Oahu Island, Hawaii.

In floristic detail, it describes the status of plant cover on the most readily visible lands, the slopes that rise above the valley bottoms and that are much disturbed by human activity, but not occupied with actual settlement and cultivation. Some ecological interpretations of recent disturbance history also appear.

Floristic and zonal vegetation comparisons with southeast Oahu cast the Marquesan field data into an instructive form that should be useful in the comparison of Marquesan plant cover with that of Hawaii and of other islands in the dry tradewind zones of the world.

SECONDARY PLANT COVER ON UPLAND SLOPES, MARQUESAS ISLANDS, FRENCH POLYNESIA[1]

BY

BRYCE GILMORE DECKER[2]

FOREWORD

The publication of this article has been delayed for nearly twenty years. Except for some changes in botanical nomenclature suggested by F. Raymond Fosberg of the Smithsonian Institution, the text has not been substantially revised to include changes in the Marquesas Islands that have occurred since then, nor reference to scientific work and botanical exploration in the Marquesas since the early 1970s. Much of the information in this monograph and more on the plant cover of houseyards and cultivated sites appears in my dissertation: *Plants, Man and Landscape in Marquesan Valleys, French Polynesia*; University of California, Berkeley (Geography), 1970.

THE MARQUESAS ISLANDS

The archipelago, comprising nine principal islands (Lat 7°50'S; Long 138°50'W), is politically part of French Polynesia (Polynésie française), which is an overseas *département* of France. The group lies about 1300 km NE of the entrepot for the country, Papeete, at Tahiti in the Society Islands.

Long accessible only by sea, a first aerial link with Tahiti and the outside world was established well after this study ended, with the completion of an airfield on Uahuka Island in 1970.

Total land area, about 1060 sq. km. (Adamson, 1936) approximates that of the single island of Tahiti (1040 sq.km.) and is about two-thirds the size of Oahu, the island on which Honolulu is located (1564 sq.km.). When the small area of these volcanic remnants is considered, their peaks rise to remarkable heights. Hivaoa, Nukuhiva and Uapou all exceed 1200m, an elevation comparable to the highest on Oahu. Most Marquesan topography is quite as ruggedly dissected and spectacular as Oahu's Waianae mountain

[1]Field research for this study in 1963-64 was supported by the Foreign Field Research Program conducted by the Division of Earth Sciences, National Academy of Sciences—National Research Council, and sponsored by the Geography Branch, [Office of Naval Research, Contract Nonr-2300 (09)].

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range, or the interiors of Tahiti and of other Pacific high islands with approximately similar geological histories.

The Marquesas share with Hawaii a dry tradewind landscape of arid lower slopes and moist high interiors that are always green with an important difference. Marquesan droughts sometimes last three to five years and may be very severe to both ecology and economy.

A mostly Polyesian population of about 5000 (4800 in 1962) supplements income from copra sales and public works with subsistence gardening, fishing and shooting of feral goats, cattle and sheep that freely roam the uplands above the deep valleys and canyons that contain all the villages and most of the cultivations.

FIELD WORK

During a broader study of plant cover as it reflects the influence of man (Decker, 1970), field work concentrated in and near two representative inhabited valleys; Puama'u Valley on NE Hivaoa Island, and Vaipaee Valley on Uahuka Island. Those islands are separated by 120km of open sea.

In the course of approximately nine months' residence, plant cover types were mapped in detail. Notes and voucher specimens documenting floristic composition were made in these and other localities on five islands. Some collections and data derive from a prior nine-months' residence as a private traveler in 1960. Sets of specimens have been deposited in herbaria in Hawaii (BISH), California (UC), Washington, D.C. (US), and Paris (P).[1]

PERTINENCE OF FRANK EGLER'S ECOLOGICAL WORK ON SOUTHEASTERN OAHU

Advantage has been taken of floristic and climatic similarities between the Marquesas and Hawaiian Islands to apply to the Marquesas a convenient scheme of vegetation description devised by Frank Egler for the island of Oahu, with some modification. Papy (1955) used Egler's approach in a comparable treatment of the vegetation of the Society Islands.

In the Marquesas, as in Hawaii, a secondary vegetation containing many species of wide tropical distribution, and introduced since the arrival of man, occupies most localities below 800-900 meters. An impressive number of such species is common to both archipelagos, particularly in the drier localities, as will be seen.

Climatically, both Hawaii and the Marquesas lie in regions of dry easterly tradewinds so that all low-lying land is subject to desiccation by prevailing winds that blow most of the time from the same quarter. The desiccation is most pronounced on slopes that lie in leeward rain shadows.

With elevation, the regional dryness is slaked by orographic showers that fall onto the heights and keep the mountains green.

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[1]Abbreviations indicate herbaria as listed in Index Herbariorum.

Briefly stated, the moist-dry transition, so visible in the landscape and ecologically fundamental, is employed as an important vegetation boundary. In 1947, Frank Egler elaborated a xerotropical floristic area and xerotropical vegetation zones for SE Oahu (see fig. 1). His approach accommodated three important aspects of the secondary plant cover of Oahu, aspects generally shared in common with Marquesan plant cover: 1) the abrupt, conspicuous transition from dry to moist environments; 2) a distinct ecological segregation of species into two floras—pluviotropical and xerotropical—corresponding to their adaptations to one or the other ecological area; and 3) the confusing mosaic of structural types resulting from complex and unrecorded disturbance history.

Within each zone dominant species lend the various cover types a characteristic texture and morphology. But on Oahu, the dominant species were viewed by Egler as clearly xerotropical or pluviotropical. He saw them growing on either side of a moisture boundary that he mapped as a simple line. Thus, his main geographical demarcation relied upon an ecological criterion, the moisture boundary between the two zones.

In the arrangement of Marquesan zones and floras, the reader should note an important departure from Egler's arrangement for Oahu. I was not able to distinguish a moisture line as clearly as Egler did. In the Marquesan landscape, the transition between pluviotropical and xerotropical zones is marked by dominant cover types of its own. Accordingly, I describe a discrete Marquesan transitional zone and list a transitional flora.

Vegetation dynamics interested Egler, too, and he had much to say about the subject. In the time ordinarily available for a field study, the course of succession is impossible to predict. His approach assures that neither difficulty with tropical successional relationships that are obscure, nor details of disturbance history that cannot be known, need interfere with a logical arrangement and useful description of vegetation.

I use plant cover synonymously with vegetation in one strict sense of the latter: that is when vegetation refers to the entire complex blanket of plant life of a place. Plant cover types are visible elements that may be differentiated from the total mosaic of plant cover and mapped as discrete types.

THREE FLORAS

The Xerotropical Flora

In order to establish a xerotropical zone for the Marquesas, a floristic comparison is made here between Egler's lists of xerotropical species from southeast Oahu and mine from the Marquesas.

In the lists that follow, only Marquesan xerotropical species appear. The first two lists compare in a very general way the relative abundance of those xerotropical species common to both SE Oahu and the Marquesas. The third list includes the additional Marquesan species that do not appear in Egler's SE Oahu flora.

An interrogation point [?] precedes *Oxalis corniculata* and *Psilotum nudum* because they were seldom collected and then not as part of a distinctly xerotropical cover. I have omitted *Commelina diffusa*, which is pluviotropical and may have appeared in Egler's xerotropical flora in error. Critical taxonomic work remains for plants identified by genus alone. Where names have seen revisions, the name used in my dissertation appears here in parentheses.

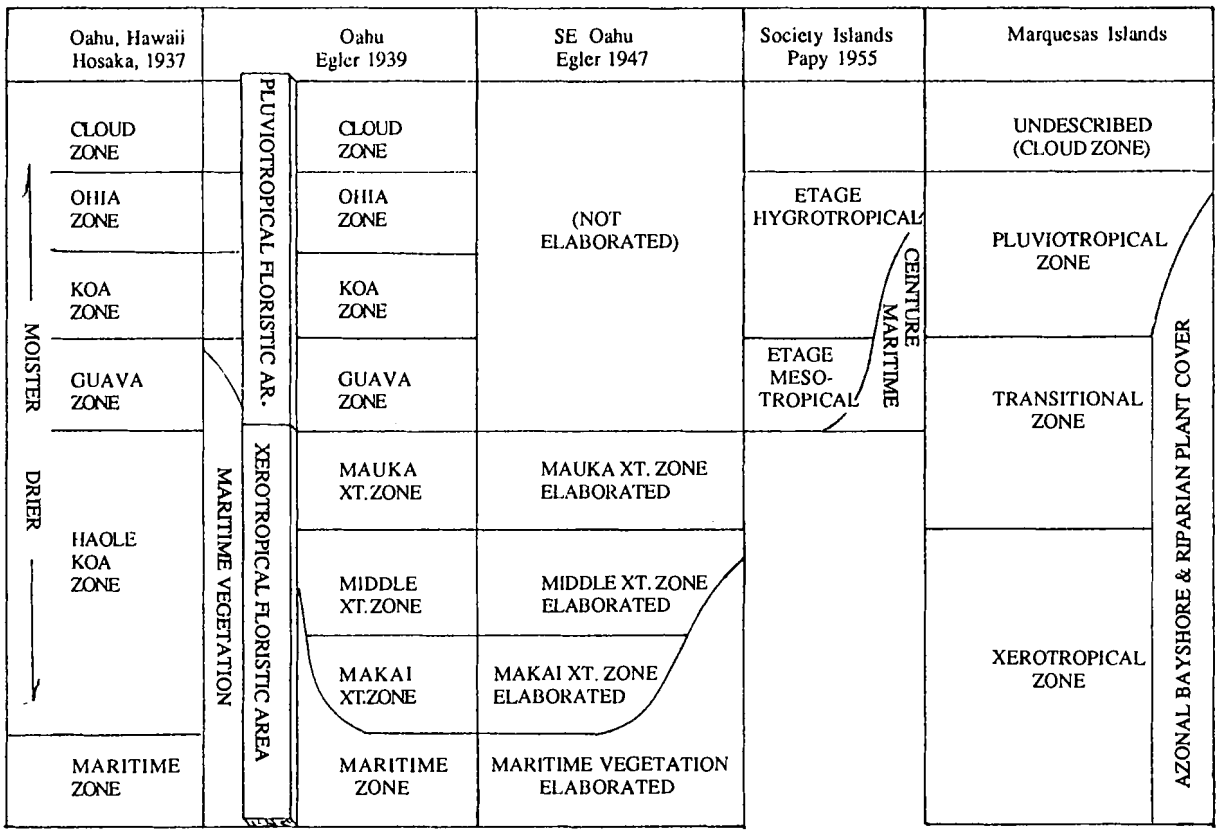

Figure 1. Marquesan Floral Zones Related to Earlier Work in Hawaii and the Society Islands.

