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SIM Report No. 25  
Scientific Investigations in Micronesia  
1949-  
The Vegetation of Micronesia - Part 1  
by F. R. Fosberg  
Pacific Science Board  
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THE VEGETATION OF MICRONESIA  
(Part 1)

SCIENTIFIC INVESTIGATIONS IN MICRONESIA  
Pacific Science Board  
National Academy of Sciences-National Research Council

F. R. Fosberg  
Pacific Vegetation Project  
Submitted 8 December 1959.

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**SCIENTIFIC INVESTIGATIONS IN MICRONESIA**

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between

**THE OFFICE OF NAVAL RESEARCH**

and

**THE NATIONAL ACADEMY OF SCIENCES**

The SIM (Scientific Investigations in Micronesia) Program developed as a successor to the former CIMA (Coordinated Investigations of Micronesian Anthropology) project with an enlarged scope that includes field research in the physical, biological, and life sciences. Field work under SIM has been conducted in the islands of the Trust Territory in Micronesia, the Gilbert Islands and the Tuamotu Archipelago since 1949. The field research has been carried out in cooperation with universities, museums, research institutions, and government agencies under this project of the Pacific Science Board of the National Academy of Sciences-National Research Council, supported by the Office of Naval Research and aided by financial assistance from other sources.

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## PREFACE

This report is Part 1 of a statement of the present knowledge of Micronesian vegetation. It is based on work sponsored by the U. S. Commercial Company (1946), the Office of the Quartermaster General, U. S. Army (1949), the Office of Naval Research (1950-1956), the Corps of Engineers, U. S. Army (1951-1956), the U. S. Geological Survey (1951-1956), and the Pacific Science Board (1949-1956). It is in the nature of a progress report on the work of the Pacific Vegetation Project and is submitted to fulfill, partially, obligations to all of the above agencies, as well as to provide a usable treatment of the land vegetation of this large oceanic area. Specifically this document is submitted as a partial report on work done under Office of Naval Research Contract N7-onr-29154, NR 388 001. Our gratitude is very deep to the agencies concerned for their continued support and their patience. Part 2, in preparation, will cover the remaining archipelagoes and isolated islands of Micronesia. More detailed reports are planned, based on further study of data in hand and continued field investigations.

The material in certain sections of this report have been submitted in more or less their present form to the Engineer, Armed Forces Far East, as sections of military geology and military geography reports. It is thought desirable to include them here also, in order to have all existing information on Micronesian vegetation summarized in one report. The text of the present document was duplicated and issued by the Office, Chief of Engineers, Department of the Army, Washington, as Engineer Intelligence Study 257, dated December, 1958 (issued December, 1959).

In addition to the agencies listed above, it is a pleasure to acknowledge my indebtedness to the Library of Congress, the U. S. National Herbarium, the Bernice P. Bishop Museum, the Government of Guam, and the Administration of the Trust Territory of the Pacific Islands for facilities and support that contributed in large measure to making possible the work reported here. Among numerous individuals who have assisted in one way or another, and to whom thanks are due, I must make special mention of a few. Mr. and Mrs. Peter J. R. Hill, Mr. and Mrs. Ernest G. 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 U. S. C. C. Micronesian Economic Survey Party and the U. S. 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 provided transportation, information, and company in the field on several occasions. Mr. Edwin H. Bryan has been helpful in many ways and on many occasions. Mr. 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.

F. R. Fosberg

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Figure 54. Guam.

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(Fosberg, Jan. 1954).

Figure 54b. Brackish marsh with Paspalum vaginatum and patches of Scirpus. Gravel in foreground thrown into marsh by storm. Near Camp Bright.  
(Fosberg, Jan. 1954).

## INTRODUCTION

### A. Purpose

This study of the vegetation of Micronesia is intended primarily as a reference for military personnel and others interested in the natural features of Micronesia. It may also serve as a guide to further studies by showing the ways in which vegetation serves as an indicator of terrain conditions.

