

THE VEGETATION OF
MICRONESIA

1. GENERAL DESCRIPTIONS, THE VEGETATION OF THE MARIANAS ISLANDS, AND A DETAILED CONSIDERATION OF THE VEGETATION OF GUAM

F. RAYMOND FOSBERG

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F. RAYMOND FOSBERG

*Research Associate in Vegetation Studies
The American Museum of Natural History
Botanist, United States Geological Survey*

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INTRODUCTION

IN 1946, FOR THE REPORT of the United States Commercial Company Economic Survey of Micronesia, I wrote a description of Micronesian vegetation from observations made during that survey. It was, perforce, superficial and hastily done. Even so, and though unpublished, the paper apparently has been subsequently useful to a number of scientists and others concerned with Micronesia. It is the only extant account in English of the vegetation of that area. Many errors and inadequacies have been detected in that treatment, and it seems appropriate to present a revised, but still preliminary, sketch of the vegetation of Micronesia. This embodies the data included in the 1946 account, supplemented by the results of further study of that material, together with the results of later field work: surveys in the Marianas, Palau Islands, and some Caroline atolls in 1950, supported by a SIM (Scientific Investigations in Micronesia) fellowship under the auspices of the Pacific Science Board; visits to most of the northern Marshall Islands in 1951 and 1952; a two-month reconnaissance of Guam in 1953 and 1954; and a number of shorter visits to Guam and the Marshall Islands since 1954. All work after 1950 has been carried out as part of my duties as botanist on the staff of the United States Geological Survey, the 1951-1954 part of it being undertaken for the office of the Engineer, United States Army Forces Far East. In addition to the data made available by field work, the present report includes information gathered during an extensive examination of much of the available literature on Micronesian vegetation and flora. The completion of the study of all the material available and its presentation in final form will take considerable time. Meanwhile this preliminary account may satisfy the needs of at least some of the people interested in the vegetation and geography of Micronesia.

It is a pleasure to acknowledge my indebtedness to the institutions listed above, as well as to the United States Navy, the Office of the Quartermaster General, United States Army, and the Government of Guam, for facilities and support that made possible the work here reported. The Bernice P. Bishop Museum, the United States National Herbarium, and the

Library of Congress have generously provided facilities for work. Among the numerous individuals who have assisted in one way or another I must make especial mention of a few. Mr. and Mrs. Peter J. R. Hill, Mr. and Mrs. Ernest Holt, and Mr. and Mrs. Robert P. Owen provided welcome hospitality, companionship, and transportation for extended periods in Micronesia, as well as stimulating discussion of local geography and vegetation. The members of the Economic Survey Party and the United States Geological Survey Guam Party were both helpful and stimulating as field colleagues. Mr. Larry Bonham provided valuable information on the vegetation of Pagan. Mr. Manuel Calvo, of the Guam Department of Agriculture, provided transportation, information, and company in the field on several occasions. The Governor of Guam, the Honorable Richard Barrett Lowe, was generous with cooperation and hospitality. Mr. Edwin H. Bryan has been helpful in many ways and on many occasions. Dr. Harold J. Coolidge has given constant support and encouragement. To the Reverend Hugh O'Neill is due my deep gratitude for encouragement and facilities at a time when this project might otherwise have been abandoned. Dr. Frank E. Egler, Dr. Jack McCormick, and Mr. Peter Mattson have all read and made many constructive criticisms of the manuscript. Lastly, my associate, Miss Marie-Hélène Sachet, has worked tirelessly in compiling information from the literature and going over the manuscript many times. To all, my most sincere thanks.

Geographically, Micronesia covers a large section of the earth's surface, but is mostly water (fig. 1). There are approximately 117 islands, atolls, or closely associated groups of islands, but they are so small that altogether they constitute less than 1000 square miles of land. Stretching over 27 degrees of latitude and 44 degrees of longitude, Micronesia shows, as would be expected, great variation in climate and also much diversity in topography. In geological character the islands range from low coral atolls through raised coral islands and a great variety of volcanic islands to masses of metamorphic rock. For an excellent introduction to the general ge-

ography of Micronesia, see Gressitt (1954).

To produce a detailed account of the vegetation of such a varied area as Micronesia from observations made during a total of 12 months of field work is manifestly impossible. Many of the islands have never been visited by a botanist. With the advantage of previous experience with Pacific and tropical vegetation, however, it has been possible to arrive at an understanding of the major vegetation types and successions present and to write a general account of the plant communities and their distribution. For those islands and groups actually visited, or for which recorded information is available, individual accounts are presented. Relatively few of the southern atolls in the Marshall Group were included in the surveys, but it is probable that no major differences will be found from those described in the same climatic belts. Those atolls that are in the extreme south are likely to be wetter and more luxuriant than any so far described, but this greater precipitation probably does not result in more than minor differences in the vegetation. In the Carolines all islands not visited (except Fais which is topographically somewhat like Angaur and Peleliu) are low atolls, or low, isolated, coral islands. They are not likely to be very different from those atolls already described, but it is regrettable that there is reliable information on so few of the Caroline atolls.

The physiognomy of a vegetation (directly the result of the growth forms of the plants comprising it) is influenced mainly by four factors: (1) available water, depending on climate, exposure, and drainage; (2) substratum; (3) animal (including human) influences; and (4) history, principally that of climatic change and human activity. Thus it is that a major vegetation type or formation, such as montane rain forest, presents essentially the same appearance in the Pacific islands as in tropical America, even though there may be no species and but few genera in common.

The composition of a vegetation is related to the same four factors, but with an all-important additional one—geographic position, with the attendant particular regional floras on which to draw for component species. Available water and substratum are largely selective factors, determining the composition by excluding those species not well enough adapted to a given total environment

to establish themselves or to persist against competition. History and geographic position determine the flora available to be selected from, as well as influencing the other two factors.

Thus, in the text that follows, the physiognomic features described will be familiar to those who have had an extensive experience with tropical vegetation, while most of the species will be familiar only to those who are acquainted with the floras of the tropical Pacific.

The major climatic, topographic, and geologic features of the major island groups in Micronesia that influence vegetation may be briefly summarized, as follows:

The Marshall and Gilbert Islands, as well as Wake and Marcus Islands, are all atolls or low coral islands, with only a few meters, at most, of elevation above the sea. There is a major gradient in rainfall from north to south in the Marshalls, with the extreme northern islands quite dry, the southern ones very wet. A similar arrangement, but reversed, exists in the Gilberts. Typhoons occur but are not frequent in the Marshalls and are very rare in the Gilberts.

Nauru and Ocean Islands are elevated coral islands, platforms of limestone and phosphate rock, surrounded by cliffs and narrow coastal strips. Their climate is extremely variable, with occasional severe dry seasons.

The Marianas can be divided into two groups. The northern chain consists of young, mostly still active volcanoes, with steep slopes of ash and lava. The southern ones, from Farallon de Medinilla southward, are older, much worn-down volcanoes, capped or surrounded with elevated limestone terraces. The characteristics of the vegetation and available climatic data indicate that the Marianas, as well as the western Carolines, are in a climatic area with moderate dry seasons and many, often severe, typhoons.

The Western Carolines consist of three high islands or groups of islands and a number of low coral atolls. Of the high islands Fais is a somewhat elevated coral island. Yap is a mass of metamorphic and volcanic rocks surrounded by a wide fringing reef, and the Palau Group is complex. Its northern island, Babeldaob (Babelthuap), is a low, extensive, eroded volcanic mass, which has extensions

southward in Koror, Ngarakabesang, Malakal, and Aulupse'el Islands. The remainder of this group, to the south, is of elevated limestone, extremely dissected, steep, and rugged. The southernmost islands, Peleliu and Angaur, have rugged limestone ridges on extensive limestone platforms elevated a few meters above sea level. The entire group is surrounded by, or arranged on, a huge, almond-shaped barrier reef about 50 miles long. To the north of this, but usually associated with it, are two small atolls, Kayangel (Ngaiangl) and Ngaruangel.

The Central Carolines are all low atolls except the Truk Group, which consists of a cluster of small volcanic islands, the largest of which is Tol (Ton) Island, 361 meters in height, surrounded by a barrier reef on which are a number of reef islets of coral limestone similar to those on atolls.

The Eastern Carolines consist of two high islands, Ponape and Kusaie, and eight low coral atolls. Ponape and Kusaie are basaltic volcanoes, 791 and 630 meters in altitude, respectively, younger than the volcanic islands to the west but much dissected by erosion.

The climate of the Eastern and Central Caroline Islands is wet and not strongly seasonal. Westward in the group the seasons become more marked. Climatic data on the low islands of the Carolines are especially needed. Typhoons occur occasionally in the eastern and central islands and have caused serious damage a number of times within the present century.

The subject of classification of vegetation is in such an unsatisfactory state, especially with regard to tropical vegetation, that it seems inadvisable to try to force the array of Micronesian types into any of the schemes in vogue. Furthermore, most of the islands have not yet been studied in sufficient detail to allow any sort of true classification of the vegetation for the area as a whole. It is, in general, desirable to classify vegetation on the features of the vegetation itself and to exclude topographic and other habitat features as much as possible. However, at the scale of the general treatment of Micronesia, and because of the paucity of information on many of the islands, more understanding and clarity can be achieved by bringing in both plants and habitats as may seem necessary, and to arrange the descriptions in a classification of situations rather than strictly of vegetation

types. Where more detailed information has been available on certain islands, such as Guam, this arrangement is less satisfactory and is superseded in the part of the paper that deals specifically with Guam by a system based more directly on the vegetation.

While the concept of plant indicators is an old one and has been widely applied in temperate regions, in the tropics it has been little used, although it is fully as valid; potentially it may be even more useful. Information on environmental conditions in the tropics is less readily available than for other regions and is more difficult and expensive to collect.

One of the main objectives of much of the work on which this report is based was to gather as much information as possible on the extent to which the vegetation types of Micronesia can be used as indicators of environmental conditions, especially ground conditions that are not easily determined without actual local exploration. Some correlation was determined, on the basis of both recorded information and of new data collected in the field. In the General Descriptions of Vegetation Situations and Types, below, a paragraph is included after each major vegetation type, pointing out such indicator significance as is fairly reliably recognized. Many of the data are in such a preliminary state that they must be carefully worked over and checked before indicator relationships can be considered established.

On the basis of the admittedly inadequate information available on climate and vegetation, as well as the physiographic characteristics of the islands, an attempt has been made to indicate on a map of Micronesia (fig. 1) certain natural boundaries that seem to be of significance in the study of the vegetation of the islands. These, except for such obvious features as elevated limestone, recent volcanism, and sword grass, are not claimed to be objectively determined boundaries. They have been worked out on the basis of what is known of climate, substratum, and the general aspect of the vegetation. Because adequate objective criteria for the delimitation of natural regions are lacking, boundaries of this sort may be suggestive and may prove useful when the time comes to present a formal account of the biogeography of the Pacific area.

GENERAL DESCRIPTIONS OF VEGETATION SITUATIONS AND TYPES

MANGROVE FORMATION

THIS IS A WIDESPREAD and distinctive type of vegetation found throughout the tropics wherever there are low, muddy seashores, quiet bays, deltas, or estuaries. Only rarely do minor developments of mangrove occur under other site conditions. A sinking coastline obviously favors the development of this type, though situations can be imagined where a rising coast may expose tidal mud flats that were previously too deeply submerged for mangroves to take root. More likely, however, most exposed situations even on sinking coastlines would be covered by fringing reefs.

MANGROVE SWAMPS

Plates 1-3; plate 32, figure 2;
plate 33, figure 2

These are the natural vegetation of tropical, salt-water mud flats. Available mud flats are converted into this type of swamp almost as soon as they are formed because of the mode of propagation of the trees that form the bulk of the mangrove vegetation. Seeds of the mangroves of the family Rhizophoraceae have the peculiarity of germinating while still on the tree. From each seed a large, torpedo-shaped seedling, mostly root, is produced which hangs suspended from the fruit; when it reaches a certain stage, it falls to the water or mud beneath. If the tide is sufficiently low, the tree sufficiently tall, and the mud soft enough, the seedling may thus plant itself neatly in the mud. If not, it falls in the water or onto the surface of the mud, and at high tide, floats away, ready to take root at any place where it may be cast up or stranded in a suitable habitat. A large part of the conspicuous drift material left by the tide on tropical beaches is made up of these strange-looking seedlings, although few will develop on a beach exposed even to moderate waves. Their abundance in the water makes it almost certain that any exposed mud flat or other appropriate habitat will quickly become populated by a thriving stand of mangroves. This habit of the seedlings of planting themselves under and around the periphery of the parent trees makes it equally certain

that as soon as the first stand has reached fruiting age a new crop of seedlings will be planted, and the flat will be occupied by as dense a growth of mangroves as it can possibly support. Meanwhile seeds of other seashore and mangrove plants will drift in with the tide or be brought by birds, wind, or other means and take root, providing that portion of this distinctive vegetation which does not belong to the true mangrove family (Rhizophoraceae).

In general appearance the mangrove swamp is a dense broad-leaved evergreen forest, low near its outer edge but becoming 15 to 20 meters tall or even taller inward. It has a uniform, fine-grained, dark green appearance from above. The leaves tend to be entire, leathery, and rather small. Other than the peculiar seedlings mentioned above, the most striking thing about the trees of this vegetation is the strange appearance of the various types of aerial roots (pl. 2, fig. 1) and pneumatophores. Almost every mangrove species has some means of aerating its underground system in the form of thickened, spongy prop roots, high thin buttresses, knees, or thin, vertical conical projections. The form that these organs take is characteristic for each species, and the trees can be identified from them alone. The abundance of these pneumatophores, especially of the prop roots of the species of *Rhizophora*, makes progress for a man on foot through some parts of a thick mangrove swamp difficult or almost impossible. The easiest way to study mangroves is from a boat in the innumerable tidal channels that wind and intersect throughout the swamps.

Mangrove swamps in Micronesia are not so extensive or well developed as those in the subcontinental region farther west. Considerable areas exist around all the high islands in the Carolines in the form of narrow fringes along many stretches of coastline, with large swamps in estuaries and in filled lagoons (as in Kusaie). They are a much less conspicuous element in the vegetation of the Marianas and Marshalls. In the Marianas, only around the southern half of Guam is there any im-

portant development of this formation, and the creation of the large naval installations around Apra Harbor has destroyed the most extensive areas formerly existing on this island.

The principal tree species found in the mangrove vegetation in Micronesia are *Rhizophora mucronata*, *R. apiculata*, *Bruguiera gymnorrhiza*, *Sonneratia caseolaris*,¹ *Xylocarpus granatum*, *Lumnitzera littorea*, *Barringtonia racemosa*, *Heritiera littoralis*, and *Excoecaria agallocha*. Shrubs are *Clerodendrum inerme*, *Acrostichum aureum*, and *Nypa fruticans*; lianas are *Derris trifoliata*, *Smythea lanceolata*, and *Dalbergia candenatensis*, with *Davallia solida*, *Nephrolepis acutifolia*, and several orchids as epiphytes. A number of other species in each of these categories occur in Palau and Yap, or locally elsewhere, and several species from the strand flora, such as *Hibiscus tiliaceus*, *Hernandia sonora*, *Pemphis acidula*, *Intsia bijuga*, and *Wedelia biflora*, may occasionally or under special conditions be found with the mangroves. This strand infiltration occurs mainly near the edges of mangrove swamps, inland, or near the periphery of the distribution of the formation in Micronesia.

An interesting impoverishment of the mangrove flora takes place as one goes eastward or northward from Palau, where by far the greatest number of species are found. Northward in the Marianas, of the tree species, only *Rhizophora mucronata*, *Bruguiera gymnorrhiza*, *Xylocarpus moluccensis*, *Heritiera littoralis*, and *Lumnitzera littorea* are found on Guam, and in Saipan there is only one, *Bruguiera gymnorrhiza*, but two species of strand trees are added, *Hibiscus tiliaceus* and *Hernandia sonora*. In addition, several of the shrubby species are found here in the swamps, and at least one mangrove species, *Excoecaria agallocha*, occurs in strand vegetation. *Acrostichum* lines marshy shores as far north as Pagan. Eastward, *Xylocarpus granatum* seems to go no farther than Ponape. Other species stop at Kusaie, except *Sonneratia caseolaris*, *Rhizophora mucronata*, *Bruguiera gymnorrhiza*, and *Lumnitzera littorea*, which occur in the Marshalls, especially in the south. *Bruguiera gymnorrhiza* occurs very

rarely in the northern Marshalls, but is known there as isolated individuals (Bikini).

MANGROVE DEPRESSIONS

In the Marshalls are few examples of true mangrove swamps, with muddy or silty bottoms, but a modification, which has been termed "mangrove depressions" (Fosberg, 1947), occurs here and in the atolls of the Carolines. In these, several of the species of trees characteristic of mangrove swamps, especially *Bruguiera gymnorrhiza* and *Lumnitzera littorea*, as well as *Pemphis acidula* and *Intsia bijuga*, found elsewhere on dry limestone rock, grow in clear water in rock-lined depressions. Other depressions are muddy but separated from the sea. The water in different depressions is of varying salinity, and the floristic composition seems to differ with salinity. Some, at least, of the mangrove depressions in the Marshall Islands are abandoned taro pits into which the natives have thrown *Bruguiera* seedlings.

Nypa SWAMPS

Farther west, in the Malayan region, there is, according to various writers, a distinction between mangrove swamps and *Nypa* swamps, the latter being characterized by dominance of the stemless palm, *Nypa fruticans*. This is scarcely the case in Micronesia except in Guam, where extensive stands of *Nypa*, generally regarded as introduced, occur along some of the estuaries on the east coast. Elsewhere *Nypa* colonies (pl. 3) occur very widely in mangrove swamps, especially in openings, and along estuaries and tidal channels but can scarcely be considered to form a separate association or formation.

Barringtonia SWAMPS

A somewhat comparable situation exists with *Barringtonia racemosa*. This small tree is common along tidal channels in most mangrove swamps, seldom forming large stands except in Guam. Here, at least along the Talofof River estuary, occur extensive pure stands of this species in flat bottomlands inundated by the highest tides. These *Barringtonia* swamps have a dense, even canopy and little undergrowth. The ground beneath is peaty and firm, though wet, at least in the channels

¹ While this paper was in press it has been shown that the correct name for this species is *Sonneratia alba*.

between the root masses of the trees. As most of the Guam *Barringtonia* forest is in fresh water, this type is again referred to below in the section on the coastal plain.

Acrostichum SWAMPS

Acrostichum aureum is perhaps the most widely distributed of all plants of the mangrove formation, being found in both hemispheres, and extending in the Pacific to the southeastern islands of Polynesia. It is commonly mixed with other vegetation but occasionally, especially in the Marianas, forms rather extensive marshes and zones around bodies of water, usually brackish but in some areas fresh. It may form pure stands but is frequently mixed with *Clerodendrum inerme*, and in some places also with *Hibiscus tiliaceus*, as around Lake Susupe (pl. 24) on Saipan.

ENVIRONMENTAL RELATIONS OF MANGROVE SPECIES

Only a rough idea has been gained of the factors that control the local distribution of the principal species of the mangrove formation. A definite zonation is commonly observed, which may be sharply defined or blending. It may be correlated with a gradient inland from sea water through brackish to fresh. In general *Sonneratia* (pl. 1, fig. 2) seems able to withstand the most extreme saline conditions. Coral rock or sand substrata also may favor this plant and may be responsible for its extension farthest seaward. It does not occur in the innermost portions of the swamps or in mangrove depressions. *Rhizophora* (pl. 1, fig. 1) is ordinarily seen in situations almost as marine as those where *Sonneratia* is found, but usually on muddy or silty bottoms only. It seldom extends to the inner borders of the swamps and is not found in mangrove depressions. *Bruguiera* does not come so near to the open sea as the two foregoing but does occur inland as far as any trace of mangrove swamps is found. It is one of the principal components of mangrove depression vegetation and is found in pure stands in some of the landlocked ponds in the southern Palau Islands. It seems to be commonest in brackish rather than very saline situations. *Lumnitzera* and *Xylocarpus* both seem to grow mostly in habitats similar to

those of *Bruguiera*. *Barringtonia racemosa*, as a mangrove species, is seen chiefly along estuaries and tidal channels. It is, however, by no means confined to mangrove swamps. *Excoecaria* was found only in relatively open areas in mangrove vegetation but is also seen in rocky places in strand vegetation. *Nypa* patches (pl. 24) are found along estuaries and in openings near the inner edges of mangrove swamps, never much exposed to the open sea. In Guam the heavy waves of sea water driven in by the 1949 typhoon did considerable damage to the *Nypa* swamps. *Acrostichum* is found in open places and around the inner edges of the swamps, and, though able to endure very brackish water, it grows in some cases in perfectly fresh water. It may be characteristic of early stages in the successional development of this vegetation. *Clerodendrum* usually occurs around the edges, in openings, and with *Acrostichum*, and also extends into the strand and other types of vegetation, even to higher altitudes. The distribution of epiphytes on mangrove trees is very curious. They seem to occur on relatively few individual trees, but there in great abundance (pl. 2, fig. 2). Towards the inner borders of the swamps they become much more common and generally distributed.

There is no sharp boundary between mangrove swamps and fresh-water swamps (see p. 27). It is highly doubtful that the mangrove species really require salt water in their physiology. It has been demonstrated that the American mangrove, *Rhizophora mangle*, at least in its early stages, grows better without salt water (Egler, 1948). It is likely that most or all of these species are confined to saline areas by competition and migration ability rather than by physiological necessity. The boundaries between the mangrove and most forest types on dry land are sharp and easily seen.

INDICATOR SIGNIFICANCE

As an indicator the mangrove formation, in general, reveals a number of things. It dependably indicates flat land, exactly at sea level, usually with tidal channels, and water with at least some salinity. Cover from the air is usually complete. Mosquitoes are likely to be abundant. Spiny or prickly plants are absent, but at least one noxious tree, *Excoe-*

caria, is likely to be present, the latex of which is poisonous to the skin of many people and very dangerous if it happens to splash, squirt, or be rubbed into the eyes. Undergrowth is sparse. The substratum is ordinarily muddy, often very soft, but passability varies greatly with the different local types included in this formation. If *Rhizophora* is the dominant genus of trees in a swamp, it is likely to be nearly impassable to a man on foot, both because he will mire down in the mud and because he will have great difficulty in cutting through, even with a machete, the densely interlocking aerial roots. Where *Sonneratia* is abundant, travel is much easier. The substratum is more likely to be firm coral silt or sand, though it may be mud. The roots form a firm platform only several inches below the

surface, and, though the erect, slender pneumatophores are a nuisance, walking is almost always practical and fairly easy. *Bruguiera* is likely to be in soft mud, sometimes an organic muck that is extremely soft and jelly-like. If the stand is dense, the horizontal roots just under the surface of the mud, with their loop-like knees, give a precarious but passable footing. Otherwise travel is difficult. A dense stand of *Nyssa* is almost impossible to force one's way through. Between the plants the soil is usually soft and muddy. Open stands may be passable. Mechanized equipment is likely to mire down in any mangrove swamp. I have seen a bulldozer, in Guam, in the relatively firm *Barringtonia racemosa* phase of the formation bogged down so that it was scarcely visible.

STRAND VEGETATION

Plates 4-10, 23

Normally the strand is that portion of the land immediately adjacent to the seashore, under direct influence of salt water and spray. Thus on ordinary coastlines the strand is an extremely narrow belt at the top of the beach or on rocks just above high-tide level. Its flora is made up of halophytes. Fleshiness is the most common and obvious adaptation of these plants. Their sap is usually noticeably salty.

In Micronesia the strand is one of the most extensive vegetation types, occupying much more area than would be expected, even allowing for the enormous length of coast line bounding the islands; this is because the vegetation of coral atolls is almost entirely of a strand character (pls. 5-10), and the great majority of Micronesian islands are atolls or have barrier reefs with islets that are equivalent to atoll islets. These islets are not more than a few meters high at most and are exposed to the saline influence both of spray that blows in from the ocean, and of the brackish ground water.

Ecologically the strand may be regarded as comparable to a rather early successional stage, under ordinary conditions arrested in its development towards a mesophytic forest. Of unusual interest is the fact that in the interior of some of the wider islets of the low islands of the Carolines and southern

Marshalls, the development has been allowed, by the wet climate, lower salinity, and luxuriance of vegetation, to progress substantially towards a mesophytic condition. In some of them, except for the abundance of strand species, one could say that a true mesophytic forest type had been produced. Here, however, it is regarded as the wet end of a series of strand types based on the gradient of available moisture.

The vegetation of raised coral limestone may be regarded as belonging in the same succession, but because of the much lower salinity, different environment, and far richer flora, it is discussed separately (p. 21).

Normal strand vegetation exists on such portions of the coast line of all the high islands as are not occupied by mangrove swamps, and even on some of the mangrove coasts it occurs on a line of beach either outside or inside the mangroves. The strand around high islands may be volcanic or coral sand or gravel beach, coral rocks or bluffs, or volcanic rocks or bluffs. There are four main situations.

ON BEACHES OF HIGH ISLANDS

Plate 23, figure 1

Beaches, and sand flats or small dunes immediately behind them, present even more rigorous conditions than other strand situa-

tions, because they are made up of loose, shifting sands. Rather few plants have developed adaptations to cope successfully with this factor, especially as it is often complicated by high salinity, strong sunlight and heat, and the drying effect of wind. The plants so adapted have been able to occupy a habitat where there is little competition, and which is uniform over vast distances. Most of these successful plants also have means of readily crossing large stretches of sea, either by floating or by sticking to the feet or feathers of birds. Thus isolation has been incomplete, and little local evolution has taken place among strand species. Therefore one meets the same species on tropical beaches throughout the Indo-Pacific region, and some of them even in the Atlantic. Naturally there are usually some local additions to this strand flora in different regions. It is usually richer in continental or subcontinental regions and poorer the farther one goes from such places.

The relative uniformity of physical conditions on beaches leads to the development of a characteristic vegetation type, varying locally but recognizable anywhere. Most obvious and universal in this type, and usually occupying the position of most extreme exposure to salt water, coming down virtually to high-tide mark in places, is the beach morning-glory (*Ipomoea pes-caprae*¹). It is found throughout the tropics, wherever a beach vegetation develops, and is frequently dominant in the vegetation. Sharing its place in the loose sand on the beach slope may be *Sporobolus virginicus*, a harsh wiry grass, and *Thuarea involuta*, a trailing, mat-forming grass.

In Micronesia the only sandy beaches of volcanic material known to me are around the young volcanoes of the northern Marianas and a few at the mouths of rivers in southern Guam. Even there they are very restricted. The vegetation seems to be made up almost entirely of beach morning-glory, which grows in profusion.

Because corals, calcareous algae, Foraminifera, and mollusks live in great abundance in tropical waters, most beaches are of calcareous

¹ The Micronesian plant is *I. pes-caprae* subsp. *brasiliensis* (Linnaeus) van Oostroom, sometimes regarded as a species distinct from the *I. pes-caprae* of the Indian Ocean.

sand, composed of pulverized fragments of the skeletons or shells of these organisms. The vegetation on the lower part of the beach, just above high tide, is composed principally of grasses or beach morning-glory and other strand creepers, but at the top of the beach, and on the sand flats and small dunes immediately behind it one finds a much more complex vegetation. There may be a forest (pl. 23, fig. 1) of *Messerschmidia argentea*, *Hernandia sonora*, *Pandanus tectorius*, *Thespesia populnea*, and *Pisonia grandis*, and in some areas *Calophyllum inophyllum*, *Casuarina equisetifolia*, and *Guettarda speciosa*. The most important strand forest, the coconut plantation, is described below (p. 25). Scrub of *Scaevola sericea*, *Suriana maritima*, and *Wedelia biflora* is commonly found, as well as a varied herbaceous vegetation of *Ipomoea pes-caprae*, *Paspalum vaginatum*, *Thuarea involuta*, *Lepturus repens*, *Triumfetta procumbens*, *Boerhavia diffusa*, *Vigna marina*, and various introduced weeds that can thrive in spite of the salt. They survive apparently because their shallow root systems draw only on the upper few centimeters of sand, which are washed more or less free of salt by the rain (even though some of them can withstand complete washings with storm waters). Such weeds are *Eragrostis amabilis*, *Vernonia cinerea*, several species of *Euphorbia*, *Phyllanthus*, *Portulaca oleracea*, *Chloris inflata*, *C. radiata*, and, most obvious of all, *Cenchrus echinatus*. These sand flats merge insensibly into the more stable materials of the coastal strip.

Certain beaches are made up of large fragments of rock or boulders. On the active parts of these beaches, there is little or nothing in the way of vegetation. At the tops of beaches and on the rubble or boulder flats behind them, the vegetation is essentially that of the rock strand.

ON ROCKY COASTS OF HIGH ISLANDS

Plate 4

Except in the northern Marianas, coastlines of volcanic rock are not common in Micronesia. Where coasts have been lowered they are commonly lined by mangrove swamps, and where they have been raised there is an elevated fringing reef. In the northern Marianas the vegetation on rocks

exposed to salt spray is largely *Scaevola sericea* and *Wedelia biflora*, which form a thick scrub. In especially exposed places tufts of *Fimbristylis cymosa* are scattered over the rocks. Elsewhere in the few places where there is a volcanic rock strand, such as certain spots on Truk, Ponape, Kusaie, and rocky headlands on Babeldaob and Ngarakabesang in the Palaus, an open growth of *Pandanus* is common, with a scrubby scattered vegetation of *Scaevola*, *Wedelia*, *Derris elliptica*, and a herbaceous cover of *Ischaemum*, *Ipomoea pes-caprae*, and *Fimbristylis cymosa*. *Casuarina* forest and *Hibiscus tiliaceus* thickets are equally at home in strand localities and in second growth away from the sea, but the areas away from the sea are much larger; these types are described below.

Limestone rock strand is much more common in Micronesia than volcanic strand, and its vegetation is richer and more varied. Ordinarily on rocks there is a scrub or scrubby forest, with *Pemphis acidula*, *Scaevola*, *Capparis cordata*, *Hernandia sonora*, *Terminalia samoensis*, *Barringtonia asiatica*, *Pandanus*, *Thespesia*, *Excoecaria*, and *Casuarina*, tangled with vines of *Canavalia microcarpa*, *Mucuna*, and *Ipomoea tuba* (often mis-called *I. alba*). On the most exposed areas may be patches of *Fimbristylis cymosa*, forming a thick turf or scattered tufts. *Pemphis* often occurs in pure stands on limestone rock (pl. 4), and, in Micronesia at least, it seems to be almost confined to such habitats. This type of strand grades without a break into the vegetation of raised coral limestone, described below.

It seems probable that the local character of strand vegetation may be determined to a certain extent by the frequency and severity of typhoons. On Guam, the typhoon of November, 1949, produced several very conspicuous results. In some spots the vegetation on limestone rock just above sea level was completely killed, and in others only a few *Pemphis* roots remained alive (pl. 34, fig. 2). *Hernandia* trees and others were completely stripped of leaves, and the young growth was killed back. Either areas of young *Casuarina* on sand flats were killed outright, or young growth was blackened. In many exposed sandy stretches the sand itself was removed in great quantities. In coconut plantations as

much as a meter in depth of sand was washed out, leaving great mats of roots exposed, and in places the trees remain standing on top of a root mass a meter or so high (pl. 34, fig. 1). Almost all undergrowth had been killed.

Mention should perhaps be made here of the extensive beds of several "sea grasses" which are to be found in shallow water on reef flats and in bays. These communities have not been carefully studied, and only a general statement concerning their composition can be given, with no analysis of the distribution of the species. Of the algae almost nothing is known. Common seed plants are *Enhalus acoroides*, *Diplanthera uninervis*, *Thalassia hemprichii*, *Cymodocea rotundata*, and *Halophila ovalis*. These are so seldom found fertile that even their identities are often doubtful. *Enhalus* is the most conspicuous of the "grasses" that form dense beds where the water is reasonably quiet. *Diplanthera* and *Thalassia*, often with *Halophila*, form a sort of turf on shallow reef flats. These communities are important in supplying protection for small fish, both the young of the large food fishes and fish that never reach a large size but form the food for the larger fish.

ON CORAL ATOLLS AND LOW CORAL ISLANDS Plates 5-10

By far the most important areas of strand vegetation are on the atolls and other low coral islands. These are bodies of flat land built up from the skeletons of lime-secreting organisms, as much as several square kilometers in area and entirely covered by strand vegetation. The substratum is calcium carbonate derived from corals, calcareous algae, Foraminifera, and mollusk shells. In a typical atoll this is unconsolidated material in the form of sand, gravel, and broken rock, piled on a reef platform which is at or just above sea level. In the majority of Micronesian atolls examined there has been some consolidation of loose material, and in places bare, rough, beach limestone is exposed. Frequently there are depressions, marshes, or taro patches in or near the center of the land area. A normal transect across an islet from the inner or lagoon beach outward is as follows: The lagoon beach and the area immediately

behind it are sand; in the interior a higher humus content is developed, proportional to the rainfall, often with marshy spots, artificial depressions filled with muck for taro growing, or brackish ponds, in some places rock bottomed. As the outer beach is approached the material becomes coarser and more gravelly. Just inside the outer beach it is pure broken coral rock, usually forming a broad low ridge up to a meter or more higher than the flat, then extending in the form of shingle down to the surf line and reef flat, which is a wave-cut platform a few to many meters in width, exposed at the lowest tides. Here and there at any part of the platform the underlying rock, usually the consolidated material mentioned above, may be exposed. In general, the narrower the islet is from inner to outer beaches, the coarser is the material of which it is composed. Of course, there are local variations of this pattern, as in islets that are almost entirely sandy or others that are entirely of gravel or broken rock.

The vegetation varies in relation to the substratum and the history of human occupation. In many cases, what the original vegetation was can scarcely even be surmised, as most of the atolls in Micronesia have long been under human occupation. Any attempt at interpretation of the original state should await a detailed study of all the atolls, in order that any small undisturbed fragments of vegetation may be located and information from them pieced together. Only a description of present conditions is given herein, amplified by information from a few places where what seems to be original vegetation is still preserved.

Most of the islets except a few of the smallest and a few of the driest have been planted to coconuts (pl. 9, fig. 2) or coconuts and breadfruit. Thus, the basic vegetation is a planted forest of *Cocos nucifera*, with usually a large admixture of *Artocarpus altilis* and some other trees. The coconut plantation comes right down to the inner beach, with a scattering of wild trees, such as *Calophyllum inophyllum*, *Hernandia sonora*, *Pemphis acidula*, *Cordia subcordata*, and *Messerschmidia argentea*, and occasional bushes of *Scaevola sericea* and *Sophora tomentosa* along the beach above high-tide level. Undergrowth near the inner beach is scanty, except on the

wettest atolls, where several ferns, *Wedelia*, *Vigna marina*, and other plants form a dense ground cover. Commonly a sparse growth of *Lepturus*, *Ipomoea pes-caprae*, *Euphorbia chamissonis*, *Triumfetta procumbens*, *Thuarea*, *Fimbristylis cymosa*, *Cassytha filiformis*, and weeds covers the ground. The villages are ordinarily on the inner beaches, under the trees. Various weeds and cultivated plants are found around them.

In the interior, especially on the wetter islands, breadfruit is likely to be abundant, sometimes even more so than the coconut, even occurring in pure stands. The breadfruit trees are often of enormous size, in places towering above the coconut palms, and, as on Nomwin, may in places form a thick canopy that tends to shade out undergrowth. Other trees, such as *Morinda citrifolia*, *Pandanus*, *Guettarda speciosa*, *Pisonia grandis*, *Ochrosia*, *Hibiscus tiliaceus*, *Premna obtusifolia*, *Eugenia* sp., and, in some islands, one or two species of *Ficus*, are common, but ordinarily form a second story, not reaching the height of the breadfruit and coconut forest. Undergrowth, often very dense unless periodically cleared, consists of small individuals of the second-story trees plus *Wedelia biflora*, *Polypodium scolopendria*, *Nephrolepis*, *Asplenium nidus*, and *Tacca leontopetaloides*. In the Carolines, *Piper* is also found in the undergrowth, except in the most shaded parts of this forest. Controlling this undergrowth, particularly where it is made up of *Wedelia* and *Premna*, is one of the major problems of the native agriculturist.