Explanation of Figure. Egler (1939) described xero- and pluviotropical floras for Oahu, Hawaii, and extended to the whole of that island the vegetation zones described earlier by Hosaka (1937:201-211) for Kipapa Gulch, which naturally transects the gamut of Oahu vegetation zones. In a major monograph, Egler (1947) elaborated the xerotropical zones of southeastern Oahu. After tentative application of the xerotropical and pluviotropical concepts of Egler to Tahiti, Society Islands (Papy, 1948, not in figure), Papy (1955, fn., 176) recanted, after a climatological analysis indicated to him that the entire land area of the Society Islands was too moist to be called xerotropical. Papy did put the lee sides of the Society Islands into a mesotropical zone which appears equivalent to Egler's guava zone and at least part of my Marquesan transitional zone. Egler (1939,4; 1947, 405-406) emphasized the azonal character of maritime vegetation and Papy and I have followed suit. The pluviotropical guava zone reaches the shore on windward Oahu but not in the southeastern sector of that island. The pluviotropical zone extends to the shore in the Marquesas and, as Papy noted, in the Society Islands, too. Papy (1955, fn.,176) preferred the word hygrotropical to pluviotropical for etymological reasons, but rather different names seem appropriate for Papy's zones because he attempted to define them climatically in a way that Egler pointedly eschewed. Egler used the adaptations displayed by arrays of growing plants to define the moisture regimes at their sites. (Egler, 1947, pp. 391-295; Papy, 1954, 1955).

There are other symbols. An asterisk "*" precedes species common or widely distributed in the Marquesas; "(TR)" precedes species with ranges that extend into the transitional zone, described below. Locally established species are followed by a list of localities where they were observed. Species lacking a qualifying symbol or annotation are of occasional occurrence.

I. XEROTROPICAL SPECIES OF THE MARQUESAS WIDESPREAD OR DOMINANT IN SOUTHEAST OAHU:

Acacia farnesiana (local on Tahuata, Nukuhiva, Eiao)
(TR) **Ageratum conyzoides*
(TR) *Bidens pilosa*
(TR) **Cassia occidentalis*
**Cenchrus echinatus*
(TR) **Chrysopogon aciculatus*
**Cynodon dactylon*
**Dactyloctenium aegyptium*
Desmodium triflorum (local at Puamau football field)
**Eleusine indica*
(TR) **Emilia sonchifolia*
Eragrostis amabilis (*E. tenella*)
**Euphorbia hirta*
(TR) **Indigofera suffruticosa* (absent at Vaipaee)
Leucaena leucocephala (Egler's *L. glauca*; local on Uapou, Nukuhiva, & Hivaoa at Puamau)
**Macroptilium lathyroides* (*Phaseolus lathyroides*)
**Malvastrum coromandelianum*
(TR?) *Oxalis corniculata*
**Passiflora foetida* var.
Peperomia blanda (*P. leptostachya*)
Plumbago zeylanica
**Portulaca oleracea*
(TR?) *Psilotum nudum*
Ricinus communis
Setaria verticillata
Sonchus oleraceus
Tricholaena rosea (Egler's *T. repens*; local on Hivaoa, Uapou, Tahuata)
**Waltheria indica* (Egler's *W. americana*)
Xanthium strumarium (Egler's *X. saccharatum*)

The second list comprises Marquesan xerotropical species that were less abundant on SE Oahu, occurring there on less than 80% of Egler's field lists. It will be noted that some of these species are, however, common and widespread in the Marquesas.

Modifying symbols below are used as in the first list above.

II. MARQUESAN XEROTROPICAL SPECIES NEITHER COMMON NOR WIDESPREAD IN SOUTHEAST OAHU:

Amaranthus viridis
**Canthium odoratum*
(TR) *Capsicum frutescens*
Cardiospermum halicacabum

Catharanthus roseus
**Cyperus javanicus*
(TR?) *Cyperus rotundus* (local on Puamau football field; on Nukuhiva and Uahuka in villages)
**Digitaria setigera* (*D. pruriens*)
(TR) *Dodonaea viscosa*
(TR?) *Dolichos lablab* (apparent escape from cultivation at Puamau)
(TR) *Eugenia cumini* (introduced on all islands but widely naturalized only in vicinity of Bay of Traitors, Hivaoa)
Euphorbia prostrata
Gossypium barbadense
(TR) *Melinis minutiflora* (Nukuhiva, Hivaoa, Fatuiva)
(TR) **Morinda citrifolia*
Ocimum gratissimum
Panicum maximum
(TR) **Psidium guajava*
(TR) *Psidium guineense* (*P. guajava* and *P. guineense* were not distinguished in the field and many of the specimens remain unnamed pending study)
Salvia occidentalis (local at Taiohae on Nukuhiva)
(TR) **Synedrella nodiflora*
(TR) *Tecoma stans* (local, southern Nukuhiva)
Tephrosia purpurea
**Vernonia cinerea* (var. *parviflora* in Marquesas)

The enumeration of Marquesan xerotropical plants concludes with 45 more species that grow intimately along with the plants on the two lists above. None are listed by Egler from SE Oahu, but many of them are in fact common on Oahu and elsewhere in Hawaii. See, for example, the floristic enumerations for Hawaiian vegetation zones (Ripperton & Hosaka, 1942), game bird habitats (Schwartz & Schwartz, 1949), ecosystems (Fosberg, 1972), and Oahu dry-grass communities (Kartawinata & Mueller-Dombois, 1972).

III. MARQUESAN XEROTROPICAL SPECIES ABSENT FROM EGLER'S OAHU LISTS:

(TR) *Abrus precatorius*
Abutilon grandifolium
**Abutilon hirtum*
**Achyranthes aspera* (*A. indica*)
Aristida sp. (collected only at Oea on Nukuhiva)
Asclepias curassavica
**Caesalpinia bonduc*
Caesalpinia major
(TR) **Casuarina equisetifolia*
(TR) **Celastrus crenatus*
Celtis pacifica
(TR) *Cerbera manghas*
Cleome viscosa
(TR) **Colubrina asiatica*
**Cordia lutea*
(TR) *Cordia subcordata*
Eragrostis xerophila (native to Marquesas)

(TR) **Erythrina variegata*
Eugenia sp.
(TR) *Ficus prolixa*
Fimbristylis separanda (E. flank of Taiohae Bay, Nukuhiva)
Gossypium hirsutum var. or ssp.
(TR) *Guettarda speciosa*
Ipomoea macrantha (*I. tuba*)
Jatropha gossypifolia (local at Vaipaee)
Melochia pyramidata (Taiohae, Nukuhiva & Hakahetau, Uapou)
Ocimum basilicum
Ocimum sanctum (Hakehetau, Uapou)
**Panicum reptans* var *marquisense*
Peperomia spp, (in crevices of outcropping boulders)
(TR) *Phyllanthus amarus*
Pisonia grandis
(PT & TR) **Polypodium scolopendria*
**Rhynchosia minima*
Salvia coccinea (collected on Uahuka only)
(TR) **Sapindus saponaria*
(TR) **Sida acuta*
Sida hybrids (*Sida acuta* and *S. rhombifolia* are apparently hybridizing, according to F. R. Fosberg in personal communication.)
Sida paniculata (local on Tahuata, Uapou, Nukuhiva)
**Sida rhombifolia* (*)
(TR) *Thespesia populnea*
Tribulus cistoides
(TR) **Triumfetta rhomboides* (*T. bartramia*)
**Waltheria tomentosa* (Marquesan native species)
(TR) **Xylosma suaveolens* subsp. *pubigerum*

The Transitional Flora

Excepting the yards and gardens, certain areas in the transitional zone are as rich in species as any part of the lower elevations. Most of the plants are readily assignable either to the xerotropical or pluviotropical floras. A few very common species, however, lie athwart the transition: *Casuarina equisetifolia, Desmodium incanum, Miscanthus floridulus, Nephrolepis hirsutula, Premna serratifolia, Psidium* spp., *Sapindus saponaria, Xylosma suaveolens.*

The looming dominance of several of the latter in very visible cover types dictated the utility of a transitional zone and flora for descriptive purpose, although it departs from the elegant division that Egler was able to map for southeast Oahu. It may be argued that a similar transitional zone exists on Oahu; *Psidium guajava* is there so distributed, as perhaps also in Tahiti (See fig. 1). The visibly dominant species on Oahu cover types, however, were in Egler's (1947) view either xerotropical or pluviotropical, as already noted.

The list that follows is annotated as were the xerotropical lists above with the symbols "(XT)" and "(PT)" to denote xerotropical and pluviotropical species respectively.