### B. Scope

This Guide embodies the data included in the 1946 report of the United States Commercial Company Economic Survey of Micronesia 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 (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; and a two months reconnaissance of Guam in 1953 and 1954. The 1951-54 work was undertaken for the office of the Engineer, U. S. Army Forces Far East. In addition to the data made available by field work, this report includes information gathered in an extensive examination of much of the available literature on Micronesian vegetation and flora. Completing the study of all the material available and presenting it in final form will take a 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.

### C. Method of Presentation

To produce a detailed account of the vegetation of such a varied area as Micronesia from observations made during a total of twelve months of field work is manifestly impossible. Many of the islands have even yet never been visited by a botanist. With the advantage of a certain amount of previous experience with Pacific and tropical vegetation, however, it has been possible for the author to arrive at some 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 in the extreme south are likely to be wetter and more luxuriant than any described. This greater precipitation probably does not result in more than minor differences in the vegetation, however. 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 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-form of the plants comprising it - is influenced mainly by four factors: 1) available water, depending on climate, exposure, and drainage; 2) substratum; 3) animal (and human) influences; and 4) history, principally that of climatic change and human activity. Thus it is that a major vegetation type of formation, such as a 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--that of 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 notes to follow, the physiognomic features described will be familiar to those who have had any extensive experience with tropical vegetation, while most of the species will be familiar only to those who are acquainted with the flora of the tropical Pacific.\*

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\*It will be noted that botanical rather than common names generally have been used for the plants. This usage is because in Micronesia few plants have familiar English names, and there seems little point in using local native names or Japanese names which do not appear in available books.

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## PART I. ESSAY ON THE NATURE OF VEGETATION

The term vegetation, used in any but a purely popular sense, correctly means the plant cover of an area of the earth. It is a term used to indicate an aggregate of plant communities, rather than individual plants or species. It is necessary to emphasize this because of the frequency with which the word vegetation is erroneously used in speaking of particular plant species.

No useful understanding of any plant ecological work, other than some phases of autecology (the environmental relations of separate species), is possible until the idea of plant communities is grasped. Vegetation, as a mosaic of plant communities, is a product of, and is dependent upon, a large number of conditions. On the one hand, it is dependent upon the species present, and upon the inherited characteristics of each of them. On the other hand, it is dependent upon the nature of the environment, and the interactions between that environment and the plants. In both these respects, the factors of chance and probability play a leading role. The science of ecology, in a broad sense, involves the study of these dependencies and other interrelationships between organisms and their environments.

Historically, one of the earliest phenomena of vegetation is the colonization of a bare area, either on soil or rock. Such an aggregation of plants cannot be called a truly random assortment. Here, as in all later stages in the development of vegetation, the environment exerts a selective action, severely limiting the number of kinds of plants that may become established to populate the area. Only a relatively few species are able to withstand the rigors of such a site, i.e. the heat, rapid erosion, lack of humus, exposure to wind and rapid evaporation, etc. Such of these species as are available in the form of viable propagules may make up the first stages of the new vegetation.

The selective effect of the environment is commonly formulated in terms of the action of limiting factors such as low temperatures, lack of water, or acidity of the soil, etc. which prevent certain species from growing. It can be formulated equally well in terms of the degree to which the environment is able to satisfy the requirements of the various species involved. There is no doubt that certain plants are definitely eliminated by individual limiting factors. However, it is probable that the greater proportion of available species are not thus eliminated. It seems likely that the composition of the vegetation is more largely determined by the degree to which the environment satisfies the requirements of the species present. Those whose needs are most fully met will become most important in the communities while those least satisfied will be eliminated by competition.

This will become more and more true as the vegetation develops toward maturity and as competition for the resources of the environment increases.

As plants appear in a new environment, they immediately become a part of that environment, altering it to a certain extent, changing its capacity to meet the requirements of various available species. This alteration may eventually cause changes in the composition of the new plant community. Such a process may be likened to a chain-reaction, going on as long as it produces significant changes in the environment. As the available physical space fills up and as competition increases the rate of change slows down. At the same time more and more plants enter the vegetation, whose influence is such as to create or maintain conditions not unfavorable to themselves. Thus, of course, change in the environment tends to become less, and eventually, providing no extraneous general, secular, or catastrophic changes are taking place, an equilibrium may be reached. In the terminology of many ecologists, vegetation in such a state of equilibrium or relative stability is called climax.