Occasionally, especially on the wider islets, there are dry grassy openings with *Thuarea*, *Paspalum conjugatum*, *Digitaria*, and *Lepturus*, and marshes with *Cyperus javanicus* and *Jussiaea*. These marshes are almost entirely planted to taro-like plants such as *Cyrtosperma chamissonis* and *Colocasia esculenta*. In fact, on the wetter islands large excavations have been made to create artificial marshes, filled with muck from decaying vegetable matter, for the cultivation of these plants along with sugar cane, bananas, and even certain ornamentals which do not thrive in the drier or more saline conditions on dry land.

The breadfruit does not, ordinarily, live close to the outer beach although (except in

the drier islands) the coconut does. Just inside the beach is usually a dense, brushy strip of forest (pl. 9, fig. 1) with *Morinda*, *Messerschmidia*, *Soulamea amara*, *Pipturus argenteus*, *Terminalia samoensis*, *Pandanus*, *Cordia*, *Pisonia grandis*, and *Guettarda*, often tangled with *Canavalia*. This may be well developed near the passages between islets. At the top of the outer beach is a row of *Messerschmidia argentea*, and outside this a fringe of *Scaevola sericea* (pl. 7, fig. 1) sloping from the surface of the beach up to a height of as much as 5 or 6 meters. This fringe of *Scaevola* backed by *Messerschmidia* along the outer beaches is one of the most constant features of atoll vegetation.

On the drier islands in the Marshalls the strip of brushy xerophytic vegetation normally just inside the outer beach becomes very extensive, in some areas covering whole islets. *Scaevola* is the most important constituent of this vegetation, with *Pisonia* assuming dominance towards the interior and the inner side if the area is large. This *Scaevola* brush has little or no undergrowth and, where extensive, may be accepted as an indication of a dry climate.

In the sparser places in this brush, as well as in openings near the outer beaches, *Lepturus repens*, *Thuarea involuta*, *Fimbristylis cymosa*, *Cassytha filiformis*, *Triumfetta procumbens*, *Ipomoea pes-caprae*, and, in the northern Marshalls at least, *Boerhavia diffusa* form a thin ground cover.

On sand spits, the narrow ends of islets, and other places more than usually exposed to salt spray, is a lower brushy vegetation of *Scaevola sericea*, *Suriana maritima*, *Euphorbia chamissonis*, and small plants of *Messerschmidia* and of *Pipturus*, with *Lepturus*, *Ipomoea pes-caprae*, and *Triumfetta* between. Where the substratum is of rock, this may be largely replaced by *Pemphis*.

On pitted rock platforms, especially on the seaward sides of islets, a pure forest of *Pemphis acidula* (pl. 5) may be found in places, forming a dense, fine-textured growth up to 6 meters in height. The tree trunks may be up to 25 cm. or more thick and furnish the hardest wood found in the region. The seedlings of *Pemphis* in such situations start in tiny pockets of sand in erosion pits in the limestone. For such a hard wood, the trees

grow very fast. A fairly continuous cover may be formed in as little as 10 years and may reach 5 meters in height. The most conspicuous forests of this type are found on fairly dry atolls. In certain locations *Pemphis* forests are found growing on sand. Whether such a condition results from the drifting of sand over a rock substratum or whether this type of vegetation can gain a foothold on sand is not yet known.

On most of the atolls with moderate and heavy rainfall, which include the great majority in Micronesia, the interior of the islets was undoubtedly occupied originally by a more luxuriant forest, still of a strand character but more mesophytic than much of the present atoll vegetation. Remnants of this, or of an advanced secondary forest which is probably similar, still exist here and there, especially in the northern Marshalls. It has largely been replaced by coconuts. Usually it is a mixed forest (pl. 6, fig. 2), of varying proportions of *Guettarda*, *Pisonia*, *Cordia*, *Allophylus*, *Intsia*, *Eugenia*, *Ficus*, *Ochrosia*, *Soulamea*, *Barringtonia*, *Premna*, *Pipturus*, *Scaevola*, *Morinda*, *Pandanus*, *Messerschmidia*, and other trees and large shrubs. Any one or most of these genera may be lacking, and the forest is quite variable in stature, density, canopy, and amount of undergrowth.

A peculiarity of atoll vegetation is that almost any one of the above trees may be found in pure stands. This is especially true of *Pisonia grandis* and *Ochrosia oppositifolia*. From old records, as well as from modern indications, it appears that pure forests of *Pisonia* (pl. 8, fig. 2) were once one of the most characteristic and widespread features of atolls. Pure stands of other plants, such as *Scaevola*, *Pemphis*, *Lepturus*, *Sida*, *Portulaca*, *Messerschmidia*, and *Triumfetta*, are also occasionally found. The common occurrence of pure stands on atolls, unusual for tropical vegetation, is puzzling. It may be related to the generally rigorous nature of the salty atoll environment, as well as to the very small total number of plant species available.

In general, the pattern of vegetation on an atoll seems to be correlated largely with salinity, which, in turn, is controlled by the amount of rainfall and the area of continuous land surface. The body of ground water in the surface layers of an islet will be fresh to

the extent that the addition of rain water overbalances the inward diffusion of sea water. Casual observation suggests that the roughly concentric arrangement of vegetation types from extremely halophytic on the outside to more mesophytic in the interior represents a typical succession, or "halosere." It is much more probable, however, that these are arrested successional stages corresponding to the salinity of the ground water and the intensity of salt spray.

Around the villages and in cultivated and denuded places the weed vegetation is conspicuous. The more common weeds are shallow-rooted herbs, mostly annuals, living in the surface layers of soil that are kept washed somewhat free of salt by the rain. The more obvious species are *Cenchrus echinatus*, *Chloris inflata*, *Cynodon dactylon*, *Digitaria pruriens*, *Paspalum conjugatum*, *Eragrostis amabilis*, *Fleurya ruderalis*, *Portulaca oleracea*, *P. samoensis*, *Phyllanthus amarus*, various *Euphorbia* species, *Centella asiatica*, *Hedyotis biflora*, *Eclipta alba*, and *Vernonia cinerea*.

Strand conditions prevalent on atolls form a drastic limiting factor to permanent human occupation. The number of economic as well as other plants that can grow there is greatly restricted. Ordinary agriculture is out of the question. The coconut, *Pandanus*, and *Tacca* are the only food plants that will grow on virtually every atoll, including even the moderately dry ones. As wetter conditions are encountered the number of plants increases somewhat, but extraordinary methods must be resorted to in order to increase the food supply. The tendency for humus to disappear from the soil must be counteracted, and conditions more moist than normal must be maintained. Salinity and the extremely calcareous nature of the soil are further unfavorable factors. Breadfruit will, of course, grow in all but the drier situations. It and coconuts are the staple foods on most atolls. Low swampy places in the centers of some islets are excavated, and patches of taro (*Colocasia* and *Cyrtosperma*), with bananas, sugar cane, and other plants, are raised in muck produced from decaying vegetable matter thrown into the water and mud. A few fruit trees, such as limes, soursops, and certain varieties of bananas, are raised in fertile

protected spots, even outside the excavations. *Pandanus* in many varieties is everywhere (pl. 6, fig. 2). But, even at best, the inhabitants of atolls are forced, by the conditions of their environment, to utilize absolutely everything that grows there. The result is that, generally speaking, there are few plants on an atoll that are not used.

Certain islets were seriously denuded during World War II, either by the fighting or for other reasons, but early concern about the revegetation of these areas has proved quite unfounded. Vegetation has come back very rapidly. The succession has been different under different conditions. In some places, where the actual ground surface was not seriously altered, or where there is enough moisture to compensate for compaction of the surface, a woody vegetation of *Messerschmidia*, *Pipturus*, *Scaevola*, and other shrubs and trees tangled with *Ipomoea tuba*, *Canavalia*, and other climbers, has promptly reestablished itself. In compacted areas pure stands of *Ipomoea pes-caprae* (pl. 10, fig. 1), *Vigna marina*, or *Fimbristylis cymosa* are first to appear, or in some places mixtures of these and various weeds, notably two introduced woody species of *Pluchea*, *P. odorata* and *P. indica*. All of these are replaced sooner or later by an almost pure dense mat, a meter or more in depth, of *Wedelia biflora* (pl. 10, fig. 2). The factors influencing or causing the differences in these successions are not clear, and the eventual course of the successions is not known. This problem deserves much more study.

ON LOW ISLETS ON BARRIER REEFS AROUND HIGH ISLANDS

Around most of the high islands in the Carolines there are low islets resembling those on atoll reefs. They correspond almost exactly to atoll islets in their vegetation and environmental conditions. The only significant difference is that there may be more species in some of the wetter vegetation types on barrier islets. Some of these species are normally high-island ones.

ENVIRONMENTAL INDICATIONS

Strand vegetation, in general of course, indicates salinity. Places along the seashore

that display a substantial number of plants not normally found in strand vegetation are likely to indicate fresh-water springs. In the interior of atoll or barrier-reef islets special luxuriance of the vegetation, dense breadfruit forest, and taro patches are good evidence that the ground water may be fresh enough to be potable. They indicate, as well, a generally wet climate. Dryness of climate and salinity of ground water are indicated by extensive areas of *Scaevola* brush and xerophytic forest. Coconut or mixed coconut and breadfruit plantations indicate sandy or gravelly soil and, especially if dense, rather

little undergrowth, easily traveled through. Taro patches indicate soft mud, which may be shallow. A strip of xerophytic brushy forest at the top of a beach usually marks rough, broken, coral rock, ordinarily forming a low ridge. *Pemphis* scrub or forest is usually good indication of coral rock, often very rough. In either *Pemphis* or *Scaevola* scrub the growth is so thick that it must be traversed with the aid of machetes, and with *Pemphis* such cutting is difficult because of the hardness of the wood. Beach forest of *Pisonia*, *Hernandia*, and *Casuarina* usually has little undergrowth and is easily traversed.

VEGETATION OF RAISED CORAL LIMESTONE

Plates 11, 12, 25-31

PRIMARY VEGETATION

One of the most important and extensive vegetation types in Micronesia is the forest found on limestone that has been significantly elevated above sea level. Large areas of this occur in the southern Marianas, the southern half of the Palau Islands, and on Nauru and Ocean Islands.

It may be assumed that the limestone was laid down in the form of reefs which accumulated debris on their tops, as is seen in the low islands, and that it was subsequently elevated to its present position. During and after elevation three important processes operated to modify its surfaces: weathering of the rock to produce a residual soil, erosion, which tended to remove all loose or residual material, and solution, which pitted the surface of the rock and produced the extreme dissection and roughness evident in many places. Two strikingly different surfaces have been produced, depending upon whether the first or the last two of these processes have been dominant in an area. One is a relatively smooth surface with a usually thin layer of reddish or brownish soil, the other a dissected, often fantastically rough, hard limestone surface, called in Polynesia "feo" (pl. 23, fig. 2; pl. 34, fig. 2). In the latter, soil exists only in cavities and crevices, if at all. Large areas of the first type are found where there are extensive terraces, level or only gently sloping. The second type occurs on cliffs, bluffs, near the edges of terraces, and on cer-

tain areas of comparatively level terrace. All except the last of these are easily understood, as the drainage is rapid and effective on these steep and porous slopes. The last may be the result of internal drainage or some such cause. In many places a similar rough surface produced by different causes often exists on talus slopes and debris cones at the bases of cliffs. The distribution of these three surface types has been the determining factor in the pattern of present-day vegetation types and agricultural land (pl. 25). It is on elevated limestone of this sort that phosphatization has taken place, providing enormous deposits of phosphate rock. Although these are the source of important fertilizers, their presence has no obvious effect on the natural vegetation pattern. However, the mining of the phosphate rock for fertilizer destroys utterly the original forest and is followed eventually by the development of a scrubby second growth. It is possible that the absence of any noticeable direct influence on the vegetation by phosphate rock, in spite of the essential role of phosphorus in plant nutrition, may be evidence that the soils on the non-phosphatized limestone are sufficiently rich in phosphorus.

The vegetation of elevated limestone is a modified strand type; in fact, as noted above, the boundaries between the two are difficult to delimit. It is, especially in the aspect found on level areas with soil, or in very wet places, much more advanced than is the

strand in the particular vegetational succession leading from extreme halophytic scrub to mixed wet tropical jungle, the mesophytic formation of the tropics. Here the succession has progressed until the vegetation is a moist forest or a true rain forest or jungle, but still with many strand species or derivatives of them. The salinity has decreased to almost zero, except on sea cliffs and similar locations exposed to spray, with a resulting decrease in fleshiness and other characteristics of plants exposed to saline environments. Many halophytic species are able to persist, possibly because the calcareous substratum is likely to be alkaline. However, numerous other species have been added, and the flora is enormously richer than that of the strand vegetation from which this type was derived.

The most striking impression gained upon looking at the forest of these raised limestone areas is of its extremely mixed character (pls. 12, 25). Locally certain species tend to be dominant, but the type in general is hard to characterize by reference to dominant or even universally characteristic species. Certain habitat types may be separated out, most of which may best be described in connection with their particular islands or groups of islands. The highly developed forest on comparatively level land with some soil has been mostly destroyed, to give place to Japanese sugar plantations. Enough remains on Guam to show that it was a tall, closed-canopy forest, largely dominated by enormous wild breadfruit (*Artocarpus*) and banyan (*Ficus*) trees. With the exception of the abundance of these two trees the composition of this forest is probably not greatly different from the average of that on rough limestone.

Generally speaking, the most common trees on inland areas of elevated limestone belong to the genera *Ficus*, *Pandanus*, *Artocarpus*, *Intsia*, *Elaeocarpus*, *Aglaiia*, *Fagraea*, *Pipturus*, *Cycas*, *Claoxylon*, *Boerlagiodendron*, *Laportea*, *Eugenia*, *Premna*, *Guamia*, *Hernandia*, *Pouteria*, *Erythrina*, *Randia*, *Melanolepis*, *Cynometra*, *Semecarpus*, *Meryta*, *Pongamia*, and *Dracaena*. The undergrowth is of many genera, prominent among which are *Psychotria*, *Clerodendrum*, *Morinda*, *Tarenna*, *Polyscias*, *Maesa*, *Ficus*, and *Eugenia*. The whole may be tangled with such vines as

Canavalia, *Mucuna*, *Operculina*, *Caesalpinia*, *Gymnosporium*, *Freycinetia*, and *Schefflera*. Naturally, no single stand of this vegetation has all the genera listed above. Some are restricted to one area or the other. In Palau, most of this type of forest is on steep slopes (pl. 11, fig. 2), while in the Marianas it is largely on flat terraces and cliffs (pl. 11, fig. 1; pl. 30, fig. 1). Also, in Palau, many more species enter into the composition, and a characteristic feature is the abundance of tall, very slender palms, especially on the ridges.

Epiphytes, especially ferns, are common in these forests and are abundant in their wetter aspects. *Asplenium nidus*, *Polypodium scolopendria*, *Davallia solida*, and *Nephrolepis acutifolia* are common, both as epiphytes and on the ground, though, indeed, there is little difference between these two habitats on the rough phase of the limestone. Many smaller ferns and orchids are found on tree trunks and branches, along with abundant bryophytes and algae in wet areas.

The strangling habit is common among species of *Ficus*. Seedlings germinate on tree limbs, begin life epiphytically, then send down aerial roots which enter the ground and may be so numerous as to surround and kill the host tree. This habit was noticed particularly in Palau and Guam.

On bluffs and seaward slopes the forest is likely to be more brushy, with several additional genera, such as *Mammea*, *Barringtonia*, *Cordia*, and *Casuarina*. Some of the inland genera, such as *Artocarpus*, *Elaeocarpus*, and *Boerlagiodendron*, may be lacking. On cliffs a scrub is found, with some of the forest plants in dwarfed form, but with conspicuous additions such as *Bikkia*, *Capparis*, *Jasminum*, *Hedyotis*, *Canthium*, and various strand plants. At the tops of bluffs and cliffs, near the edges of terraces, especially in the Marianas where the exposure is to the open sea rather than to lagoons as in Palau, there often occurs a strip of dense scrub, possibly induced by wind and salt spray, made up of such genera as *Canthium*, *Eugenia*, *Jasminum*, *Callicarpa*, *Capparis*, *Psychotria*, *Scaevola*, *Bikkia*, *Pemphis*, and *Myoporum*. In places of extreme exposure this scrub becomes prostrate or gives way to a herbaceous ground cover of *Zoysia* sp., *Heliotropium anomalum*,

Hedyotis albido-punctata, *Evolvulus alsinoides*, and other species.

On the lower terraces in the Marianas the rainfall is evidently low enough so that species with the ability to lose their leaves during dry seasons have predominated. This has resulted in a monsoon type of forest, a rainy-green deciduous forest which lets in sufficient light so that the introduced lime berry (*Triphasia*), a viciously thorny shrub that is the scourge of travelers wherever it occurs, has in many places been able to invade the forest and form an impenetrable undergrowth. Among the trees that drop their leaves, at least facultatively, during dry seasons, are species of *Ficus*, *Erythrina*, *Laportea*, *Hernandia*, and *Pisonia*. Because of the time at which these observations were made, it is not altogether certain that some of the effects described are not due to the typhoon of November, 1949, and thus some of the species may not be deciduous at all. Only further observation during dry seasons which do not follow typhoons will clarify this point.

SECONDARY VEGETATION

Plates 21, 22, 28; plate 30, figure 2

Disturbance and clearing bring out great differences between the rough and smooth types of substratum mentioned above. On all the southern Marianas except Guam the Japanese cleared every available hectare of land with sufficient soil for agriculture. Thus, at one stroke the entire area of the smooth type of surface was converted from forest to grassland (sugar plantation). The rough type was not much disturbed except by logging and the construction of military installations. On Guam large areas of the smooth type are in coconut plantations. In addition, other extensive areas are now covered with almost pure stands (pl. 31, fig. 1) of *Pandanus tectorius* (*P. fragrans* Gaudichaud) which are regarded as the result of clearing in past times. It is realized that much more detailed study is needed to establish this as a fact, but observations of what appear to be successional stages leading up to this forest suggest that it is a sound conclusion.

In the Marianas are extensive areas where, owing to cultivation or to war activities, virtually all the soil has been cleared off the limestone surface. On these places, very ex-

tensive especially on Rota, a uniform vegetation of varying mixtures of *Ipomoea indica* and *Passiflora foetida* is found. Apparently because of the lack of soil few other plants are able to invade it. *Melochia* makes some headway, but little difference was noted between 1946 and 1950. The blanket of the two vines is quite dense and as much as 30 cm. in thickness. When the morning-glories (*Ipomoea*) are in bloom the display is quite showy.

The usual result of clearing and disturbance is the appearance, first, of thick growths of herbaceous weeds which grow in great luxuriance. Among these are *Cassia occidentalis*, *Malvastrum coromandelianum*, *Sida*, *Crotalaria mucronata*, *Asclepias curassavica*, *Euphorbia cyathophora*, *E. hirta*, *E. hypericifolia*, *E. prostrata*, *E. thymifolia*, *Phyllanthus amarus*, *Cleome viscosa*, *Portulaca oleracea*, *Mitracarpum hirtum*, *Borreria laevis*, *Blechum brownei*, *Sesbania sesban*, *Amaranthus spinosus*, *A. viridis*, *Emilia*, *Vernonia cinerea*, and *Bidens pilosa*, and a number of weedy grasses such as *Eragrostis amabilis*, *E. pilosa*, *Eleusine indica*, *Cenchrus echinatus*, *Chloris inflata*, and *C. radiata*. Later, brushy patches appear with *Melochia*, *Leucaena glauca*, *Morinda citrifolia*, *Carica papaya*, *Triphasia trifolia*, and other species, or large areas become covered with pure stands of *Melochia* (Rota and Saipan), *Leucaena glauca* (Guam), *Casuarina* (Saipan), or *Jatropha gossypifolia* (Tinian). Following this, or without this stage in the Palaus, vigorous secondary thickets or forest appears, made up of *Macaranga*, *Pipturus argenteus*, *Hibiscus tiliaceus*, *Casuarina*, *Abroma*, *Pithecellobium dulce*, and *Pandanus*, often with a dense undergrowth of shrubs such as *Triphasia*, *Morinda*, and *Melochia*. On Saipan, and to some extent on other islands, *Acacia confusa* (pl. 21, fig. 2) and *Albizia lebbek* form solid stands, either singly or together, and quickly take over sizable areas. *Casuarina equisetifolia* (pl. 26, fig. 1) does the same, but does not mix with the other two. Stands of these three species seem, in fairly dry situations, to exclude almost all other plants, but in wet places an abundant undergrowth appears beneath them.

Species of *Operculina*, a huge liana, cover large areas of this secondary forest as well as of bare ground, with a dense blanket of

tangled, large-leaved vines (pl. 22, fig. 2). In the areas on Angaur and Peleliu where the forest was killed but not removed by military activity, these vines covered the bare skeletons of the trees sufficiently to simulate the appearance of a living forest.

Some idea of the rapidity with which secondary forest develops may be gained from the fact that on Angaur, in 1946, large areas denuded in 1943 were covered by a dense stand of *Macaranga*, *Pipturus*, and *Abroma* 2 to 3 meters in height. In 1950, these same stands were from 10 to 15 meters in height and still very dense.

AS INDICATOR OF ENVIRONMENTAL FEATURES

It can be taken as virtually certain that no surface supply of fresh water is available on the limestone substratum under this type of vegetation. However, an extensive area of continuous elevated reef limestone is almost certain to be underlain by an abundant supply of ground water, which may be obtained by drilling, and which often appears as springs at sea level or at contacts with underlying volcanic material. These contacts are very obvious because of the sharp difference in vegetation and drainage pattern. The porous nature of the limestone makes it certain that all the rain that falls on an area percolates into the ground to augment the lens-shaped body of ground water, none being lost by run off. This porosity, however, also makes it necessary to be extremely careful to avoid pollution. Drainage from garbage disposal, sewage, waste oil, and leakage from oil or gasoline storage are all certain to drain directly downward into the body of fresh water, and such pollution, once accomplished, is practically permanent.

The limestone substratum, whether smooth or rough, is almost certain to be firm and is especially suitable for airfields and as a foundation for construction of all sorts. It is significant that all but one of the airfields and strips constructed by the United

States armed forces in Micronesia, and a considerable number in Okinawa (Colwell, 1946), were built on this sort of substratum. Coral rubble for surfacing roads and air strips is also certainly abundant in such situations. For the latter purpose it is well to distinguish between the forest that indicates smooth, soil-covered limestone and that on bare, rough rock, as the protective layer of soil maintains the limestone in a much softer, more workable condition than that exposed to air.

The perfect drainage on limestone makes the estimation of humidity affecting storage conditions much simpler than in other areas. The only factors that must be taken into consideration are the actual amount and incidence of rainfall, the temperature, and the effect of the vegetation itself in inhibiting evaporation. Here the difference between the permanently closed canopy of a rain forest and the seasonally open one of monsoon forest is important.

The effect of a limestone substratum on ease of travel varies, but varies more or less in relation to the vegetation. The smooth, soil-covered type of surface is easily traversed, unless the vegetation is second growth, in which case the undergrowth is likely to be dense and extremely thorny. If the undergrowth is of *Triphasia*, foot travel is impossible, and clothing is torn to shreds when one attempts it or clears trails or camp sites. In the rough, pitted, or dissected type the undergrowth is not so much of a problem, but the surface itself is very destructive to shoes, clothing, and any other equipment that comes in contact with it, and, if extreme, causes serious risk of bodily injury. Although cliffs are common, they are usually easily climbed because of the rough nature and the firmness of the limestone.

In areas where *Pandanus* is common, mosquitoes of the genus *Aedes* may be very abundant. In spite of the lack of standing water, they breed in abundance in the water collected in the bases of the leaves.

VEGETATION OF ROUGH LAVA FLOWS

In the northern Marianas occasional fresh, rough, lava flows, which usually originate on the sides of the volcanic cones and spread fan-wise to the coast, often form extensive,

gently sloping plains that stretch down to the sea, where they protrude as peninsulas (pl. 20). Nearly all of them end in low cliffs. Their surface is often incredibly rough, fully

as much so as that of ordinary pitted limestone, though less than in extreme examples of it.

The vegetation on these flows is a thick forest, thinning out to scrub near the sea. It has the same mixed appearance as that on limestone, and when examined is found to be made up largely of *Pipturus*, *Ficus*, *Melanolepis*, *Randia*, *Aglaia*, *Pandanus*, *Hibiscus tiliaceus*, *Morinda citrifolia*, and *Psychotria mariana*, with occasional *Trema*, *Elaeocarpus*, *Guamia*, *Pouteria*, and *Premna*. The last five occur especially towards the upper reaches of the flows. Undergrowth is sparse except for young trees of the above genera, and such vines as *Abrus*, *Operculina*, and *Freycinetia* (near the heads of flows). *Asplenium nidus* and *Polypodium scolopendria* are very common; *Pteris quadriaurita* and *Nephrolepis biserrata* less so, on the rough lava surface and to some extent in the trees. The species men-

tioned are all among those found on limestone in the southern Marianas, and the aspect of the vegetation is virtually identical with that on limestone. Much of this forest has been cleared and planted to coconuts, especially where soil has accumulated on the lava.

The similarity of the vegetation types on raised coral limestone and on rough lava flows, if, indeed, they are not to be regarded as one type, suggests that the physical characteristics, rather than the calcareous nature of the substratum, determine the vegetation on raised coral limestone. At least physically, rough lava and pitted limestone are similar, although chemically they are very different.

The indicator significance of this vegetation is the same as that for the type on rough coral limestone, except for such items as the use of the actual material itself. Indeed, they would be hard to distinguish from the air except by their geographic situation.

CASUARINA FOREST

Plate 19, figure 2; plate 24, figure 2; plate 26, figure 1

In the northern Marianas especially, but also in Saipan and Guam and locally elsewhere, are stands of pure *Casuarina equisetifolia*. They occur on both limestone and volcanic substrata, at high and low elevations, and on all types of slopes. There seems to be no common topographic factor in their habitats, but all young stands seen were on ground recently denuded or in extreme pioneer situations. In fact, no *Casuarina* trees were seen, no matter how old, that would not logically have had such conditions for their seedling stages, except the scattered ones that come up in grass. It is apparent that, although the older trees of this species exist quite satisfactorily in competition with other species, its seedlings can stand little or no shade or root competition except from grass. Trees of all ages are very susceptible to fire. *Casuarina* are among the most success-

ful colonizers of denuded areas, new volcanic material, and fresh sand flats, and, if protected from fire, will rapidly build dense, tall forests. Where they are dense enough to produce a heavy layer of "needles" on the ground, there is little undergrowth, except in very wet situations. Whether such lack is due to the chemical nature of the material or to the fact that the dry spongy layer prevents seeds from getting sufficient water to germinate has not been determined.

There are few common features indicated by this type of forest, except ease of penetration, lack of undergrowth, and a thick cushion of the deciduous branchlets or "needles." Visibility is fairly good. Considered in relation to particular topographic features, there is little doubt that significant and useful correlations could be worked out.

COCONUT PLANTATIONS

Plates 9, 18

The most extensive type of agriculture in Micronesia is coconut culture. Coconuts are produced by large palms which are grown in plantations on many types of land, from flat strand to elevated limestone plateau, lava

flow, and weathered volcanic slopes. Though usually planted in pure stands, in many places coconuts are mixed with breadfruit in varying proportions. Because such forests are planted, the trees are ordinarily regularly

spaced and, when well cared for, fairly free from underbrush. If the plantations are neglected, thickets of *Premna*, *Wedelia*, and other aggressive weedy species, and dense brakes of young coconut seedlings, self-sown, fill the spaces between the trees.

The ground between coconut trees is filled by a dense mat of thick, cord-like roots (pl. 34, fig. 1) just below the soil surface, so closely packed that it is hard to see how any other plant could gain a foothold.

It is highly improbable that any of the extensive coconut forests in Micronesia, or anywhere else for that matter, are "natural." Even the original home of the tree is unknown. In spite of the seedlings from drifted nuts occasionally seen, man seems to have been the usual agent for the distribution of the coconut.

In recent years the coconut has been virtually wiped out on Rota, Tinian, and Saipan by the attacks of a weevil (*Bron-*

tispa). This insect is now controlled by an introduced parasite, and the coconut plantations may be expected to reappear in those areas. In the Palaus, a rhinoceros beetle (*Oryctes*) has done great damage to coconuts, almost eliminating them locally, but this pest seems to be abating, and vigorous steps are being taken by the Trust Territory Administration to hasten its control.

So diverse is the terrain occupied by coconuts that, again, generalization is difficult as to features that are indicated by coconut plantation. It is usually traversable and open, always an indication of present or past human activity. Mosquitoes are likely to be common, as broken shells and old leaf bases, as well as trunk cavities, provide breeding places. Food and potable drinking water, logs for temporary construction, and leaves for thatch are available wherever there are coconuts.

VEGETATION OF COASTAL PLAINS

Plates 13, 14, 24

GEOGRAPHY

In Micronesia the coastal plain is a strip, usually quite narrow, of flat land behind the strand and behind the mangrove swamps on some of the high islands. It is ordinarily not more than a few meters above sea level, or not even that high. The substratum may be coral sand or rubble, or volcanic soil and debris from the slopes above, and is often quite high in humus content in the marshy places and taro patches. The boundaries between coastal plain and strand are often indefinable.

Such a strip is found around stretches of the coasts of Truk, Ponape, Kusaie, Babeldaob, the west coast of Saipan, on the central west coast and in valley mouths on the south and east parts of Guam, and narrowly around parts of the peripheries of such elevated coral islands as Rota, Nauru, and Ocean. Little of this habitat was seen on Yap, as the mangrove swamps commonly come right up to the bases of the slopes, though there may be significant amounts of coastal strip on some parts of its coast.

This strip may be the result of a slight elevation, perhaps a eustatic shift in sea level, as in Truk, where the foundation is calcare-

ous, exposing a fringing reef upon which debris is deposited from above. A slight lowering may also produce a coastal plain in valley mouths where filling in the manner of delta formation may take place. Where the land is too high for mangrove swamps, a coastal plain may be found. Also included here as coastal plain are lower areas, where the water is fresh, or almost so, with consequent distinction from mangrove swamps.

VEGETATION

Probably the original vegetation on this flat land was mostly tall primary rain forest, such as is described below (p. 27). Some of this, not much modified, still exists on Babeldaob, and perhaps a little on Ponape and some on Kusaie. Most of the land of the coastal strip has, however, been cleared and occupied by human populations for so long that it has an entirely different character and shows little or nothing of the appearance of the original forest.

The coastal plain is the area that is most favored as a place to live by the native populations of the high islands. As a result, it is mostly under cultivation. The vegetation of the coastal plain may be roughly divided into

two types or patterns depending on whether the substratum is relatively dry firm ground, or marsh and swamp.

The dry ground, where the villages are situated, is largely dominated by coconut (pl. 13, fig. 1) and breadfruit plantings, which are the most important agricultural crops. *Terminalia*, *Calophyllum*, *Ficus*, *Casuarina*, mango (*Mangifera*), and other large trees are common, with the addition in the Carolines of *Parinari glaberrima*. Groves of the ivory nut (*Metroxylon amicarum*), either natural or planted, are found on these coastal areas, especially in Truk and Ponape. *Pandanus* is common, as are thickets of *Macaranga*, *Acalypha*, *Morinda*, *Hibiscus*, and other secondary small trees. Yams (*Dioscorea*), *Alocasia*, bananas (*Musa*), *Curcuma*, and other useful plants are planted under the trees. Open areas are planted to dry-land taro, manihot, sweet potatoes, and other small crops. Undergrowth in places where cultivation is not active is largely of several species of *Dryopteris*, *Nephrolepis*, *Wedelia*, *Hedychium*, and various weeds. Openings dominated by *Ischaemum*, *Paspalum*, and other weedy grasses may represent patches of sweet potatoes planted by the Japanese during the war and since abandoned.

The marshes, where not under cultivation, are largely overgrown with brakes of the tall *Phragmites karka* (pl. 14), or with dense patches of *Scleria*, *Scirpus*, *Paspalum*, *Panicum*, *Saccharum*, or other sedges and grasses (pl. 32, fig. 1; pl. 33). On Saipan, Guam, and Truk are large areas of pure stands of *Phragmites*, a cane-like grass 2 to 3 meters in height (pl. 14). Scattered in these brakes may be occasional *Pandanus* trees. *Cyrtosperma* (pl.

13, fig. 2) and *Colocasia* are extensively cultivated in marshy places, especially on the coastal plain, and are important items in the diet of the inhabitants.

Swamp forests are a common feature of coastal plain and valley bottoms. In places they are extensions inward of the mangrove vegetation, changing in composition as the water becomes fresher. *Barringtonia* swamps may extend well up some rivers. A common swamp vegetation is an almost impenetrable tangle of *Hibiscus tiliaceus* (pl. 24, fig. 1). *Metroxylon amicarum* groves occur in swampy places on Truk.

The coastal plain vegetation, both primary and secondary, merges almost imperceptibly into the vegetation of the lower slopes of the mountains, and might be treated in the same category with it, though such factors as drainage and soil are very different.

ENVIRONMENT

On the drier parts, conditions of penetrability and substratum are such as might be expected from a mixture of habitations, cultivation, tree agriculture, and thicket. Passage is easy. Mosquitoes are likely to be abundant, and water supplies polluted.

The wet parts are passable on foot if cultivated, in spite of the deep mud. Reed brakes are practically impassable except for short distances. The ground beneath is mud and the canes are so dense as to require constant cutting and pushing aside, and the effort wears a man out in a short time, especially in hot weather, when the windless atmosphere is damp and steamy. Mosquitoes are abundant. It is impossible to see more than a yard or two ahead.

LOWER PRIMARY FOREST

Plate 15, figure 1

VEGETATION

There seems little doubt that the coastal plain and the slopes up to about 300 meters in altitude on the volcanic islands in the Carolines were once completely covered with a well-developed, tropical rain forest. Some remnants of this persist even today, after hundreds of years of destructive human activity on the part of the natives and a few years by Europeans and Japanese. On the west coast of Babeldaob and the north coast

of Ngarakabesang in the Palaus, on the tops of some of the mountains in Truk, and on the slopes of Kusaie (pl. 15, fig. 1) are areas of varying size that seem relatively undisturbed. Perhaps the largest continuous areas are on Ponape.

This forest is of large trees, in many places forming a dense canopy. Undergrowth is sparse in the parts that are well shaded and on not too steep slopes. Ferns, both terrestrial and epiphytic, are abundant. Where this

type still exists on the coastal plain, with a gradual transition into mangrove swamps, as in the river valleys on Babeldaob, a spectacular type of jungle is to be seen, similar to the imaginative jungle pictures often seen in books. Large-leafed climbing aroids, festooning vines, huge gingers, and great buttressed tree trunks clothed with epiphytic ferns and orchids overhanging dark pools and streams are the striking characteristics of this aspect of the forest. Farther up the slopes tall, straight tree trunks, deep shade, ferns, and thin underbrush of shrubs and of seedlings of the trees form the dominant notes where the forest has not been seriously disturbed. In most places, however, there has been more disturbance. Trees have been cut for logs; roads, trails, and fortifications have been constructed; small areas have been cleared; and landslides have torn great gashes on the slopes. With more abundant light, dense tangles of undergrowth and vines line the edges of the forest and make penetration difficult and walking impossible without the constant aid of a machete.

As with most primary tropical forests, the composition of this type is exceedingly varied, especially on Palau. During our visits, there was little opportunity for systematic study of these areas. The trees are so large that they must be cut or climbed for any material to be secured—processes that are laborious and time consuming. Consequently only a suggestion of the great number of genera represented can be given here. *Parinari*, *Campnosperma*, *Cynometra*, *Dysoxylum*, *Semecarpus*, *Ficus*, *Calophyllum*, *Clinostigma*, *Ptychosperma*, *Elaeocarpus*, *Randia*, *Fagraea*, *Eugenia*, *Pittosporum*, *Horsfieldia*, and many other genera of trees form the basic structure of the forest. *Freycinetia*, *Canavalia*, *Piper*, *Schefflera*, *Caesalpinia*, and *Merremia*, and several aroids, several asclepiads, and especially several large species of *Ipomoea* form tangles around the edges and in the canopy.