THE TRANSITIONAL FLORA

(PT) *Aleurites moluccana* (in deep ravines and box canyons)
(XT) *Amaranthus viridis*
(PT, XT) *Bidens pilosa*
(XT) **Caesalpinia bonduc*
(XT) *Caesalpinia major*
(PT) **Canthium barbatum*
(XT) **Canthium odoratum*
(XT) *Capsicum frutescens*
(PT) *Carica papaya*
(XT) *Cassia occidentalis*
(XT) **Casuarina equisetifolia*
(XT) **Celastrus crenatus*
(XT) *Celtis pacifica*
(XT) *Cerbera manghas*
(XT) **Chrysopogon aciculatus*
(PT) *Coffea arabica*
(XT) **Colubrina asiatica*
(PT) *Commelina diffusa*
(XT) **Cordia subcordata*
(XT) **Cyperus javanicus*
(PT) **Cyperus kyllingia*
(PT) *Cyperus marquisensis*
**Desmodium incanum*
(PT) **Digitaria henryi* (zonal status doubtful)
(?) **Digitaria radicosa* (*D. timorensis*; adventive on open sites; zonal status doubtful)
(XT) **Digitaria setigera* (*D. pruriens*)
(PT) *Elephantopus mollis* (still spreading on Hivaoa, Nukuhiva & Fatuiva)
(PT) *Elephantopus spicatus*
(PT) *Emilia fosbergii* (*E. javanica*; extent of occurrence uncertain)
(PT) **Emilia sonchifolia*
(XT) **Erythrina variegata*
Eugenia sp.
(XT) *Eugenia cumini*
(PT, XT) **Ficus prolixa*
(PT) *Gleichenia linearis*
(PT) **Glochidion* sp.
(XT) *Guettarda speciosa*
(PT) *Hibiscus tiliaceus*
(PT) **Hibiscus tiliaceus* var. *sterilis*
(XT) **Indigofera suffruticosa*
(PT?) *Ipomoea* sp.
(XT) *Ipomoea macrantha* (*I. tuba*)
(PT) *Ipomoea obscura*
**Miscanthus floridulus*
(PT, XT) **Morinda citrifolia*
Morinda umbellata var. *forsteri* (col. Puamau only)
(PT) **Nephrolepis biserrata*
(PT) **Nephrolepis hirsutula*
(XT) **Ocimum gratissimum*

(XT) *Ocimum sanctum* (collected only on Uapou)
(PT) *Oplismenus compositus*
(?) *Oplismenus hirtellus*
(PT) **Pandanus tectorius* sensu lato
(XT) **Panicum reptans* var. *marquisense*
(XT) *Passiflora foetida* var.
(XT) *Phyllanthus amarus*
(XT) *Pisonia grandis*
(PT, XT) **Polypodium scolopendria*
**Premna serratifolia* (*P. tahitensis*)
(PT, XT) **Psidium guajava*
(PT) **Psidium guineense*
(PT) *Santalum insulare* (native to Marquesas)
(XT) **Sapindus saponaria*
(XT) **Sida acuta*
(PT) **Stephania hernandifolia* (not collected at Puamau)
(XT) **Synedrella nodiflora*
(XT) **Thespesia populnea*
(XT) **Tricholaena rosea* (locally established on Hivaoa, Uapou, and Tahuata)
(XT) **Triumfetta rhomboidea* (T. bartramia)
(XT) **Vernonia cinerea*
(PT) *Wikstroemia coriacea* (*W. foetida*)
(XT) **Xylosma suaveolens* subsp. *pubigerum*

The Pluviotropical Flora

Egler (1939) left the pluviotropical vegetation of Oahu without detailed floristic lists such as he subsequently (1947) published for the southeastern Oahu xerotropical. Several prominent Oahu pluviotropical species were mentioned, however, that are abundant enough for indicator use in the Marquesas. They include *Aleurites moluccana*, Coffea arabica, *Commelina diffusa*, *Cordyline fruticosa*, *Gleichenia linearis*, *Paspalum conjugatum*, and *Psidium guajava*.

Psidium guajava seems to be primarily pluviotropical, but it extends well into the xerotropical zone and is prominent in the transitional zone. In rainy periods *Commelina diffusa* likewise may be seen in ground cover of the transitional zone.

The other species seem to be reliable Marquesan pluviotropical zone indicators, particularly *Paspalum conjugatum* and *Gleichenia linearis*. On Uahuka, however, *P. conjugatum* has not yet become established and *Coffea arabica* remains only locally naturalized. With the notable exception of *G. linearis*, which forms conspicuous and extensive fernbrakes, none of these Hawaiian indicator species is widely dominant in the Marquesas. In addition to *G. linearis*, the characteristic indicator of pluviotropical conditions in the uplands is *Hibiscus tiliaceus*.

The enumeration of pluviotropical plants below includes few native Marquesan species, because they were not encountered in the sampled localities. It would be right to expect them because the higher pluviotropical zone abuts the cloudy heights that are rich in species peculiar to the archipelago.

The list does comprise the common plants from secondary pluviotropical plant cover types subject to disturbance by grazing, trampling and fire in the areas studied or

traversed. The list should grossly delimit the pluviotropical zone on all the inhabited Marquesas islands.

Where the range of a species extends into the transitional zone, its name is preceded by "(TR)" as in the foregoing lists. Again, asterisks denote the widespread species most often encountered.

Adenostemma lanceolata (A. lavenia)
Ageratum conyzoides
Aleurites moluccana
Alocasia macrorrhiza
Asplenium nidus
Athyrium sp.
Barringtonia asiatica
(TR) *Bidens pilosa*
Calophyllum inophyllum
**Canna indica* (not common in uplands and fallow)
(TR) **Canthium barbatum*
(TR) **Carica papaya*
**Centotheca lappacea*
**Cocos nucifera*
(TR) **Coffea arabica*
(TR) **Commelina diffusa*
Cordyline fruticosa
Cyathula prostrata
Cyperus brevifolius
(TR) *Cyperus kyllingia*
(TR) *Cyperus marquisensis* (native species)
Desmodium heterocarpon var. *strigosum*
(TR) **Digitaria henryi* (on open trampled ground; PT status doubtful)
Dioscorea alata
Dioscorea bulbifera
Dioscorea esculenta var. *fasciculata*
(TR) **Elephantopus mollis* (limited distribution on Fatuiva, Hivaoa & Nukuhiva)
(TR) **Elephantopus spicatus*
(TR) *Emilia fosbergii* (*E. javanica*)
(TR) **Emilia sonchifolia*
Fimbristylis nukuhivensis (native species)
Freycinetia spp. (at least two native spp.)
(TR) **Gleichenia linearis*
(TR) *Glochidion* sp.
(TR) **Hibiscus tiliaceus*
(TR) **Hibiscus tiliaceus* var *sterilis*
Histiopteris incisa
**Inocarpus fagifer* (*I. fagiferus*)
(TR) *Ipomoea* sp.
(TR) *Ipomoea obscura*
**Lycopodium cernuum*
**Mangifera indica*
Marattia sp.
(TR) **Morinda citrifolia*
Nasturtium officinale
(TR) **Nephrolepis biserrata*

(TR) **Nephrolepis hirsutula*
(TR) **Oplismenus compositus*
(TR) **Pandanus tectorius* sensu lato
**Paspalum conjugatum*
**Paspalum paniculatum*
Peperomia spp.
Piper latifolium
Pipturus argenteus
(XT, TR) *Polypodium scolopendria*
(XT, TR) **Psidium guajava*
(TR) *Psidium guineense*
Pteris sp.
(TR) *Santalum insulare* (native species)
Schizostachyum sp.
Sphenomeris chinensis
Spondias dulcis
(TR) *Stephania hernandifolia*
Tacca leontopetaloides
Tectaria marchionica (native species)
Terminalia catappa
**Thelypteris opulenta*
Urena lobata
Vanilla planifolia
Weinmannia sp.
(TR) *Wikstroemia coriacea* (*W. foetida*)
Xanthosoma sagittifolia

PROMINENCE OF STRAND SPECIES IN FORESTS OF THE INTERIOR

A remarkable feature of the Marquesan inland secondary forests is the persistent dominance in them of species widely associated in tropical countries with the saline environments of the shore, or, when not distinctively plants of the shore environments, at least demonstratively capable of dispersal by ocean currents, as shown by Guppy (1906, 528-531; 1917, 86-87).

Egler hesitated to elevate the distinctive Oahu maritime plant community of salt-tolerant species to a zonal rank comparable to his xerotropical and pluviotropical. He saw that many maritime species thrived in inland localities miles away from the shoreline. "...[the] mountainward ... boundary [of the maritime zone] is generally independent of ecologic controls and is very indefinite. That is, edaphic and atmospheric factors, although they play a role in limiting the seaward ... extension of non-maritime communities, do not on the other hand control the [mountainward] limit of most strand plants. Fortuities in terrestrial migration account for the highly irregular and unpredictable distribution of strand communities." (Egler 1947, 405)

Egler also emphasized that "this flora, always thought to be remarkably adapted for transportation by currents, is perhaps as remarkable for its relative lack of adaptations for terrestrial migration." (Egler 1947, 405-406)

A number of Marquesan plants fit that description. They regenerate well in Marquesan inland sites and can be called widely naturalized there:

Caesalpinia bonduc
Colubrina asiatica
Cordia subcordata
Erythrina variegata
Guettarda speciosa
Ipomoea macrantha
Hibiscus tiliaceus
Morinda citrifolia
Pandanus tectorius sensu lato
Premna serratifolia
Sapindus saponaria
Thespesia populnea

Most of those species grow in forests below about 500m, but the dominance of at least two, *Hibiscus tiliaceus* and *Pandanus tectorius*, extends to the very margins of the cloud forest.

Plate 1: Forest dominated by *Pandanus tectorius* and *Hibiscus tiliaceus*. *Gleichenia linearis* fernbrake occupies the ridge crest above. Vaikivi, interior of Uahuka Island.

In Oahu, Egler found little evidence of reproduction of the maritime species transported inland. In obvious contrast, in the Marquesan interior, regeneration of a significant number of maritime and large- or buoyant-seeded plants has not been hampered in any obvious way by presumed deficiencies in dispersal mechanisms nor by competition from other species.

The strand species display every evidence of permanence in the upland vegetation. It is interesting that they vary considerably in their apparent moisture requirements and segregate themselves into the three Marquesan floral zones.

It is conceivable that ancient Polynesians carried at least some of these strand plants inland. All were employed in the aboriginal economy. Their inland prominence reinforces a view that aboriginal alteration of the vegetation below the cloud zone must have been profound, coincident with the establishment there of the shore species. The primeval vegetation would have been suppressed in the clearing for cultivation of these and other useful but less persistent plantings, and by the use of fire.