It is unfortunate that the climax has usually come to connote a static condition. Actually, it is probable that no truly static condition ever exists in vegetation. Since the community is made up of populations of individuals that are constantly reproducing and dying, and therefore changing, at least fluctuation is to be expected in the composition of every community. Moreover, it is likely that secular change in the environment, such as that due to major cycles in the earth's relation to the sun, is never entirely absent. Added to this, a gradual wastage of the physical components of the environment — soil, plant nutrients, topographic relief, etc. — must be expected. It becomes clear, upon reflection, that vegetation is always dynamic to a greater or lesser degree. What are known as successions happen when change is relatively rapid. When the change is very slow, or only fluctuating around a condition of equilibrium, this condition may be called climax. The expression "relatively stable vegetation" might well be used instead of climax with less chance of ambiguity. The term "virgin forest" is commonly applied where relatively stable vegetation persists because man has not disturbed it. In the tropics "primary forest" is the relatively stable undisturbed forest of moist or wet country at not too high altitudes.

One of the important problems in the study of vegetation is determining the rate and probable direction of change. If this is solved for any particular type of vegetation, prediction and some measure of control become possible, and a further key to the nature of the environment may be provided.

The first and truly basic stage in the study of any vegetation is description. Without accurate knowledge of what the vegetation is, there is little use in trying to understand it or make use of it. Much of the information conveyed by a description of vegetation may be arranged in three categories, namely (1) location (or distribution), (2) composition, and (3) structure and physiognomy. A fourth, successional position or "dynamic status" is important if known, but may often be determined only after critical and sometimes lengthy study. To render the description meaningful, as much information as is available concerning the environment is usually added.

Of these categories, the first, location, needs no explanation except to point out that, in a dynamic system, location in time (date) is as important as location in space.

Composition is the array of kinds of plants which make up the vegetation, and their relative numbers.

Structure is the arrangement of the different sorts of plants in the vegetation, not by species but by growth forms, or categories of plants that are similar in outward form, though not necessarily related botanically. Thus the tulip tree, plane tree, beech, birches, oaks, maples, ashes, hickories, and elms that make up the winter-deciduous tree growth form are not closely related by evolution but present a similar appearance and the identical adaptation of dropping their leaves in winter. The structure of vegetation is responsible for its appearance or physiognomy, which is the basis of the major divisions in many classifications of vegetation. The reason for this emphasis on physiognomy lies in the probability that growth forms actually do represent significant adaptations to specific environments. A predominance of a certain specific growth form would then indicate that the vegetation as a whole was a reflection of the environment to which that growth-form was a response.

Since there are in the world a great number of different kinds of vegetation, it is necessary, as a means of conveying ideas about them and as an approach to understanding them, to have some sort of classification or systematic arrangement.

Many and various classifications of vegetation have been proposed, based on a variety of different features, but none so far are completely satisfactory. This is neither cause for especial surprise nor criticism. Considering the small amount of reliable descriptive information available on vegetation, as such, it is more surprising that any real progress has been made.

The great subdivisions of vegetation are, traditionally, forest, grassland, and desert, with such intermediate categories as scrub, savanna, and others. These, it will be noticed, are units characterized by physiognomy.

Such major subdivisions of these as tropical rain forest, winter-deciduous forest, prairie, tundra, chaparral, etc. are often called formations. Some students call them "formation types" and term the various geographical expressions of them "formations." These large categories, again, are delimited by physiognomic differences, and may generally be taken to indicate differences in climate, though not always. The winter-deciduous forest formation occurs where there is a wet summer and a severe winter, the winter being a dry season because water takes the unavailable form of ice. In tropical regions with high rainfall throughout the year we have "rain forest." If there are marked wet and dry seasons in the tropics we may have "dry-season deciduous" or "rainy-green" forest.

Smaller subdivisions, often called associations, are characterized by particular combinations of species, in other words, by local peculiarities in composition. Thus, in the deciduous forest formation of eastern North America, we have beech-maple and oak-hickory associations.