The lower primary forest is one of the two

vegetation types in Micronesia that are of great importance as sources of timber for construction purposes. A properly conducted timber survey would yield, as a by-product, much valuable information on the composition, structure, and behavior of this type. The Japanese maintained several small sawmills to utilize this resource. There seems little question that this forest and that on the raised limestone on the north end of Guam, if managed properly, would be capable of supplying the lumber needs of Micronesia. For this reason it is imperative that no more of the forests than have already been cleared be utilized for agricultural purposes. Most of the slopes still wooded are so steep that they will not support a permanent intensive agriculture, because leaching and erosion are very active in such a wet climate. The need for timber is so great and so constant that it would be very wise to conserve any tall forest that still remains. Lumbering operations must, for the same reasons, be supervised with great care, so that they do not produce a scrubby, decadent condition in these forests, as has occurred in many parts of the world. Proper utilization for lumber is also entirely consistent with watershed protection, except perhaps on very steep slopes.

ENVIRONMENT

This type of forest indicates slopes of volcanic soil, often well weathered, largely clay in nature. There are usually streams of fresh water. The lack of undergrowth makes traverse easy, except for fallen trees and occasional thorny vines, wherever the canopy has not been destroyed. Where this has happened there is likely to be an impenetrable tangle of vines and brush. Visibility, except in brushy areas, is excellent for short distances. The ground under foot may be very slippery because of the clay. *Semecarpus* is a tree in this forest that causes severe contact dermatitis in some people. The sap or latex is especially dangerous.

SECONDARY FOREST ON SLOPES

Plates 21, 28

VEGETATION

As noted above, much of the primary forest has been cleared and the land used for agricultural purposes. This is true of most of the

area of the volcanic islands up to about 200 meters in altitude. Above this elevation the slopes become so steep that they have been less disturbed.

Although most of this land is too steep to be suitable for ordinary agriculture, because of erosion and leaching, an indigenous type of cultivation has been evolved that is eminently well suited to such terrain. This is a mixed planted forest of coconuts and breadfruit. From a distance such a stand resembles natural forest rather than planting. Spacing and arrangement are not at all regular, but are more suited to the terrain. Bananas, citrus, papayas, dry-land taro, yams, and *Alocasia* are commonly raised on the slopes beneath the trees, along with other minor crops. In wet depressions and seepy places are small patches of wet-land taro and in some places *Cyrtosperma*. In general the ravines seem to be planted more completely to breadfruit, while the ridges are given over to coconuts. The slopes between the two average about equal proportions. On Ponape and Palau some slopes are planted to pure stands of coconuts.

On some of these slopes are thickets of native shrubs and trees. These may indicate former cleared areas that were not replanted to coconuts and breadfruit. Recent clearings, such as those made by the Japanese during the war for sweet potatoes and cassava, first grow up to dense grass, largely *Paspalum*, *Digitaria*, and *Ischaemum*, then are taken over gradually by shrubs and small trees of a weedy type—*Macaranga*, *Commersonia*, *Glochidion*, *Acalypha*, *Melochia*, *Premna*, *Boehmeria*, *Hibiscus*, and other genera. If not burned this becomes in a few years typical secondary forest of the above genera, plus others, with a dense tangle of underbrush and an abundance of vines, mainly *Canavalia*, *Ipomoea*, *Merremia*, and *Cayratia*.

On Ponape and Kusaie most of the slopes occupied by secondary vegetation have been taken over by stands of one species, *Hibiscus tiliaceus*, which in many places forms an impenetrable tangle, so dense as to exclude most other plants. *Hibiscus* plants are scarcely to be considered trees. They are

coarse, extensive, tangled, shrub-like plants with springy trunks and branches up to 10 cm. or more in thickness, rather low, presenting a virtually unbroken surface of large, dark green leaves to the light. This *Hibiscus* scrub seems to be favored by steep slopes. In places, along the paths of landslides, it reaches almost to the tops of high mountains well into the upper forest zone.

In the Marianas and western Carolines much of the land that would be expected to bear secondary forest has been burned so frequently that the forest has been replaced by coarse grassland, a type that is discussed below. However, thickets and tangled forests of *Macaranga*, *Glochidion*, *Parinari*, *Pandanus*, *Dracaena*, and *Symplocos* are common. In certain localities *Leucaena glauca* forms dense, pure stands, with nothing beneath it except its own seedlings, which come up as thick as a lawn. In the volcanic portions of Guam is a secondary type of mixed forest consisting of many of the species found on raised limestone, but characterized by the scattered occurrence of the introduced *Areca catechu*, the betel palm. This forest is quite variable in composition. Often it includes coconut palms and even bamboo clumps. It may be much overgrown by vines and frequently has a spiny undergrowth of *Triphasia*. It is termed "ravine forest" from its frequent occurrence in ravines and on steep slopes (pl. 35).

ENVIRONMENTAL INDICATIONS

Secondary growth indicates human activity, past or present. It is likely to be dense, tangled, and difficult to penetrate until it gets quite old. An old, undisturbed secondary forest, with a closed canopy, gradually becomes more open beneath, as the undergrowth yields to shading and perhaps root competition, and becomes similar in its environmental aspects to primary forest in the same locations.

MONTANE RAIN FOREST AND CLOUD FOREST

Plate 15, figure 2

CHARACTERISTICS

Botanically, perhaps the most interesting type of vegetation on tropical islands or tropical mountains is the scrubby, wet, drip-

ping, mossy forest that occurs on steep slopes and crests extending into the cloud zone. The thin, leached soil and steep, windswept terrain do not permit the growth of tall trees.

Except in sheltered ravines and occasional flat places the trees have a low bushy growth habit, some with bare trunks and branches and broom-like tufted tops. On the crests they are even more gnarled and dwarfed. Mosses and liverworts cover everything to such an extent that the terms "moss forest" and "mossy forest" have been applied with good reason. Epiphytes are more abundant than in any other type of vegetation. Ferns are omnipresent. Undergrowth is so dense as to make it necessary to cut one's way at every step with a machete when traversing such a forest.

There is no definite correlation with altitude in the distribution of the cloud forest. It may be found above 500 meters on one tropical island, down almost to sea level on another, and in a belt between 1000 and 2000 meters on another. In continental areas it is usually quite high, and two belts, a true cloud forest and a montane rain forest just below it, can be recognized. In the Andes, for example, a great belt of forest of these types extends from about 1000 to 3500 meters in altitude. The determining factors for cloud forest seem to be mainly rugged topography and a cloudy climate, with almost continuous rain. In Micronesia these conditions obtain only on Ponape and Kusaie (pl. 15, fig. 2), and two belts, cloud forest and montane rain forest, can scarcely be distinguished.

Although cloud forest is a definite forest type found in the tropics wherever proper conditions prevail, the variation in composition is greater than that of almost any other general sort of vegetation. Diversity of flora is encouraged by geographic remoteness or by any sort of broken terrain resulting in isolation. The fact that this cloud forest is characteristically a montane or insular vegetation insures extreme isolation, and local endemism is more highly developed here than in any other part of the area.

Owing to the economic bias of the 1946 survey, when I visited Ponape and Kusaie, very little time was spent in this interesting part of the vegetation in Micronesia, because of the comparative paucity in economic species and the fact that in Micronesia people do not live there. Consequently the information available as to the local diversity in

physiognomy and the actual floral composition is meager. Prominent genera of trees are *Elaeocarpus*, *Astronidium*, *Clinostigma*, *Cyathea*, *Claoxylon*, *Eurya*, *Timonius*, and *Psychotria*, with vines such as *Piper* and *Freycinetia* climbing on their trunks and forming tangles. The undergrowth is mostly of a multitude of fern species, with small specimens of the trees and a number of lesser shrubs. *Marattia*, *Dryopteris*, *Tectaria*, *Polypodium*, *Lindsaya*, *Elaphoglossum*, and *Asplenium* are abundant fern genera, occurring both terrestrially and epiphytically. This type of forest is the home of an abundance of filmy ferns, *Trichomanes* and *Hymenophyllum*. Orchids of a number of genera are also common, some terrestrial and some epiphytic.

Although economic plants are not at all prominent in this forest, the vegetation as a whole is of tremendous economic importance. A blanket of such a dense, moss-covered vegetation, with the quantity of humus that the cool temperature permits to accumulate, acts like a great sponge to soak up the water that continually falls on it, passing it on to the porous basaltic rock on which it grows. This rock forms the natural water reservoir that makes continuous human activity possible on these islands. As long as this cover is maintained intact, there need be no worry about a continuous water supply for any reasonable human population. Such a need is so much more important than any other economic factor on an island, that it is unthinkable that this area should be used for any other purpose than as a watershed.

The native populations here do not live in the cloud forest. In fact, except for a few hunters, they seldom if ever go there. Grazing is the only activity that will ever likely encroach on this forest, and it should be discouraged. For preservation of such a forest, hunting or any other means of reducing populations of wild hogs, deer, cattle, or other introduced large animals that happen to gain a foothold, should be given every sort of encouragement. This type of forest, at least on islands, is rapidly broken down by the trampling, rooting, or browsing of large animals, as it originated in the absence of such animals, and the component trees are not able to withstand these disturbances.

ENVIRONMENT

The cloud forest indicates a continuous humidity of almost saturation, a very high rainfall, little sunlight, cool temperatures, and, in places, high winds. The slopes are steep, the ridges narrow, the footing is insecure and slippery, and the undergrowth is so dense as to be a continuous obstruction. On the ridges the vegetation may be dwarfed

and scrub-like, and it is almost impossible to cut trails through it. The leaves and moss cushions are likely to be so wet as to saturate clothing in a few moments. Water supply is usually not a problem, but camp sites are sometimes very hard to find, and waterproof camping equipment is essential. Dry wood is scarce. Trails in this type of forest become canals of mud after very little use.

DWARF VEGETATION ON OPEN CRESTS

On summits or high slopes of many tropical mountains there appears a vegetation characterized by its dwarf stature and dense, wet, tussocky nature. This, as is the cloud forest, is dependent on high rainfall, but with the additional factors of frequent high winds and extreme exposure. The paramos of the Andes and the "open bogs" of the Hawaiian Islands are good examples from parts of the world where this type is prominent and well known.

Floristically the composition is usually even more varied than in the cloud forest, as isolation is more extreme and evolution has taken various paths without the check of continuous influx of plants from adjacent areas. Here are often found great numbers of very restricted, endemic species. The plants found are often dwarfed specimens of the components of the forests below, with a liberal admixture of others characteristic of such exposed areas.

If this vegetation were not of such extreme scientific interest, it would be scarcely worth

mentioning in a report on Micronesia, as it occurs only on the summits of a few peaks on Kusaie and Ponape. On Kusaie there was a brief opportunity to study this type, but I was not able to spend the time necessary to climb the highest peaks on Ponape, so I know nothing about them except from reports of others (Glassman, 1952; Hosokawa, 1952). On these peaks the dwarf vegetation is mainly of ferns—*Nephrolepis*, *Gleichenia*, *Davallia*, *Lycopodium*, and other genera—with great banks of mosses and liverworts. A few trees of *Elaeocarpus* have gained a foothold, or perhaps have persisted, their trunks embedded in great moss cushions, with epiphytic orchids and ferns in abundance. The presence of *Blechnum orientale*, *Gleichenia linearis*, *Lycopodium cernuum*, *Melastoma malabathricum*, and a dwarf *Isachne* related to *I. confusa* suggests an affinity with the next type to be discussed, though the nature of this relationship is obscure.

"SAVANNA" OR GRASSLAND VEGETATION

Plates 16–20, 35–40

CHARACTERISTICS

On the volcanic (and metamorphic) portions of many of the high islands are grasslands of varying extent. These are most extensively developed on Guam, and Safford (1905) has called them "savannas" (although they are not flat, nor do they always have scattered trees, as the word suggests). There they coincide, roughly, with the limits of the volcanic portions of the island. The vegetation of the northern Marianas is mostly of this sort, and there are large areas of it on Palau and Yap. It is characterized by a pe-

culiar and very interesting aggregation of species of plants which varies somewhat from island to island but which is easily recognized wherever encountered. Ecologically this type presents some intriguing problems, the answers to which are by no means all available yet.

The plants characteristic of this type of vegetation are *Miscanthus floridulus*, *Heteropogon contortus*, *Dimeria*, and various other small grasses; many sedges, principally species of *Fimbristylis*, *Scleria*, and *Rhynchospora*; ferns and related plants, such as

Gleichenia linearis, *Lycopodium cernuum*, *Cheilanthes tenuifolium*, *Lygodium scandens*, and *Blechnum orientale*; shrubs and herbs, such as *Geniostoma*, *Eurya*, *Melastoma malabathricum*, *Pandanus*, *Myrtella benningseni-ana*, *Glossogyne tenuifolia*, *Nepenthes mirabilis*, *Morinda pedunculata*, several species each of *Hedyotis*, *Euphorbia*, and *Phyllanthus*, and a number of others. Some of these species are confined to savanna areas. Many of them extend into or persist in other types of vegetation, especially secondary ones. Sometimes one will be found growing in an almost incongruous place. On Guam and Saipan, *Miscanthus*, for example, grows in several places on bare limestone (pl. 40, fig. 2), though it is normally a good indicator of volcanic soil. In these spots, sword grass is found to be exposed to strong winds or to full sun and often is not accompanied by any of its habitual associates. It is the association of any considerable number of savanna plants, together with the typical physiognomy of the savanna, that makes them of use as indicators. In some islands the occurrence of several of these species in an otherwise limestone region is sufficient to suggest a search for a volcanic exposure.

This vegetation is quite variable in aspect, because of the varying degree of dominance of several of its principal components and the varying composition of the type from island to island. In its most extensive form it is dominated by sword grass, *Miscanthus floridulus* (pls. 36, 39), with other species occurring in burned or eroded spots or on rock outcrops. On Guam many level or gently sloping areas are covered by a low, finer grassland of *Dimeria chloridiformis* (pl. 35, fig. 1; pl. 36 fig. 1). Scattered bushes occur, and often seedlings and small trees of ironwood, *Casuarina equisetifolia* (pl. 36, fig. 1; pl. 37). These are apparently much more noticeable now than formerly, at least in the Marianas, and it is said locally that the Japanese planted them. The natives remark that they have been there only since the war. In 1946 they were mostly small, 1 to 3 meters in height. In 1950, in some areas they had become much more abundant, and many were small trees. It is highly unlikely that the Japanese had time to plant *Casuarina* during the war, especially on Guam. More likely

these seedlings are a normal part of the vegetation, resulting from a continuous rain of the small-winged seeds blown up onto the savanna from the abundant stands of ironwood along the coast. The restrictions on the normal activities of the natives during the war reduced the number of fires and permitted more of these seedlings to grow large enough to be seen. On Saipan there were areas in 1946 where recent fires had killed most of these young ironwood trees. Further evidence lies in the fact that Safford (1905), observing almost 50 years earlier, regarded *Casuarina* as a normal part of the savanna flora.

In some areas in the western Carolines is a low, mixed vegetation of shrubs, a number of sedges, *Gleichenia*, *Lycopodium cernuum*, several small grasses, *Nepenthes*, *Hedyotis*, scattered larger shrubs and small trees, and *Pandanus* (pl. 16). In others there are mixed grasses and *Pandanus*, and, in still others, almost solid stands of *Gleichenia*. It is interesting to note that, while *Miscanthus* dominates large areas in the Marianas, in the Carolines it has been found only on Ponape, though there are apparently a number of suitable habitats for it on the other islands. *Saccharum spontaneum* has been occasionally mistaken for *Miscanthus*.

ORIGIN AND DEVELOPMENT

There seems little doubt that the Micronesian islands were, before the advent of man, almost entirely forested except, perhaps, for the fresh volcanic slopes of the northern Marianas and possibly small areas of impervious soil elsewhere. The forest types are summarized, as far as I can reconstruct them, in the preceding sections of this report. Large areas of these forests, especially in the western part of Micronesia, have been in some manner destroyed and replaced by herbaceous vegetation. It seems most probable that man-made fire has been the principal agent of this destruction.

None of the Micronesian forests can be said to be particularly susceptible to fire in their natural condition, as none is especially dry in character. All known on volcanic substrata tend to retain the moisture that falls on them, even under dry-season conditions, yet these are the ones that have principally been replaced by grassland, while the exceed-

ingly well-drained limestone types seem to resist fire completely.

The intervention of man has, of course, resulted in clearing as well as burning. When a forest is cleared, a natural drying out follows. Burning is usually resorted to for disposal of the debris from clearing. Humus is burned from the soil. After cultivation is abandoned, weeds and pioneer species of various sorts naturally take possession. Then, during any prolonged dry season, fires may easily start where they could not have in the original forest. In the absence of fire, the normal succession soon leads, in a naturally forested region, to typical secondary forest. However, if the area is burned, this succession is altered. Some plants, particularly tree seedlings, are killed. Others, especially the group mentioned above as characteristic of the savanna, which may not have been able to exist in the competition encountered before the fire, are enabled to gain a foothold. If there is no further fire, these are gradually crowded out by the normal secondary flora. However, if fires continue, those plants that are more capable of surviving them, having deep-seated rhizomes or other persistent parts, tend to become more and more dominant. The forest succession is further retarded and the association of pioneer species is encouraged by the burning out of the natural humus from the soil and by the inevitable formation of erosion scars. It is probable that the longer this repeated burning is continued, the longer it will take for a normal succession to be reestablished after the burning is discontinued. Merrill (1912) has discussed this problem from a slightly different viewpoint, with emphasis on similar vegetation in the vicinity of Manila, Philippine Islands. His conclusion is that grassland in these portions of the tropics definitely results from and depends on the activities of man.

In Guam before the war the savanna was burned over almost every year, the fires being set deliberately by the inhabitants to get rid of the sword grass and encourage better forage species. There is, of course, no better way to perpetuate sword grass. On Saipan less than a year after a forest fire had burned off a forest of *Acacia*, killing every tree, sword grass, which had existed in poor condition under this forest, had produced a

solid stand up to 2 meters in height.

On virtually every island in the Carolines and southern Marianas on which savanna vegetation of any sort is encountered, one can detect burned stubs of grass or other plants here and there. Even on Ponape, where this type would not be expected because of the wet climate, limited open areas occur, dominated by *Gleichenia linearis*, where some of the plants characterizing savanna elsewhere can be found. Here the natives said that fires were frequently set merely for amusement. Glassman (personal communication, 1950) said that he saw an area of *Gleichenia* on Ponape, well up in the rain forest, that had been burned several weeks previously. This is entirely likely, as herbaceous vegetation in well-drained situations, even in wet climatic areas, dries out rather quickly during a series of dry days and will burn under such circumstances. It is significant that the surrounding forest apparently does not suffer significantly from these fires.

On Yap it was possible to detect various stages in the formation of this vegetation. Certain areas showed the results of clearing and abandonment, others the result of a single fire, still others those of repeated fires. These developmental stages in savanna vegetation were seen on areas of soil formed from schist. On Rumung Island, at the north end of Yap, is a large savanna of well-developed grassland, with scattered *Pandanus* trees, on soil from this same kind of schist. I did not visit this place, but photographs and notes by Dr. Josiah Bridge establish its character definitely. In the Gagil and Tomil districts is a broad strip of weathered volcanic material, purplish red in color, with manganese nodules very abundant on the surface. Here the fern-shrub phase of savanna vegetation is extensively developed. There are abundant evidences of burning. In 1950, a view of this strip from the air suggested that the erosion scars were larger and more abundant than in 1946.

It is interesting that, in the northern Marianas, extensive areas of sword-grass savanna lie on slopes of unconsolidated ash and cinders (pls. 18-20), where there seem to be no evidences of recent burning. On steeper slopes, primarily of lava, *Casuarina* is one of the earliest invaders, and forests are formed,

but there is little evidence that even *Casuarina* commonly invades the main ash slopes of these volcanic cones. There seems to be a striking correlation between grassland and those slopes that are more or less at the angle of repose of this loose material. Steeper slopes, ravines, and more level areas at the base, all tend to have trees. On the higher slopes of some of the islands, such as Alamagan, there appears to be a sparse woody vegetation mixed with the savanna, and a tree fern has been described from there. But, generally, this habitat seems to be the natural home of the sword-grass type of vegetation.

Bridge (personal communication, and Bridge and Goldich, 1948) has noted a high correlation between bauxite deposits and the fern-dominated phase of the savanna vegetation. It is certain that on the known bauxite areas this is the present vegetation. Whether it has always been so is conjecture, in any event, but a lateritic material such as bauxite would doubtless give rise to an extremely sterile soil. It may be significant that the only well-developed savanna area on Truk is on the trachyte cap of Mt. Witipon where there is a significant quantity of bauxite in the residual soil. If an area of bauxite could be protected from fire for some years, the question of whether or not this material could support forest might be settled.

One of the interesting problems connected with this type of vegetation is the origin of its flora. Many of the species are scattered through the Indo-Pacific region. Some of these may have followed man in his early migrations or may have crossed the seas by natural means and accumulated in burned areas after the advent of man. But these explanations do not take care of the endemic plants in the flora. Micronesian endemics such as *Myrtella benningseniana* (pl. 39, fig. 2), *Ischaemum longisetum*, *Dimeria chloridiformis*, *Hedyotis tomentosa*, *Hedyotis korrensis*, *Geniostoma micranthum*, and *Phyllanthus saffordii* (pl. 36, fig. 2) appear to be confined to the savanna. They probably did not originate since man started burning the vegetation. If the bauxite areas have always been open, the problem disappears. If not, such endemics may have originated ages ago on the slopes of the volcanoes of Palau and the southern Marianas, when these were young

and similar to the present condition of the bare northern Marianas, and may have maintained a precarious existence as rare plants on peaks and crests, landslides, and ravine walls through the long periods of time when forests were almost the only vegetation on these islands. Against this suggestion is the probability that loose ash slopes may never have existed in the southern Marianas, at least, but that the volcanic materials were extruded under the sea. A more acceptable suggestion may be that in areas of old, gentle topography and impeded drainage, savanna has existed for ages, giving ample time for a flora to have originated. This is in line with Beard's suggestion (1953) that such conditions are responsible for many tropical American savannas. That an extensive old erosion surface has existed and still persists in small remnants on Guam has been suggested by geologists (Tracey, verbal communication). In any case, when man arrived on the scene and began to open up larger areas by burning, an opportunity came for the spread of endemic savanna plants, and now they have wide ranges.

Where volcanic substratum comes in contact with limestone there is commonly a sharp line of demarcation between the savanna on the volcanic soil and the forest on the limestone.

The problem of why this savanna vegetation does not develop when limestone soils are subjected to the same treatment of repeated burning has not been solved. It may be that, owing to the richer nature of the limestone soil, a more lush secondary vegetation is quickly developed, and the drying that makes fire possible is less pronounced. The undergrowth in the forest on limestone is usually sparse and perhaps not very inflammable. There is also the fact that many of the limestone areas are so rough that they are seldom cleared, which applies to some of the driest of them. Certainly the secondary growth on limestone, as on Peleliu and Angaur, and on the low islands, very rapidly produces a dense and absolutely complete cover. On Truk, Ponape, and Kusaie, where even on volcanic soil the revegetation is rapid and the resulting vegetation is very dense, savanna areas are restricted or almost absent.

A comparison of the acidity of soils on limestone with those on volcanic material shows a striking difference. Limestone soil, as would be expected, is around pH 7.5 or above, while soil on volcanic material is usually pH 6 or below, more often around pH 5, or even lower, especially when the top soil has been eroded away. Such a variation in acidity may very well explain why, if savanna plants cannot withstand high alkalinity or the competition of the plants that normally grow in alkaline soil, there will be little chance for a savanna of the composition described to appear, regardless of the history of the limestone area.

Considerable interest has been expressed in the possibility and desirability of reforesting the savanna areas, especially on Guam. Certainly steps should be taken to reduce the erosion that is taking place and to improve the watersheds that are sources of public water supply. It should be emphasized, however, that the desired effect may be gained more cheaply by the elimination of fires alone, and that, without elimination of fires, no program of reforestation can possibly have great success. Fire will destroy deliberately planted tree seedlings just as readily as those planted by natural agencies. Because the region is a naturally forested one, succession will take care of the reforestation if given a chance. This is amply shown by the young *Casuarina* forests that have appeared in some areas on Guam in the few years since the Japanese occupation. Observations made in 1950, 1953, 1954, 1956, and 1957, however, show that, in spite of laws against burning, fires are again becoming of frequent occurrence.

VARIATIONS

In the ravine bottoms in savanna areas, some thicket or gallery forest usually develops, generally of a mixed type, often secondary in appearance. The deeper the ravine, ordinarily, the taller is the forest. Undoubtedly the existence of this forest reflects the closeness of ground water to the surface. The frequent fires doubtless do enough dam-

age to assure that the forests commonly will be secondary in nature.

If the ravines are shallow and quite wet, the vegetation may be a dense stand of reeds, *Phragmites karka* (pl. 38, fig. 2), which stand out as a somewhat greener band against the brownish or grayish yellow-green of the sword grass. The reed stands may often be tall enough to be almost level with the sword grass on higher land, concealing the ravine from view except for the difference in color.

ENVIRONMENTAL SIGNIFICANCE

This readily identifiable type of vegetation in nearly all locations indicates a volcanic substratum. Except in the northern Marianas, this substratum is a weathered volcanic material; the slopes are usually less steep than on limestone; there are few extensive flat areas; surface drainage is usual, owing to the impervious nature of the soil; and the stream patterns are typically dendritic. Water may commonly be found in the ravines, either on the surface or by digging, except in the driest seasons.

In wet weather the thick clay soil collects on boots in clumsy balls, and the bare slopes and trails are as slippery as though greased. In dry weather the fine, impalpable red dust is most annoying to eyes and nostrils.

Sword grass in dense stands is almost completely impenetrable by man for any distance. It does not yield to a machete and must be broken down by main force. The scabrous edges of the leaves cut like razors when drawn through the hands. The atmosphere is hot and dusty where the grass is tall, and a man is exhausted after progressing but a short distance. Travel on ridge crests is, however, frequently not difficult. Well-developed *Gleichenia*, or staghorn fern, is almost as difficult, but can be traversed. It forms a wiry tangled mass, with stalks that leave sharp ends when broken. The mixed type, with *Gleichenia*, *Nepenthes*, and *Hedyotis*, is usually sparser, much more low-growing, and offers little obstacle to traverse.

There is great danger of fire in any of these types in dry weather, especially in the sword grass, which burns with great vigor.

VEGETATION OF THE MARIANAS ISLANDS

THE MARIANAS CHAIN IS composed of 15 islands (plus various tiny satellite islets) arranged in a long arc running north and south between latitudes 20° 32' N. and 13° 15' N. and between longitudes 144° 24' E. and 146° 04' E. The regional climate is tropical. Temperatures show relatively little seasonal variation, with monthly averages between 24° and 27° C., and extremes of 18° and 35° C. Precipitation, between 2000 and 2500 mm., is strongly seasonal, with the rainy season occurring from July to October. Trade winds are rather constant but with some weak westerly monsoon influence in summer and with relatively frequent storms and typhoons from the southeast and east. Typhoons average about one a year in the Marianas. Excessive runoff in some areas and excessive percolation in others, as well as the seasonal distribution of rainfall and the effects of typhoons, cause the general aspect in most places in the Marianas to be less humid than would be expected from the total precipitation.

The flora of the Marianas is not large; both native and naturalized species probably do not total more than 500.

A number of sketches of the vegetation of the Marianas have been published by various persons, beginning with Gaudichaud (1826) and including Marche (1891), Prowazek (1913), Kanehira (1934), Hosokawa (1934), United States Geological Survey (1944), and Gressitt (1954), as well as descriptions of a number of individual islands, notably Guam. (See Sachet and Fosberg, 1955.) Most of these impress the reader with their superficial nature or their high degree of generalization, which actually reflects a paucity of reliable information. With the exception of Safford (1905) these writers made only short visits and saw very few islands. No one has studied the entire group, even superficially, and only Guam has been studied more than casually.

The Marianas Archipelago can be divided readily on several bases into a northern group of young, mostly somewhat active volcanoes, and a southern group of older islands of elevated coral limestone and old, weathered,

volcanic rocks. The northern group has not been subjected to a great degree of human disturbance, but in the southern group the disturbance has been such as to alter the entire appearance of the landscape. The vegetation of the northern group is predominantly grassland, probably of a primary nature, with subordinate areas of forest. That of the southern islands is predominantly forest, with some grassland, the greater part of which is secondary in origin, resulting from human activity.

Man has been a factor influencing the vegetation of the Marianas, especially the southern Marianas, for at least 3500 years. Alexander Spoehr (1955) reports a radiocarbon date that indicates about that age for archeological remains found on Saipan and allows 4000 years since the entry of man into Micronesia. At the time of the occupation of these islands by Spain, about 400 years ago, the native population was estimated to number many tens of thousands. The profound effect of these people on the vegetation cannot be doubted, when the abundance of archeological remains and the plantings of bamboo, coconuts, and other economic plants in remote inland localities far from present-day habitations are considered. Very little is known of their culture and activities or of the nature of the vegetation at the time of the early visits by Europeans. Enough is recorded, however, to show that there have been great changes since that time. These are treated in such detail as is feasible with present knowledge in the descriptions of the individual islands. Their general nature may be summarized.

On old volcanic soils the clearing and burning of forest have been general. In places a secondary forest has resulted; in others a great expansion of secondary savanna from probably small areas of primary savanna has taken place. Much erosion and deterioration of the soil have accompanied this process, making the savanna more stable than might be expected. The most conspicuous invasion by tree species to be seen at present is by the fast-growing but very fire-susceptible *Casuarina*.

On limestone soils, if fertile, the forest has been cleared and replaced by coconut plantations, open fields and gardens, pastures, or by scrubby secondary forest. On the shallower soils and the deep red soil on hard limestone the forest has generally persisted, except where cleared for military installations or attempts at farming, but one of its important components, *Intsia bijuga*, has been generally logged out. War activities have resulted in conspicuous deterioration, though this is hard to distinguish from typhoon damage. In many places coconut groves have replaced areas of forest, though on Rota, Tinian, and Saipan beetle damage has now eliminated them. Cleared land, where abandoned or unused, has rapidly grown up to a tangled second growth. In many areas such introduced woody species as *Triphasia trifolia*, *Jatropha gossypifolia*, *Pithecellobium dulce*, *Muntingia calabura*, *Nypa fruticans*, *Cananga odorata* (pl. 29, fig. 2), and especially *Leucaena glauca* have occupied certain habitats, changing the aspect of the vegetation conspicuously. Many of these plants were introduced very early during the Spanish occupa-

tion. Some are confined principally to Guam. Others have spread throughout the principal islands of the southern group, and a few have even reached the northern islands.

Two interesting vegetational relationships between the northern and the southern groups should be mentioned. One is the existence on rough lava flows on some of the northern islands, especially Alamagan, of a forest type that is similar in aspect and even to some extent in composition to that on rough limestone in the southern Marianas. This similarity suggests that the physical nature of the substratum may be of more importance than the chemical factors. The other relationship is the close similarity of the *Miscanthus* grassland, the principal vegetation of the loose porous ash slopes in the northern group, to the usually secondary grassland, predominantly *Miscanthus*, which occupies most of the steeper eroded slopes of old volcanic materials in the southern Marianas. The northern Marianas grassland, however, is poorer in species, both introduced and native, than that on Guam, for example.

THE NORTHERN MARIANAS

There has been no general vegetation survey of the nine northern islands of the archipelago, and only on Pagan has there been any attempt to determine the areal extent or relations of cover types. This undertaking was in connection with a geological survey and was definitely a secondary consideration. Very brief notes are available in accounts by Corte (1875), Marche (1891), Fritz (1902), Prowazek (1913), and Kanehira (1934). Three of the islands were examined by the present writer on short visits in 1950. Some information has been gleaned from photographs taken in 1945, lent by Dr. A. H. Banner, and some of a very general character from aerial color photographs made by Messrs. J. I. Tracey, Jr., David B. Doan, and S. L. Schlanger, and from photomosaics lithographed by the 64th Engineer Battalion, United States Army Forces Far East.

The general picture of the vegetation pattern on the northern Marianas volcanoes, where they have not been covered by recent

ejecta, is that steeper ash slopes are clothed by a dense coarse grass; ravines cut in these slopes are filled by woods and thickets; steep exposures of lava rock are either bare or covered by *Casuarina*; gently sloping rough lava flows, if not too recent, are covered by mixed forest; and the flatter areas and more moderate slopes near the sea, by coconut plantations. Recent volcanic material, if loose and fine-grained, is gradually colonized by grasses and grass-like plants, principally *Miscanthus floridulus*. Lava is likely to be colonized by ferns and trees, especially *Casuarina*. Sea cliffs and beaches have shrubs such as *Scaevola sericea*, often sparsely scattered, and talus may have dense thickets of *Hibiscus tiliaceus*.

URACAS (FARALLON DE PAJAROS)

Neither field data nor published information is available on the vegetation of this active volcano except for a brief account by Fritz (1902, p. 116). One species of sedge, *Fimbristylis urakasiana*, has been described

from it. Excellent aerial color photographs, taken in 1952 by the members of the Guam party of the United States Geological Survey, suggest that the greater part of the island is covered by fresh volcanic material, lava and ash, which apparently supports no vascular vegetation whatever. Two lighter-colored rocks of older material protrude from this younger layer and show a thin grassy vegetation, possibly of *Miscanthus floridulus* (pl. 17). No woody plants can be discerned. These facts accord with the observations of Fritz, who speaks of a volcano with no vegetation but with fragments of an older island with sparse plants on its red rock. His party planted coconuts, *Casuarina*, and other plants. These are not evident on the recent photographs.

MAUG

This is a cluster of three small islands, obviously parts of the rim of the crater of a partially submerged volcano, arranged in a ring around a "lagoon" which was the old crater. The eastern island is largest, reaching an elevation of 218 meters. These islands are very steep and rocky, and the slopes are for the most part covered by a coarse grass, probably *Miscanthus*. Information is scanty, no recent visitors having made any records of vegetation or collections. Fritz wrote a brief account, republished by Prowazek. The present author has made notes from photographs taken in 1945 and generously lent by Dr. A. H. Banner. In addition to the grass, low scrub patches with *Scaevola* and *Wedelia* occur on all the islands. The eastern island, according to Fritz (1902), has some trees, including coconuts, *Terminalia*, *Pandanus*, *Boehmeria*, *Hernandia*, and *fago* (*Ochrosia*, according to Safford, 1905, and modern Guamanians, but Prowazek, 1913, interprets it as *pago* and cites it as *Pariti tiliacea* [*Hibiscus tiliaceus*], which actually may be more probable). Fritz reports a coconut grove on the west coast, on a wide ridge. The United States Hydrographic Office Sailing Directions (1952) report that the higher slopes of East Island are covered with trees. Modern air photographs show patches of forest on the higher slopes and dense scrub below the grassy slopes along the shore and running up ravines.

ASUNCION (ASSONGSONG)

This island is a steep volcanic cone, still showing occasional signs of activity. Concerning it also there is a dearth of information. In addition to information from Prowazek's account (1913), the United States Hydrographic Office (1952), and the Banner photographs, we may quote from Beechey's narrative (1831, vol. 2, p. 438), "Time must have made an agreeable alteration in the appearance of this island since it was visited by La Pérouse. Instead of a cone covered with lava and volcanic glass, and presenting the forbidding aspect he describes, we traced vegetation nearly to the summit, and observed woods of palm-trees skirting its base; particularly in the southwest side." La Pérouse visited the island in 1786; Beechey, in 1827.

If one can judge from the photographs, the higher slopes are covered by *Miscanthus* and little else. There is some brush on the more moderate lower slopes, and on the south side, especially around the former Japanese village, are some forests and coconut plantations. The forest extends irregularly more than halfway to the summit. Woody vegetation runs farther up the ravines. *Cocos*, *Carica*, *Morinda*, and *Musa* are identifiable from the photographs, while Prowazek adds *Terminalia*, *Pandanus*, *Hibiscus*, and bread-fruit trees. It is interesting that he records *Carica*, which apparently achieved a wide distribution even in such remote islands rather early after its introduction during Spanish times, although, according to Safford (1905, p. 216), the natives, at least of Guam, do not care much for its fruit.

AGRIGAN (AGRIHAN)

This island is a recently active (1917) volcanic cone 965 meters high, composed largely of beds of loose ash with some interbedded basaltic flows. Its flora is reasonably well known through the collections of Kanehira, Hosokawa, and Fosberg, though no separate list has been published. Little is on record about the vegetation, as the visits of all botanists who have stopped there have been very short. Since the visit of Fritz in 1901 there has been volcanic activity, possibly of a major character, as he records the altitude of the central peak as only 750

meters. His brief characterization of the vegetation (1902), however, is not discrepant from the account below, summarized from personal observations and from notes published by Kanehira (1934) and Hosokawa (1934).