THE NATURALIZATION OF COFFEE AND OTHER CULTIVATED PLANTS

Most of the cultivated plants of the world are heliotropic. It is not at all unusual to see certain of them escape garden or field to grow adventitiously in sunny, open sites. That is true of many garden ornamentals, most of which have short evolutionary histories in cultivation and retain some aggressiveness in the wild state. *Plectronia scutellarioides* (*Coleus blumei*) and *Catharanthus roseus* are excellent examples from the Marquesas. Presumably all historically introduced, some of the conspicuous upland fugitives from cultivation include:

Acacia farnesiana
Bixa orellana (in dry stream courses)
Caesalpinia pulcherrima
Canna indica
Coffea arabica
Eugenia cumini (especially around the Bay of Traitors, Hivaoa)
Eugenia uniflora (locally established around Bay of Traitors, Hivaoa)
Melia azedarach
Nicotiana tabacum
Ocimum basilicum
Psidium spp.
Ricinus communis
Salvia coccinea (Uahuka)
S. occidentalis (Taiohae, Nukuhiva)
Sorghum halepense
Stenolobium stans
Tricholaena rosea
Vitus sp. (at Hanaiapa, Hivaoa)

The phenomenal status of *Coffea arabica* as a thoroughly naturalized tree in most of the islands holds some ecological interest. *C. arabica* is one of the few cultivated species that prefers a semi-shaded habitat. In the Marquesas there are exceedingly few real ombrophiles at the lower elevations. *C. arabica*, with either some obscure measure of

aggressiveness in shaded situations or utter lack of local competition for such a niche, has effectively formed a shrubby understorey in the older secondary forests. Did nothing like it grow in that niche before its introduction in the nineteenth century? The understorey of small coffee trees, their own seedlings sprouting densely, is most remarkable beneath the dense forest canopy of *Hibiscus tiliaceus* in the humid back valley ravines, There, in the deep shade, virtually all other macroscopic green plant life is absent, but *Coffea* thrives.

THE XEROTROPICAL ZONE AND XEROTROPICAL COVER TYPES

A xerotropical vegetation dominated by low grasses and suffrutescent herbs prevails over extensive areas on most of the islands, particularly at the lower elevations, above or adjacent to coastal cliffs, in places well removed from the islands' central heights. As a rule, the suffrutescent plants grow most densely in ravines on sheltered, less disturbed slopes, and toward the interior. A number of xerotropical shrubs and trees are also encountered toward the interior and in sheltered ravines. Relic xerotropical forest with closed canopy exists outside the study area on Hatutaa and in places on leeward Nukuhiva.

The gentle sweep of broad interfluves in the xerotropical zone of southwestern Uahuka, the weathered remnants of cinder cones, and the grey, yellow-brown of the sparse vegetation are reminiscent of Easter Island landscapes, even to the dark coastal cliffs above a reefless white and purple sea. In the Puamau study area, by contrast, there is little xerotropical cover and it is confined to the very steep slopes of the gravely denuded mountain, Namana, on the northwestern side of the bay.

Except in relic localities inaccessible to foraging animals, the present xerotropical plant cover reflects in obscure degrees the influence of those animals. Soil erosion associated with their activity has utterly denuded plant and soil cover from many localities. The spread of certain historically introduced plants has almost certainly been facilitated by the presence of goats, sheep, cattle, horses and asses.

Animals have gravely denuded terrain in these localities: windward Fatuiva, southern Tahuata, northwestern and eastern Hivaoa,northern Uahuka, northeastern Uapou, western and northwestern Nukuhiva, and most of the entire islands of Eiao and Mohotane.

The influence of fire in this zone is problematical. No burning was observed of the xerotropical cover, but it is surely combustible in drought, and residents report that fires do occur. Both heavy grazing and a desire to leave forage for the animals may have served to reduce the incidence of casual burning of the range. The xerotropical zone constitutes the most significant grazing range on most islands.

Dominance of individual species varies considerably from place to place, although the whole floras of the xerotropical cover do not differ much from island to island. Certain species, by their local dominance, alter the physiognomy of a landscape. *Indigofera suffruticosa*, for example, introduced in historical time, had assumed wide dominance in the feral cattle, horse and goat ranges in northwestern Hivaoa west of Hanamenu in 1963, affording to that inclined plateau district a soft verdure quite in contrast with the barren, sparsely vegetated aspect of similar slopes elsewhere. In northeastern Hivaoa, a densely-growing grass, *Tricholaena rosea* (see discussion below) was rapidly colonizing the xeric slopes. Invading more slowly, the whipstem tree, *Leucaena leucocephala* has formed dense thickets over much of southern coastal Nukuhiva since its introduction in the nineteenth century (Drake 1893, 58-59). Similarly, a shrub with succulent branches, *Jatropha gossypifolia*, has begun to form its malodorous thickets on the steep slopes that flank the village of Vaipaee, on Uahuka.

Seaward Xerotropical Cover

In the driest outermost xerotropical localities two species are almost always present in some abundance: the low grass *Panicum reptans* and suffrutescent, sparingly-branched *Waltheria indica*. Several other common species usually combine with those two:

Abutilon hirtum
Cassia occidentalis
Cenchrus echinatus
Euphorbia hirta
Malvastrum coromandelianum
Ocimum gratissimum
Passiflora foetida var.
Portulaca oleracea
Rhynchosia minima
Sida rhombifolia
Vernonia cinerea

Plate 2: Seaward xerotropical plant cover on grazed terrain, southern Uahuka Island. The view is toward the south, overlooking the narrowed lower reach of Vaipaee Valley.

In general, the suffrutescent herbs and shrubs are more common in ravines and on undenuded, steep slopes where thickets may be dense enough to defy easy penetration by humans and large animals. Species are listed below in approximate order of observed frequency, with species reference to southwestern Uahuka, except as noted.

Grasses and Sedges:
- *Panicum reptans*
- *Cenchrus echinatus*
- *Tricholaena rosea* (obs. only on Hivaoa, Tahuata, Uapou)
- *Cynodon dactylon*
- *Dactyloctenium aegyptium*
- *Digitaria setigera* (D. pruriens)
- *Setaria verticillata*
- *Eragrostis amabilis* (*E. tenella*)
- *Fimbristylis separanda* (seen only at Taiohae)

Herbs:
- *Rhyncosia minima*
- *Vernonia cinerea*
- *Euphorbia hirta*
- *Portulaca oleracea*
- *Passiflora foetida* var.
- *Synedrella nodiflora*
- *Ageratum conyzoides*
- *Salvia coccinea* (seen only on Uahuka)
- *Amaranthus viridis*
- *Asclepias curassavica*
- *Cleome viscosa*
- *Euphorbia prostrata*
- *Ipomoea obscura* (seen only at Puamau)
- *Tribulus cistoides*
- *Xanthium strumarium*

Suffrutescent Herbs:
- *Waltheria indica*
- *Sida rhombifolia*
- *Malvastrum coromandelianum*
- *Abutilon hirtum*
- *Cassia occidentalis*
- *Ocimum gratissimum*
- *Macroptileum lathyroides* (*Phaseolus lathyroides*)
- *Sida paniculata* (seen only at Nukuhiva, Uapou, and northeastern Tahuata)
- *Catharanthus roseus*
- *Sida acuta*
- *Sida hybrids*
- *Triumfetta rhomboidea* (*T. bartramia*)
- *Phyllanthus amarus*
- *Melochia pyramidata* (seen only on Nukuhiva and Uapou)
- *Ocimum sanctum* (Uapou only)

Shrubs and Trees:
- *Gossypium barbadense*
- *Gossypium hirsutum* var. *taitense*

Gossypium hybrids[1]
Jatropha gossypifolia (only at Vaipaee on Uahuka)
Waltheria tomentosa (*W. lophanthus*)
Cordia lutea
Gossypium hirsutum var. (collected Uahuka only)
Tephrosia purpurea
Ficus prolixa
Leucaena leucocephala (established on Nukuhiva, Uapou, and locally at Puamau, on Hivaoa)
Acacia farnesiana (locally established at Vaituha on Eiao; Taiohae, Nukuhiva; & Vaitahu, Tahuata)
Tamarindus indica (occasionally planted)
Albizia lebbeck (occasionally planted)

Inland Xerotropical Cover

This cover type lies between the seaward xerotropical and transitional cover types. It embraces most of the species listed above for the seaward xerotropical cover and is notably enriched by several shrubs and trees. Most of the species listed below also grow farther inland, in the transitional cover types, but these listed extend well seaward into the xerotropical zone beyond the farthest seaward salients of the transitional cover types.

Abrus precatorius
Caesalpinia bonduc
Caesalpinia major
Celastrus crenatus
Celtis pacifica
Chrysopogon aciculatus
Colubrina asiatica
Eugenia sp.
Guettarda speciosa
Ipomoea macrantha (*I. tuba*)
Morinda citrifolia
Polypodium scolopendria
Psidium guajava
Psidium guineense
Sapindus saponaria
Sorghum halepense (zonal status doubtful; seen at Puamau, on Hivaoa, only)
Thespesia populnea

Along the upland bordering Vaipaee canyon to the east, north of Tahoatikikau crater, the topography lies virtually level upon a steep precipitation gradient. It is possible there to distinguish a broad range of vegetation transition. Open woodland stands of *koku'u* (*Sapindus saponaria*) may be seen extending from the densely wooded transitional zone into inland xerotropical cover. Among these trees and between individuals and clumps of shrubs a dense cover of the suffrutescent herbs is characteristic. Excepting where animals traverse such cover frequently and create paths, penetration is arduous. *Ocimum gratissimum*, *Sida* spp. and *Triumfetta* are dominant at Vaipaee. *Indigofera suffruticosa*, abundant in such localities on other islands, is conspicuously absent here.

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[1]Introgressive hybridization apparently occurs between the native *Gossypium hirsutum* variety and the introduced, naturalized *G. barbadense*, according to Paul Fryxell in personal correspondence.

Where density of the brushy canopy thins sufficiently to admit sunlight, typical low-growing xerotropical grasses and herbs cover the ground beneath.

In open, sunny places where animals congregate and along upland trails, *Malvastrum coromandelianum* is conspicuous, along with *Cynodon dactylon, Euphorbia hirta, Cenchrus echinatus, Dactyloctenium aegyptium* and less commonly *Amaranthus viridis* and *Euphorbia prostrata.* After prolonged rains these same open sites support an ephemeral explosive growth of annuals, and certain perennial pluviotropical heliophiles including *Vernonia cinerea, Ageratum conyzoides, Portulaca oleracea, Sida* spp., *Emilia sonchifolia, Elephantopus spicatus, Cyperus kyllingia,* and *Digitaria henryi* (Hivaoa only).