This process of subdivision, reflecting actual differences in plant cover, may be carried down to a very local sort of variation. Whether or not it is necessary to classify vegetation down to these local minor variations depends entirely on whether one's purposes are served thereby. If it is desirable to discuss such variations, it is often essential to have names for them that will convey information on their characteristics and relationship to other types.

The comprehension and classification of vegetation has been seriously hampered by lack of carefully recorded, accurate, descriptive information. The assembling of this sort of data is expensive and time consuming. One must be on the ground to obtain the raw facts. This means that the various regions of the earth must be visited and examined carefully by vegetation students. Specimens of the plants must be gathered for study and identification. Notes must be taken on their occurrence, arrangement and abundance, as well as their behavior, life-histories, and habitat preferences. Information on the environment must also be recorded. These studies cannot be made hastily, but must be carried on as meticulously as studies in experimental chemistry.

Since the study of vegetation is an expensive, long-term process, it may be asked what the practical significance is that makes the expenditure worthwhile.

In order to exist and carry on his activities in the changing and diverse environments on the earth, man must either adjust himself and his activities to these situations or manage and manipulate them to fit his needs and desires. Both of these processes are facilitated by an understanding of the environment.

Vegetation is a major component of man's total environment, and it serves as indicator of, or reflects, many other components. Any attempt to understand vegetation better is an approach toward the ability to live and function more effectively within the environment, as well as to manipulate or modify it for any desired purposes, and to do so wisely. This is particularly true when vegetation is observed in connection with studies of other major environmental factors such as climate, the earth itself, or its mantle of soil.

Man's effort to modify and improve his environment is everywhere evident. The scope of such attempts varies a great deal: an extremely local one is the creation by the use of clothing of an immediate environment warm enough in which to live. Major attempts at changing the environment are extensive irrigation projects, widespread agricultural developments, and the creation of cities. Evidence of ill-considered or poorly managed modifications is also widespread, in the form of abandoned projects, ruined, worn-out or eroded land, and poverty.

Numerous throughout history are the military campaigns which failed because the rigors of winter environments were not properly estimated, the relation between insects and disease was not understood, or the natural advantages of terrain and vegetation of the country were not utilized as well as they were by the enemy.

From a military point of view, a long-term policy on such investigations is especially necessary. Most military operations are carried on in a state of emergency. Any information, to be of use, must be available immediately. Such studies as those of climate, substratum, and vegetation must be done before an emergency arises, as there is no chance to carry them out effectively or satisfactorily on an emergency basis.