The vegetation, though locally varied, is separable into two main complexes. The steep ash slopes which cover the greater part of the island are clothed with dense sword grass (*Miscanthus*) and cut by ravines which are wooded well up towards the top of the mountain. The *Miscanthus* is dense, well over head high, and difficult to traverse. The crater, at the summit, has not been examined botanically. The coastal benches and bluffs are covered by a mixture of thickets and woods of *Casuarina*, *Ficus*, *Hibiscus tiliaceus*, and various other native trees where the terrain is too steep or rough for the planting of coconuts. Coconut plantations occur where there are small bits of reasonably level land. The coconut plantations, though containing undergrowth, may be penetrated and traversed readily, but the patches of woods may be locally dense and tangled. If the woods are made up of *Casuarina* they are usually open, but may be impassable if on cliffs and steep bluffs. Forests of *Ficus* and miscellaneous other trees may afford considerable obstruction, and if *Hibiscus tiliaceus* is dominant they may be impossibly tangled.

The general characteristics of the vegetation of this island suggest a relatively dry climate, even if allowance be made for the effects of the extremely rapid drainage through the coarse volcanic ash. Epiphytes are not common on the trees, and leaf epiphytes are wholly absent. The increasing abundance of ferns which is found towards the upper parts of the wooded ravines shows that the humidity, at least, is greater there. This may well be due to the cloud cap that often covers the upper part of the mountain. Surface water seems to be entirely absent except during rainy weather, when apparently there is some runoff in the ravine bottoms.

PAGAN

Pagan (pls. 18, 19) is the largest of the northern Marianas and has the best-known flora and vegetation. The island is composed

of two high volcanic centers connected by a wide, low isthmus. The more northern one of these, Mt. Pagan, 570 meters in elevation, has been active recently, and minor activity, such as warm springs and emissions of steam and hot gases, can still be observed. The topography is very diverse, much of it steep and rough, and the surface is made up of relatively fresh lava flows and beds of ash and coarser pyroclastic material. Slightly elevated reef limestone of limited extent is found on the east and north coasts.

Plant collections have been made on Pagan by Marche, Kanehira, Hosokawa, Anderson, Bonham, and Fosberg. A catalogue of the vascular flora has been prepared on the basis of these (Fosberg, 1958). A small fossil flora has also been found and has been reported by Fosberg and Corwin (1958). The geology was thoroughly studied in 1954 by Corwin, Terman, Bonham, and Viele and an extensive report has been published (1957). Notes on the vegetation were made in connection with the geological study by Bonham. Brief notes were published on the vegetation by Marche (1891), Fritz (1902), Kanehira (1934), and Hosokawa (1934), and I was able to make records and photographs during a short stop in 1950. From these sources the following summary has been written. A vegetation map prepared by Bonham has been published in connection with the military geological report (Corwin *et al.*, 1957).

The present-day vegetation of Pagan gives a general impression of semi-aridity; indeed, large areas would be classed physiognomically as deserts. This is probably not so much a reflection of climatic dryness as of an extremely porous substratum and of the pioneer nature of vegetation occupying surfaces of recent volcanic ejecta. In the very few low wet areas, such as to the west and southwest of the Freshwater Lake or Inner Lake (pl. 19, fig. 1), thickets of broad-leaved trees are fairly luxuriant, and in places bordering the lake the conditions are somewhat marshy. Luxuriant patches of woods also occur in hanging valleys on the west side of the south end of the island. A mixed scrub forest of low stature forms thickets and patches up to several acres in extent on plains north and south of Mt. Pagan and in places extends up

the lower slopes of the volcano. Scrub forest occurs also on steep slopes on the west shore of the isthmus and chokes numerous ravines throughout the island. No investigation has been made of the actual composition of this forest, but it is said to contain 15 or more species of trees. It varies in height from 3 to 8 meters and in density from open park land to dense tangled thicket. Undergrowth is sparse, but low, tangled branches of the trees cause serious obstruction to movement in denser areas.

The loose volcanic ash which covers large areas, especially on the west side, is vegetated largely by an almost pure stand of sword grass, *Miscanthus floridulus* (pl. 19). This forms a coarse, harsh, brake-like grassland 1 to 3 meters in height and in places very dense. On the steepest slopes and above 250 meters in elevation this grass tends to be shorter and the clumps more widely spaced. Above 450 meters it is sparse to absent.

Lava flows (pl. 18) may be virtually bare, as on the northeast side of Mt. Pagan; they may support scattered clumps of *Miscanthus* and trees of *Casuarina*, as on the east and southeast sides of Mt. Pagan and the central upland of the southern part of the island; or, as on many of the flows and lava cliffs to be seen along both sides of the island, they may be covered by almost pure forests of *Casuarina* (pl. 19, fig. 2). *Casuarina* and the fern *Nephrolepis hirsutula* are among the earliest invaders on new lava. These two species were found well established on a fresh black *aa* flow in the depression at the west base of Mt. Pagan in 1950. This flow has been dated by Tanakadate (1940) as having occurred in 1925. It shows no visible weathering.

On plains of ash soil the vegetation is generally grassland (pl. 19, fig. 2) with scattered trees or clumps of trees. The trees may be *Pandanus*, *Casuarina*, or any of a number of broad-leafed species. Many of these areas were under cultivation before World War II and are now weedy; they have rows of *Casuarina* and other trees planted by the Japanese as windbreaks. *Jatropha gossypifolia*, a fleshy-stemmed shrub, introduced by the Japanese in the late 1930's, has spread and now dominates large areas in the central

part of the island. Clumps of trees of various kinds mark the sites of houses, still existing or not. On the gently sloping northwest part of the island is a large coconut plantation. Smaller ones occur in many parts of the island, both on plains and on talus cones. Coconuts are also common in ravine mouths and on steep slopes above the sea. The large plantations are of relatively recent date, but there is no way of knowing the age of the smaller clumps of coconuts that occur mixed with other vegetation on various parts of the island. Some may very well date from pre-European times.

A small, slightly raised coral reef on the east coast is the only known locality on the island for *Pemphis acidula*, *Capparis cordata*, and several other plants of rough limestone habitats, but they may occur on similar reefs on the north end of the island.

The vegetation on steep slopes, rough ground, and relatively fresh lava has been little disturbed by man's activities. The sword grass has been burned over large areas, but such burning does not seem to be much of a deterrent to *Miscanthus* itself. In favorable places, the grass, after being burned in 1954, grew to waist height within six weeks. This burning may, however, tend to eliminate associated species and to keep *Casuarina* from gaining much of a foothold. Much of the area of more gentle ash slopes and plains, as well as talus cones, has been, as noted above, very much altered by man. The cultivated areas were abandoned after World War II and allowed to grow up to weeds, but they are being gradually reoccupied at the present time. The coconut plantations were not changed except to be choked with weeds and young coconut seedlings.

ALAMAGAN

This island (pl. 20) is a dormant volcano, in many respects similar to Agrigan. Plant collections and notes on the vegetation have been made to about the same extent and by the same people as those on Agrigan. Topographically, in addition to steep ash slopes somewhat dissected by ravines, this island has gently sloping lava flows extending from the base on the north and southwest sides.

The south end is a high bluff, with tremendous recent landslides and great talus slopes at its base, all almost devoid of vegetation. There are two craters. As on Agrigan, surface water is absent except during rainy weather.

The dominant vegetational feature, as on the other northern Marianas, is the sword grass on the ash slopes. These slopes are cut, well towards the top, by deep ravines which are densely wooded with mixed broad-leaved forest made up of many species. The upper middle slopes have a sparse scattering of woody vegetation, which Kanehira (1934) describes as a continuous stand of tree ferns, branched at the base, the bases never less than 1 meter in diameter. This tree fern is a species of *Cyathea* not found elsewhere. The uppermost slopes are thickly covered by sword grass. In the crater, according to Kanehira, are bushes and grasses, the latter occupying plots at the foot of the vertical walls.

In the lowlands, steep eroded areas, bluffs, broad ravines, and talus, if wooded, are covered by thickets with tangled undergrowth. The outstanding feature here, however, is the gently sloping surface of the lava flows. These flows, where reasonably smooth, are planted to coconuts. In places, however, they are exceedingly rough and covered by a type of forest resembling that on the rough limestone in the southern Marianas. The forests are made up of *Ficus prolixa*, *F. tinctoria*, *Pipturus*, *Pouteria*, *Hibiscus tiliaceus*, *Elaeocarpus joga*, *Melanolepis*, *Premna*, *Morinda citrifolia*, *Guamia*, *Psychotria mariana*, *Trema orientalis* var. *argentea*, *Randia cochinchinensis*, and other trees. Undergrowth is generally very sparse, the two most important components being the ferns *Polypodium scolopendria* and *Asplenium nidus*. Towards the seaward edge, just as in the forests on limestone in the southern Marianas, the stature of this vegetation is much lower, and shrub species are more numerous. *Pandanus* is commonest on bluffs over the sea, and *Casuarina* was seen only in such situations.

Judging by a greater abundance of epiphytes, as well as by the generally more luxuriant appearance of the vegetation and by the presence of tree ferns in important

numbers, Alamagan is distinctly wetter than Agrigan, where the conditions of the substratum are similar.

GUGUAN

Guguan is one of the most uninviting of all tropical islands. Almost no one has visited it for botanical investigation, and it has no inhabitants. Fritz (1902) gives the only useful account of the vegetation. This description is more than 50 years old, and there has been some volcanic activity since, judging from the apparently fresh lava that covers large areas, especially on the northern part. Fritz said the northern part was of recent volcanic ash and was covered by grass and the parasitic *Cassytha*. In the ravines were numbers of *Pandanus* trees. In the south part there is a valley where Fritz planted coconuts, *Casuarina*, beans, and gourds. It is not known if they survived. On modern aerial photographs the interior is covered chiefly by barren black lava, with some grass visible near the edges.

SARIGAN

This is a dormant or extinct volcano, conical in shape and just over 550 meters in elevation. From the few brief reports and photographs available, the steeper slopes seem to be covered by *Miscanthus*, as is usual for these young islands. The lower slopes have coconut plantations, except where too steep as on the southwest side, or where there are lava flows as on the north point. Such flows are forested, and there are a few scattered coconut trees. Forest, or thicket, also runs up the ravines. There are a number of species of woody plants, but *Hibiscus tiliaceus* is especially prominent, forming tangled thickets laced with morning-glory and other vines. Near the summit is some scrubby growth, including tree ferns.

ANATAHAN

Anatahan is also an extinct or dormant volcano with a broad, shallow crater and with high remnants of the rim forming peaks to the east and west of it. The steep slopes are cut by deep ravines, giving the sides a folded aspect. In these ravines there is said to be some surface runoff during rains.

The lower slopes are thickly wooded, as is also the south side of the high western peak. There are many coconut plantations in the valleys and on lower slopes not far above the sea. The ridges on the steeper slopes are covered by *Miscanthus* grassland, with the ravines between them wooded. It is not certain whether the broad plain on the bottom of the crater is grassy or covered by thickets. It is probably swampy or marshy. *Pandanus* is common in the thickets and woods near the

shore and on the slopes above. About abandoned dwellings are *Citrus* trees and banana plants. There are said to be breadfruit trees in the valleys. A popular account (Maruyama, 1954) of the life of the Japanese castaways who occupied the island from 1944 to 1951 gives a vivid impression of the island and its vegetation, though little scientifically acceptable information on the vegetation is included.

THE SOUTHERN MARIANAS

In geology, topography, and soils, as well as in vegetation, these southern islands in the Marianas chain contrast strongly with the nine northern ones described above. Because their topography and soils are such as to make them far more satisfactory for human occupation, disturbance resulting from such occupation has altered them conspicuously, not only in their vegetative cover but in the character of their soils.

These islands are essentially masses of old volcanic rock, much of it the result of submarine eruptions, covered completely or partially by caps and terraces of ancient to modern reef limestone which has been elevated by tectonic movements to varying heights, up to as much as 474 meters above the present sea level. During their history repeated changes in level have occurred, and extensive faulting has taken place. Erosion, transgression of the sea over at least large parts of the land, marine planation, the building up of new reefs, and their elevation to form terraces have all contributed to the creation of the present landscape. No volcanic activity subsequent to the Miocene period is known to have occurred. On Guam, at least, some land surface has possibly been continuously available since the early Miocene or before.

The volcanic portions of the islands are best exposed on Guam, to a lesser but important extent on Saipan and Rota, much less on Tinian, and not at all on Aguihan and Medinilla. Topographically they are generally sharply dissected and characterized by abundant surface drainage and complicated drainage patterns. Remnants of gent-

ler, ancient relief are present on Guam and on the summit exposure on Rota. The soils on these volcanic exposures are either highly weathered lateritic clays or very immature, partially weathered, recently exposed materials.

The limestone parts of the southern Marianas are of several sorts. Most conspicuous are terraces and cliffs of hard limestone, with surfaces either covered by thin to moderately thick soil, or bare and eroded into a harsh surface of pits, rough masses, and pinnacles, with soil only in pockets and cracks. There is no surface water, and drainage is internal. Certain areas of limestone contain large proportions of volcanic or clay material and are termed argillaceous limestones. These are often much more weathered. They have produced karst topography characterized by knobs and sinks, which has generally been worn down to a rounded but very complicated surface of rather low relief. There are locally great thicknesses of soil and, in the filled sink holes, marshy places. Finally there are areas of lime sand forming flat, low terraces near the coasts, which are mixed, in places, with some volcanic material. Here are marshes and swamps with deep accumulations of muck of high organic content.

Before the advent of man the limestone areas were doubtless almost entirely forested. Even now they are predominantly so, except for the large areas that have been cleared and maintained in a clear condition on and around military establishments. The agriculture is largely tree agriculture and cultivation of small garden plots. The Japanese maintained large areas in sugar cane, but

these have been abandoned since the last war and in large part have grown up to second-growth thickets. Little may now be said about the original vegetation of the argillaceous limestones, as it has been completely altered by agricultural activities. The soils here are the most fertile in the Marianas. The coastal sandy areas have been planted largely to coconuts, but some portions still remain in *Casuarina* forest and strand forest. The marshes are covered either by reed brakes or by swamp forest. The hard limestone terraces and cliffs, where not cleared for military purposes or for farms, still bear the characteristic mixed forest of the limestone in varying states of modification.

The volcanic areas are characteristically covered by savanna vegetation, but large areas in valley bottoms, ravines, and on steep slopes have a mixed forest or thicket, highly modified by man, which is here termed "ravine forest." This is best developed on Guam.

FARALLON DE MEDINILLA

Apparently no botanist has ever visited Medinilla, and Fritz (1902) is the only person ever to make any botanical observations there. No specimens have been seen from this tiny scrap of elevated coral, and the only modern information available is from a few aerial color photographs taken by geologists of the United States Geological Survey Guam party in 1952 and a photomosaic map. The island has been frequently used as a bombing target, from which the vegetation has apparently suffered, although in the photographs it appears to be not very different from what Fritz described.

Even the size of this island has been a matter of uncertainty. Brigham (1900, p. 64) gives its length as 2 miles and its height as 50 feet. Fritz says it is 30 meters high. The United States Hydrographic Office (1952) gives its height as 266 feet but is noncommittal as to its other dimensions. From a photomosaic map by the United States 64th Engineer Base Topographic Battalion (1952a) its greatest length was determined to be 2.75 kilometers and its greatest width as

0.5 kilometer. Its shores are steep cliffs, and great blocks are said to be loosened from the mainland of the island. It is apparently entirely limestone. Fritz states that the plateau is covered by brush about 4 meters in height and a savanna with small grasses and Liliaceae. The plants he mentions by Chamorro names are *talisai* (*Terminalia*), *gulus* (*Cynometra*), *lada* (*Morinda citrifolia*), *ahgau* (*Premna*), and *nunok* (*Hernandia* or *Ficus*). He says there were papaya trees but no coconuts. He planted coconuts, *Casuarina*, beans, and other plants, but there is no record of whether or not any of them survived. No coconuts are apparent on the photographs. Part of the island still seems to be grassy or almost bare.

SAIPAN

The second largest of the Marianas and about 474 meters in altitude, Saipan (pls. 21-24) has a complicated geological structure and great topographic diversity. Added to this in its effects on the vegetation is a history of human occupation of at least 3500 years, including occupation by the aboriginal Chamorros, domination and alteration by four successive foreign cultures, and a major campaign of World War II. Scarcely an acre of the island has not been profoundly disturbed. As a result the vegetation pattern is neither simple nor stable.

The island is elongated in a north and south direction and has a main mountain mass extending from near the north end about three-fourths of the way to the south end. It is dominated by Ogso Tagpochau (Mt. Tapochau) in a more or less central position, and at the north end is the precipitous Pidos Kalahe (Mt. Marpi), 256 meters in altitude. The highest peaks are of limestone, notwithstanding the statement that Mt. Tapochau is an extinct volcano (United States Hydrographic Office, 1952), but some of the ridges and slopes are masses of old and deeply weathered volcanic rock. Some of the geological formations are of mixed volcanic and calcareous materials. East of the mountains the land slopes generally rather steeply to the sea except for the large Hagman Peninsula which is somewhat elevated, relatively level limestone. Similar slightly ele-

vated land makes up most of the southern fourth of the island. On the west side along the southern three-fourths of the island is a low, flat, coastal plain mostly of calcareous sandy soil. It is narrow at the north and much broader southward. On this are some marshy areas, especially a large one behind the village of Chalan Kanoa that contains a body of open, almost fresh water called Lake Susupe (pl. 24).

In all probability the greater part of the island was originally forested, mostly with the typical mixed forest found on limestone in the Marianas. Of this a few altered remnants remain, one near the top of Ogso Tagpochau, some on and around the base of Laderan Bañadero at the north end, and some on cliffs and terraces here and there along the precipitous eastern side, as between Puntan Laulau Katan and Puntan Hagman. The composition of these forests varies locally, in places being dominated by *Cynometra*, *Barringtonia*, *Erythrina*, or by a mixture of trees. *Pandanus tectorius* and *P. dubius* are generally common with *Pisonia grandis* on lower sites, *P. umbellifera* on higher, and with *Ochrosia oppositifolia*, *Bleekeria*, *Ficus*, *Pouteria*, *Laportea*, *Melanolepis*, *Guamia*, *Aglaiia*, *Claoxylon*, *Hibiscus tiliaceus*, and *Randia* as other important components. At the edges of terraces on the windward (east) side this vegetation becomes stunted to a dense scrub in which shrubs such as *Scaevola sericea*, *Jasminum marianum*, and *Canthium odoratum* become abundant. On the actual cliffs exposed to constant salt spray driven by the trade winds is a scrub of *Pemphis*, *Bikkia*, *Scaevola*, *Hedyotis*, and dwarfed examples of many of the above-named plants (pl. 23). *Ipomoea tuba* is common from the dense forest to the exposed cliffs. Some of the cliff tops are open or semi-open, with grassy spots of *Zoysia tenuifolia*, *Stenotaphrum micranthum*, *Gossypium*, *Hedyotis albido-punctata*, *Myoporum*, *Phyllanthus marianus*, and other plants. At times the spray blowing up over these cliffs is so thick that visibility of features several miles away is obscured. Near the edges of these cliffs a dwarfing of the leaves of *Scaevola sericea* is very striking and not observed elsewhere even under similar conditions.

All the level land was put into sugar cane by the Japanese (pl. 21, fig. 1). There is no record of what was there before, though some of it must have been mixed forest, either primary or secondary. As the island at one time supported a large Chamorro population, probably most of the forest on level land would have been second growth on their abandoned fields and dwelling sites. Such second growth was probably dominated by *Macaranga*, *Melochia*, and *Hibiscus tiliaceus*, with blankets of *Operculina ventricosa* (pl. 22, fig. 2). Sugar growing was not resumed after the last war, and the cane fields have been gradually invaded by different woody plants, forming uneven mixed thickets, with the cane persisting in many places. *Pennisetum purpureum* or elephant grass has become dominant locally; *Passiflora foetida* and *Ipomoea indica* are abundant and quickly cover any open land (pl. 22, fig. 1). On some level areas in the south part *Saccharum spontaneum* has formed, in a short time, a thick, brake-like growth. Whether this wild cane is descended from *Saccharum spontaneum* cultivated in the Japanese experimental plots or is a progeny of cultivated sugar cane that has produced seed is not known. At least two strains of *Saccharum spontaneum* are recorded as having been cultivated experimentally by the Japanese.

Many areas of level and sloping ground have been covered either since World War II or during the Japanese occupation by pure or mixed stands of *Albizia lebbek* and *Acacia confusa* (pl. 21, fig. 2) and others by *Casuarina equisetifolia*. The first two were said to have been planted by the Japanese for charcoal. All these species tend to exclude undergrowth. In the case of the two legumes the dense shade produced may inhibit other vegetation. The *Casuarina*, which makes a thinner shade, lays down a thick blanket of "needles" through which, in drier parts, a seed would not be likely to get enough moisture to germinate, or through which buried seedlings might not penetrate—at least, seedlings are not found. Where this mulch was moist, many plants were observed to be gaining a foothold. On the sandy coastal plain *Casuarina* is very common, in places dominant. Here *Pithecellobium dulce* is also

a common tree. Its bark was used in Spanish times for the tanning of hides.

Parts of the coastal plain have been reoccupied by the Chamorros and are planted to various garden and field crops. Some of the marshy places are used for the culture of taro and related plants. Others, including the area east of Lake Susupe, are covered by brakes of *Phragmites karka*. Parts of the latter, at least, were previously in rice. Rice culture was practiced by the ancient Chamorros and was carried on by the Japanese wherever the land was suitable. West of Lake Susupe is swampy land, with a scrubby vegetation of *Hibiscus tiliaceus*, *Clerodendrum inerme*, *Acrostichum aureum*, scattered *Casuarina* trees, and patches of *Paspalum vaginatum* (pl. 24, fig. 1). Some low places and roadsides are occupied by *Panicum purpurascens*.

The volcanic areas, such as the "sabanans" south of Laderan Tagpochau, Ogso Talofoto (Densinyama Ridge) to the north, part of the hills around Fañunchuluyan Bay, and the slopes east of Laderan Tagpochau, are mostly covered by *Miscanthus floridulus* and associated species. On undisturbed areas of this type, this coarse, tall grass is dominant but tends to be invaded by *Casuarina*. When fires occur, the *Casuarina* saplings are killed, but the *Miscanthus* recovers very rapidly. In places such areas are also invaded by *Acacia confusa*, which tends to shade out the grass and cause it to become very loose and elongated. Fires, here also, kill the trees but merely burn off the shoots of the grass, leaving the root crowns to send up a new crop of shoots. In eroded areas *Gleichenia linearis*, *Lycopodium cernuum*, *Chrysopogon aciculatus*, *Heteropogon contortus*, *Cantharospermum scarabaeoides*, *Scaevola sericea*, *Desmodium umbellatum*, and many less common species make up the vegetation. The first pioneers on this bare clay are *Sphenomeris chinensis* and *Gleichenia*. Some of the areas occupied by *Miscanthus*, such as the east slopes of Sabanan Dandan and areas above Bahia Laulau (Magicienne Bay), are seen, when eroded, to have a layer of fine red soil, up to a meter or more in thickness, underlain by hard coral limestone. In at least two places (the north slope of the peak of Ogso Tagpochau and the pass in the center of the is-

land southwest of Fañunchuluyan Bay), *Miscanthus* was found growing directly on a limestone surface. Thus, although *Miscanthus* usually may be taken to be an indicator of volcanic or lateritic soil, it is not fully reliable as such. On Saipan, at least, where it is found on limestone it is not accompanied by its normal associated savanna species (on Guam there are exceptions to this statement).

The strand zone is made up mostly of cliffs on the eastern side and is dominated by *Pemphis acidula* scrub. Where it is sandy, something resembling the normal, widespread, strand vegetation of the Pacific occurs, with *Hernandia sonora*, *Thespesia*, and *Pisonia grandis* as the most important trees and with *Thuarea involuta* and *Ipomoea pes-caprae* beneath and running out onto the beach (pl. 23, fig. 1). On the west coast, *Casuarina* is conspicuous, but most of the strand forest has been destroyed. At Tanapag is a tiny mangrove swamp containing *Bruguiera gymnorhiza*, *Thespesia populnea*, *Hibiscus tiliaceus*, *Hernandia sonora*, and *Acrostichum aureum*.

The vegetation of Saipan in general has been so disturbed that it is now mostly in a state of rapid change. Secondary successions of various types are taking place. Fire is a frequently recurring factor, and areas are being cleared for cultivation or for construction. Between 1946 and 1950 (the times of the two visits on which the present account is based), many areas had changed almost beyond recognition. The northern part of the island has been closed to the public by the authorities since 1949, because of the presence of unexploded ammunition. These disturbed areas can be expected to come gradually back to a forested condition in most parts. The level portions in the southern two-thirds of the island will probably be more and more intensively occupied and cultivated. And, of course, no one can predict with certainty the course of military policy and the extent or amount of maintenance of the military installations. The present account must be regarded as mainly a series of notes and impressions applying to conditions from 1946 to 1950, against which changes can be assessed.

TINIAN

This island (pl. 25) is essentially a terraced platform of elevated reef limestone, with a locally irregular surface mostly varying between 50 and 100 meters in altitude. Some rather extensive areas near the north and south coasts are lower, while prominences on the three main uplands extend well above 100 meters. The highest points are 178 meters on Carolinas Ridge and about 160 meters at Lasso. A few small exposures of volcanic rock are known, but they are not extensive enough to make much difference in the general limestone environment. The varied topography includes flat plains on the more extensive terraces, long irregular lines of cliffs that bound the terraces, areas of old karst topography with sink holes, and local exposures of sharply dissected limestone. Some of the plains have deep clay soil, mostly red but locally black. The bottoms of depressions in the karst areas have deep marshy soil, some have pools of water in rainy seasons, and one has a permanent pond called Hagoi (Lake Hagoya), on the north end of the island. Elsewhere the internal drainage is very effective, as would be expected in limestone country. There are no surface streams, and the only permanent surface water is the pond mentioned above. Except for a stretch of the southeast coast, the island is surrounded by low cliffs, occasionally with beaches at the base.

Numerous writers (Anson, 1748; Byron, 1773; Wallis, 1773; Gilbert, 1789; Gaudichaud, 1826) have given brief descriptions of the vegetation of the island in the eighteenth and nineteenth centuries. Marche (1891) briefly referred to it, as did Alvarez Guerra (1887). Fritz (1901, 1906) and Prowazek (1913) gave brief accounts of the island during the German occupation, and Kanehira (1937), Hosokawa (1934), and Matsue (1932), during the Japanese period. Together these give only the sketchiest idea of the vegetation and the changes it has undergone. During the Economic Survey in 1946, I spent several days on Tinian, and the observations made then are the principal basis for the present account.

Nothing but conjecture is possible about the original vegetation of Tinian. When dis-

covered by the early explorers, Tinian was densely populated by Chamorros (30,000 according to Anson's informant) but, along with the other Marianas, was depopulated by the Spaniards about the beginning of the eighteenth century. Unquestionably the intensive occupation by the aborigines largely altered or destroyed the original forest which must have completely covered the island. During the eighteenth and nineteenth centuries the Spanish governors maintained the island in a depopulated state as a pasture for great herds of wild cattle which supplied meat for the garrison on Guam. The early visitors mentioned thousands of cattle, hogs, and chickens, as well as goats, dogs, cats, possibly buffalo, and even guanaco. This large population of four-footed animals, descendants of introductions by the Spaniards, unquestionably had a profound effect on the vegetation and may well have been entirely responsible for the open, park-like landscape so enthusiastically described by Anson. He reported (1748, p. 415) open "lawns," "their turf quite clean and uniform, it being composed of a very fine trefoil, which was intermixed with a variety of flowers," alternating with patches and clumps of woods. These woods were in part open beneath and "quite free from all bushes and underwood," as would be expected from the presence of "at least ten thousand" cattle. Anson also mentioned quantities of coconuts and breadfruit, and guavas, limes, sweet and sour oranges, as well as "water-melons, dandelion, creeping purslain, mint, scurvy-grass, and sorrel." A rapid change must have taken place, however, because 23 years later (in 1765) Byron (1773, p. 116) described the same ground in far different terms: "The trees stood so thick, and the place was so overgrown with underwood, that we could not see three yards before us . . . our shirts and trousers . . . were in a very short time torn all to rags by the bushes and brambles; at last, however, with incredible difficulty and labour, we got through; but to our great surprise and disappointment, we found the country very different from the account we had read of it: the lawns were entirely overgrown with a stubborn kind of reed or brush, in many places higher than our heads, and no

where lower than our middles, which continually entangled our legs, and cut us like whiplash." Wallis (1773) described the island as one continuous thicket, with the cattle not nearly so abundant as Anson had described. Gilbert (1789) found conditions essentially the same as those described by Wallis.

Gaudichaud (1826), visiting the island in 1819, wrote that the forests had almost disappeared and were replaced by fields, which, when abandoned, had been invaded by thickets of *Psidium*, *Citrus*, *Triumfetta*, *Sida*, *Gossypium*, and *Waltheria* entwined with *Guilandina* [*Caesalpinia*], *Convolvulus*, and other vines. On the mountains he described a mixed vegetation of native and imported plants, among which he mentioned orange, lemon, coconut, and papaya, and towards the summit (possibly of Carolinas) a forest of *Unona* [*Guamia*], *Rauwolfia* [*Cerbera?*], *Pisonia*, and other trees. Thickets surrounded one of the lagoons and marshes apparently the other, where the animals came to drink.

Marche (1891) merely noted that the vegetation was very "poor" and that coconuts were the only tall trees. Fritz (1901) said the vegetation was not especially luxuriant. He mentioned a forest zone in the south, the trees 10 to 15 meters in height, passing gradually to a scrub 4 meters tall of guava, lemon, orange, and *Annona* trees. This passed in turn to a savanna which covered by far the greater portion of the island. But, instead of grass, this was a guava scrub 0.5 to 1 meter tall, with here and there, especially where the land slopes to the sea, expanses covered with creeping vines and a parasitic plant similar to dodder [*Cassytha*]. He wrote that in especially dry seasons the entire plant cover of the savanna "died," but in the rainy season it came back to life. By Fritz's time the number of wild cattle had apparently diminished greatly. His native informants said there were 600 to 700 head. It may be that many had starved as a result of the encroachment of unpalatable shrubs on the savanna. The development of thickets and the gradual emergence, as gathered from these successive accounts, of the introduced guava as a dominant suggest that such starvation may well have happened. Von Prowazek (1913),

the other German writer who treated Tinian to any considerable extent, contributed very little further information.

During the 1920's the Japanese cleared every square foot of Tinian that had level soil (pl. 25). In Matsue's book describing the process (1932) are colored panoramic views showing the landscape before the forest had been cleared and after the clearing. The portion shown in the first panorama at least was then densely forested. Although the Japanese collected many plants on Tinian, their accounts of its vegetation are so meager as to be of practically no value, although Hosokawa (1934) mentioned mixed forests on limestone and almost pure stands of *Guamia*.

When visited by the United States Commercial Company Economic Survey party in 1946, the island had just been the scene of one of the heaviest actions of World War II and had been converted into a tremendous air base, with two large airfields and a network of roads. The cane plantations had been abandoned for at least two years, although both the Japanese and American Armed forces had used some of them for farms and gardens to produce vegetables and other food plants. The following two paragraphs are quoted virtually verbatim from the description of the vegetation written by me at that time, except for corrections made later in the names of the plants.

The vegetation of the cliffs separating the terraces, and of the exposures of rough limestone such as just north of Tinian City, is typical of that found on rough limestone throughout the area but perhaps drier and more devoid of undergrowth than usual. This is a low, subxerophytic forest of many kinds of trees, locally dominated by *Cynometra*. A similar vegetation occurs on the sea cliffs, but on the west side more moisture than usual seems available, which is reflected in an undergrowth of ferns that is more luxuriant than that found elsewhere. Near the base of these cliffs *Barringtonia asiatica* is one of the commonest trees. The sea cliffs in many places are so steep that they support only a brushy vegetation, with *Myoporum boninense*, *Bikkia mariannensis*, *Hedyotis albido-punctata*, and *H. foetida* common in it, and

showing quite strongly the characteristics of strand vegetation, probably because of the exposure to salt spray. The most surprising discovery here was *Heliotropium anomalum*, not previously known nearer the Marianas than Wake Island. On exposed headlands there is an interesting transition of the vegetation from low forest to brush, mainly *Scaevola*, which becomes lower and lower, then changes from *Scaevola* to *Myoporum* and to *Heliotropium*. Open spaces are filled with a solid turf of *Zoysia*. Species of *Evolvulus*, *Vicia*, and other genera seen nowhere else were found here in these turfy places. Low cliffs above the ocean are often covered with a solid stand of low bushes of *Pemphis acidula*. On still lower rough rocks near sea level *Pemphis*, *Messerschmidia*, and a variety of *Excoecaria agallocha* are dominant.

On the soil-covered terrace surfaces not a trace of the original forest remains. The Japanese had cleared and planted to sugar cane or other crops every patch of arable soil (pl. 25). In 1946 this area was mostly very weedy open ground with large patches of sugar cane and Napier grass (*Pennisetum purpureum*) persisting in it. Different parts had been abandoned for different lengths of time and consequently showed different weed floras, but none had come back to any sort of secondary forest. Some areas which had been abandoned for only two and a half months at the time of our visit had such a luxuriant growth of weeds as to appear to have been fallow much longer. In the Mt. Lasso area on eroded places the strand species *Vigna marina* and *Ipomoea pes-caprae* were found at 150 meters in altitude and well inland. On a terrace below the southeast side of Carolinas Ridge is an area of deep black soil that was apparently planted to sweet potatoes by the Japanese. In 1946 it was covered by a pure stand of a grass that was probably *Paspalum vaginatum*, though this is an unusual site for this species. The plant was sterile at the time it was seen and was not identified with certainty. On the south part of the island, especially near Tinian City, one of the commonest weeds was *Jatropha gossypifolia*, which forms large thickets about 2 meters high. It was introduced by the Japanese as an ornamental (T. Tuyama, un-

published information) and in 1937 was seen (by Tuyama) only as a short hedge. In less than 10 years it had spread and dominated large areas.

Conspicuous in the landscape on the flat parts of the island in 1946 were dense wind-breaks of *Casuarina equisetifolia* and of *Acacia confusa*. Seen from the air in 1950 these species had begun to spread and to invade the nearby fields. By the time of the geological and soil survey in 1950–1951 the fields that were open in 1946 had so grown up to thickets as seriously to impede the surveys.

In 1946 a narrow strip of trees lined the edges of the depression of Lake Hagoya, while the actual marshy land around the open water was a reed brake of *Phragmites karka*. Seen from the air in 1950 the open water had diminished, and the reeds had increased accordingly. Schnee (1911) gives the vegetation of this lake as *Acrostichum aureum*.

A striking feature of this island is the complete absence of savannas dominated by sword grass (*Miscanthus*). This lack is, of course, correlated with the absence of extensive exposures of volcanic rock. Tinian is the only one of the larger Marianas that lacks this conspicuous vegetation type. A concurrent result is also the absence of many species that are commonly found in association with *Miscanthus*.

It is very probable that the original vegetation of the island was a moist forest similar to that found on the northern plateau of Guam, though possibly less wet. Most of the early accounts emphasized the dryness of the soil. Some mentioned the salubrious climate, but those writers who visited Tinian in the wet season did not agree with such a statement, and some characterized it as the worst climate that they had encountered. Judging by present Marianas forests on limestone, the forest may have been dominated by *Artocarpus*, *Ficus*, *Intsia*, *Premna*, *Pisonia*, *Hernandia*, and other large trees. It may have been deciduous in extremely dry seasons (occasionally, not every year, February to May), with a moderate clothing of epiphytic plants such as orchids and ferns, and it may have had a fairly well-developed undergrowth of *Guamia*, *Maytenus*, *Cycas*, *Geni-*

ostoma, *Piper*, and large ferns. Towards the edges of cliffs and on high summits the forest was probably dwarfed and similar to that existing in such situations at the present time. The vegetation of the actual cliffs and strand situations also was probably very similar to the present vegetation. In some ravines and broken terrain traces of a taller forest still exist, but in it the introduced *Delonix regia* is conspicuous.