The onset of rainy weather also favors the suffrutescent herbs, and a usual public works project involves cutting away from trails the rank thickets of *Ocimum gratissimum, Indigofera suffruticosa* and *Triumfetta rhomboides* that appear in the course of a few moist weeks.

Plate 3: Transitional forest cover gives way to inland xerotropical cover on the far slope; view toward southwest overlooking Vaipaee valley 1 km above the village; camera's elevation about 180m.

Denuded Xerotropical Slopes

Whatever the vegetation cover of Mt. Namana, northwest of Puamau Bay, may once have been, its dike-shot brown aretes, cliffs, and buttress ridges appear nearly barren today, utterly stripped of soil; yet groves of large trees remain in deep ravines and on some of the gentler slopes. In a narrow zone between the groves and the highest denuded slopes, exposures of red-yellow soil, rilled by rainwash, announce the presence of goats and the persistence of denudation processes that began in the nineteenth century. Few observant travelers have failed to note the association of goats and sheep with degradation

of soil and vegetation in places that are either remote from habitation or comparatively inaccessible to hunters because of steep and otherwise difficult, broken terrain.

The condition of Mt. Namana, razed by goats and erosion, is typical of fully the eastern third length of Hivaoa, which is mostly denuded, barren mountainous country above imposing coastal cliffs. Clinging here and there to the brown, rocky slopes are large, solitary banyans called *aoa* (*Ficus prolixa*). Their spreading canopies incline parallel to the prevailing slope, and in these situations, they lack their usual pendant aerial roots. The contrast between the sparkling green foliage of these massive pale-trunked giants and the parched barren setting is as arresting as the sad reality that most of the growth that once surrounded the trees has vanished. The *aoa* seems to survive by virtue of a remarkable, proliferated system of ramifying roots that strike off from the base of the trunk along the rocky ground to seek crevices often some meters distant.

Apart from the banyans, the plant life on these denuded surfaces is scant. In crevices of weathered rock, once apparently a subsoil "C" horizon, one finds scattered depauperate individuals of *Waltheria indica*, *Panicum reptans*, *Abutilon hirtum*, *Cassia occidentalis*, *Euphorbia hirta*, *Vernonia cinerea*, and *Ageratum conyzoides*.

Turfs

Grassy turf formation, which constrains soil erosion on certain maritime slopes heavily used by animals, was noted in several localities around Puamau Bay. The turfed sites lie before salt-laden sea breezes at low elevation, on interfluves above sea cliffs. Several species of low-growing rhizomotous grasses participate: *Panicum reptans*, *Digitaria henryi*, *Dactyloctenium aegyptium* and *Cynodon dactylon*. On Uahuka, turfs of *Chrysopogon aciculatus* were noted in a similar maritime locality just east of Hokatu village. In general, *C. aciculatus* is associated with more moist conditions than commonly prevail on animal ranges near sea level. It is worth mention that where some soil remains, and granted favorable growing weather, a spontaneous pioneer revegetation of denuded slopes in the xerotropical zone proceeds rapidly after the animals are removed.

Grass Cover, *Tricholaena rosea* Type

Tricholaena rosea, a grass of tropical African origin, was reportedly brought from Tahiti to northeastern Hivaoa around 1950 by the late Edouard Friedman of Puamau, where it became known as *mutie etua*, or "Edouard's grass".

Since then, its spread has been phenomenal. The grass entirely covers all the xerotropical slopes between Eiaone and Hanapaoa to the west of Puamau, and well-established patches were noted all along the northern coast of Hivaoa from Natue to Hanamenu. It has been introduced on at least two other islands, Tahuata and Uapou.

Tricholaena does not seem to thrive in the driest seaward sectors; in fact, it grows inland on open sites well into the transitional zones.

An example of replacement of transitional zone vegetation by *T. rosea* was related by a credible observer on Hivaoa. In the valley of Eiaone, just west of Puamau, Mr. Henry Lie, a resident there for fifty years, has watched *Miscanthus floridulus* (discussed below) a conspicuous tall grass disappear from the valley's precipitous western flank under grazing pressure from his goats and sheep, only to witness a subsequent invasion of the same locality by *T. rosea*.

Similarly, patches of *Tricholaena rosea* may be seen in openings within the *Miscanthus* grass cover at Puamau, although the sequence of disturbance and revegetation there is unknown. *Tricholaena* also grows sporadically even in the pluviotropical *Gleichenia* fernbrakes along ridgecrest trails.

Where it is well-established, *T. rosea* grows 50-100cm tall with numerous branching culms in clumps spaced closely together so that unbroken stands of the grass result. The usual xerotropical shrubs and suffruticose herbs remain visible in the observed *Tricholaena* stands, but less abundantly than in typical xerotropical cover elsewhere. The capacity of this grass to invade sparsely vegetated, eroding uplands must be regarded as auspicious as long as unconstrained foraging animals move freely over their ranges.

The advent of *mutie etua* is much appreciated in Puamau where suitable horse forage is ever in short supply, as in all the larger humid valleys. For that reason alone, one might predict a rapid dissemination of the grass over the archipelago.

THE TRANSITIONAL ZONE AND TRANSITIONAL COVER TYPES

The vegetation of the transitional zone, like that of the adjacent zones, occupies diverse well-drained land at a wide range of elevation. In its present condition, the zone is characterized by more woody growth than prevails in the xerotropical zone and especially by the distinctive *Miscanthus floridulus* tall grass cover. Salients of transitional vegetation extend down ravines into the xerotropical zone and penetrate along rising ridgecrests into the pluviotropical zone.

Transitional cover type are physiognomically diverse, occur in mosaic, and reflect a corresponding diversity of land types and kinds of disturbance.

For example, at Puamau, the crest along one of the prominent ridges may be taken as typical. From a point in mid-valley, the ridge rises to abut the back wall of the great Puamau amphitheatre. Flanks drop sharply to either side of the narrow crest. Substrates along the crest include surfaces as varied as rock outcrops, old Polynesian stone platforms, excavated pit defenses, and deep lateritic soil. Grazing, burning, traffic by animals and humans, and even some clearing and planting complicate the recent disturbance history. On such a ridge, nearly all the transitional cover types may be represented: forest, scrub, *Casuarina* groves, *Pandanus* groves, *Miscanthus* tall grass, *Tricholaena* grass, along with patches of pluviotropical cover—*Gleichenia* fernbrake, and saliants of *Hibiscus* forest that here and there rise from the more humid ravines to overtop the ridge.

At Vaipaee, transitional vegetation occupies a large fraction of that basin along a crescentic belt that intersects the axis of the valley about half a kilometer above the village. The crescent curves to the north and east to include most of the western and northern flanks of the Vaipaee drainage.

Transitional Cover on Grazed Ranges

On the slopes of certain interfluves marked by animal activity and active erosion scars in friable, yellow-red, residual soil, the relatively dense cover afforded by suffrutescent herbs in the inland xerotropical zone gives way to a more open transitional cover of low grasses, herbs and shrubs. Locally, the low fertility seems affirmed by a turf of *Chrysopogon aciculatus* in which the shrubs and suffrutescent herbs appear scattered, spindly, and comparatively small. The latter include *Psidium* spp. *Morinda citrifolia, Triumfetta rhomboides, Waltheria indica, Desmodium incanum, Indigofera suffruticosa*

(not yet introduced at Vaipaee in 1963), and the fern *Polypodium scolopendria*. Another fern, *Nephrolepis hirsutula*, is the only other plant in the herbaceous assemblage that sometimes approaches a status co-dominant with *Chrysopogon aciculatus*. Toward the moist interior, fewer and fewer xerotropical species occur. Unforested, grazed areas grade into a trampled *Gleichenia* fernbrake. *Mangifera indica* occurs sporadically and often, along trails. That tree is not apparently as subject to the depauperate chlorosis that here afflicts the few other scattered trees, notably *Hibiscus tiliaceus* and *Pandanus tectorius*.

Plate 4: Transitional landscape, central Vaipaee valley, view toward northwest. The nearer slope displays little evidence of fire or other disturbance in recent years. *Miscanthus floridulus* tall grass (light tone) is mixed with growth of woody scrub. Compare it with far upper right (summit elevation 620m), where *Miscanthus* was burned over about three years before the photo was taken in 1964. Gentler slopes on the nearer ridgecrest (elevation about 275m) are no longer grazed and its transitional range is reverting to scrub and wood, but *Miscanthus* is still absent. Transitional forest on colluvium below *Miscanthus* covered slopes is perhaps 20 to 30 years old, as are the coconut palms in the valley bottom. Vertical jointing appears in the prominent stratum at mid-slope. Prevailing wind blows from right to left; the moister area is to the right, the drier to the left.

Other herbs occur in transitional range cover in varying abundance: *Ageratum conyzoides, Cyperus brevifolius, C. javanicus, C. kyllingia, Passiflora foetida, Synedrella nodiflora, Vernonia cinerea.*

Another upland grass, *Paspalum paniculatum*, enters grazed cover very prominently on Nukuhiva and to some extent on Hivaoa and other islands, but not at all at Vaipaee, where it is not yet established. *Tricholaena rosea* invades these localities at Puamau. Another recently introduced grass, *Melinis minutiflora*, had become similarly established among transitional range species in one locality above the bluff just east of the Catholic mission compound in Puamau.

Transitional Scrub

In the ravines and swales below the transitional ranges and wherever the transitional forest thins, a cover of typical transitional scrub appears.

The shrubs and small trees most abundantly seen are *Psidium guineense, P. guajava, Celastrus crenatus, Colubrina asiatica, Premna serratifolia,* and *Morinda citrifolia.* All of them at times approach the stature of trees, even *Colubrina.* When crowded, clambering *Celastrus* sometimes grows several meters up through the foliage of other plants, deriving enough support from its neighbors to acquire arborescent bulk. In addition, the usual trees of the transitional zone grow scattered among the shrubs.

A characteristic ground cover accompanies the transitional scrub where the canopy admits sufficient light for *Nephrolepis hirsutula, Desmodium incanum, Polypodium scolopendria,* and *Indigofera suffruticosa.* Locally, *Indigofera* assumes dominance, as does *Tricholaena rosea,* encroaching upon such open scrub at Puamau.