# The Vegetation of Micronesia

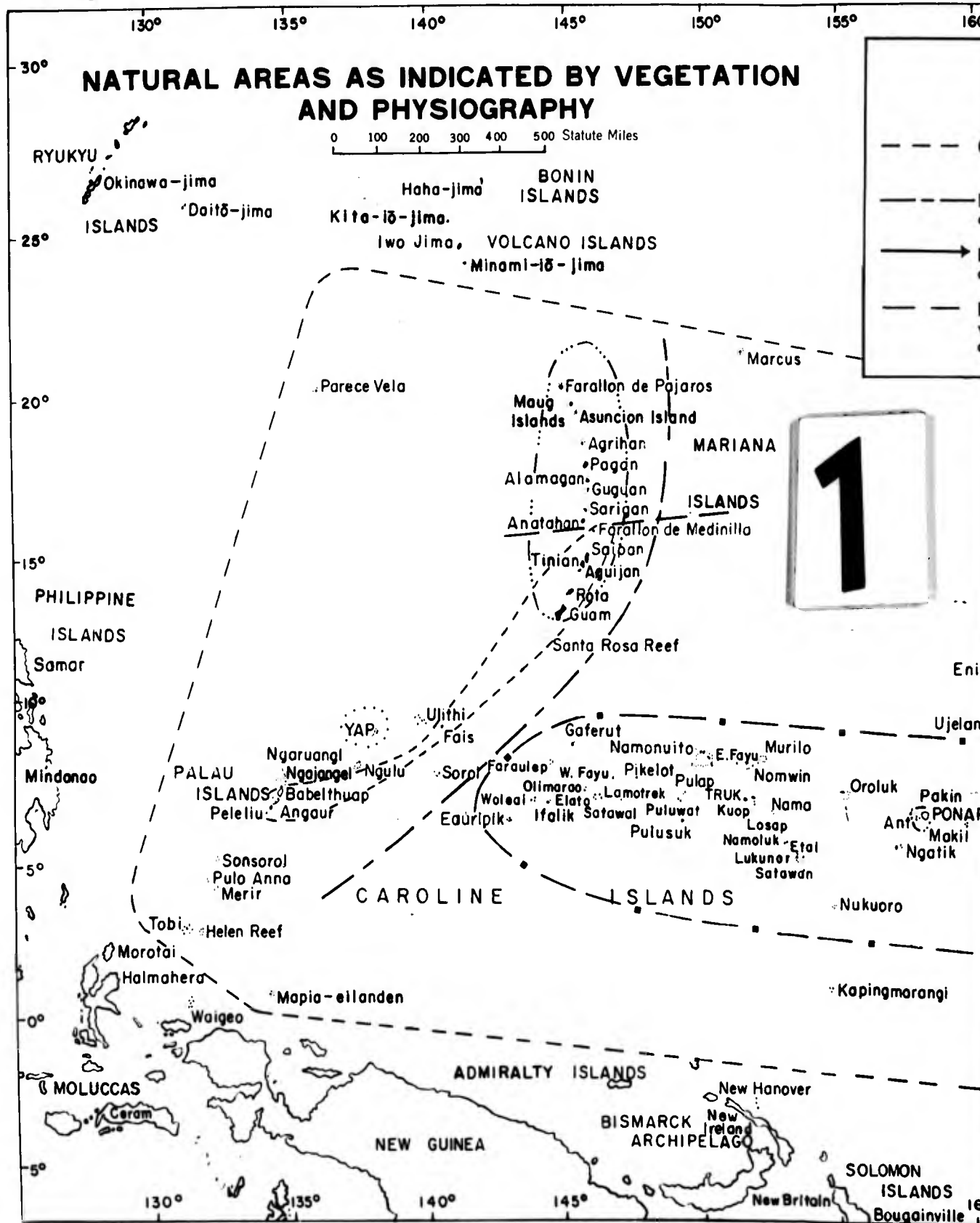
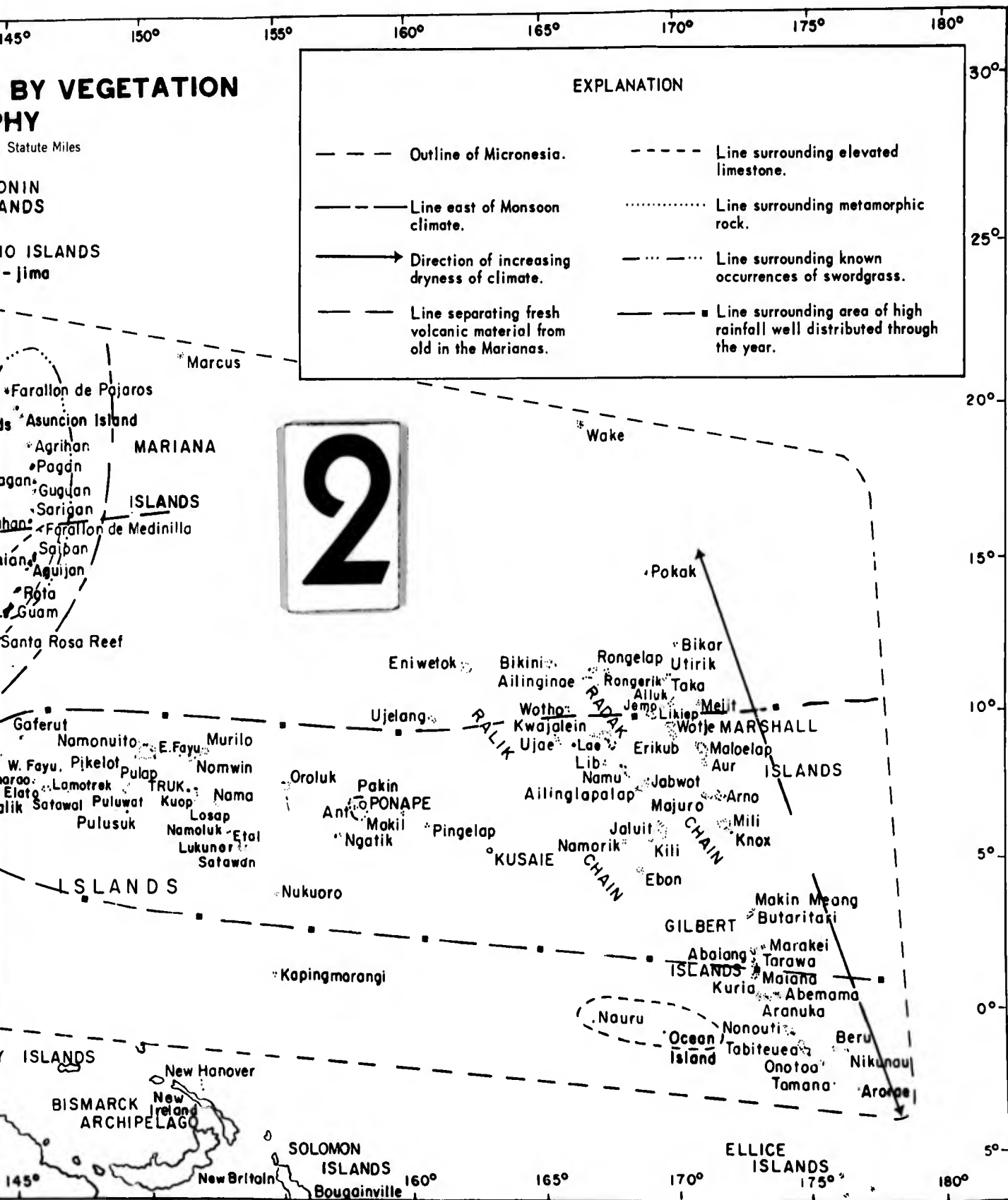