AGUIGUAN (AGUIJAN)

This small island (pl. 26) is just south of Tinian and in geological structure is essentially similar to it, being a limestone platform with several flat terraces. Little if anything has been written on its vegetation, and I have not studied it, except briefly from the air in 1950. As with Tinian, the Japanese cleared the level places for sugar-cane plantations and planted windbreaks of *Casuarina* on the uppermost terrace. The plantations were still more or less dominated by the persisting cane and by Napier grass in 1950. Most of the cane has since died. The other parts are wooded, but the undergrowth, at least, has been affected by the large number of feral goats that inhabit the island. The composition of the forest is apparently similar to that on the rough limestone and the cliffs of Tinian. A bamboo and the flamboyant, *Delonix regia*, as well as *Leucaena glauca*, are conspicuous introduced plants. *Jatropha gossypifolia*, as on Tinian, is locally common, probably because it is unpalatable to the goats. Much of this information was gathered from unpublished photographs kindly furnished by Mr. George Peterson, which he took in 1954, and others, by Mr. Clifton J. Davis, which he took in 1954 and 1955.

ROTA

Although many earlier botanists visited Rota (pls. 27, 28), especially during the Japanese period, no significant account of its vegetation has been located in the literature. Gaudichaud (1826), Marche (1891), Fritz (1901), Prowazek (1913), Seidel (1915), Hosokawa (1934), and Kanehira (1936) have all published accounts of the island that mention vegetational features, but from all these

no clear idea of either the character or the pattern of the vegetation can be gained. Seidel (1915, facing p. 192) gives a map purporting to show the distribution of the vegetation types as well as the topography, indicated by contour lines. Neither the contours nor the vegetation on this map is very convincing, and the paper that it accompanies seems to have been entirely compiled from previous, inadequate accounts. The present account is based on observations made in less than a week spent on the island in 1946 and 1950, with brief opportunities to see it from the air, and from a few strips of aerial photographs and a published photomosaic (United States 64th Engineer Base Topographic Battalion, 1952b). Such observation is quite inadequate for an exact description to be given but makes possible a generalized account.

Rota has an area of 85 square kilometers. It is principally a series of limestone terraces rising one above the other, surrounding a volcanic core which protrudes slightly through the topmost plateau (to an altitude of 496 meters) and is also exposed on the slopes of the south side of the island. Depending on the angle from which the island is viewed from the air or sea, there appear to be from five to 11 terraces. They seem mostly to slope gently towards the sea, but on the ground this is imperceptible in many places. There probably has been some local faulting which has confused both the regularity of the terraces and the slope of their surfaces. The limestone surface itself varies from being fairly smooth and covered by a significant layer of soil, to bare rock, deeply pitted and rough, in places much dissected. The volcanic hill at the top is smooth and rounded in its contours. The exposed volcanic material on the south forms a rather steep but variable slope, cut by small streams which issue from the base of the limestone cliff above (pl. 28, fig. 2). These streams have eroded small ravines in large parts of the surface, while some areas have been, from ancient times, terraced for rice and taro culture and irrigated by water from the streams.

The island formerly had a large population of Chamorros who unquestionably modified most of the vegetation rather drastically. It was largely depopulated by the Spanish at

about the beginning of the eighteenth century. The rougher parts of the island were probably not cleared by the aborigines, and during the period between the depopulation (1700) and the Japanese occupation (1914) the original forest vegetation had time to recover even on areas that had been completely cleared. Kanehira (1936) says that when he visited Rota in 1932 the entire island was covered by impenetrable forests that could not be traversed even with the aid of an axe and that he was forced to grope his way along hunters' footpaths. But when he returned in 1935 he found much of the island cleared for sugar planting and roads running to all parts. In 1946 there was some relatively undisturbed forest on areas where the soil was too thin for agriculture; areas with soil had been planted to sugar cane but were subsequently abandoned and in places were growing up to second-growth scrub and forest. Areas still under cultivation by the natives were rather insignificant in size, although scattered in various sections of the island. An aerial photomosaic prepared from photographs taken in 1946 shows that about one-fourth of the total area was covered by well-developed forest, but this was divided into many small parcels and rather narrow, concentrically arranged areas resulting from the roughness of the land near the cliffs which bound the various terraces.

The vegetation of the island was probably originally rather simple. On the limestone parts a mixed forest existed, varying from semi-xerophytic, more or less dry-season deciduous on the lower terraces, all the way to a wet forest (pl. 27), though scarcely a true rain forest, on the highest terraces. The best parts of this forest were undoubtedly cleared, and what is left is of medium stature, rather degraded by logging and, in places, by bombing.

The lowest terrace, a sort of coastal plain, best developed along the north coast, still possesses remnants of a strand type of forest of *Hernandia sonora*, *Thespesia*, *Hibiscus tiliaceus*, *Barringtonia asiatica*, *Pandanus tectorius*, *P. dubius*, *Ochrosia oppositifolia*, *Pisonia grandis*, *Guettarda speciosa*, and other trees and shrubs. On the spray-swept beach *Messerschmidia argentea*, *Scaevola sericea*,

Excoecaria agallocha, *Pemphis acidula*, and *Sophora tomentosa* are more abundant. In going back from the actual coast to the strand forest one encounters also various plants, such as *Cycas circinalis*, *Terminalia catappa*, *Laportea*, *Macaranga*, *Mammea*, *Premna*, *Morinda citrifolia*, *Allophylus*, *Melanolepis*, *Pipturus*, *Intsia*, *Grewia*, *Ficus prolixa*, *F. tinctoria*, *Albizia lebbek*, *Pithecellobium dulce*, and *Muntingia calabura* (the last three introduced but completely naturalized), as the forest gradually changes to the subxerophytic forest of the lower several terraces. In this dry type, especially on cliffs and rough areas, *Cynometra ramiflora* is in many areas a dominant or exclusive species. *Casuarina* is locally common or in some areas abundant. A tangled undergrowth of *Colubrina*, *Jasminum*, *Callicarpa*, *Phyllanthus*, *Mucuna*, *Ipomoea*, and other native plants competes with dense, spiny thickets of *Triphasia trifolia* to make penetration difficult. Much of this forest has been cut, and weed patches and thickets remain (pl. 28, fig. 1). Coconut trees were formerly abundant but are now gone because of the ravages of the *Brontispa* weevil. Ferns are common in the shade at the bases of the cliffs. On open, vertical cliff faces, too steep for forest, a sparse shrubby vegetation is found in which *Bikkia*, with large white flowers, is conspicuous. Breadfruit trees, at these altitudes, are usually of the seedless sort and persist from planting. The soil on much of this lower terrace land is very thin. Places were observed where it had been raked together into windrows parallel to the contours, exposing the bedrock between the rows, in order to obtain sufficient depth for planting sweet potatoes and perhaps other garden crops. On many of the thin-soil areas on these and more elevated terraces the soil has been so washed away following clearing that the limestone in places resembles a rough pavement. Here the revegetation to secondary thickets is very slow, and the vegetation is principally a mat of *Passiflora foetida* and *Ipomoea indica*.

The most extensive terrace is a gently sloping one between 150 and 200 meters on which the air strip and the ruins of Shimaparu are located. Here the original forest had been mostly cleared. Even in 1946 secondary

thickets were occupying many areas, but cultivation continued in places. At these altitudes the forest changes imperceptibly to a wetter type which on the topmost terraces is very luxuriant and has a full canopy. In these wet parts the principal trees are *Elaeocarpus joga*, *Hernandia labyrinthica*, *Fagraea berteriana*, *Pandanus*, *Guettarda*, *Ficus prolixa*, *F. tinctoria*, *Artocarpus mariannensis*, *Pipturus*, *Laportea*, *Guamia*, *Claoxylon*, *Boerlagiodendron*, *Macaranga*, *Pisonia umbellifera*, and others, with *Psychotria*, *Piper*, *Discocalyx*, *Maesa*, and other shrubs and many ferns in the undergrowth. *Freycinetia* and *Alyxia* are common lianas. Epiphytic ferns and orchids are abundant. Around the edges of clearings and along roads *Premna* and *Tarenna* are common, and great lianas of *Mucuna gigantea*, *M. urens*, and *Flagellaria indica* festoon the margins of the forest and make penetration difficult.

Most of the topmost terrace has been cleared and is covered by grass, cultivated fields, and in places by large patches of Napier grass. A considerable area on the southwest side is bare and fantastically pitted and pinnacled, the result of phosphate mining by the Japanese. The highest point on the island is a knoll of volcanic material protruding up through this limestone terrace. It is partly covered by a dense, low forest of *Acacia confusa*, apparently introduced by the Japanese, and partly by grassy or fern-covered, open areas dominated by *Paspalum* and *Gleichenia*, with *Blechnum orientale* forming conspicuous rosettes.

The vegetation of the volcanic soil on the south slopes (pl. 28, fig. 2) contrasts conspicuously with that of the rest of the island. It is typical sword-grass savanna, dominated by *Miscanthus floridulus*, with the ravines densely wooded with breadfruit, mango, and various native trees thickly tangled with undergrowth at the edges. The *Miscanthus* is frequently burned, and the savanna shows conspicuous erosion scars cut into the very acid, bright red or, in lower layers, mustard-yellow, clay soil of the steeper slopes. The vegetation of the partially healed scars is characterized by small shrubs such as *Myrtella*, *Geniostoma*, and *Wikstroemia*, and herbs such as *Gleichenia* and other ferns,

Fimbristylis, *Euphorbia*, *Heteropogon*, and *Chrysopogon*, as well as many weeds (a weed, as the term is used in this paper, is an aggressive pioneer species). On the gentler slopes are apparently prosperous little farms with breadfruit and mango trees, maize patches, and gardens with various cultivated plants. In marshy areas along the streams that here characterize the terrain, and especially in the former irrigated land where the Chamorros are said to have cultivated rice, *Alocasia* is generally dominant. Some rice plants were found persisting. Clumps of bamboo are common here, especially in the wooded ravines, and in sheltered moist places bananas are abundantly planted. In the garden plots dry-land taro, *Xanthosoma*, maize, sweet potatoes, and tapioca are the commonest plants. When these plots are abandoned they are quickly covered by a tall growth of weeds.

GUAM

Guam (text fig. 2; pls. 29–40) is the largest and southernmost island of the Marianas. It is almost 50 kilometers long and from 7 to 15 kilometers wide. The highest point, Mt. Lamlam, is 406 meters in altitude. The northern half of the island is mostly limestone, with three small volcanic hills protruding through it. The largest part of this, to the north, is a flat plateau of hard limestone. This plain slopes gently to the southward from about 200 meters to about 100 meters at the narrow waist of the island which is an old karst surface of an argillaceous limestone, worn down into rounded hills and marshy-bottomed sinks. There is no surface water in the northern part except for several springs. The southern half of the island is in sharp contrast. It is of ancient, deeply weathered volcanic material, plastered here and there with patches of limestone, the largest of which is the Mt. Lamlam-Mt. Alifan Ridge, which makes up the backbone of the island. High peaks of volcanic material are Mt. Tenjo, not far south of the center of the island, and a number of sharp prominences south of Mt. Lamlam. In this southern half are numerous streams and one large river system, the Talofof. The mouths of the valleys hold small estuaries surrounded by

small areas of flat land. Higher up there are flat or gently rolling areas as well as rugged terrain. Small remnants, sometimes termed "mesitas" (pl. 37, fig. 2), of an ancient erosion surface, with fine red soil, are scattered here and there. Rock exposures occur on ridges and steep, eroded slopes. Along the west side near the middle of the island is a coastal plain of varying width, interrupted by cliffs. This in its broadest part extends halfway across the island and includes the extensive Agaña Swamp, or marsh, fed by a large spring in the argillaceous limestone area. Much of the remainder of the periphery is bounded by cliffs and steep slopes, interrupted by flat valley mouths.

The soils are quite varied. On the hard limestones of the northern plateau and its southern extensions along the coasts is a bright red, highly lateritic soil, generally shallow but deep in low spots. On the argillaceous limestone is a brown soil, perhaps the best on the island agriculturally. In the valley bottoms is alluvial clay soil, or, in marshes and swamps, a deep, highly organic muck. On the coastal plain and other narrow strips of low coastal land at valley mouths or at bases of cliffs the soil is a somewhat altered coral sand, more rarely in the southern part a sand of heavy volcanic minerals. The soil of the volcanic portions of the island is a deep red, purplish, or yellow clay, highly acid in most places and containing little humus except in the surface.

No detailed systematic study of the vegetation of Guam has been made, but its vegetation is the best known of any of the Marianas. Much scattered descriptive material is available. Gaudichaud (1826) spent several months on the island in 1819 and left a valuable account which shows a considerable degree of understanding and helps to explain present conditions. Safford spent a year on Guam as a government official just after the transfer of the island to United States jurisdiction in 1899. His book (1905) and other works (1902-1904) give a very interesting and comprehensive account of the plants and an account of the vegetation. Merrill (1914, 1919) and Merrill and Perry (1946) provided a rather complete listing of the flora but without much information on the vegetation.

During World War II a number of American service men made collections and studied the flora and vegetation. Walker and Rodin (1949) reported on the additions to the known flora. A paper on the vegetation by Glassman (1948) also resulted, which was the most adequate published work on the subject up to that time. The present study is based on observations made during six visits, aggregating somewhat more than three months, in 1946, 1950, 1952, 1953-1954, 1956, and 1957. It can, at best, be regarded as a reconnaissance study, but gives a rather complete descriptive outline of the vegetation types and pattern. (See Detailed Consideration of the Principal Vegetation Types on Guam, p. 54, below.)

The greater part of Guam is forested, but substantial areas, especially in the southern half, are covered by coarse grass, and smaller parts are in pasture or under various kinds of cultivation. There are few large stretches of uniform vegetation. Most of the island is covered by a mosaic of small patches of extremely varied appearance. The forests are mostly second growth, many of them irregular thickets, generally dense, tangled, and often with spiny undergrowth.

Limestone areas are usually wooded, except where they have been cleared for agriculture or other purposes and except for some vertical cliffs. The original forest on limestone was of large trees, with a thick canopy overhead. A long history of disturbance by the Guamanians and by frequent typhoons, together with the destructive effects of World War II and subsequent military activities, has left little undisturbed primary forest on the island. Weed patches, partially revegetated clearings, thickets of fast-growing, soft-wooded, weedy trees and scattered bare skeletons of dead forest giants are more characteristic than is the forest which originally occupied most of the island. Scattered patches of the latter remain here and there on the northern plateau and especially on cliffs and relatively inaccessible terraces around the steep coasts of the northern half of the island.

Much of the plateau is occupied by areas cleared for military establishments, either active or abandoned. Some of these are rela-

tively bare of vegetation. Others have grown up to tall grasses, thickets, and large areas of *Leucaena*, a tall, feathery-leaved shrub or small tree which has increased enormously since the war. Coconut groves are found in many parts, both on the plateau and along the coast. The lower central part of the island has been subject to disturbance for a much longer period. Much of it is under cultivation, mostly in small patches, or in larger areas of pasture, with diverse thickets, *Leucaena*, bamboo clumps, and small coconut groves. A large reed marsh, Agaña Swamp, occupies the section of the center just east and north of Agaña. Other marshes are found along the west coast from Piti to south of Agat, with small mangrove swamps interspersed.

The southern volcanic half of the island is a complex mosaic of grassland and patches of forest (pl. 35). Low land in the valleys of the Talofofa river drainage and of some of the other rivers is occupied by extensive swamp forests and occasional cultivated clearings. In these valleys, as well as on uplands along the east coast, are large coconut plantations. Patches of mangrove occur at the mouths of the rivers.

The grasslands or savannas (pls. 35-40) of the volcanic soils are believed to be mostly, but not entirely, the result of extensive and repeated burning over many years. Much of the grass is tall, harsh sword grass, with

sharp-edged leaves, which forms a very dense growth, especially on slopes. Ravines in these areas are filled with thick growths of coarse reeds, which stand out from the rather similar sword grass by their brighter green color (pl. 38, fig. 2). Level areas are more usually covered by a softer, bluish green, low grass (pl. 35, fig. 1). Erosion scars are grown over by small bushes and tangled ferns (pl. 38, fig. 1).

When left unburned for a few years the grasslands may be abundantly invaded by *Casuarina* trees (pl. 36, fig. 1), which may eventually form open forests. These trees are, however, very susceptible to fire, and stands of them of any extent in the savanna have grown up only since the Japanese invasion in 1941. At the present time they are again being destroyed by fire.

The forest patches in the volcanic region occupy a substantial total area but are much broken up by ridges and flats covered by grass. The woody vegetation on volcanic soil in many respects resembles that on limestone, but tends to be thicker, lower, more bushy, and characterized by betel-nut palms. The forests (pl. 35) are more commonly found in ravines, valley bottoms, and steep slopes; they were undoubtedly much more extensive before the Chamorro people arrived on Guam and their destruction has been especially rapid since the coming of the Europeans.

DETAILED CONSIDERATION OF THE PRINCIPAL VEGETATION TYPES ON GUAM

GUAM IS HISTORICALLY the most important island of the Marianas and has been studied most. As noted above (p. 11), the classification of types used in the description of its vegetation differs from that of vegetation situations and types in other parts of Micronesia (pp. 12-34). Because it is not desirable to attempt to squeeze the vegetation categories that emerge upon more careful study into the highly generalized arrangement used for the whole of Micronesia, the vegetation of Guam is treated in detail separately.

The significant vegetation types found on

Guam and some of their variants, grouped ecologically, are described below. Probably few, or none, of these exactly represent any of the original vegetation of the island but are rather the results of modification by man. In many, this modification has been profound or complete, and in some it has been so recent that no subsequent equilibrium has been attained, and the vegetation is still changing rapidly. The types described first are the most stable and perhaps are nearest the original ones, while those that are treated last are the result of recent disturbance and are still changing rapidly.

FORESTS OF ELEVATED HARD LIMESTONES

Plate 29, figure 1; plate 30, figure 1

The mixed mesophytic, broad-leaved evergreen forest of the elevated limestone terraces, plateaus, and slopes must originally have been the most widespread vegetation type on Guam. The entire northern half of the island, except for Mt. Santa Rosa and two smaller volcanic outcrops and the beaches, is of hard limestone. Around parts of the southern half, on both east and west coasts, there are "ramparts" or other areas of hard limestone, and the high Mt. Lamlam-Mt. Alifan Ridge and the hill west of the Fonte River are also of this rock. These areas were, and in small part still are, covered by a tall, dense, mixed forest, mainly of evergreen dicotyledonous trees. In the central part of the island the argillaceous limestone may have borne the same sort of forest, but because it was the most suitable agricultural land, the original vegetation of this area has been completely altered. Its secondary vegetation is treated below.

It is difficult to be certain of the character of the original vegetation, even of the hard limestone areas. Guam has been inhabited by man for possibly several thousand years, but of this period virtually nothing is known except for the last 430 years. For most of the latter period, until 1941, the total population

has not been large, but at the time of Magellan's visit in 1521 there must have been tens of thousands of aborigines. The influence of these people on the vegetation is hard to estimate but could not have been negligible. Since Magellan's time, although the population has been smaller, the people have been much better equipped to destroy the forests. Also, since that time they have been ably assisted by the cattle, goats, deer, and other four-footed animals brought by the European conquerors. The actual changes effected by these influences up through 1941 cannot be well traced, but undoubtedly the local diversity of forest types growing on an essentially uniform substratum and in the absence of much local climatic variation is one result.

Beginning with the Japanese invasion in 1941, the rate of change in most of the vegetation types on Guam was enormously accelerated. Battles were fought in the forests with highly destructive modern weapons. Enormous areas were cleared and scraped by bulldozers and changed permanently; they are discussed below in a section on weedy vegetation. In the following paragraphs the main present-day aspects of this forest are discussed.

Because of the presence, virtually every-

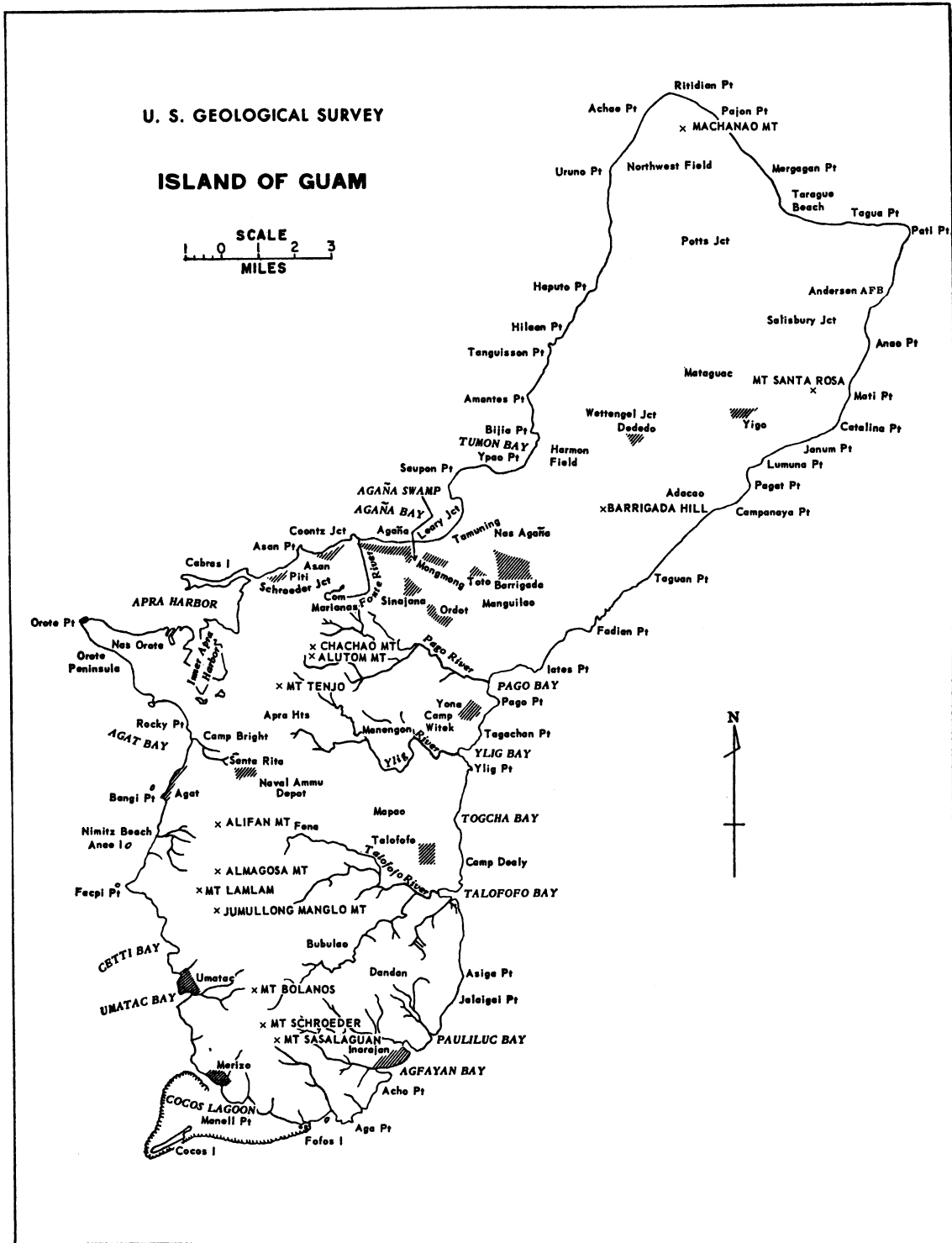


FIG. 2. The island of Guam.

where, of species that generally occur in secondary vegetation and even of introduced plants, such as *Triphasia*, *Cestrum*, and *Carica*, and because of the uneven, brushy nature of almost all the remaining forests, it seems best to regard the present-day forests on the plateaus and terraces as modified. In a few places the disturbance may not have been great enough to change the structure and composition entirely, but as a whole what is presently growing on these areas is considered to be modified forest, probably much of it not truly secondary, if this term is taken to mean forest that follows clearing.

Generally, this modified forest of limestone areas has a thinner, more irregular canopy than primary tropical forest usually has, and consequently more abundant undergrowth. Several introduced species have become common in the undergrowth, notably *Triphasia trifolia* and *Morinda citrifolia*. The two species of *Pandanus*, *P. tectorius* and *P. dubius*, have probably greatly increased in abundance. *Intsia*, formerly much more common, has been logged out, until it is in many parts of the island quite scarce. Logging of this species, the *ifil* of the Guamanians, was carried on rather continually in the early part of the present century, and large trees are now not often seen. Where found in Guam, large trees of *Intsia* seem to be characteristically almost leafless though still living. This is not true of the same species elsewhere, and the reason is not obvious unless it is due to exposure as the surrounding forest is cleared or destroyed.

In many areas on the northern part of the island most of the large trees of various species are dead or in very poor condition. Several reasons are advanced for this—insect damage, typhoon damage, damage from military activities when fighting was intense in these areas, and exposure from partial clearing. Probably no one of these explanations accounts entirely for the large areas dominated by white skeletons towering above the lower growth in the forest. All the above-mentioned factors, and still others, may together be responsible for this condition. Examples can be seen west of Andersen Air Force Base and west of Northwest Field.

In this present-day forest, though it varies continuously, several more conspicuous or

frequent aspects occur. These are described below and, where possible, are localized and correlated with topography and other features. It must be remembered, however, that in a continuously varying vegetation by no means all examples will fit any of the described categories.

Artocarpus FOREST

The most widespread aspect of the limestone forest is dominated by large trees of the wild breadfruit or *dugdug*. This is *Artocarpus mariannensis*, closely related to the cultivated breadfruit, *Artocarpus altilis*, but differing in the entire or few-lobed leaves, pubescent and brownish beneath, and the consistently seedy fruit, as well as in the softer, yellower, more fine-grained wood. A secondary dominant species that is locally quite as abundant as *Artocarpus* is *Ficus prolixa*, a large banyan. This is called *nunu* by the Guamanians. The trunk of this tree, which may be enormous, is not a clear column as in *Artocarpus*, but an entwined and fused mass of large, tough, aerial roots, some of which also hang from the branches and form smaller secondary trunks like pillars supporting the branches.

Besides the above-mentioned dominants this forest is likely to have *Aglaiia*, *Ochrosia*, *Premna*, *Tristiropsis*, *Elaeocarpus*, *Intsia*, *Pisonia*, *Claoxylon*, and *Pandanus* as fairly large trees, and smaller individuals of all of these, as well as *Guamia*, *Cycas*, *Morinda*, and *Triphasia* in the understory. Locally any of the above trees may become common or even dominant.

Generally most of the trees in these forests form a dense second story 10 to 15 meters in height, with *Pandanus* and *Elaeocarpus* commonly most abundant. Overshadowing this is a discontinuous layer of *Artocarpus* and *Ficus* which may be from 20 to 25 meters in height or even taller. Locally these two may be up to a meter in diameter, the *Ficus* even more, but most of the *Artocarpus* are much less. The understory and shrub layers are not sharply separated. They vary in density inversely with the age of the forest and the density of the upper layers. In a forest that has not been logged or cleared for many years, it is possible to walk around rather freely with little trail cutting. In

younger or sparser stands the ground is likely to be choked with shrubs, vines, and luxuriant ferns.

This type of forest is found over large parts of the northern plateau, on the hard limestone on the east coast as far south as Talofof Bay, and on the Mt. Lamlam-Mt. Alifan Ridge. It is no longer continuous over extensive areas because of the widespread military activities of the past few years. Good examples may be seen on the road from Yigo to Agafo Gumas, about 1 kilometer northwest of Yigo. When this type of forest is cleared, some large trees are often left standing which usually become unhealthy and die in a few years. The *Artocarpus* trees seem to stand the exposure resulting from clearing longer than most others.

MIXED MOIST FOREST

East of Mt. Santa Rosa and for an undetermined distance north and south along the strip just behind the edge of the coastal cliff, there is a type of forest (pl. 30, fig. 1) similar to that dominated by *Artocarpus*, but almost completely lacking that genus. Here no one tree is especially outstanding in the landscape, though various ones may be so locally, especially *Tristiropsis* and *Claoxylon*. *Mammea* may be common here. Old stumps and logs of *Intsia*, the *ifil* of the Guamanians, are frequent, said to date from logging operations in 1912. This logging may account for the presence in this area of large trees of secondary species such as *Macaranga*, growing with the other trees enumerated under the *Artocarpus* type.

Forest similar to this is also found on the terrace behind Tarague Beach. Here *Ochrosia* and *Cycas* are the most abundant trees. *Cycas* makes up the understory.

Mammea TYPE

On the eastern escarpment of the plateau, as at Anao, except where it is vertical, the dominant tree is *Mammea odorata*, the *chopag* of the Guamanians. This is seldom a large tree; locally it may make up the greater part of the forest on steep slopes, ledges, and terraces. The forest varies from being rather uneven to uniformly dense, with a smooth canopy as seen from the air. It is

usually of medium height and has a well-developed undergrowth. *Aglaia*, *Guettarda*, *Cynometra*, *Bleekeria*, *Guamia*, *Ochrosia*, and *Ficus* are generally frequent, and on the gentler slopes and terraces below the cliffs *Pisonia grandis* is common in places. Here *Hibiscus tiliaceus* is an important component, as well as, locally, *Barringtonia asiatica*.

Cordia TYPE

On the steep slopes and cliffs behind Tarague Beach on the north end of the island, the forest is locally dominated by *Cordia subcordata*, with *Aglaia*, *Macaranga*, *Premna*, *Cycas*, *Morinda*, *Cynometra*, *Guamia*, and *Pipturus* common. This forest is not tall and not particularly dense, but rather difficult to walk through because the limbs of *Cordia* tend to be low, very widely spreading, and tangled just above the ground.

Merrilliodendron FOREST

On terraces at Haputo is an example of what may have been a more widespread forest type, a tall forest, perhaps 30 to 45 meters in height, dominated by trees of *Merrilliodendron megacarpum* and *Ficus prolixa*, the latter less abundant but taller. The second story, only about 4 meters in height, is of saplings of *Merrilliodendron* and the lowest layer, from 0.5 to 1 meter in height, is of seedlings of the same species. This tree seems completely tolerant of shade. *Ficus* seedlings are not found in these layers because they start as epiphytes in the crotches of trees, then send roots down the trunks of their hosts, and eventually surround them with a network of roots and "strangle" them to death. Hence the name "strangling figs" is commonly applied to such species. The resulting habit is referred to as the "banyan" growth form.

Pandanus FOREST

Common on interior areas on the plateau are forests made up of an almost pure stand of *Pandanus tectorius*, the screw pine or *kafu*. The trees in any one stand appear to be about the same age, 10 to 15 meters in height, the trunks 10 to 20 cm. in diameter. The prominent stilt roots of the *Pandanus* add to the *Flagellaria*, *Cestrum*, *Triphasia*, *Nephrolepis*,

and other components of the dense undergrowth in making walking difficult.

Pandanus forest (pl. 31, fig. 1) is probably a secondary type, though its exact status is extremely hard to determine. Study of successional relations in these forests would be time-consuming and uncomfortable but possibly very enlightening. There is every conceivable transition between this and the *Artocarpus* and mixed forest types, but the pure *Pandanus* is very conspicuous and covers considerable areas. Good examples may be seen along the highway northeast of Dededo.

HALOPHYTIC AND XEROPHYTIC SCRUB

Plate 4

On terraces and cliff edges not very far above the sea on the east and north coasts and on vertical limestone cliffs and their tops is a scrub of varying heights and densities that may be a response to extreme salt spray, to dryness resulting from too good drainage, to excessive transpiration due to the exposure to winds, or to any combination of these and other factors. It is low, tangled, often

stiff, and conceals pits, pinnacles, and other dangerous irregularities in the limestone. Good stands of such scrub, showing considerable variation, occur south of Campanaya Point on the lowest terraces a few meters above sea level.

Near the sea, *Pemphis acidula* (pl. 4) is by far the most abundant component and, where exposed to strong, spray-laden winds, may form almost a mat. Back a short distance *Scaevola*, *Guettarda*, *Mammea*, *Messerschmidia*, *Clerodendrum inerme*, *Pandanus dubius*, *P. tectorius*, *Hibiscus tiliaceus*, and *Ochrosia* may all be present in dwarfed forms. On the steep cliffs, *Bikkia*, *Hedyotis foetida*, *Cycas*, *Triphasia*, *Scaevola*, *Mammea*, and *Phyllanthus mariannensis* all may be important components. At the tops of higher cliffs any of these may be present, but *Triphasia*, *Ficus prolixa*, *Colubrina*, *Jasminum*, and *Cynometra* are likely to be prominent. Scrub is not universally present in the afore-mentioned sites but may in places give way to forest. On steep cliffs the density is likely to vary with the steepness of the cliff and the number of crevices, ledges, and other irregularities.

RAVINE FOREST OF SOUTHERN GUAM

Plate 35

In valleys and ravines and on certain slopes in the volcanic portion of Guam is an important type of forest that differs somewhat from that on the plateau limestones. As its floristic composition is rather variable, it may conveniently be termed ravine forest. Good examples can be seen in the heads of ravines both north and south of the road between Apra Heights and Camp Witek. In addition to occupying ravines and slopes in the volcanic area, this type or variants of it occur on outcrops of Bonya and Maemong limestones (D. B. Doan, personal communication) in the Talofofu drainage. The south side of the Talofofu Valley is forested largely with this type, which also alternates with swamp forest in the valley bottom. Where the valley bottom is flat there is generally swamp, while on low hills and ridges the forest is similar to the ravine type.

This forest is usually an uneven mixture of many kinds of trees, of rather low stature,

brushy, and tangled. The canopy, if any, is only a few meters above the ground, and its upper surface is typically irregular. Because of the characteristic occurrence of this type of forest in ravines there is seldom a great continuous extent of woods. The small patches naturally vary in character with the depth of the ravines and the steepness of their sides. A typical occurrence has a belt of very thick scrub around the edges, gradually changing inward to forest. In the ravine bottoms the forest may be tall enough and dense enough to permit free passage, or it may be low and tangled or sparse and choked with brush and saplings. A tree layer and a shrub and herb layer can usually be distinguished in the deeper parts of the ravine, but towards the edges, these merge and become indistinguishable.

This forest type is variable in composition from place to place but generally much poorer than the forest on the limestone

plateaus. The inclusion of the lowland limestone hills of the Talofofu basin adds considerable variety to the total list of species growing in the ravine forest. However, the aspect and principal species on this limestone are not much different from what are generally found in the ravines. A more intensive study would most assuredly result in separation of one or more distinct types on this limestone. For purposes of the present study and with the information at hand, it seems better to merge them.

Most abundant trees in the ravine forest are *Hibiscus tiliaceus*, *Pandanus tectorius*, *P. dubius*, *Ficus prolixa*, *Glochidion mariannensis*, *Areca catechu*, *Premna obtusifolia*, *Cocos nucifera*, and, more locally, *Artocarpus mariannensis*, *Cananga odorata*, *Ochrosia oppositifolia*, *Bleekeria mariannensis*, *Calophyllum inophyllum*, and others. Shrubs are commonly *Triphasia trifolia*, *Cycas circinalis*, *Timonius glabrata*, *Morinda citrifolia*, *Piper guahamense*, *Geniostoma* sp., and, rarely, around the edges, *Cyathea lunulata* and *Melochia hirsutissima*. *Medinilla rosea*, *Freycinetia torresiana*, *Flagellaria indica*, and *Lygodium scandens* are common climbers. Epiphytes occur, but not abundantly. Herbs on the forest floor are *Oplismenus compositus*, *Centotheca lappacea*, a large species of *Scleria*, and several ferns.

The most nearly characteristic species, and the one that most generally sets this forest off from the plateau forest, is the betel palm, *Areca catechu*. This species is almost always present in the ravine type and is apparently lacking in the plateau forest, except that it is

found rarely on Mt. Lamlam. *Calophyllum*, also lacking from the plateau forest, is often found in the ravine forest. *Glochidion* is much more common in the ravine type. There are, however, no tree species restricted to this type. The difference is more one of aspect and of average or percentage composition than of mutually exclusive species.

There seems no doubt, because of the widespread presence of *Hibiscus tiliaceus*, *Areca catechu*, coconuts, *Triphasia*, and even bamboo, that this type is secondary. The abundance of artifacts, especially broken pottery, as well as scanty historical evidence, shows that these parts of Guam were densely populated in pre-Spanish times, and undoubtedly the ravines were used largely for agriculture—taro and rice growing and coconut culture. Betel chewing was a widespread or universal habit, and the betel palms (*Areca*) now found here are probably descendants of planted ones.