Additionally, where the scrub is traversed by trails, virtually all the common weedy herbs and grasses tolerant of upland soils appear in the ground cover along the way.

Tall Grass Cover of *Miscanthus (Kakaho)*

It did not reach Hawaii, but on other xeric high islands across the central Pacific from the Marianas to Mangareva, *Miscanthus floridulus* is the principal and aboriginal constituent of tall grassland maintained by periodic burning. Conspicuous wherever they arise in the Marquesas, broad swaths of the straw-yellow (green only after prolonged rainy weather) *kakaho* grass occupy ascending buttress ridges and other steep slopes above almost every Marquesan valley.

As one of the more dramatic elements in the Marquesan landscape, the rising swaths of tall grass and their combustibility did not escape the notice of at least one early observer, suggesting the probable antiquity of the aboriginal practice of burning, on which the continued maintenance of this distinctive cover seems to depend.

The first clear record of burned vegetation was made by Georg Forster (II, p.9) from the deck of the Resolution off Tahuata in 1774, but he did not note the nature of the burned vegetation. William Crook was the first to write, in 1797-1799, that on the slopes around Resolution Bay (Vaitahu, at Tahuata I.), "...the inferior ridges produce only reeds." (Sheahan 1952; cxl,cxlv). Crook's Marquesan vocabulary offers the word *kaukahhu* for reed (ibid., lxxv), which term appears equivalent to the modern *kakaho.* His reeds were almost surely *Miscanthus floridulus*, and it may be noted that his description of the "inferior ridges" still applies at Vaitahu, almost two centuries later.

Some months later, after Crook had removed to Nukuhiva, in the northern Marquesas, he observed there a burning of similar slopes.

> "About the month of August ... The appearance of the Soil upon these inferior ridges was barren; and they were only covered with burned Grass or Reeds. These are often set on fire, toward the lower part of the ridge, from whence the flame naturally spreads to the higher Ground." (Sheahan 1952, clxxiv).

Miscanthus floridulus attains a height of over two meters as a dominant in its typical transitional zone stands. In dense growth, penetration is arduous because of the stiff cane-like culms and microscopically serrate leaf margins that lacerate the flesh. Within the transitional zone it often gives way quite abruptly to forest or scrub. At the unforested margins of its range, it grades into the suffrutescent herbs and scattered shrubs of the inland xerotropical cover, or, on the moist side, into pluviotropical *Gleichenia linearis* fernbrake. At both these extremes of its range, it tends toward scattered, depauperate clumps that attain lesser heights—1 to 1 1/2 m or less.

The woody species that grow in some of the *kakaho* stands are all typical of the transitional zone. Most often seen are the *Psidium* spp. Less abundant but still common are *Morinda citrifolia*, *Celastrus crenatus*, *Pandanus tectorius*, *Hibiscus tiliaceus*, *Xylosma suaveolens* and *Casuarina equisetifolia*. Several of the species acquire unusually attenuated habits as stems lengthen to overcome shading by the grass: *Psidium*, *C. crenatus*, and *H. tiliaceus*.

Certain *kakaho* stands are so full of woody growth as to appear moribund, suggesting a successional trend toward transitional thicket or forest should the growth remain long free of fire. Excellent examples are the mixed *kakaho* and thicket on the western flank of Vaipaee canyon between the upper village and the great bend of that valley. Where the grass had burned in recent years, as in the extreme northwest corner of the valley, the shrubs were not so much in evidence.

According to local informants, the *kakaho* in the latter locality was swept by fire in the drought period preceding 1963.

Another striking feature of *Miscanthus* stands is their confinement to very steep slopes. Because the grass does grow here and there on gentle slopes, the prevalent occurrence is not easily explained on any obvious edaphic basis.

The key to the problem seems to be that grazing stock are excluded from these tall grasslands by both man and the terrain. Cattle and horses are typically present in uplands near villages but by nature shy away from the steeper slopes. Generally fair game to hunters, the more sure-footed sheep and goats are uncommon near villages. When present, sheep and goats remove the tall grass, as related above in the case of Eiaone. *Miscanthus floridulus* would appear to be rather coarse fodder, but both horses and cattle eat it readily, particularly when it is putting out tender new shoots.

At Vaipaee, the once extensive herds of cattle and horses on the high ridges west and north of the valley had been removed over a year prior to 1964. The peculiarities of plant cover there still reflected their presence, however. At the brink of every *Miscanthus*-clad precipice, where the slopes at the top would have invited the presence of the large livestock, the tall grass abruptly gave way above to transitional scrub or range cover.

Transitional Forest Cover Types

The forest of the transitional zone is richer in arborescent species than any other spontaneous vegetation at low elevation. Certain tree species aggregate in groves. Others appear throughout the transitional zone, both as forest and scattered in scrub and *Miscanthus* grassland.

Two species best characterize the forest by their abundance over all its range: *Xylosma suaveolens* subsp. *pubigerum* (*pi'api'au*), and *Sapindus saponaria* (*koku'u*).

In the shade of their closed canopy, the forest types exclude most herbaceous ground cover. As a rule, much bare soil is visible between fallen leaves and litter, and the undergrowth, if any, comprises tree shoots, scattered ferns and scant growth of *Oplismenus compositus*. *Xylosma* positively inhibits all other growth beneath its crown.

On its pluviotropical margin, transitional forest grades into *Hibiscus tiliaceus* forest or gives way to *Gleichenia* fernbrake. Where the forest extends all the way to the xerotropical margin with no interposition of other transitional cover types, it gives way rather abruptly to inland xerotropical cover.

Transitional Forest in Valley Bottoms and Ravines Above the Sea

This forest type or its remnants is frequently encountered around the shore, in uninhabited valleys behind small bays, on talus below sea cliffs, and in the plunging ravines and foreshortened hanging valleys above the cliffs themselves.

From a distance the assemblage of trees presents an airy lightness and diversity of foliage textures reminiscent of North American deciduous forests in late spring. Foliage is a light, bright green. Grey-white trunks prevail. The trees are of uneven heights, and the great banyans (*Ficus prolixa*) tower here and there above all the others. Close inspection reveals tropical growth habits: massive coalescing trunks and pendant aerial roots of the banyans, bar-like prop-roots of *Pandanus* angling stiffly outward from its trunk, and the curious ground-clasping roots of *Pisonia* that appear to flow octopus-like about and over rocks.

On the other hand, groves of *Xylosma* resemble nothing as much as a forest of birches or aspens except for their seasonal clusters of small black berries. *Xylosma* bark is light grey. Its leaves oscillate in the wind on long, pendant twigs; and yellow and fallen, they litter the otherwise barren ground beneath.

The forest in the ravines above Puamau Bay at the foot of Mt. Namana is typical. Trees include the common *Xylosma* and *Sapindus*, as well as *Thespesia populnea* (*mi'o*), *Erythrina variegata* (*netae*), *Ficus prolixa* (*aoa*), *Hibiscus tiliaceus* (*hau, fau*), *Carica papaya* (*vi papai*), *Morinda citrifolia* (*noni*), *Canthium odoratum* (*kotai*), *Pisonia grandis* (*pu'atea*), *Pandanus tectorius* (*ha'a, fa'a*), and *Premna serratifolia* (*va'o va'o*). Deep in the ravines occasional *Aleurites moluccana* (*ama*) and *hau* suggest the presence of perennial moisture there.

In similar groves elsewhere *Celtis pacifica* appears occasionally, as in long-abandoned Natue Valley, east of Puamau. In a few valley bottoms distant from habitation, *Cordia subcordata* (*tou*), a marketable cabinet timber, still occupies a sub-dominant position in the forest, as again, at Natue.

Finally, certain economic species, planted or spontaneous, appear sporadically in these same ravines and valleys, including *Capsicum frutescens* (*neva*), *Ceiba pentandra*

(*uru uru*), oranges (*anani*). Coconut palms appear where droughts are not too severe or where ground water is available and so often occupy a small area at the foot of a ravine just behind the shore.

Transitional Forests on Upland Slopes and Inland Ridgecrests

Most of the trees listed in the foregoing section appear also in the upland transitional forest. *Cordia subcordata*, however, was not encountered away from the valley bottoms, and *Celtis pacifica* and *Pisonia grandis* are uncommon far inland of coastal and xerotropical localities.

All too often the transitional zone near large settlements is sufficiently disturbed that forest stands, unbroken by new or old garden clearings, burns, and the like, are not extensive. The situation gives rise to a landscape mosaic of forest interrupted by gardens, thicket, *Miscanthus* grasslands, and denuded places. This is the situation that prevails at Puamau just south of Mt. Namana.

Closed forest nearly always includes *pi'api'au* and *koku'u* as co-dominants except as the latter is in local demand to fire bakers' ovens as at Puamau. *Mi'o*, also in demand by local wood carvers, is not prominent in the closed forest but may be common in upland parkland at forest margins.

Along ridgecrests, salients of transitional cover rise above the pluviotropical vegetation that prevails in the inland valleys. In addition to the trees listed above, several pluviotropical trees here enter the forest including prominently: *Pandanus tectorius* and *Hibiscus tiliaceus*, and also *Glochidion* sp., *Canthium barbatum*, *Coffea arabica* (except on Uahuka), and occasionally *Cocos nucifera* and *Mangifera indica*.

The profile of these ridgecrests is also marked by discrete groves of *Pandanus* and *Casuarina*, now discussed separately.

Pandanus Groves in the Transitional Zone

Pandanus tectorius abounds in the Marquesan interior throughout the transitional and pluviotropical zones. Whatever its importance in traditional economy may have been, the species is entirely feral today. I never once saw *Pandanus* used for thatch in the Marquesas. For plaitwork, the spineless, cultivated *P. tectorius* variety *laevis* is exclusively utilized. The latter bears only a Tahitian name, *paeore*. Presumably, it is not indigenous to the traditional Marquesan economy.

The wild pandan grows rarely behind the beach. Where moister zones approach the sea, however, *Pandanus* may be seen atop cliffed peninsular interfluves and in the plunging ravines that at intervals notch the barren coastal cliffs.

It is common to see groves extensive enough to form a distinct cover type and most conspicuously perhaps, in the ridgetop groves that cover rocky outcrops and old stone platforms, and up and down ravines within *Miscanthus* tall grasslands.