Outstanding variants of this type are stands of *Calophyllum* in the Talofofu region, groves of *Areca* or of *Areca* with *Hibiscus* in various places, and pure stands of *Cananga* in the Fena River area (pl. 29, fig. 2). All these species may be of aboriginal introduction. In the Umatac and Merizo areas, as on the slopes of Mt. Schroeder, *Artocarpus mariannensis*, the *dugdug* of the Guamanians, is a dominant component of this type. It is scarce or lacking in most ravine forest areas.

There seems to be no way of deciding, from information at hand, what the original forest of southern Guam was like.

WET LANDS

Plates 32, 33

Wet land is not very extensive in Guam, but it is widely distributed on the southern half of the island. It occupies sufficiently different topographic situations that a number of distinctive vegetation types have developed to occupy it.

Ground where the water table is either permanently at the surface or sufficiently near it to make the soil permanently wet may, in Guam, be conveniently divided into marsh and swamp, depending on whether the vege-

tation is predominantly herbaceous or woody. Several types of each exist on Guam. Bogs, wet areas with thick peat accumulations, do not exist on the island and are rare in all lowland tropics, unless peat swamps are considered bogs; in that case the *Barringtonia* swamps of Guam may be regarded as bogs. A few borings also indicate that peat may underlie at least the larger of the *Phragmites* marshes. The extent of this accumulation has not yet been determined.

Marshes are found in low places along the coast, along streams, in depressions and sink-holes in the argillaceous limestone region, and in small, poorly drained spots and in depressions and ravine bottoms in volcanic soil. Mostly they contain fresh water, though some close to the beaches may be brackish. Swamps are found chiefly along river beds essentially at sea level and in certain coastal areas. There is also a swampy depression, transitional in character between reed marsh and swamp, east of the high ridges of Mt. Lamlam. Little or no wet ground exists on the northern part of the island, with the exception of a few marshy spots around Mt. Santa Rosa and Yigo. The drainage in the limestone is too nearly perfect.

The wet areas of Guam are occupied mostly by single species or mosaics of patches of single species, rarely by mixtures of a few species. Invasion and successional change undoubtedly occur very commonly, but in the time devoted to studying these types of vegetation little definite evidence of such invasion and change was recorded.

The ground in all the marsh and swamp types of vegetation is usually soft, and in none of them can it be depended upon to support vehicles. Crossing such areas on foot may or may not be feasible, depending on the season and on local conditions. The vegetation itself, in the woody and reed types, usually makes progress extremely laborious. The *Barringtonia* swamp is an exception in that walking, except for fallen trees and knee-deep water, is fairly easy. The firmness of the ground here is deceptive, however, as heavy vehicles, such as caterpillars, bog down.

MARSHES

It is almost certain that on Guam, as in most wet tropical areas, marshes are merely stages in successions leading to woody vegetation, usually swamp types. In some of the marshes succession seems to be active; in others, more or less retarded. What the factors may be that retard the process of vegetational change is not known, but it is clear enough that in some cases man's activities may create and tend to maintain open conditions, even in areas of waterlogged soil. It is possible that many areas are now open and marshy only because they were cleared

out and used for rice cultivation by the Japanese during the last war.

REED MARSH

This is by far the most frequent type of marsh vegetation. It is dominated by the tall tropical reed *Phragmites karka*, often in pure stands. This plant forms hollow canes the thickness of a man's thumb and 2 to 4 or even 5 meters in height. Ordinarily a stand of these canes is so dense as to make penetration by a man on foot difficult. Stands are seen in which the canes may average less than 10 cm. apart. The individual canes, though tough, are easily bent or crushed. The color of a stand of *Phragmites* is a medium green except when in flower, when the whole stand assumes a bronze color and a soft fine texture because of the loose, fine tassels of flowers (later fruits). Flowering occurs in winter, but the exact periodicity has not been recorded. It extends at least from December into February.

Although some areas of this type are large, especially that adjacent to Agaña, called Agaña Swamp, smaller patches and narrow belts are more common, making up mosaics with swamp forests and with the savanna. Reed marshes are found on soils derived from either volcanic or calcareous materials but are confined to areas that are wet with seepage, or under standing or running water for the greater part of the year, and that never really dry out. Therefore their presence is a reliable indication of surface water, or of ground water very near the surface, either fresh or somewhat brackish. Because of its habitat requirements, this vegetation type is found only on the south half of the island. The total area occupied by this type is actually quite large, though little would show on a vegetation map, because the individual patches are mostly small.

One important feature of this type is the masking of minor topographic irregularities because of its tendency to grow in low wet spots. An unwary observer might very likely describe as smooth or undulating an area of coarse grass which was actually cut by shallow ravines. The general surface of the sword grass on the dry slopes and that of the reeds in the ravines may be rather continuous, and somewhat similar in appearance,

though the ground beneath may vary by a meter or more in relief and be as different as rough rock and soft mud.

Scirpus MARSH

Plate 32, figure 1

Actually submerged ground covered by bullrushes (*Scirpus erectus*) exists in limited areas around the base of Orote Peninsula. These bullrushes are naked green stems the diameter of a finger and rising 1 meter to 2 or even 2.5 meters from a mat of prostrate root stocks buried in the mud of the bottom. The stems are tough but soft and easily crushed, being spongy within. At the tops they are tapering and pointed, or end in a loose tassel of brown flower heads.

Dense, pure stands of this plant grow in shallow standing water, usually covering portions of small ponds which may be partly open water and partly covered by other types of marsh vegetation. The water may be slightly brackish.

Cyperus MARSH

This type is uncommon and not at all uniform. Shallow ponds occur with scattered tufts of *Cyperus*, usually *Cyperus polystachyus* but sometimes *C. odoratus* or *C. javanicus*. *Rhynchospora corymbosa* is occasionally found with them. *Cyperus odoratus* and, less commonly, *C. javanicus* also occur in local stands in ordinary low wet ground. In all these types, the dominant species is a tufted, grass-like plant with a whorl of long leaves at the top of the stem surrounding a cluster of greenish, scaly flowers. These types of marsh are of small area and unimportant, except that *Cyperus* is often a good indicator of a muddy substratum. Examples can be seen at the base of Orote Peninsula.

Paspalum FLATS

Plate 32, figure 1; plate 33, figure 2

Paspalum flats are lawn-like areas, usually wet and usually brackish, covered by a dense stand of *Paspalum vaginatum*, which is a wiry, creeping, mat-forming grass growing no higher than 30 cm., usually much less. Though this grass may grow on mud as well as sand, and often in shallow standing water, it usually provides a safe enough footing for walking. The tough mat of roots will nor-

mally support a man, even on soft mud.

Such flats are common around southern Guam near the coast, wherever there are ponds or wet ground, for example, just south of Camp Bright. They are never of large area. They often mark places where ground water seeps out near high-tide level. They may also occupy the edges of shallow ponds and the bottoms of depressions behind beach ridges, as at Umatac.

Panicum FLATS

Plate 33, figure 1

These are similar in superficial appearance to *Paspalum* flats, but are dominated by *Panicum purpurascens*. The mass of vegetation is much deeper, often 1 meter or more in thickness, and makes a much less firm mat. The stems are much longer and thicker, and the leaves and sheaths are quite hairy. Walking is not easy through this type, both because of the deep tangled nature of the growth and because the water or mud may be deep and the vegetation mat not firm. *Panicum* occurs in wet low places but more commonly in water fresher than that in places occupied by *Paspalum*. Low places used as pastures are particularly dominated by this *Panicum*, which is a good forage grass. It was brought in for this purpose by the Guam Experiment Station several decades ago and has naturalized itself thoroughly, on both dry and wet ground. On wet ground what are here termed *Panicum* flats, possibly better called wet meadows, have resulted. One such can be seen along the road at the north side of the base of Orote Peninsula.

RICE AND TARO PATCHES

These are at present uncommon on Guam, although during World War II they were much more important. Rice is now grown on only one or two farms near Talofoto, though aerial examination shows traces of paddy-field pattern in the low coastal areas for some distance south of Orote Peninsula. Marsh taro culture still exists in some of the valleys of southern Guam, such as Talofoto, but is being supplanted by the easier dry-land type of culture. The taro plant itself is also being supplanted by the yautia, which is grown on dry land. These plants are grown for their starchy tuberous corms or underground stems.

MISCELLANEOUS MARSHY VEGETATION

Vegetation that does not fit any of the common types may also be found occasionally. In places where roads or other disturbances of the ground have dammed ravines in the volcanic area there may be marshy patches of *Rhynchospora corymbosa* and *Acrostichum aureum*, ordinarily found in lowland swamp areas. In other wet spots may be found varying mixtures of sedges, grasses, *Jussiaea*, *Dryopteris goggilodus*, and other herbs of wet soil. Rarely, especially along the west coast between Agaña Swamp and Nimitz Beach, there are patches of nearly pure stands of *Ipomoea aquatica* and of *Eleocharis fistulosa*, or these may be mixed with other herbs. They both grow on muddy ground.

SWAMPS

Almost any of the above marsh types tend to be invaded by trees and shrubs and thus to develop into swamps. The brackish marshes are invaded by mangrove swamp plants, especially *Avicennia* (pl. 33, fig. 2). Little or nothing is known of the courses of successions leading to the several swamp types other than mangrove swamps.

Swamp or swamp forest of any appreciable extent occurs only at or slightly above sea level along coasts and in the bottoms of the larger river valleys. One exception to this is the patch of mixed marsh and swamp just east of the high ridge of Mt. Lamlam mentioned above.

Five types of swamp are recognized, but it should not be thought that the actual stands are all sharply separated into one or another. They tend to grade into one another and to form mosaics with patches of two or more of them, usually also with patches of reeds. The Talofoto basin contains the largest area of swamp land. Here almost all the alluvium filling the valley floor is swampy.

MANGROVE SWAMPS

These are very poorly represented indeed in Guam, in comparison with their development on islands and coasts to the south and west. Around the base of Orote Peninsula (pl. 32, fig. 2) there are a few small areas now largely destroyed or degraded by dredging or by oil floating on the water. There are also

still smaller areas east of Merizo and at the mouths of the rivers on the east coast. Only a very few of the typical species of western Pacific mangrove swamp plants are represented here, namely, *Rhizophora mucronata* (pl. 32, fig. 2), *Bruguiera gymnorhiza*, *Avicennia* sp., *Xylocarpus moluccensis*, *Lumnitzera coccinea*, *Heritiera littoralis*, *Hibiscus tiliaceus*, *Acrostichum aureum*, and *Nypa fruticans*.

Nypa SWAMPS

This swamp type is even more feebly represented. There are a few patches of *Nypa* at the mouths of the Pago, Ylig, and Inarajan valleys at the sides of the estuaries of the streams. These are of no importance, except as representative of a swamp type very well developed and yielding useful products in the Philippines, Indonesia, and southeast Asia.

Barringtonia SWAMP

A striking swamp forest type, known only in Guam, only from the Talofoto River. Where best developed it is a pure stand of *Barringtonia racemosa* 10 to 15 meters in height, close set, and with a dense, complete canopy. The tree trunks are seldom more than 20 cm. in thickness. There is no undergrowth whatever, and the trees grow on conspicuous hummocks, with muddy channels between them. These channels may hold standing water, or they may be almost dry, in areas near the sea where the water level fluctuates with the tide. The bottoms, though muddy, are firm enough to support a man on foot. Heavy equipment, such as bulldozers, mires down immediately and tends to sink in very deeply. This type does not form large areas, and in places it tends to intergrade with the *Hibiscus* swamp types.

Hibiscus tiliaceus SWAMP

This type fills most of the wet, low ground in the Talofoto basin, either as a relatively pure stand of *Hibiscus* or mixed with *Pandanus* to form the following type.

Hibiscus-Pandanus SWAMP

This type and the preceding may occur in fairly large areas, or form mosaics with *Barringtonia* swamp and reed marsh. Smaller

areas occur in the other river valleys and just east of Mt. Lamlam. This type of swamp is extremely difficult to traverse. The trees are sprawling, twisted forms, seldom or never proper trees with trunks. They are tangled together into an intricate mass of stems of all sizes, often laced with lianas of several sorts.

The foliage is dense on the outside of this mass, but beneath there is little but stems. The ground varies from being fairly firm to soupy mud. These areas are as nearly impassable, because of both vegetation and substratum, as any vegetation type on Guam except the scrub on limestone cliffs.

STRAND VEGETATION

There are, on Guam, three basic types of shoreline. The most extensive is probably pitted, emerged, coral limestone. The least developed is low, swampy coast. The remainder is sandy beach. The vegetation of the coral limestone shores is scrub of *Pemphis acidula* (pl. 4) which is described above (p. 58). It is of gnarled, twisted, hardwood bushes with small fleshy leaves with a slightly astringent taste. The mangrove vegetation of low swampy coasts is also described above (p. 62).

This leaves the vegetation of sandy beaches to be described briefly here. Actually, on the beach proper, there is no vegetation. It is principally on the beach ridge and on sandy flats just behind it that strand vegetation is well developed; it may conveniently be divided into woody and herbaceous types.

The forest on sand ridges and flats just behind beaches is in some places a pure stand of *Casuarina equisetifolia*. These stands are of mature but not extremely old trees. They are generally not more than 30 to 40 cm. in thickness and 20 meters in height. They do not form dense stands, but few other plants grow with them. This homogeneity may be due to the fact that few plants are able to establish themselves in the layer of dried branchlets or "needles" that accumulates beneath *Casuarina* trees except under very wet conditions. As *Casuarina* becomes established only under absolute pioneer conditions and grows rapidly, it is to be expected that pure stands or almost pure stands will be found.

On other sandy places the forest is of a mixed type, similar to that found generally in strand habitats in the tropical Pacific. This may be a mixture of *Thespesia populnea*, *Pandanus tectorius*, *Guetarda speciosa*, *Messerschmidia argentea*, *Scaevola sericea*, *Hernandia sonora*, and, of course, *Cocos nucifera*.

These trees may be present in varying proportions and with admixtures of others, but commonly *Thespesia* and *Scaevola* are most abundant. *Hibiscus tiliaceus* may be important locally.

Some beach ridges are covered by a pure stand of *Leucaena glauca*. This was dominant on almost the entire beach in front of Agaña, but the high waves accompanying the typhoon in December, 1953, killed most of this stand. The plant apparently does not endure sea water at all well.

Herbaceous vegetation is not prominent on Guam beaches. There are some strips of a sod of *Paspalum vaginatum* near Umatac. East of Merizo are similar strips, seaward of the woody vegetation, of *Sporobolus virginicus*. These are low, stiff grasses with wiry rhizomes. *Lepturus repens*, another halophytic grass, spreads by above-ground runners and forms patches in some habitats. The normal tropical beach vegetation of *Ipomoea pes-caprae*, *Triumfetta procumbens*, *Canavalia sericea*, *Vigna marina*, and other creeping plants is found on Guam but is relatively restricted and poorly developed. It may be that the frequency and destructiveness of typhoons are partially responsible for this restriction.

Another curious circumstance that is frequently noted is worth mention: a number of species commonly regarded as strand plants are, on Guam, found in various inland habitats. Among these are *Scaevola sericea*, *Ipomoea pes-caprae*, *Thuarea involuta*, *Clerodendrum inerme*, *Lepturus repens*, and *Fimbristylis spathacea*. These have all been found inland in one part of the world or another, but the number of them so distributed in Guam, as well as the frequency of such occurrence, is most unusual. No adequate explanation of this circumstance is apparent.

GRASSLAND OR SAVANNA VEGETATION

Plates 35-40

Volcanic soil in the Marianas is generally thought of as covered by a dense stand of sword grass, *Miscanthus floridulus*. This is only partly true, for, though *Miscanthus* is dominant in many areas, there are forests in valleys, ravines, and on many steep slopes.

In the grassland vegetation itself, there are at least five plant communities to be considered, occupying more or less distinct habitats. These may be termed (1) the *Miscanthus* community, (2) the *Dimeria* community, (3) the erosion scar community, (4) the *Phragmites* or reed community, and (5) the weed community which follows disturbance. At the present time the first four form a natural mosaic over a large portion of the volcanic part of Guam, with the fifth added where clearing and scraping of the soil have taken place, after cultivation, after overgrazing, and after serious fires. It is only a temporary community, especially when it follows fire, which does not commonly destroy the root crowns of the dominants of the other communities. These root crowns soon put forth sufficient new shoots again to dominate and slowly shade out the pioneers.

Miscanthus COMMUNITY

Plate 36; plate 37, figure 1; plate 38, figure 1

In its best development this is an almost pure stand of *Miscanthus floridulus*, a coarse, sharp-edged, cane-like grass. It grows to a height of 2 or even 3 meters in clumps so close together that it is very difficult to push through them. The color varies with the season and local moisture conditions, ranging from a bright, light green to gray-green, straw color, drab, or a dull, light brown, and these colors dominate the community and to a great extent the hills of southern Guam. In areas that have been protected from fires for some years, small *Casuarina* trees are usually scattered unevenly through this grassland (pl. 36, fig. 1).

Characteristically there are a number of secondary species growing with the *Miscanthus*, the number of species and of individuals varying inversely with the density and height

of the *Miscanthus*. Seldom, however, are they completely absent. Almost any of a large number of accessory species may be found in this community, but great abundance of them suggests recent burning, recent erosion, or a transition towards the *Dimeria* community.

The characteristic habitats of *Miscanthus* are fairly steep slopes, rocky and steep ridges, and low, moist, but not really wet places. It is in moist low places that *Miscanthus* reaches its greatest luxuriance, with fewest competing species. Good examples can be easily seen on the slopes of Mt. Alutom and Mt. Tenjo.

This community in dry periods is extraordinarily susceptible to fire. Fires, usually set or allowed to get out of control by local inhabitants, burn very rapidly up slopes and even down, if driven by a wind. The grass clumps usually burn down to the base, which generally resists burning and is capable of sending up new shoots. These fires are a serious hazard for people caught in their paths, as the fires travel rapidly, and it is not easy to move fast through sword grass. A rocky or open place in the grass is the safest spot in which to weather a fire, if a bare erosion scar or road cannot be reached.

Foot travel in a dense stand of sword grass, except on trails or ridge tops, is slow and at times almost impossible for any distance. The clumps of finger-sized canes are springy and tangled, and the leaf blades cut the skin like knives if dragged over it because of microscopically saw-toothed edges and a hard texture.

Miscanthus seems rather unsatisfactory for forage, though the young leaves and some of the accessory species are eaten by stock. Heavily grazed areas present a very low, clumpy vegetation.

Dimeria COMMUNITY

Plate 35, figure 1

This low grassland is dominated by *Dimeria chloridiformis*, a tufted, soft, hairy grass of a bluish green color, the flowering

stems up to half a meter or more in height. Even when very well developed, the tufts are far enough apart for many accessory species to be present in virtually all stands, but in a well-developed, undisturbed area they seldom make up 10 per cent of the cover. In small numbers, *Miscanthus* clumps are normally a part of the *Dimeria* type, but in large numbers they indicate a transition to the *Miscanthus* community. Large numbers of young *Miscanthus* plants suggest invasion and eventual dominance by that species (pl. 40, fig. 1). Large numbers of other native species indicate an erosion scar recently healed over, while large weed populations result from disturbance or overgrazing.

The *Dimeria* community is usually found on more or less level or gently rolling ground, seldom on steeper slopes. It is not commonly found at such low altitudes as sword grass may reach, even where conditions seem favorable. The soil is generally a fine red or brown clay resulting from weathering of pyroclastics and tuffs.

This vegetation presents no obstacle to walking, or even to motorized transport, providing the ground is not eroded in a rough fashion. It is, however, likely to alternate with *Miscanthus* patches and not to be continuous over large areas. Good stands may be seen in the saddle north of Mt. Alutom and north of the road east of Apra Heights.

Dimeria grassland is often used as pasture but will not support many animals, as the dominant species is not a first choice as forage. The stock tend to pass it by and to search out several minor species in the community.

EROSION SCAR COMMUNITY

Plate 36, figure 2; plate 38,
figure 1; plate 39, figure 2

Many of the characteristic savanna plants are pioneer species, coming up in bare soil and gradually being crowded out by the dominant species of the more stable communities. Their occurrence in small numbers in the grassland may be linked with the bare spots that are common there. The deeply weathered volcanic materials on Guam are subject to severe erosion, usually a combination of sheet erosion and slumping,

in which broad patches of material are removed by both water and wind. On the scars left by this process, after they have been exposed for a time, can be found a characteristic assemblage of species, which may include, at times, most of the flora of the volcanic grasslands. The first plant to come in abundantly is usually *Gleichenia linearis*, which spreads over the bare soil by means of its horizontal rhizomes. Shrubs such as *Myrtella*, *Wikstroemia*, *Scaevola*, *Geniostoma*, and *Melastoma* are usually found, as well as the fern *Blechnum orientale* and the grass *Chrysopogon aciculatus*. *Chrysopogon*, next to *Gleichenia*, plays the most active part in preventing further erosion, as its prostrate stems cling closely to the soil and form a dense sod.

This community is usually quite sparse, with much bare ground between the plants, which gradually fills in as more plants become established. *Miscanthus* and *Dimeria* soon invade and eventually one or the other dominates and produces one or the other of the two grass communities described above. For a long time, however, traces of the erosion scar remain in the unusual abundance of the species characteristic of such areas.

Phragmites COMMUNITY

Plate 38, figure 2

Reed brakes, pure stands of *Phragmites karka*, are so often found in wet ravine bottoms in the savanna that they may be regarded as a reliable indicator of a ponded or marshy condition or of running or standing water except in the driest season.

These canes are usually from 2 to 5 meters in height, as thick as a man's thumb, hollow, tough, and easily bent but difficult to break off. They grow in thick stands so as to cover the ground completely, the canes from 5 to 20 cm. apart. Because they usually grow up level with the top of the surrounding vegetation, they give a false appearance of smoothness to country that may be cut by ravines.

Walking through such a brake is a slow, fatiguing task, but not impossible. The canes may be pushed aside readily enough, but the soft, mucky ground, with tangled canes which snare one's feet, makes it desirable to avoid this sort of ground whenever possible.

WEED COMMUNITY THAT FOLLOWS DISTURBANCE OF SAVANNA

A varied assortment of weedy pioneers, virtually all introduced plants, appears after any serious disturbance or elimination of the vegetation of an area. The types of disturbance commonly seen in the savanna area are fire, grazing, cultivation, and clearing and removal of vegetation. After such treatment, various weeds appear, but the principal ones are *Stachytarpheta jamaicensis*, *Elephantopus mollis*, *Hyptis capitata*, *Hyptis suaveolens*, *Mitracarpum hirtum*, and *Chrysopogon aciculatus*. These may occur in mixtures, or, more usually, any one of them may be locally dominant.

Such weed communities may last several years but are soon replaced by the communities dominated by *Miscanthus* or *Dimeria*. Meanwhile they serve the function of weeds the world over in retarding erosion of the surface soil. As long as land is in active cultivation, weeds may be regarded as a nuisance, but when an area is abandoned they are the first step towards revegetation.

This weed vegetation offers no serious obstacle to traverse on foot or in vehicles, except where it may conceal ditches or holes in the ground. *Elephantopus* may be rather irritating to bare skin, but this is seldom more than a minor annoyance.

SWORD GRASS ON LIMESTONE SOIL

For some years the idea has been current that sword grass, *Miscanthus floridulus*, is a reliable indicator of volcanic soils. Some doubts about this were raised during the Economic Survey of Micronesia in 1946, but no definite exceptions were found.

In Saipan, in 1950, *Miscanthus* was found in two places growing directly on bare hard limestone. One of these spots was the north side of the summit of Mt. Tapochau, the other to the north in the Magazine area, southwest of Fañunchuluyan Bay. Two peculiarities were noticed in these stands; both were in quite exposed places, and both were pure stands of *Miscanthus*, with none of the commonly associated volcanic savanna species.

In Guam in 1953 there were reports of the occurrence of sword grass on limestone from

soil scientists and geologists. A search was made for such localities, and an even dozen of such stands were located. Unquestionably others exist.

Four of these, two on the upper ridge of Mt. Lamlam and two on the north and northeast slopes of Mt. Almagosa (pl. 40, fig. 2), were on Alifan limestone, two of them on thin soil coverings, two in crevices in bare rock. The other eight are on the argillaceous member of the Mariana limestone or on soil derived therefrom. These eight occurrences are located as follows: Piti, just above Marine Drive; 2.5 kilometers north-northeast of Sinajaña; Agriculture Farm Dairy; Agriculture Farm at Manguilao; small hill just south of Pago River bridge; bluffs south of Ylig River bridge; top of hill south of Talofof River bridge; and on small hills in Martinez Pasture at Dandan.

These stands differ greatly in many respects, ranging from a few feet above sea level, to near the top of Guam's highest peak, from sheltered to quite exposed situations, from slopes and cliffs to level surfaces. The number of associated savanna species ranges from none to 15. Most of the stands, however, had very few or none. The actual figures are: five occurrences with none; two with one each; one with two; one with three; one with five; one with 13; and one with 15. The last is a very small spot surrounded by savanna, while the others are well separated from any savanna.

Most of the occurrences are on limestone with a fair argillaceous content, and possibly all have some clay. It has been suggested that availability of silica is the controlling factor in the distribution of sword grass, but this is manifestly not the case, as there are any number of argillaceous localities where sword grass is lacking.

A single pair of analyses of ashed samples gave percentages of silica of 7.68 in the ash of *Miscanthus* from volcanic soil and 59.62 in that of a possibly comparable grass, *Penisetum purpureum*, growing on soil derived from hard limestone.

Of the Guam localities listed above, half were being actively invaded by *Leucaena*, and the sword grass showed the effects of shading in long spindly growth habit, sparseness, and in some cases dead clumps. In the

areas where sword grass is found on the volcanic soils, the grass is missing wherever a patch of forest has become so thick as to shade the ground completely.

None of the obvious factors seems adequate to account for the distribution of this species. The best explanation that has suggested itself so far is that it is likely to establish itself on any area that remains open for

a considerable length of time. It is encouraged by repeated fires. If *Leucaena*, *Triphasia*, or other woody species invade it in numbers they will eventually shade it out.

The main conclusion is that, while *Miscanthus* is generally an indication of a volcanic substratum, it must not be regarded as a completely reliable one, as at least 14 exceptions are known where it grows on limestone.

VEGETATION OF THE ARGILLACEOUS LIMESTONE AREA

The area underlain by the argillaceous member of the Mariana limestone is highly dissected and very complex terrain, but of low relief, never more than 50 meters, usually 20 or 30. Though it is an old karst topography, it has been greatly weathered, the ridges being rounded, the sinkholes plugged by clay soils, and drainage patterns produced containing intermittent streams. A deep brown soil, as much as 10 meters or more in depth, covers even some of the ridges, though the underlying limestone crops out here and there, and loose limestone fragments litter the surface in places.

This area has been occupied and used agriculturally perhaps longer and more intensively than any other part of Guam. It is cut up into many small farms which are reached by a network of roads. The result is that none of the original vegetation remains, and it is impossible to say at this time what this original plant cover may have been.

At present the vegetation is an intricate mosaic of small areas of a number of different types, with transitions between these, all of them either secondary or cultivated. Coconut trees are scattered in great or small numbers over almost the whole area. Patches of pure stands of *Leucaena glauca* are very frequent. These are dense growths with fine feathery foliage, the individual plants being up to 5 or 6 meters in height with smooth stems seldom more than 5 cm. in diameter. They usually grow only a few decimeters apart, so that often a man cannot walk between them with comfort. The ground may be covered with seedlings of the same species which quickly grow up and fill any gaps in the continuous canopy of foliage above. In stands of this nature there are seldom any other plants, except that around the edges thorny

bushes of *Triphasia trifolia* may sometimes be found, seriously impeding penetration.

In areas of relatively low relief there may be large patches of mixed scrubby thicket 3 to 4 meters in height, the trees usually contiguous but with occasional small openings. The principal woody species making up this type are *Cestrum diurnum*, *Leucaena glauca*, *Triphasia trifolia*, *Pithecellobium dulce*, *Morinda citrifolia*, *Psidium guajava*, *Carica papaya*, and *Annona* sp., in varying proportions, with local patches of *Moghania strobilifera*. Morning-glory vines of several kinds are tangled in these small trees and shrubs. The openings are grassy or, in ravine bottoms, filled with a low growth of one or more species of *Cassia*.

This scrubby growth is difficult to walk through, especially where *Triphasia* is an important constituent. The trunks may be 5 to 10 cm. or more in thickness, with low branches which are likely to be quite tangled. It is possible to progress with a machete, but it is advisable to take every advantage of what openings there are.

A mixed taller thicket or forest occupies much of the area, especially where the relief is sharper. Such vegetation ordinarily has a very uneven upper story of coconut and breadfruit trees about 25 meters in height, but these do not form a complete canopy. The second story, 3 to 10 meters in height, contains most of the small trees and shrubs listed in the low thickets described above, with the addition of *Hibiscus tiliaceus*, *Cananga odorata*, *Pandanus tectorius*, *P. dubius*, *Mangifera indica*, *Muntingia calabura*, and tangled masses of a large bamboo, probably *Bambusa arundinacea*. There may be an undergrowth of shrubs and tall herbs, often the large-leafed *Alocasia macrorrhiza* and the

aromatic *Piper guahamense*. The whole may be tangled with vines such as morning-glories. Penetration is generally less difficult than in the scrubby thickets, but where *Triphasia* or bamboo is abundant, walking may be almost impossible.

Interspersed with the foregoing types may be patches of open pasture, dominated by such grasses as *Panicum purpurascens*, *Paspalum conjugatum*, and *Paspalum orbiculare*. These grasses are either in low, marshy spots that occupy old sinks or on open rounded ridges. When the pastures are in poor condition because of overgrazing, there may be great patches of *Achyranthes*, *Stachytarpheta*, and other weeds, rarely or never eaten by the stock. A few such areas are occupied by sword

grass, *Miscanthus floridulus*. This grass is much more characteristic of the volcanic areas of Guam (see section on savanna vegetation above).

Patches of bananas, cassava, taros, and other edible plants, as well as coconut and citrus groves, are very common, usually associated with dwellings and small dooryard gardens, always well planted to ornamentals.

The details of this mosaic are constantly changing, as clearings are made, cultivated ground is abandoned, and fallow fields grow up to scrub or to patches of *Leucaena*. It can be characterized only as a complex unit the local characteristics of which are completely dependent upon the activities of its human inhabitants.

COCONUT GROVES AND PLANTATIONS

Large or small areas throughout the island are occupied by more or less pure stands of coconut palms. These have been planted chiefly by the Guamanians, both to provide food for themselves and their domestic animals and to produce copra for export. Large groves occur where there are sand flats behind beaches, as at Tarague Beach, on flat ground in some parts of the northern plateau, along the road down the east coast of the south half of the island, and in the valley bottoms in the volcanic areas. Extensive areas, for example, in the central Talofof drainage below the Fena Dam are covered by these trees. Smaller groves form a conspicuous part of the vegetation in the argillaceous limestone area, as described above, and occur here and there in almost all other vegetation types except the savanna.

These plantations are mostly mature and consist of trees 15 to 25 meters in height, either in regular rows or spaced irregularly 5

meters or more apart. The trunks are slender, and there is generally a more or less complete canopy of leaves high overhead. In most of the groves and plantations there is a thick undergrowth, often 2 or more meters in height, composed of various shrubs and young trees as well as an abundance of self-sown coconuts. Penetration of this undergrowth, especially where coconut seedlings are numerous, is difficult and laborious, even with a machete.

Copra is no longer produced in these plantations. Labor costs are so high that the copra does not pay the cost of production and shipping. Furthermore, one or more poorly understood diseases have rendered many of the trees completely unproductive, and some are actually dying. The only use made of the nuts at present is as feed for pigs, chickens, and other livestock, plus minor use for human food.

WEED COMMUNITIES

Most of the vegetation types of Guam have been disturbed rather profoundly and now contain a greater or smaller proportion of weedy species which were not part of the original plant communities. Where the disturbance has been so great as to destroy completely the original vegetation, this is often replaced entirely by communities of the ag-

gressive, mostly exotic, pioneer species commonly called "weeds."

The savanna communities, in most of their present habitats, seem to have had such an origin, but, rather than being introduced species, many of the plants, except in the earliest stages in succession, are from the nearby natural savanna areas. The assem-

blages noted below, however, are almost exclusively made up of exotic weedy plants. The vegetation on the argillaceous limestone, described above, could have been included here, but, as it forms a quite distinctive and recognizable mosaic, it is treated separately.

Disturbances of several kinds—fire, clearing, bulldozing, filling, for example—have produced bare ground in what were previously several different vegetation types. In fact, it would be possible to locate sites in almost any natural vegetation area that have been occupied by weeds. The principal situations occupied by such weedy vegetation are roadsides, clearings, abandoned cultivated fields, abandoned home sites and military installations, fills, and fire scars.

A number of factors seem to have a bearing on the original composition and subsequent course of succession in these plant communities. There seems to be some correlation with the original vegetation, the type of soil, the amount of moisture, and the kind of disturbance responsible. Pure chance in what weed seeds happen to be present in sufficient numbers may be one of the most important factors.

These weed communities are mostly ephemeral, though at least one of them, the *Leucaena glauca* thicket, may persist indefinitely so far as present observations show. These vegetation types can be only roughly classified. As in most vegetation situations, especially those in which active succession is taking place, varying mixtures occur which defy classification and which may result largely from chance. Here these mixtures do not occupy a disproportionate amount of the area, so that a rough arrangement and brief descriptions of the principal types seem feasible and possibly useful. The following are weed communities that are reasonably distinctive and that occur often enough to be more than merely accidental.

MIXED HERB TYPE

On cleared land, fills, roadsides, and burned areas, the first colonists are normally a mixture of many non-woody species which can grow on bare soil. Between the time when the first few plants appear on a bare surface and the time when the herbaceous species are

shaded out by the shrubs which eventually follow them in any reasonably moist climate, there are an infinite series of variations which together may conveniently be referred to as a mixed herb type.

About 75 species commonly occur in such places. These form innumerable combinations. Generally the assemblages and proportions occurring on volcanic soil differ somewhat from those on limestone. Also, those on bare rock differ from those on rich agricultural soil. Moisture exerts a strong influence on what species are abundant, as do season and the degree of consolidation or closing of the vegetation. These combinations are too numerous to be described conveniently. However, several striking aspects repeat themselves often enough to be pointed out, especially when completely dominated by one species.

Most conspicuous and common of the aspects of the mixed herb community is that dominated by *Stachytarpheta jamaicensis*. This herb, which grows to about 1 meter in height and has purplish blue flowers, completely dominates much ground on both volcanic and limestone soil that has been relatively recently cleared of vegetation. This is a vegetation of short duration, being relatively soon succeeded by shrubs or savanna vegetation.

In some areas, mostly in volcanic soil, dominance is assumed by *Elephantopus mollis*, a tall, disagreeably bristly plant. This is especially common after savanna or weedy vegetation has been burned. Where savanna dominated by sword grass, *Miscanthus floridulus*, has been burned and replaced by *Elephantopus*, the resulting herbaceous vegetation is likely to be short-lived, as the *Miscanthus* root crowns are not killed by fire. Within a short time the *Elephantopus* is crowded out. On burned-over weedy land this rapid succession does not take place, and the *Elephantopus* community may last until further burning, or until shrubs and trees or savanna vegetation have crowded it out by normal secondary succession.

Immediately after fire or other disturbance, the resulting bare area may be dominated by a pure stand of *Mitracarpum hirtum*, a slender herb with small leaves and tiny white flowers. This is soon shaded out by

taller herbs such as *Stachytarpheta* or *Elephantopus*.

On soil bare from whatever cause, *Chrysopogon aciculatus* tends to form a dense turf that clings very closely and firmly to the soil. This is a very low, creeping grass that may often form pure stands, especially on soil that is badly eroded. It is very important in such situations in retarding erosion. Where the above aspects of the mixed herb type occur on volcanic soil, they are expressions of the generalized weed community of the savanna, discussed above (p. 66).

A number of other weed communities do not seem to be particularly connected with the mixed herb type, although several of them occur on recently denuded grounds.

Pennisetum polystachyum COMMUNITY

Along roadsides and around recently abandoned military installations, especially on the limestone portions of the island, are extensive pure stands of a recently introduced grass, *Pennisetum polystachyum*. This is erect, about 1 meter in height, and produces conspicuous cylindrical spikes of yellowish flowers in the fall. By the middle of January this plant is largely dry and drab, and its habitats are quite conspicuous. In fact they can be picked out from a considerable distance during both flowering and dry seasons by their straw yellow or drab color.

Pennisetum purpureum TYPE

Napier grass or elephant grass, an introduction from Africa, is gaining ground in open areas and edges of secondary thickets. It is common between Tamuning and Potts Junction and seems to be spreading. When well developed it is a reed-like grass up to 4 meters in height, and after the first year it forms dense tangles. The canes are up to 1 cm. thick and branch freely. When young, this species is considered excellent forage. When older, it is tough and presents a tiring obstacle to movement on foot.

Tripsacum latifolium TYPE

About halfway between Wettengel and Potts Junctions is a small area of a grass new to Guam, *Tripsacum latifolium*. This is mentioned here because it seems to be spreading aggressively and will probably be much more

common in the future than it is now. It closely resembles a very dark green maize plant and forms dense pure stands up to 3 meters in height. It produces horizontal rhizomes, which, matted in the surface of the ground, enable it to exclude other plants.

Panicum purpurascens TYPE

Along more moist roadsides and in meadows, even where the ground is not marshy, Para grass forms pure stands. These are identical with similar vegetation described above for marshes. *Panicum purpurascens* seems to grow perfectly well on either dry ground or mud.

MIXED GRASS COMMUNITY

In some areas, especially those kept open by grazing, may be found meadow or pasture vegetation that is a mixture of several sorts of grasses, especially *Paspalum conjugatum*, *Paspalum orbiculare*, *Panicum purpurascens*, *Chrysopogon aciculatus*, *Sorghum halepense*, and others. Where grazed lightly, meadow of this sort may persist for some time before being replaced by other plants. If overgrazed, replacement takes place rapidly.

Nephrolepis hirsutula TYPE

In clearings in the forest on the limestone plateau, an almost solid stand of *Nephrolepis hirsutula*, a luxuriant fern with erect fronds 1 meter to 1.5 meters in height, is a common early stage in the development of vegetation. It is very dense, either as a pure stand or with other herbs, and will hide a man lying prone.

Carica papaya TYPE

Along newly bulldozed roadsides in the forest on the northern plateau, especially in deep red soil, a dominant stand of wild papaya springs up within a few weeks. As a relatively pure stand it seems to last only one generation, growing up rather evenly to a height of several meters before being abundantly invaded by other woody species. Then it is succeeded by a mixed shrub vegetation of the sort described below.

Carica papaya is a typical "rosette tree" having generally a single post-like trunk topped by a crown of great, palmately divided leaves. These are up to half a meter wide and have long petioles. The trunk is not

very woody but is rather pulpy and soft. When cut, the leaves and stems exude an abundant white latex. This may be irritating to tender skins because of its protein-digesting properties.

Passiflora foetida-*Ipomoea indica*
COMMUNITY

On bare limestone that has at some time been scraped clear of vegetation and soil is frequently found a mat of *Passiflora foetida* and *Ipomoea indica*, soft herbaceous vines. They cover the ground completely but usually to a depth of only a decimeter or two.

Operculina ventricosa TYPE

Around Northwest Field, *Operculina ventricosa* forms huge dense mats of coarse vines. These may be a meter in depth and are capable of smothering out other plants. The leaves are large and heart-shaped, the flowers white, and the fruits conspicuous in erect clusters.

Ipomoea pes-caprae TYPE

In clearings on sand flats behind the beach, and to a lesser extent elsewhere, bare ground is rapidly covered by a mat of beach morning-glory. This mat, under some conditions, becomes so dense as to retard invasion by other plants. The leaves are leathery and bright green, characteristically two-lobed at the apex.

MIXED SHRUB COMMUNITY

Plate 30, figure 2

On cleared limestone or limestone soil, various secondary herbaceous vegetation types are frequently followed by shrubby vegetation of varying composition. It seems impractical to try to separate this into types, except to indicate that in some areas single species tend to assume dominance. Commonly this vegetation is a mixture of *Hibiscus tiliaceus*, *Cestrum diurnum*, *Muntingia calabura*, *Triphasia trifolia*, *Leucaena glauca*, and many other species in lesser proportions. These latter include certain undoubtedly indigenous species, such as *Pipturus argenteus* and *Macaranga thompsonii*, some of ancient introduction, as *Morinda citrifolia*, and some unquestionably of post-European introduc-

tion, as *Psidium guajava*, *Carica papaya*, and *Lantana camara*.

The density and stature of this scrub are as variable as its composition. In some stands the bushes are not, or scarcely, in contact, and walking through the vegetation is very easy. The opposite extreme is a thicket with gnarled and twisted branches completely entwined and impossible to penetrate without constant and vigorous use of the machete. Abundance of *Triphasia* provides the additional obstacle of very effective spines. If *Caesalpinia major* is present, an even more formidable obstacle is encountered in the form of a clambering vine with large compound leaves that are beset with hooked prickles. A vernacular name for this species sometimes used in other tropical countries is "wait-a-bit," understatedly appropriate. Ordinarily the density of branching in such scrub is about as great near the ground as in the canopy.

In stature, this scrub grades insensibly into secondary forest, both by the maturing of some of the ordinary component species and by a gradual shift in composition with increase in tree species. The available information is insufficient for any real successional relations to forest types to be indicated.

Any one of the five most abundant shrub species may occasionally assume dominance, sometimes exclusive dominance. Of the resulting vegetation types, that with *Leucaena* dominant is treated separately. The others can be regarded as variants, with certain notable characteristics enumerated below.

Stands of *Cestrum diurnum* are ordinarily dense but not difficult to traverse, light green in color, and 2 to 4 meters in height. There are no spines, and the stems are relatively slender and easily cut.

Those of *Muntingia* tend to be less dense. The leaves are velvety and dull green. Again, penetration is not difficult.

Triphasia, as indicated above, is viciously spiny. The wood is hard but not very difficult to cut with a sharp machete. Cutting a branch, however, does not necessarily make penetration easier, as it may merely fall into a worse position. In this type the canopy tends to be above head height, with the lower part relatively open. However, even when it

seems feasible to walk through it, there are always enough low branches to make passage very disagreeable. In general, when the fine, shiny, dark green foliage of this plant seems to make up a large part of a thicket, it is simpler to go around than through it.

Though *Triphasia* is unquestionably the most painful scrub to traverse, a stand of *Hibiscus tiliaceus* is more exhausting. *Hibiscus* has no spines or other obvious disagreeable features; it merely forms an interminable tangle of twisted, winding, looping stems. A well-developed thicket of *Hibiscus* is one of the favorite types used in moving pictures for a terrible tropical jungle. Any individual stem is easily cut, but there are always many more, and when cut they may merely spring into more obstructive positions. One's feet are likely to be entangled; falls are frequent; anything being carried is caught by branch after branch. This vegetation may be of any stature up to that of scrub forest.

In all these aspects, as well as in the various mixed ones, lianas and herbaceous climbers are frequent and tend to complicate the tangles. Various morning-glories, *Abrus*, *Entada*, *Mucuna*, *Canavalia*, and *Flagellaria*, may be common. *Caesalpinia*, as noted above, adds a prickly complication here and there.

Leucaena glauca THICKET

Perhaps the commonest of all types of vegetation in cleared areas at the present time is a dense pure stand of *Leucaena glauca*, the *tangantangan* of the Guamanians. This plant is a slender, erect shrub or small tree with fine feathery foliage. It has no spines and individually is not an unattractive plant. Its pure stands are usually extremely dense, and may be of any height up to 10 meters, depending on age and wetness of the situation. The stems are commonly less than 5 cm. thick and grow so close together that one must push them aside to walk between them. Though the canopy is complete, there is usually a carpet of seedlings of the same

species on the ground. In central Guam, however, an insect attacking the pods has very noticeably reduced the seed production. Also the giant African snail seems to kill the young branches in certain areas by rasping off the green bark.

Opinions on the desirability of this plant differ violently. In some quarters it is regarded as a valuable forage (when kept cut close to the ground) and a protector and enricher of the soil. Other persons, who have tried to eradicate it or check its invasion of an area, regret its having been brought to Guam. It is probably the most widely used tree for fire wood on the island because of its abundance near populated areas. The wood is a good firewood—fast-firing and relatively long-burning. Unquestionably *Leucaena* has increased greatly in the last 12 years. In fact, the local Department of Agriculture, under the United States Navy administration, 1944–1950, caused large quantities of *Leucaena* seed to be broadcast from airplanes, especially on the volcanic southern half of the island. It is now very abundant on roadsides and over vast areas of former open fields in the limestone part of the island. On the southern part it has scarcely become established on volcanic soil. It has, however, come up as hedges lining many roads in this area, roads that have been ballasted with crushed coral. The *Leucaena* grows well as far as the coral has been spread. One unfortunate feature of roads lined with *Leucaena* is complete lack of visibility to the sides and on curves.

In other tropical areas where *Leucaena* has been introduced and has become abundant, it is said to act as a "nurse crop" for seedlings of species which will eventually replace it (Egler, personal communication). No indications that it plays such a role in Guam have been reported to date or noticed during this study. However, seeds of the appropriate species may not be readily available, so that this succession may have merely been arrested in the *Leucaena* stage on Guam.

SUMMARY

The vegetation of Guam, even more than that of most of the other islands of the Marianas Group, is vastly altered from its primitive state. The major differences in

substratum are reflected in differences in the pattern of the present vegetation as they probably were before human interference began, but the present vegetation in most

places little resembles what was originally there. Large-scale clearing and repeated burning and, above all, the introduction of large numbers of exotic species of plants, as well as of grazing animals, have permanently altered the structure and composition of the vegetation.

In general, limestone areas and moderately moist situations, such as ravines and valley bottoms, are wooded, except where they have been recently cleared or are kept clear for agriculture or other purposes. The types of forest are strikingly distinct in the several principal habitats in these situations, with those on argillaceous limestone and in ravines in volcanic soil probably the most completely altered, their floras being largely of exotic species. Something like the original composition seems to prevail in the hard limestone areas and in swamps.

The principal open areas are: recently cleared and agricultural land on limestone, lowland marshes that have not had time to revert to swamp forest, and the vast savannas or grasslands on volcanic soils, mostly in the south half of the island. These are all regarded as early successional stages which will eventually change to woody vegetation if allowed to remain undisturbed. Even the savannas, which are features of long standing, tend in most places to change over to *Casuarina* forest where not burned. Burning is, however, so frequent and general that this succession has nowhere progressed to any-

thing like a stable forest condition. Because of this frequency of burning and subsequent erosion a general mosaic pattern of the several herb, grass, and shrub communities involved has become established that is characteristic of volcanic soils except in the deeper ravines. It is considered probable that the present savanna vegetation has spread, under the influence of man, from small relict patches on areas of impeded drainage and has been augmented by introduced plants. This accounts for the presence in the savanna of endemic and localized plant species.

Future work on the vegetation of Guam could appropriately take the form of detailed phytosociological studies, more critical correlation of variations in the vegetation with those in the environment, repeated observations of permanently established areas to check present inferences as to long-term successional trends, and possibly experimental studies. The results of such a program would be of practical and theoretical interest not only on Guam but in the Pacific and other oceanic islands generally. A start has been made in this direction through the farsightedness of the Governor of Guam, who set aside five representative "conservation reserves" where such long-term research may be done. Some permanent transects have already been established in these areas which, it is intended, will be revisited and observed periodically.

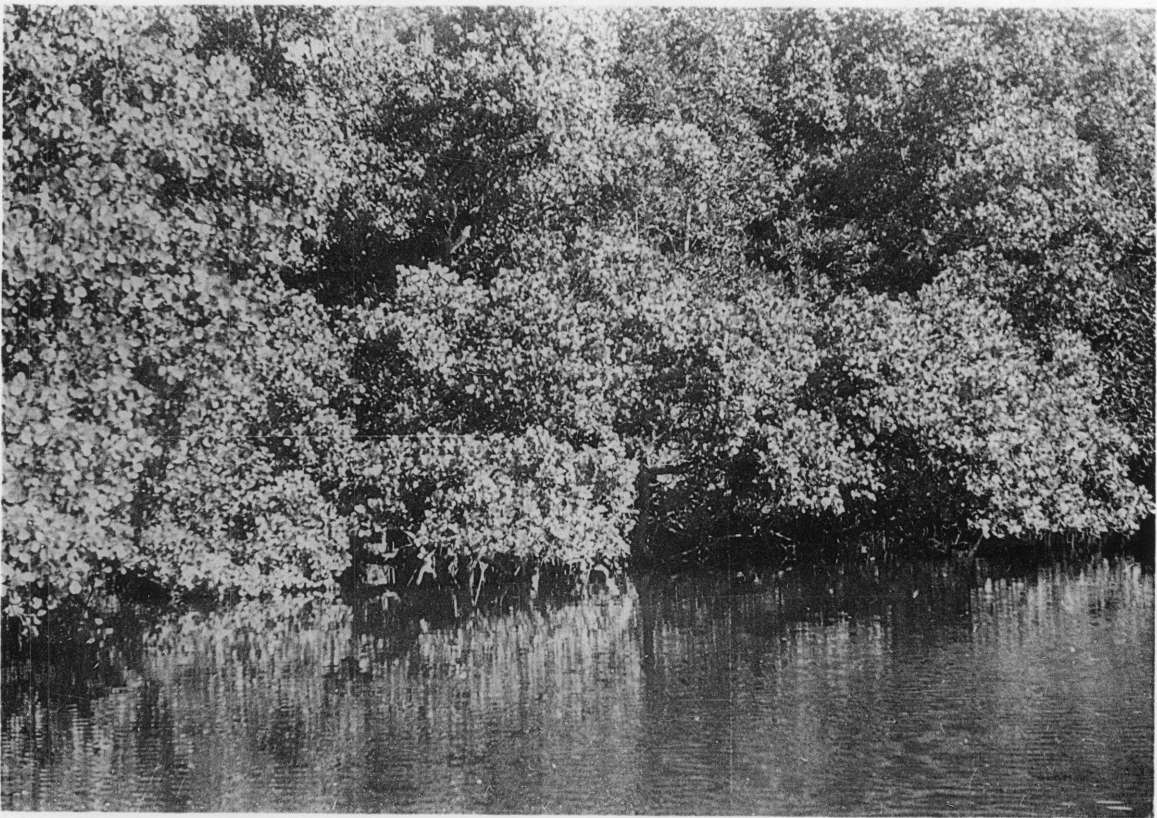
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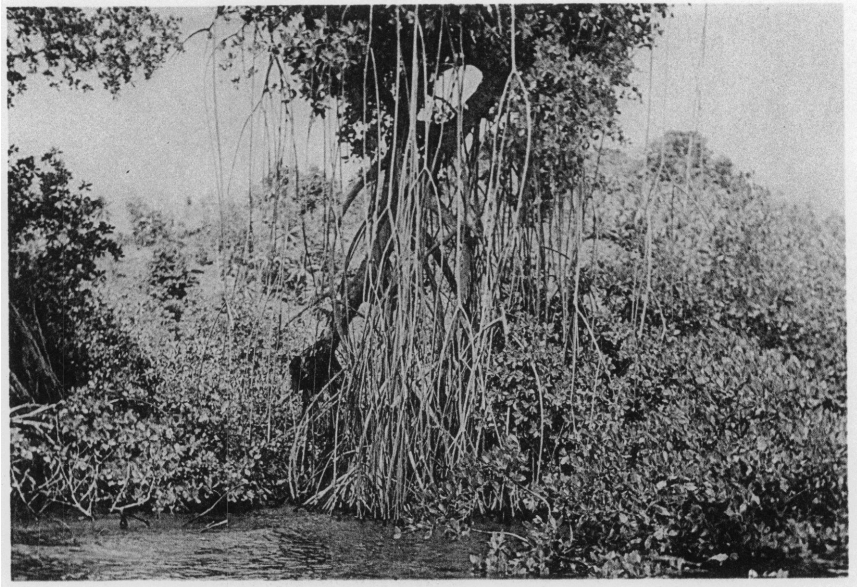
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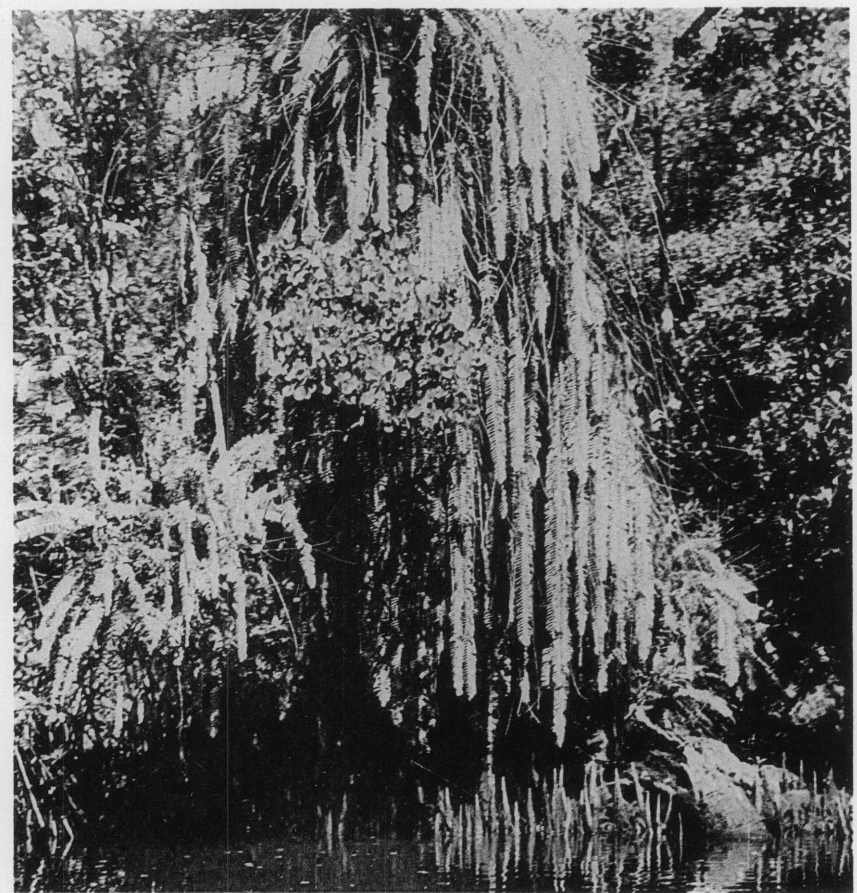
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1. Mangroves, *Rhizophora* sp., growing in shallow water. Udot Island, Truk Group. Photograph by F. R. Fosberg, May, 1946

2. Edge of mangrove swamp, mostly *Sonneratia caseolaris*. Head of Lele Harbor, Kusaie Island. Photograph by F. R. Fosberg, August, 1946



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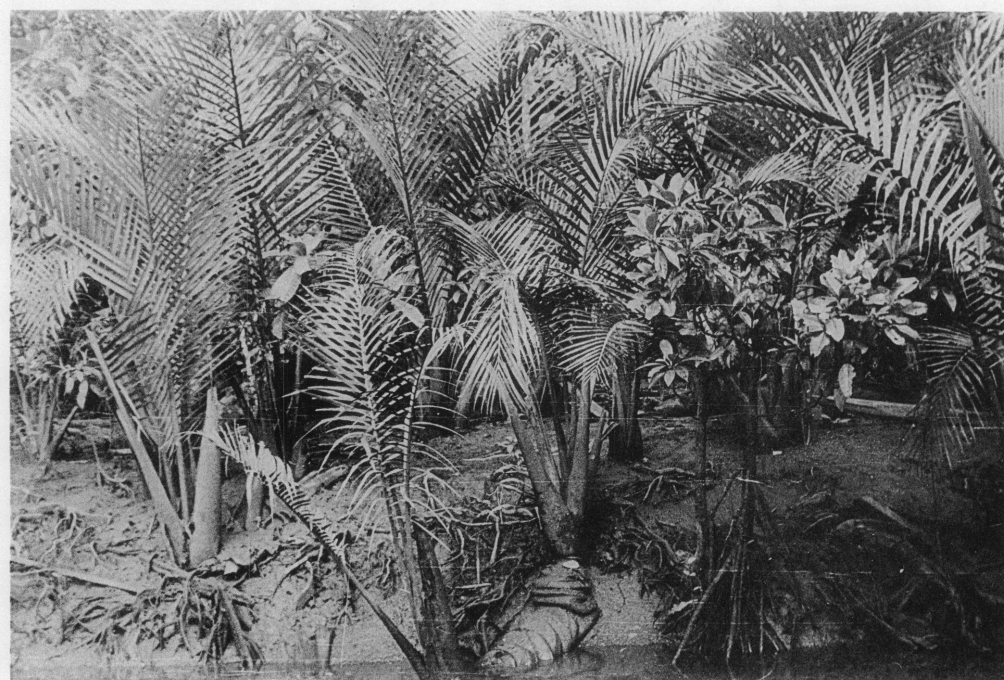


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1. Aerial roots of *Rhizophora* in mangrove swamp. Tol Island, Truk Group. Photograph by United States Geological Survey Party, ?1955
2. Epiphytic *Nephrolepis acutifolia* in mangrove swamp. North of Lele Harbor, Kusaie Island. Photograph by F. R. Fosberg, August, 1946



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2

1. Small patch of *Nypa fruticans* along channel in mangrove swamp north of Lele Harbor, Kusaie Island. Photograph by F. R. Fosberg, August, 1946

2. *Nypa fruticans*, showing buried stem exposed on edge of estuary, Ngarumiscan River, west side of Babeldaob Island, Palau Group. Photograph by F. R. Fosberg, 1946



1



2

1. Limestone terrace above sea, showing *Pemphis acidula* and other shrubs dwarfed by exposure to salt-spray-laden winds, Campanaya Bay, east coast of Guam

2. Close-up of dwarfed, prostrate *Pemphis* shrub. Same location as 1

Both photographs by F. R. Fosberg, January, 1954

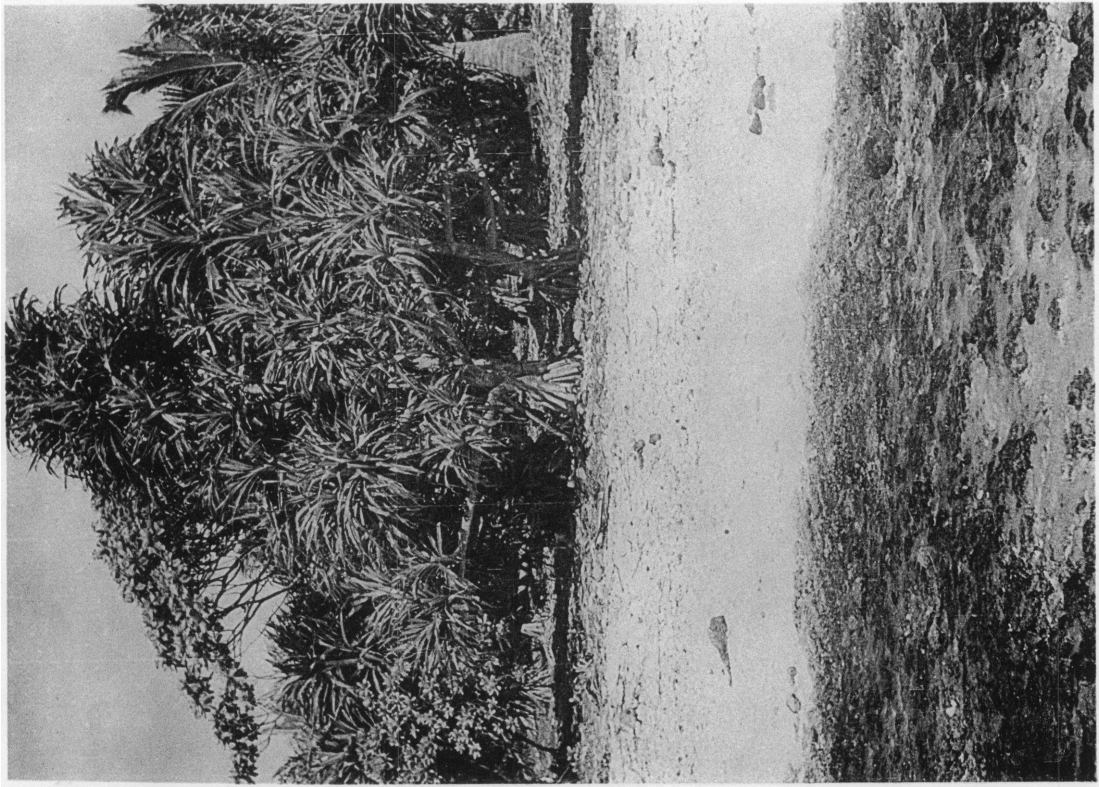


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1

Pemphis acidula forest on bare elevated reef limestone, just above high-tide level. Enelap Islet, Ujelang Atoll, Marshall Islands. Photographs by F. R. Fosberg, 1952



2



1

1. *Scaevola sericea* and *Pandanus* along outer beach. Nomwin Atoll, Hall Islands, Carolines
2. Mixed forest with *Pandanus*. Same location as 1
Both photographs by F. R. Fosberg, May, 1946



1



2

1. *Scaevola* fringe on leeward beach. Kalo Islet, Ujelang Atoll, Marshall Islands
2. Xerophytic opening in mixed scrub forest, *Scaevola* bush in foreground, with tufts of *Lepturus*, *Scaevola*, and *Messerschmidia* trees in background. Nelle Islet, Ujelang Atoll
Both photographs by F. R. Fosberg, February, 1952



1



2

1. *Scaevola sericea* colonizing sand flat at north end of Taka Islet, Taka Atoll, Marshall Islands. Photograph by F. R. Fosberg, 1951
2. Forest of *Pisonia grandis*, Almeni Islet, Bikar Atoll, Marshall Islands. Photograph by F. R. Fosberg, 1952



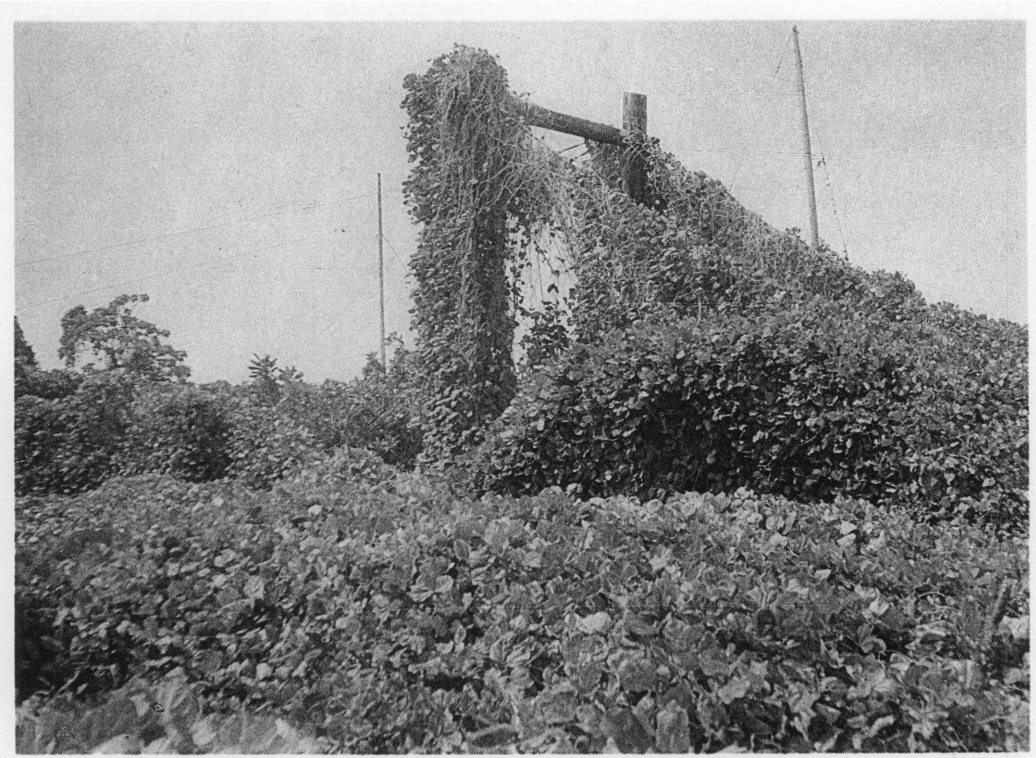
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1. Aerial view of coconut plantations on windward islets, showing crescent-shaped strips of strand scrub and scrub forest left on windward sides to protect plantations from wind and salt spray. Ailuk Atoll, Marshall Islands. Photograph by F. R. Fosberg, February, 1952

2. Opening in coconut grove, *Pandanus* on left, ground cover of *Lepturus repens*. Utirik Islet, Utirik Atoll, Marshall Islands. Photograph by F. R. Fosberg, November, 1951



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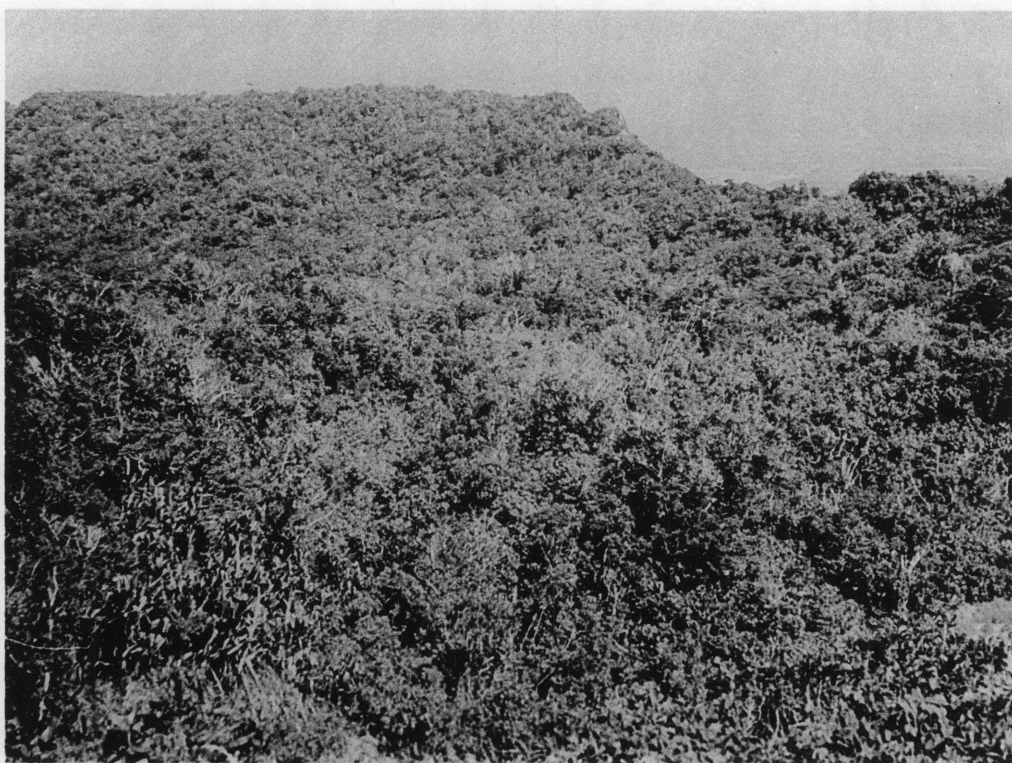


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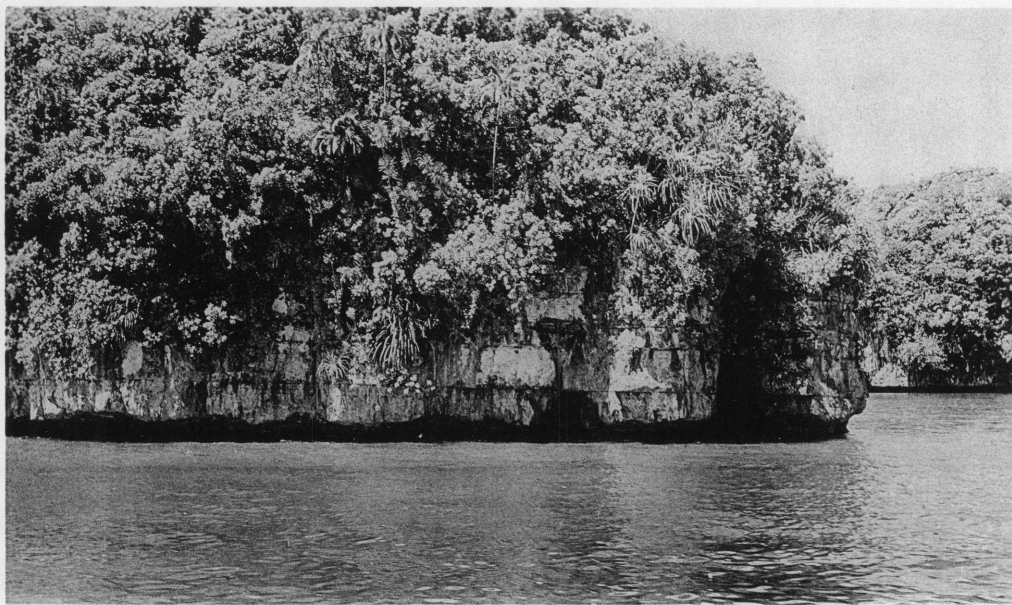
1. Installations abandoned for about four years, covered by blanket of *Wedelia biflora* and *Ipomoea pes-caprae*. Enebuoj Islet, Kwajalein Atoll, Marshall Islands

2. Opening in mixed scrub forest, covered by a deep blanket of *Wedelia biflora*. Lae Islet, Lae Atoll, Marshall Islands

Both photographs by F. R. Fosberg, January, 1952



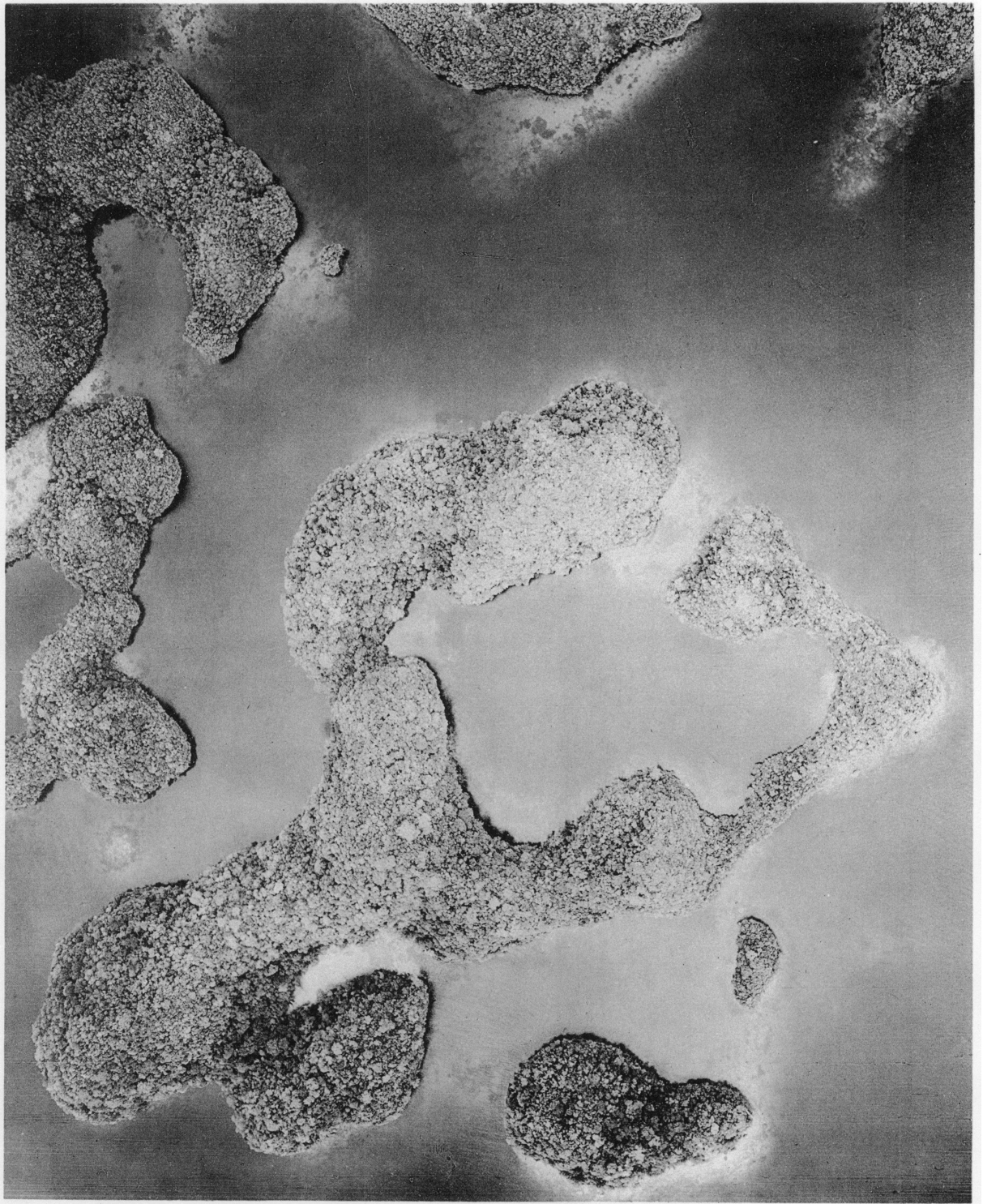
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1. Mixed forest on elevated limestone, top of Mt. Lamlam, Guam. Photograph by F. R. Fosberg, 1954