The appearance of *Pandanus* in *Miscanthus* tall grassland is interesting from the point of view of fire and succession. Several residents at Puamau asserted that fire kills *Pandanus*. The reliable informant, Henry Lie, added that "fire cooks the roots". One may hold reservations about the lethal effect on *Pandanus* of every light fire that might sweep by the trees, but in certain common circumstances, such destruction may be readily conceived.

In the course of a drought, decomposition of litter is arrested. The strap-like dead leaves, a meter or more in length, fall and accumulate beneath the crown and around the prop-roots in a high, loose pile. If the trees are also situated in a tall *Miscanthus* grassland, so much tinder-dry fuel would be available on all sides that fire sweeping the area would generate high heat. Survival of the pandans through such a conflagration would be remarkable, indeed.

Young trees are present in many grassland localities, attesting to lively seedling reproduction. Again, hot fires, were they to occur, would probably kill most of them.

Lacking more data, the role of fire in *Miscanthus-Pandanus* relationships remains moot, and interpretation of the status of present groves is difficult.

Surely, it would favor the maturation of *Pandanus* forests if burning stopped. On the other hand, the effect of many lighter fires, set at a time when the available fuel was scant or too damp to burn well, might serve the same effect, if the trees and seedlings were not all killed in a series of light ground fires.

The canopy of a mature grove of *Pandanus* is sometimes quite closed. The resulting shade and abundant litter then preclude much undergrowth. Here and there, however, sun-seeking *Psidium* preserves a place in the sun by assuming a very attenuated habit of growth, depending in part upon the larger *Pandanus* trees to support the spindly guava branches.

Groves and Forests of *Casuarina (Toa)*

Distinctive features of buttress ridgecrests in most valleys are groves of *Casuarina equisetifolia* (*toa*), a native tree of pinelike habit. In many other countries it is associated with maritime environments, but in the Marquesas, *C. equisetifolia* grows only incidentally near the sea and is common in the uplands in both transitional and pluviotropical zones. The ridgetop habitat is rather characteristic above the villages, but in fact, the tree thrives in a range of environments. Forests of *toa* cover steep, goat-grazed slopes in southern Eiaone, just west of Puamau. Elsewhere, *toa* forests dozens of hectares in extent, occur at 100-400m elevation on broad slopes in leeward Nukuhiva and Hivaoa and in the uplands of northern Tahuata. The species tolerates infertile soil and grows here and there in *Gleichenia* fernbrakes on all but sterile residual latosols.

In aboriginal times, the heartwood of *toa*, all but metal-hard, durably served Marquesans when fashioned into implements of war, so that widespread inland establishment of the tree may have been encouraged by Polynesian hands.

As *Casuarina* sheds its long, fine needle-like foliage, the duff accumulates rapidly to a depth of ten cm or more. Herbs grow sparsely in this loose, dry litter; a few scattered individuals of *Emilia sonchifolia* and *Polypodium scolopendria* are typical. At Puamau, two shrubs often appear in the soft shade on duff-covered ground—*Canthium barbatum* and *Canthium odoratum*. At Vaipaee one *Casuarina* grove was encircled by saplings of *Glochidion* sp. In the uplands of Tahuata, extensive groves of *Coffea arabica* grow amongst the *toa*.

Egler (1952, 252-256) has enumerated some of the ecological requirements of *C. equisetifolia*. Fire kills the tree, but the seeds germinate well in many burned-over sites. Strictly heliotropic, the seedlings require open sunny sites and bare mineral soil or rock. Once established, however, individuals may live for many decades if sheltered from fire.

Thus, the presence of *C. equisetifolia* on a site assures that the ground was barren of growth when seedlings established themselves and that the site has not since been burned over. Abundant growth of young-to-mature *Casuarina* trees aligned along the axes of ridgecrests around inhabited valleys seem to have sprouted along former open pathways where animal and human disturbance was once intense but more recently diminished, as hunting pressure upon feral herds has locally eliminated the animals, and as outboard-powered boats reduce the need for overland equestrian traffic.

Thickets of *Leucaena leucocephala*

Outstanding among the exotic plants that have assumed local dominance in fallow regrowth is *Leucaena leucocephala* (*atiko*; Fr. *acacia*), a deep-rooted tree of whipstem sapling habit that forms close stands. A deciduous, drought-resistant plant, *L. leucocephala* derives ultimately from Central American savannas. This leguminous tree, has spread slowly in the Marquesas; but where established, it has persisted tenaciously in both transitional and inland xerotropical localities. Thickets 6-8m tall and stem diameters up to 10cm are quite usual around Taiohae Bay, which is also a likely introduction site.

The areas of widespread establishment are limited to the islands of Nukuhiva and Uapou. For the record, on Hivaoa, two very local populations exist in Puamau village.

The attention of itinerant natural scientists has been drawn to the *Leucaena* thicket that extends more or less contiguously over most of the rugged terrain of southern Nukuhiva below 750m from Hakaui on the west to the heights east of Taiohae Bay, the port of entry.

Isolated thickets occur on the same island at Taipivai and on the northern shore at Hatiheu. On Uapou, additional large thickets, which I viewed from the sea but did not disembark to visit, extend over entire small valleys on the southern and western parts of the island. The largest valleys there, Hakahetau and Hakahau, have so far escaped being overrun. At Hakahau, small thickets occupy a few hollows on the slopes above the village; and at Hakahetau, I encountered a solitary individual on the dry slope above and west of the Catholic mission.

All ground cover is excluded within the thicket except in clearings or natural openings. Curiously, the shade of the foliage in full leaf is light and diffuse, suggesting that some factor besides shading accounts for the lack of undergrowth. The surface of the soil is covered by a thin blanket of duff composed of the fallen fine leaflets, twigs and petioles. No tendency toward a succession by native or introduced trees was observed (see Egler 1947, 417), even in senescent *Leucaena* stands where old trees become ungainly, lose their erect habit, and lean more or less perpendicular to the slope.

On one site at the xerotropical margin, on slopes above the eastern shore of Taiohae Bay, the *Leucaena* thickets grade into a seaward xerotropical cover, here much grazed by goats. The latter locality is notable for another peculiarity of site: the local abundance of *Acacia farnesiana*, which does not, however, yield dominance to *Leucaena* except in one or two ravines.

Inland, within the great Taiohae amphitheatre, the thickets occupy most of the lower portions of buttress ridges and other prominences about the valley that were probably once occupied by *Miscanthus floridulus* tall grass. In the ravines, *Leucaena* thickets give way to *Hibiscus tiliaceus* forest, but even here *Leucaena* invades cleared places and neglected coconut groves. In such open moist sites *Leucaena* grows well, maintaining foliage and

continuous growth for extended periods, to the chagrin of gardeners who would prefer to cope with less vigorous weeds.

In upland pluviotropical situations, *L. leucocephala* is less weedy and is encountered seldom in pluviotropical sites with residual soils. Tercinier, in personal communication, has suggested that the plant requires a calcium concentration not retained in the well-leached upland lateritic soils. The observed Nukuhivan habitats of *Leucaena* appear to bear out his suggestion, i.e., relatively xeric zones, skeletal soils on very steep slopes with much unweathered parent rock at the surface, and colluvial valley soils in the more moist localities.

Leucaena has extended its range rather slowly. The tree has been present at Taiohae for nearly a century at least (Drake 1893, 58-59) and remains local. Dry, ripe pods dehisced explosively on hot days at Taiohae, scattering the seeds several meters from the parent plant. More effective dispersal perhaps may be the scattering of seeds in the excrement of domestic and feral animals.

The plant is in disfavor in the Marquesas, and no effort to deliberately extend the range of the plant would be welcomed. Few recognize the several potentially great advantages of *Leucaena leucocephala*: as a source of protein-rich cattle forage and of very high-quality charcoal, and as a replenisher of soil nitrogen (Takahashi & Ripperton 1949). More immediate considerations in the minds of Taiohae resident are negative ones: the strenuous labor that clearing the thicket demands, and the unfortunate depilatory effect of the plant upon horses. Horses relish *Leucaena* foliage but lose all the long hair from their manes and tails after they eat it.

THE PLUVIOTROPICAL ZONE AND PLUVIOTROPICAL COVER TYPES

The pluviotropical, or moist, zone lies inland of the transitional zone and extends to the margins of the summit forest which is rich in species peculiar to the Marquesas and presumably much less disturbed in the course of human history than the sites that will be emphasized here. Included in the zone are all the interior forest types dominated by *Hibiscus tiliaceus*. Elevations begin near sea level in certain localities and extend higher than 900m.

Back Valley Forest

A number of garden trees persist for decades after a subsistence garden is left to grow back to forest. Inhabitants visit certain of these trees at intervals to collect their fruit. That is particularly true of coconuts, less so of breadfruit, but no grove of *Musa troglodytarum* (*hu'etu*), however remote from the village, may properly be called abandoned. Around such trees, a certain amount of clearing facilitates harvest activity, and an array of pluviotropical weeds grows in the resultant islands of sunlit ground within the forest.

In general, however, in those ravines farthest upvalley from the villages or difficult of access, few of the currently esteemed economic plants have persisted. It is likely that the more remote localities have remained out of cultivation 100 years or more, since the time of great depopulation (Schmitt 1965). That habitation—and with it, cultivation—once prevailed in these now lonely places is evidenced by the extensive stoneworks that everywhere occupy the gentler slopes.

Hau-Ihi (Hibiscus tiliaceus—Inocarpus fagifer) Forest of Backvalley Ravines and Box Canyons

In these very moist, fertile localities, conditions for pluviotropical plant growth probably approach a Marquesan optimum. Curiously, however, species diversity there is minimal in the mature forest. Of the available flora only two trees, *Hibiscus tiliaceus* (*hau*) and *Inocarpus fagifer* (*ihi*), dominate the mature forest, attaining heights of 10-15m. So dense is the shade beneath the foliage canopy that no herbaceous species tolerates the gloom.

A qualified exception is *Coffea arabica* (*kafe*) seedlings, which sprout by thousands, as described above. A fraction of them grow into spindly trees, 2-3m tall, to form a true understory. *Coffea* has invaded the pluviotropical forest of all the islands but Uahuka, where the plant is still common only in cultivation.

Ihi forms discrete groves, faring well in waterlogged soil, in streams, and along their banks. Sometimes it dominates the whole forest, as on the steep accumulations of talus and soil immediately below the cliffs of western Tahuata. Its dark yellow-green foliage distinguishes it at a distance from the equally somber but blue-green *hau.*

Aside from *hau* and *ihi*, few large trees prevail in the dank ravine bottom, excepting the long-lived banyan—*Ficus prolix*a (*aoa*)—and *Aleurites moluccana* (*ama*), *Terminalia* sp. (*mai'i*), and *Spondias dulcis* (*vi*, or *vi tahiti*).

Hau Forest on Backvalley Slopes

Above the deeper ravines, on the steep slopes of the backvalleys, *ihi* becomes uncommon and *hau* dominates the forest. Higher still, along and immediately below buttress ridge crests, *Pandanus tectorius* may in turn assume local dominance over *hau.*

Stature of this forest is shorter than in the ravine bottoms, around 5m for most trees, and the canopy is less dense, admitting enough light to support an herbaceous ground cover beneath a sparse shrubby understorey.

Coffea arabica flourishes in the understorey and is often dominant in it. Other shrubs and small trees in the understorey are: *Canthium barbatum, Glochidion* sp., *Wikstroemia coriacea, Morinda citrifolia,* and *Piper latifolium. Pipturus argenteus* appeared occasionally in such forests at Vaipaee. *Vanilla planifolia,* a succulent liana escaped from cultivation, festoons itself here and there among the branches in Puamau and many other valleys.

In the diffuse shade, *Oplismenus compositus* affords a sparse-to-dense ground cover. This grass prevails in the interior parts of Vaipaee. Several of the common ferns appear occasionally amongst the grass, notably *Nephrolepis biserrata, N. hirsutula,* and *Polypodium scolopendria.*

Depending on the locality, the *hau* forest grades variously into the mixed *Hibiscus-Pandanus* forest of the pluviotropical uplands, into transitional forest, or into ridgecrest cover types.

Bamboo Thickets

Discrete thickets of bamboo (*kohe*) appear erratically on slopes and broad interfluves in the pluviotropical zone, where they seem to persist remarkably well. F. Brown (1931, 91-92) names the bamboo *Schizostachyum glaucifolium* Munro, and calls the species indigenous to the archipelago.

Local needs for bamboo, for poles and light construction, are met largely from these groves.

Mango Groves

More common than bamboo thickets are imposing groves of *Mangifera indica* (*mako*) that occupy a space of a hectare or more in extent in the back valleys. Beneath the dense foliage of a mature grove, no other plant propagates but the mango itself, and its seedlings and root shoots may there form a dense thicket. Some of the groves increase in size if not actively discouraged. Mango persists exceedingly well in fallow regrowth. Swine root in the groves when fruit falls and probably help disperse the large seeds. Upon falling, fruits may roll several meters downhill on the steeper slopes, so that gravity plays a dispersal role. Old trees grow tall enough to rival coconut palms and banyans in height.

Hau He'e Forest Cover

The dominant in this cover type is the sterile form (*hau he'e, fau fe'e*) of the interesting dimorphic *Hibiscus tiliaceus* var. *sterilis*, which is quite probably an aboriginal cultigen, as it does not flower and must be propagated from cuttings. The fertile form, which the Marquesans call *hau ku'a*, resembles the prevalent local varieties of *H. tiliaceus*, and it reportedly flowers and sets seed normally.

Hau he'e, on the other hand, is different in most respects, easy to spy from a distance by its unusually slender, erect trunks, up to 20m tall. Close by, its leaves are seen to be one-third the size of ordinary *hau*, apiculate, and much more numerous on the branchlets.

I have seen both forms sprouting from the same cut stump, so that *hau he'e* appears to be a sport or chimaera, arising from the fertile form.

Hau he'e stems meet the local demand for long, slender, resilient poles in construction and as the handles of 10-to-15m long breadfruit-picking tools. In response to such need, *hau he'e* is cultivated to some extent, and small groves of it are to be seen on all the inhabited islands.

But there are very extensive stands of *hau he'e* at Vaipaee and elsewhere on Uahuka that far exceed any conceivable local need for long poles. *Hau he'e* dominates the fallow forest in the ravines in the northwest of Vaipaee. In a vegetatively propagated tree, its vigor and dominance there is worthy of note. It seems to occur in droughtier places than ordinary *hau* and upon the higher parts of slopes, but of course its occurrence may reflect old planting patterns more than ecological requirements.

Gleichenia Fernbrake

The pale, yellow-green fernbrakes of *Gleichenia linearis* are the most arresting element in the pluviotropical landscape. They stand forth as conspicuously there in the

vegetation mosaic as *Miscanthus* tall grassland does in the transitional zone. Both these cover types tend to occupy visibly prominent ridges and owe their maintenance to periodic burning.

The fern cover, like *Miscanthus*, occurs in great swaths on ascending buttress ridges around the valley margins, and the two cover types merge one into the other along an apparent moisture gradient. *Gleichenia*, unlike *Miscanthus*, appears not to thrive on the thin soil of steep, rocky slopes and seems to favor ridges with deeper soil and in fact, attains its most widespread development on the rolling-to-level deep latosols of the upland interfluves. Fernbrakes on the buttress ridges around the valleys are thus relatively minor facets of a cover type that becomes much more important at elevations between 300 and 900m.

Plate 5: Pluviotropical plant cover in Vaikivi, central Uahuka (elevation 435m); view toward southeast with island's summit (elevation 887m) in clouds at top left. The horse trail traverses *Gleichenia linearis* fernbrake. *Hibiscus tiliaceus* is dominant in the forest up to the clouds. *Pandanus tectorius* is co-dominant with it on the wooded ridges and nearer slopes here.

Observation in Hawaii, including quadrat studies, has established *G. linearis* as a fire-resistant plant and invasive in certain disturbed forest localities. Further, once established, the fernbrake appears relatively stable as a cover type, appearing to crowd out shoots of most other plants (Hosaka 1937; Kartawinata & Mueller-Dombois; MacCaughey; Vogl,44-46).

In vigorous, unbroken stands of *Gleichenia linearis*, few other plants occur in any but incidental abundance with the notable exception of the club moss, *Lycopodium cernuum*. Locally, groves of *Casuarina equisetifolia* seem to be invading the fernbrake, but the extensive development of this tendency would seem to be precluded by the sensitivity of *Casuarina* to fire.

Unlike the *Hisbiscus*-dominated pluviotropical forest, which is normally too moist to ignite, the fernbrake will burn after a few successive rainless days. Combustability is enhanced if the fernbrake has not been burned for several years, because in time the perennially ramifying dichotomous growth forms an accumulated tangle of dead stipes and fronds up to a meter or more deep, loosely matted beneath a sparse, coriaceous living canopy. Pertinently, the older the growth, the more difficult it is to traverse, and a frustrated hunter may set it afire simply to clear the way.

In Hawaii, *G. linearis* does not always succeed itself after burning. More often than not, burning this cover type in Hawaii seems to stimulate germination of grasses and woody species instead (Kartawinata & Mueller-Dombois; Vogl).

In the Marquesas, where none of the Hawaiian competitor species of *Gleichenia* are present, the regular succession of this fern by itself after burning is far more predictable. In the interior of Hivaoa, I observed *Gleichenia* sprouting from underground rhizomes in the ashes of a light burn of a low fernbrake that had been about 20cm tall. Elsewhere, the reports of informants about past burns were supported by other evidence, usually charred snags of trees in the midst of otherwise unbroken fernbrake.

Gleichenia does not bear repeated trampling. The plant is not palatable to livestock, but where horses and cattle traverse them, the fernbrakes are crisscrossed by countless lines of broken and trampled foliage. Under repeated trampling, the plant is unable to maintain its brittle stipes although the tangled fronds often overhang trails where they grow on slopes above the height of the animals' heads.

Within such stock-opened fernbrakes, several other species enter the cover along with *Gleichenia* and *Lycopodium*. In the uplands behind Puamau where horses are freed to rest and fatten, trampling is extensive and the grass-like sedge, *Cyperus brevifolius*, and a coarse herb, *Elephantopus mollis* (*fotapa*) are very common among the disturbed ferns. *Paspalum paniculatum* (*pufaro*), also grows among the ferns and locally forms relatively pure stands.

In the interior of Nukuhiva, in the Tovii basin, the *Gleichenia-Paspalum* association is very extensive. There, *Gleichenia* also associates itself with *Metrosideros* sp. in a kind of open fern savanna that is not elsewhere usual in the Marquesas but will be very familiar to students of vegetation in Hawaii, the Society and Cook Islands.

In both Nukuhiva and Hivaoa, *Paspalum conjugatum* is another grass often seen in the moist, grazed uplands but almost always in swales and in the semi-shade of open woods. Rather amazingingly, *P. conjugatum* was entirely absent from Uahuka in 1964, as far as I could tell in three months' field work.

Where grazing animals are not present in the fernbrake, as at Vaikivi, above the fall line in the upper reaches of Vaipaee Valley on Uahuka, the mat of fern cover is unbroken where it occurs, and the grasses and other herbs are to be found only in the path that traverses the region. In Vaikivi I could observe no tendency of the fern to invade and displace the pluviotropical forest. *Gleichenia linearis* does not grow in the shade of an unbroken *Hibiscus tiliaceus* canopy. In Vaikivi, the fernbrake had grown several years without burning. The mat of fern terminated abruptly at the edge of the foliage canopy of the forest, which was about three meters tall on the slopes. Except for a border of *Polypodium scolopendria* and *Ageratum conyzoides* in the narrow band of brighter light just beneath the thin edge of the forest canopy, a sparse cover of the shade-tolerant grass, *Oplismenus compositus* prevailed beneath the trees.

In sum, in the pluviotropical zone on poorer residual latosols, *Gleichenia* fernbrake is the most likely cover type in the presence of burning alone, giving way under the shade of *Hibiscus tiliaceus* and other trees, or, in the presence of both fire and animal pressures, to mixed *Gleichenia* and *Paspalum* grasses and other herbs.

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