2. Mixed forest on elevated limestone, steep slopes. Urukthapel Island, Palau. Photograph by Josiah Bridge, United States Geological Survey, 1947



Vertical aerial view of small islands of elevated limestone in south half of Palau Group, showing mixed primary forest. Photograph by the United States Navy

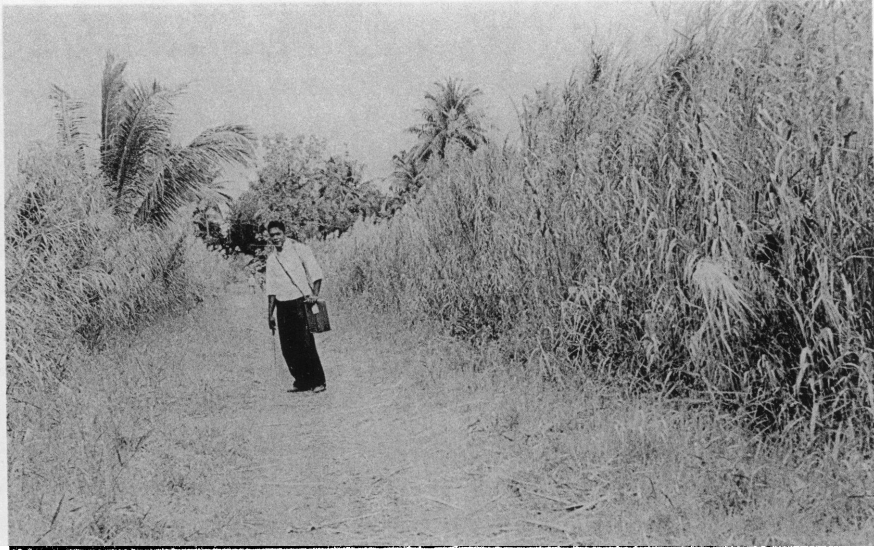


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1. Typical scene in coastal plain thickets; bare tree in center is kapok (*Ceiba pentandra*).
Dublon Island, Truk Group
 2. Taro pit with *Cyrtosperma*, coastal plain of Ulalu Island, Truk Group
- Both photographs by R. L. Hay, United States Geological Survey, 1954-1955



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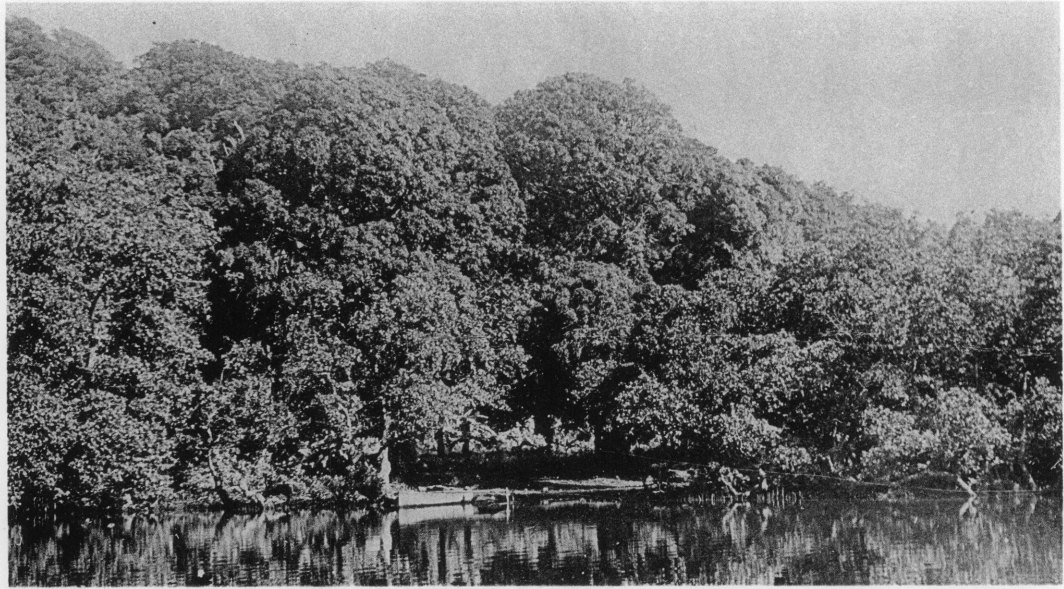


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1. Road through dense *Phragmites karka* on wet ground, coastal plain of Udot Island, Truk Group

2. Close-up view in *Phragmites* marsh, coastal plain of Param Island, Truk Group

Both photographs by the United States Geological Survey Party, 1954



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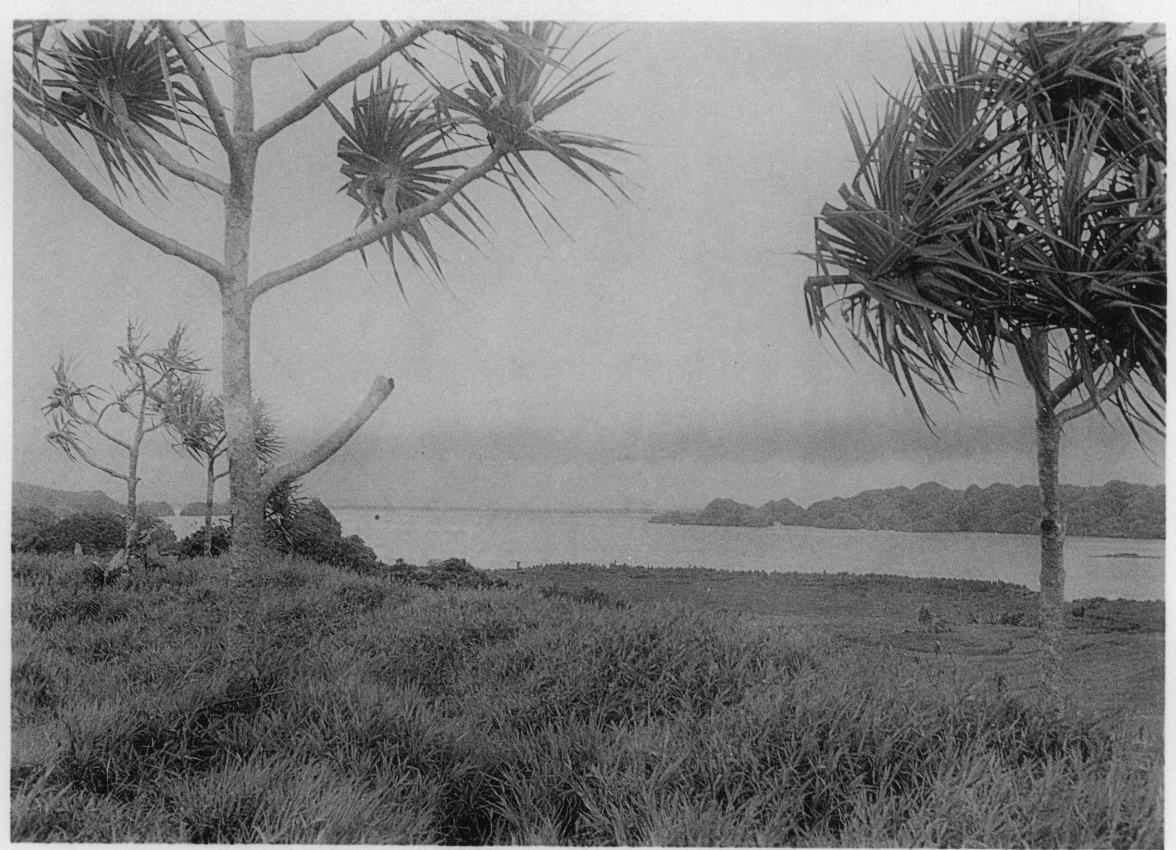


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1. Primary lowland rain forest at head of Lele Harbor, Kusaie Island
2. Montane rain forest, near top of Mt. Matante, Kusaie Island
Both photographs by F. R. Fosberg, 1946



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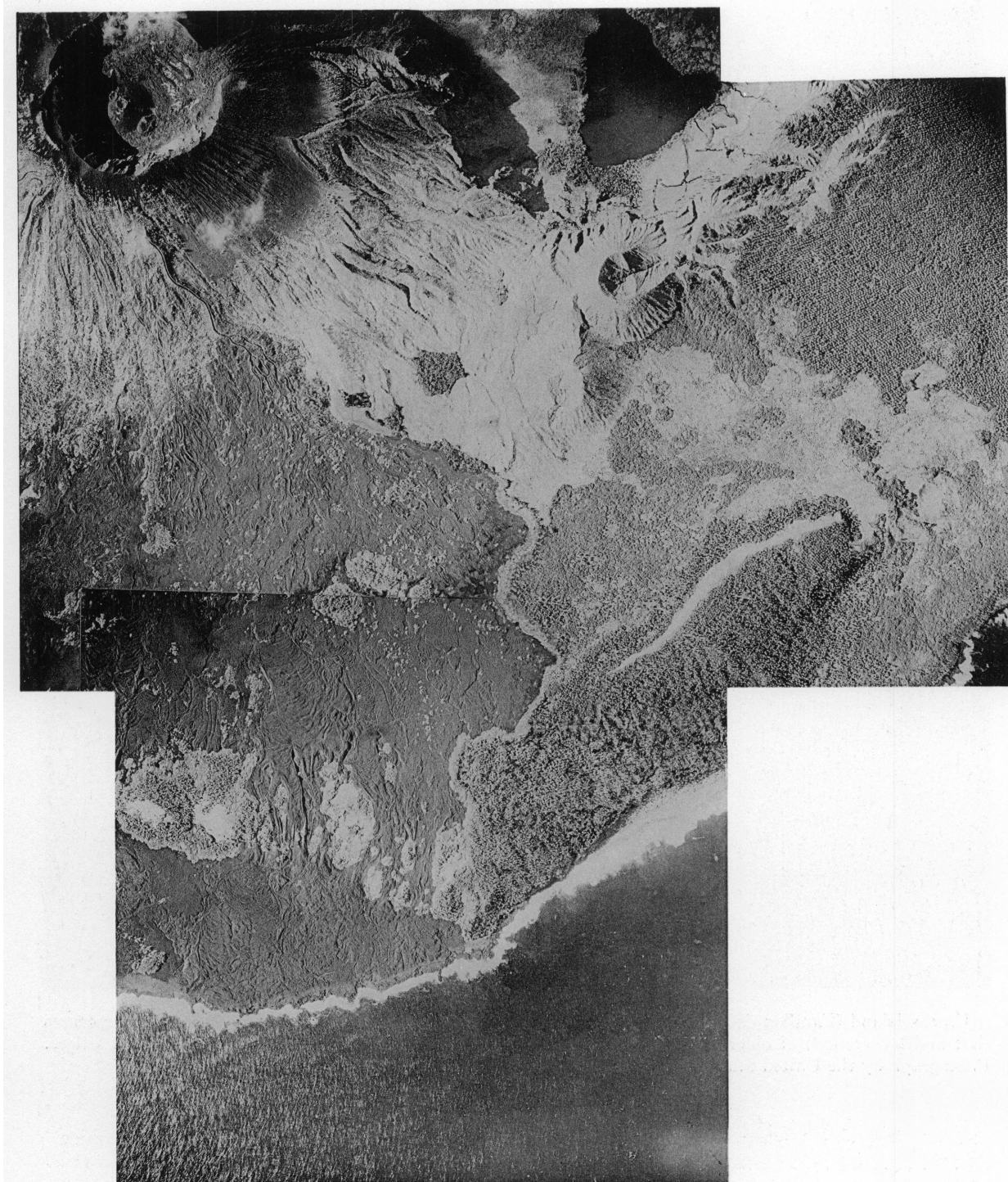


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1. Typical savanna landscape, bauxite region. Ngardmau, Babeldaob Island, Palau
2. *Ischaemum* grassland with *Pandanus* trees, northeast of Gakip, Babeldaob, Palau
Both photographs by Josiah Bridge, United States Geological Survey, 1947.



Uracas Island (Farallon de Pajaros), northern Marianas, showing fresh ash and lava slopes, two exposures (left and foreground) of older rocks which bear the only vegetation on the island, thin grasses and sedges. Photograph by the United States Navy, March, 1953



Pagan Island, northern Marianas. Mosaic from aerial photographs of north end of island, slopes of Mt. Pagan, showing *Miscanthus* grassland on ash slopes, mixed forest on lava, invasion of trees on lava flow, thickets around fresh-water lake, and coconut plantation. Photographs by the United States Navy



1



2

1. Pagan Island, northern Marianas. Freshwater Lake lined with *Casuarina*, ash slopes above with *Miscanthus*, cliffs with thickets

2. Caldera floor near Freshwater Lake, patch of *Casuarina* on lava flow surrounded by ash beds with *Miscanthus*

Both photographs by F. R. Fosberg, January, 1950



Alamagan Island, northern Marianas. Vertical aerial view of south side of island, showing coconut plantation, *Miscanthus*-covered ash slopes, and wooded ravines. Photograph by the United States Navy, January, 1952



1



2

1. Saipan, southern Marianas. Forest and thickets on limestone, with an abandoned patch of sugar cane, north of Mt. Tapochau

2. Patch of *Acacia confusa* forest on limestone

Both photographs by F. R. Fosberg, January, 1950



1



2

1. Saipan, southern Marianas. Weedy secondary vegetation along road north of Tanapag
2. *Operculina ventricosa* forming thick mat, Hagman Peninsula
Both photographs by F. R. Fosberg, January, 1950



1



2

1. Saipan, southern Marianas. Beach forest with creepers running out on beach, scrub on limestone cliffs in background, Fanagchulyan Bay

2. Scrub on rough limestone, Hagman Peninsula

Both photographs by E. R. Fosberg, 1950



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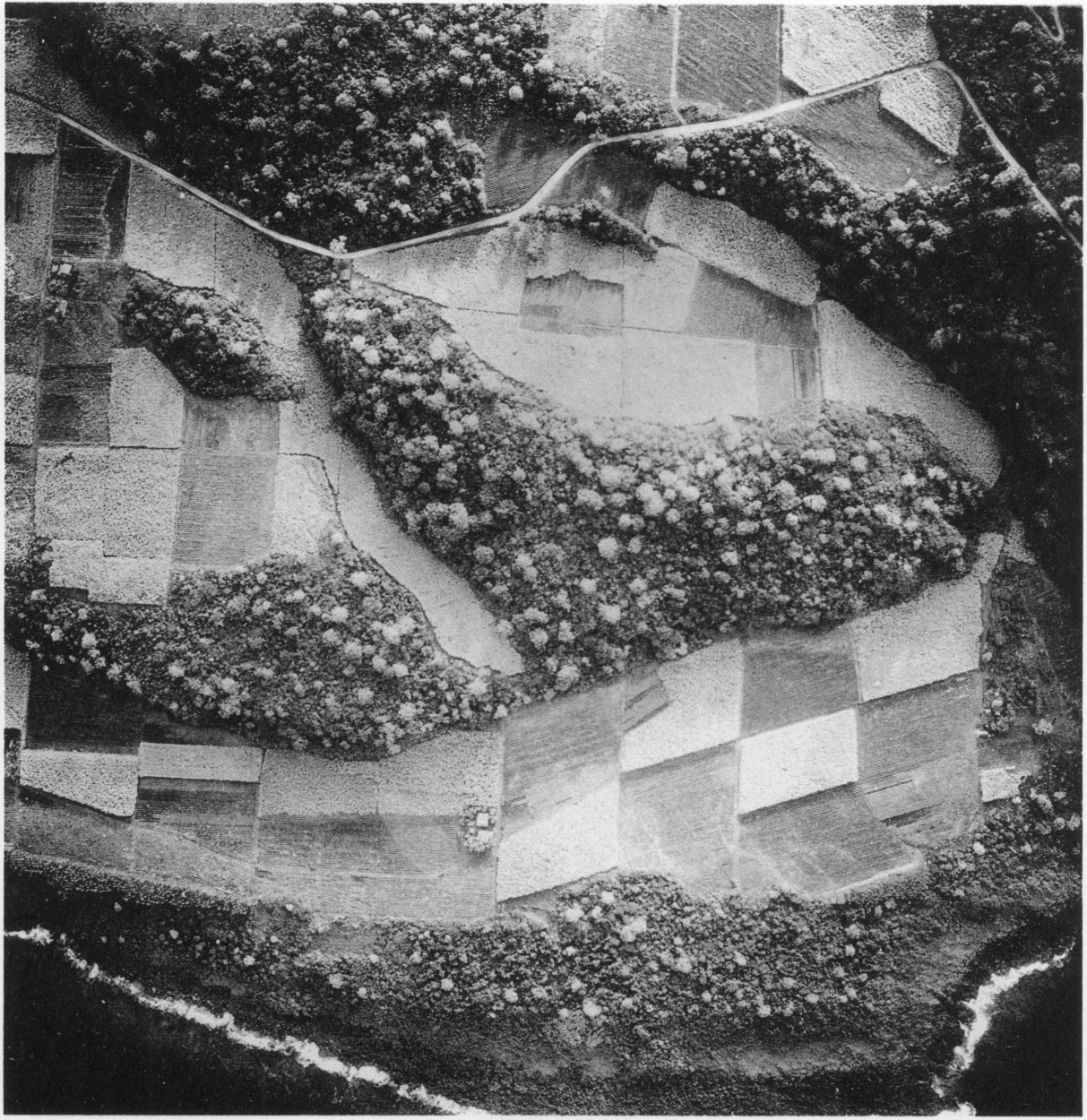


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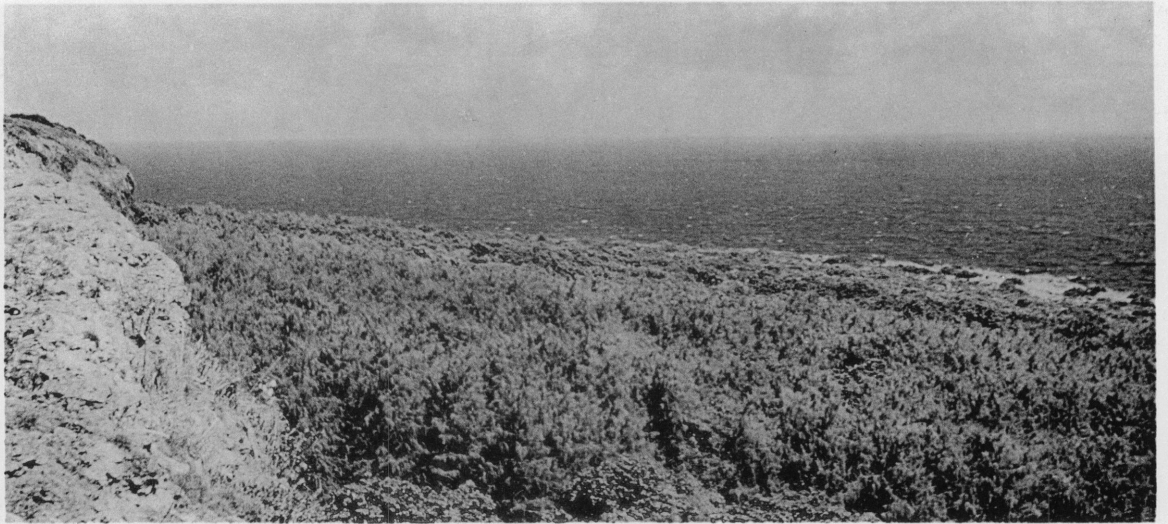
1. Saipan, Lake Susupe, Chalan Kanoa. *Casuarina* trees, *Hibiscus tiliaceus* scrub, and *Paspalum vaginatum* grass

2. *Casuarina* trees, *Scirpus* in water

Both photographs by F. R. Fosberg, February, 1950



Tinian, southern Marianas. Terraces devoted to sugar-cane culture and wooded escarpments between them showing typical vegetation on limestone in the Marianas. Photograph by the United States Navy, February, 1944



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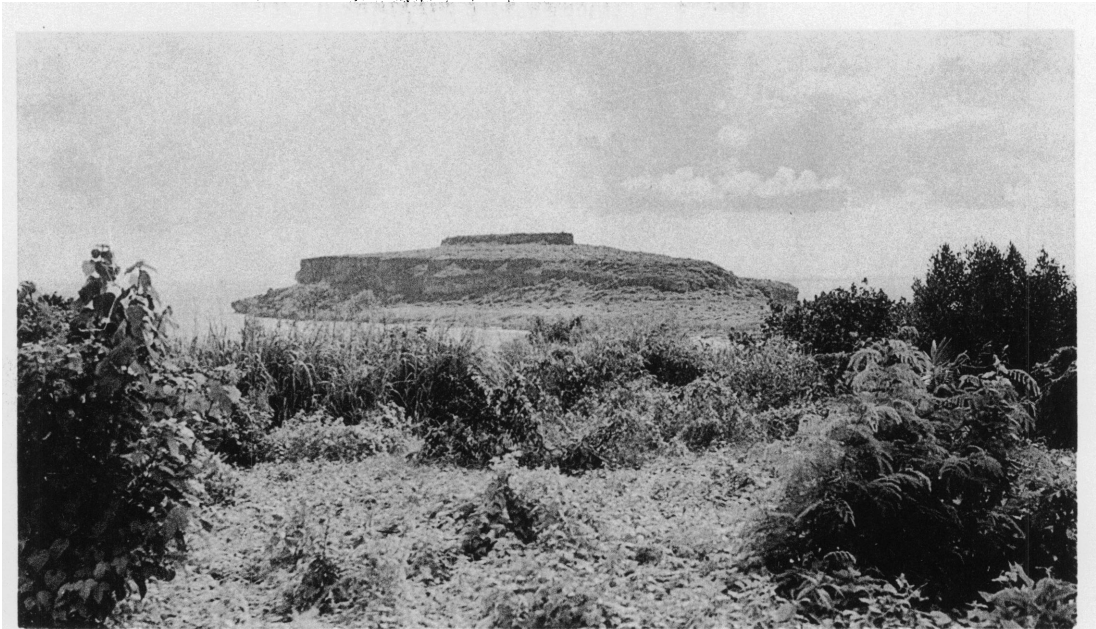
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1. Aguiguan Island, southern Marianas. Forest on lower limestone terrace. Photograph by Clifton J. Davis, November, 1955

2. Pemberton's Peak from west end, forest on rough limestone. Photograph by Clifton J. Davis, August, 1954



Rota Island, southern Marianas. Oblique aerial photograph, showing forest on rough limestone terraces; abandoned plantation land with blanket of *Ipomoea* and *Passiflora*, being invaded by shrubs and secondary forest trees, cultivated patches and wind breaks in distance, scrub on cliffs and rock strand. Photograph by the United States Navy, January, 1944



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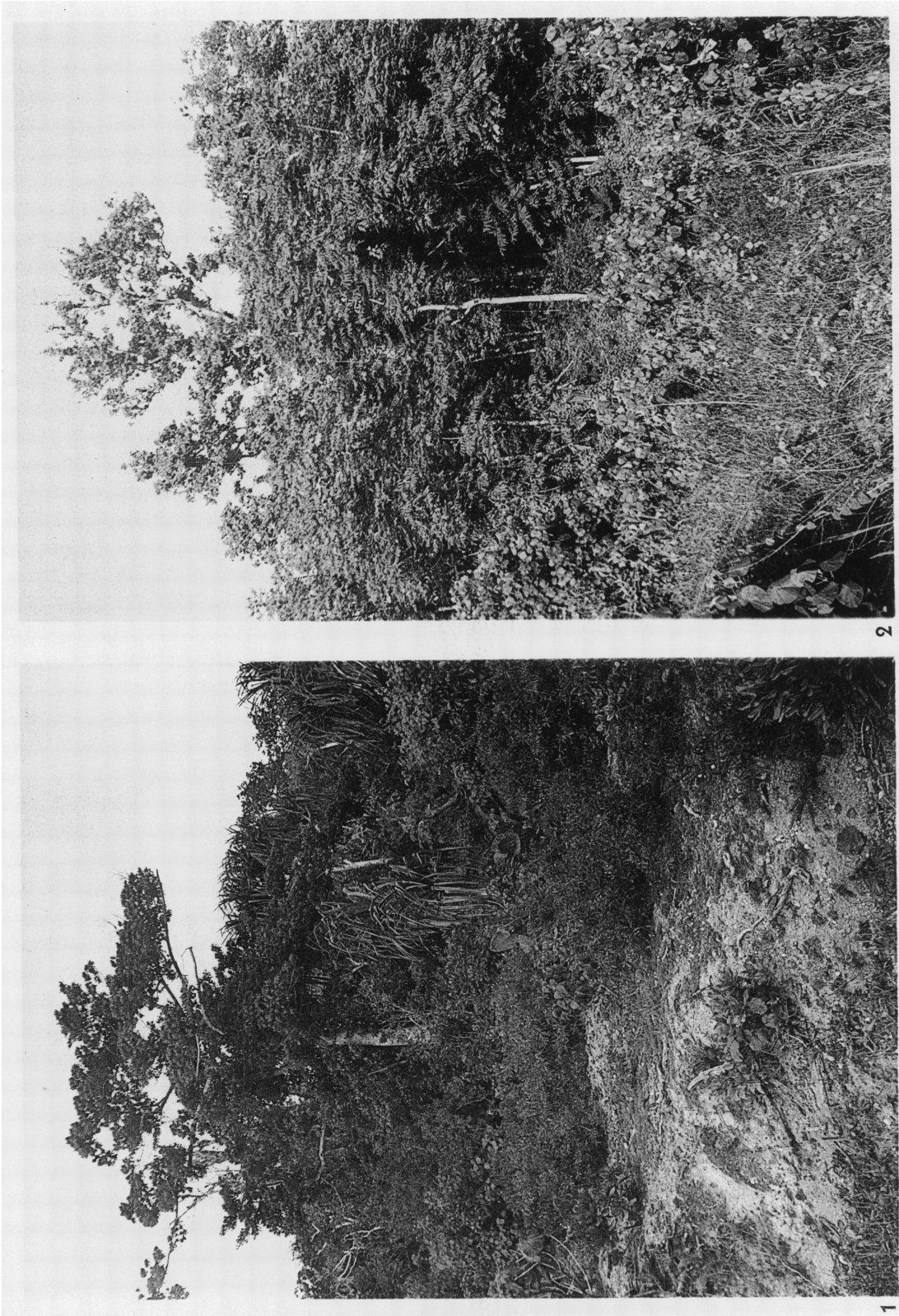


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1. Rota Island, southern Marianas. Mt. Taipingot, southwest peninsula, showing limestone terraces, scrubby secondary vegetation on abandoned field in foreground

2. South slopes, limestone above, densely forested, deeply weathered volcanic soil, grassy with wooded ravines

Both photographs by S. O. Schlanger, United States Geological Survey, 1952



GUAM

1. *Elaeocarpus joga* in forest on limestone north of Mt. Lamlam. Photograph by F. R. Fosberg, January, 1954
2. *Cananga odorata* forest above Fena Dam. Photograph by F. R. Fosberg, 1950



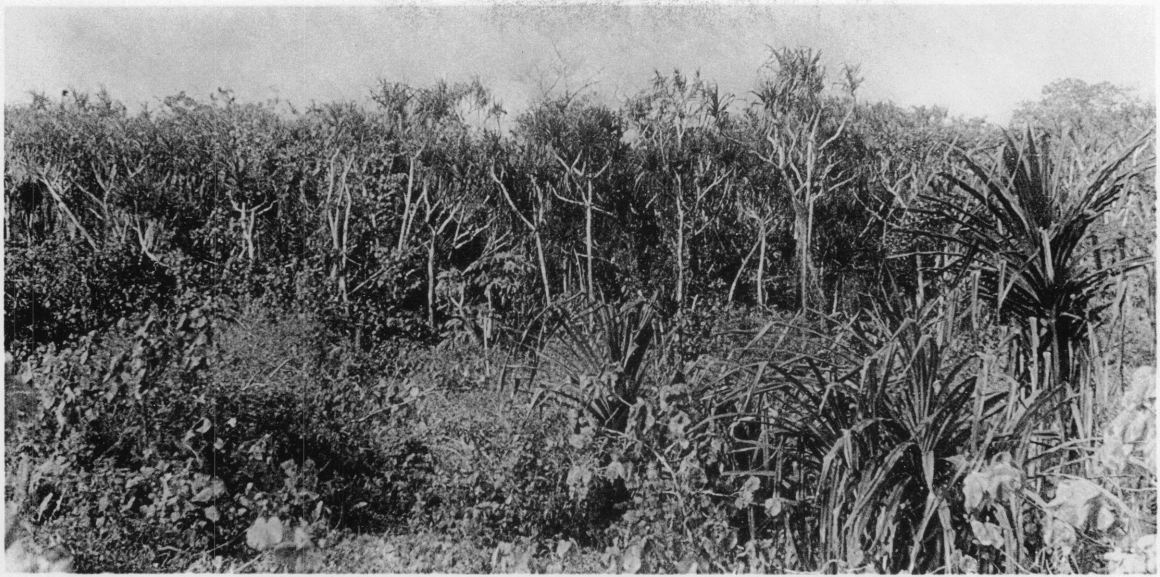
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GUAM

1. Mixed forest on hard limestone on plateau and slopes at foot of cliffs, Pajon Point. Photograph by D. B. Doan, United States Geological Survey, 1953
2. Scrubby second growth after clearing, north plateau near Campanaya. Photograph by F. R. Fosberg, January, 1954



1



2

GUAM

1. *Pandanus tectorius* forest, abandoned clearing with shrubby second growth in foreground, east of Dededo
2. Forest on limestone cliffs with *Heterospatha elata* and *Artocarpus mariannensis*. Fonte River near Agana Heights

Both photographs by F. R. Fosberg, 1950



1



2

GUAM

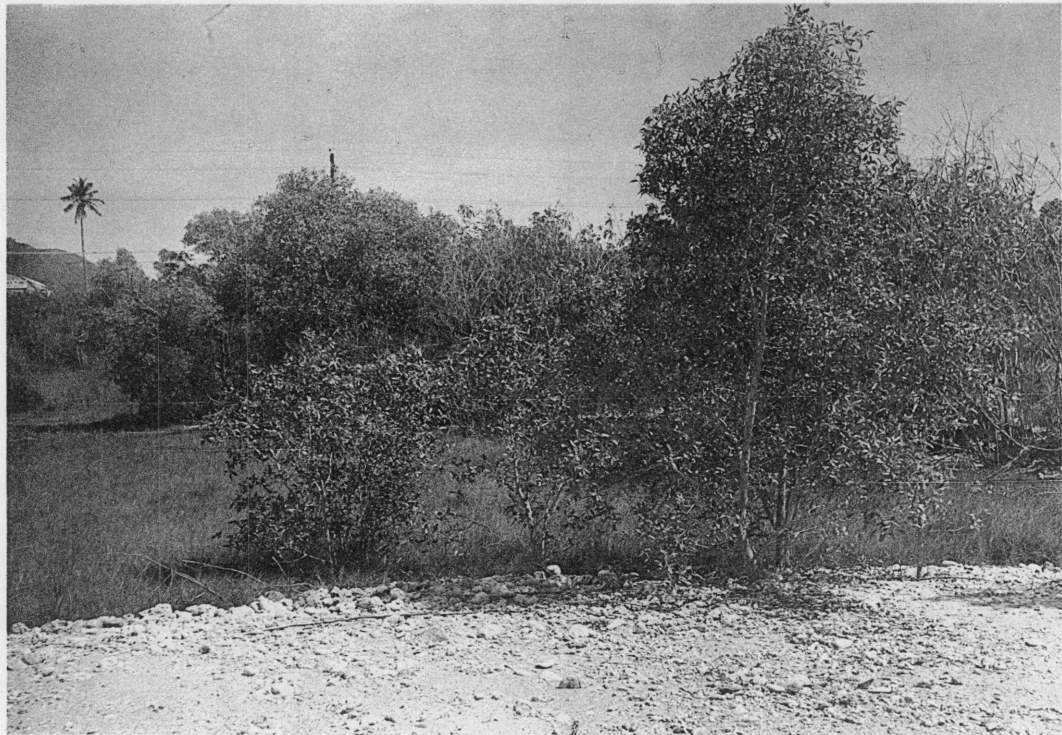
1. Brackish marsh with *Paspalum vaginatum* and patches of *Scirpus. Phragmites* in background; gravel in foreground thrown into edge of marsh by storm. Near Camp Bright

2. Mangrove swamp with *Rhizophora* at base of Orote Peninsula

Both photographs by F. R. Fosberg, January, 1954



1



2

GUAM

1. *Panicum purpurascens* marsh surrounded by reeds (*Phragmites karka*) at base of Orote Peninsula
2. Brackish marsh with *Paspalum vaginatum* and *Avicennia* trees, near Camp Bright, south of Orote Peninsula

Both photographs by F. R. Fosberg, January, 1954



1



2

GUAM

1. Coconut plantation battered by typhoon, soil washed away from roots of trees, east of Merizo
2. Rough limestone formerly covered by *Pemphis* but denuded by typhoon, showing character of limestone surface. Inarajan

Both photographs by F. R. Fosberg, January, 1950



1



2

GUAM

1. *Dimeria* grassland with scattered small *Pandanus* and *Casuarina* trees. Mt. Schroeder with patches of ravine forest in background. Near Merizo

2. Patch of ravine forest, mostly *Pandanus*, with coconut palms, weedy *Miscanthus*, and *Hyptis* in foreground. East of Talofoto (or Maemong Valley)

Both photographs by F. R. Fosberg, January, 1954



1



2

GUAM

1. View across savanna showing *Miscanthus* on slopes, *Dimeria* with clumps of *Miscanthus* in foreground, patches of ravine forest in valleys, and scattered *Casuarina* trees and active erosion scars in center. Above Merizo

2. *Miscanthus floridulus* and *Phyllanthus saffordii* at edge of erosion scar above Merizo

Both photographs by F. R. Fosberg, September, 1956



1



2

GUAM

1. Savanna vegetation showing difference between *Miscanthus* type (back) and *Dimeria* (front), with *Casuarina* in background, *Scaevola* in left foreground, east of Apra Heights

2. Wind erosion on slope of "mesita" of red clay, savanna vegetation with *Casuarina*, old dead *Scaevola* and *Casuarina* stubs exposed on slope, east of Apra Heights

Photographs by F. R. Fosberg, September, 1956



1



2

GUAM

1. Large erosion scars in red clay revegetated by *Gleichenia* and other pioneer plants, Dandan. Photograph by F. R. Fosberg, January, 1954
2. Ravine in savanna filled with *Phragmites karka*, *Pandanus* in foreground, *Casuarina* in back, east of Apra Heights. Photograph by F. R. Fosberg, December, 1953



1



2

GUAM

1. *Pandanus* savanna above Merizo

2. Erosion scar community in savanna, east of Apra Heights

Both photographs by F. R. Fosberg, September, 1956



1



2

GUAM

1. Slope with *Dimeria* and clumps of *Miscanthus*, *Casuarina* saplings, volcanic soil, east of Apra Heights. Photograph by F. R. Fosberg, December, 1953
2. *Miscanthus floridulus* growing on limestone, east slope of Mt. Almagosa. Photograph by F. R. Fosberg, January, 1954