Figure 1



## PART II. GENERAL DESCRIPTION OF MICRONESIAN VEGETATION

### A. Location and Nature of Micronesia.

Micronesia (see Figure 1. Natural Areas as Indicated by Vegetation and Physiography) covers a large section of the earth's surface, but is mostly water. There are approximately 117 islands, atolls, or closely associated groups of islands, but their areas are so small that altogether there are 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.

### B. Major Climatic and Topographic Features.

The major climatic and topographic features of Micronesia which influence vegetation may be briefly summarized as follows:

The Marshall and Gilbert 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. In the dry northern Marshalls and southern Gilberts rainfall tends both to be seasonal and irregular, with extended dry periods, a whole year with no recorded rain, though this is rare. Other years may occur with rainfall far in excess of that expected. 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 severe dry seasons.

The Marianas may 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 an area of monsoon-type climate, with moderate dry seasons and many, often severe, typhoons. In the Marianas the heaviest rain occurs in the period from July to October, but this is by no means a very regular phenomenon. From the few available figures there seems to be a slight decrease in rainfall northward in the group, but the pattern is not very clear. Orographic effects are of great importance

in the total picture and in causing local variations. Anything like adequate records are completely lacking for the group north of Saipan.

Of the western Carolines, three are high islands or groups of islands. Fais is a somewhat elevated coral island. Yap is a mass of metamorphic and volcanic rocks surrounded by a wide fringing reef. The Palau group is complex. The northern island, Babelthiap, is a low, extensive, eroded volcanic mass, with extensions southward in Kror, Arakabesan (Ngarakabesang), and Malakal islands. The remainder of this group, to the south, is of elevated limestone, extremely dissected, steep, and rugged. The southernmost ones, 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 and Ngaruangi.

Climatic data on the low islands of the Carolines are especially needed. The eastern Carolines are very wet and the climate is not strongly seasonal, the seasons becoming more marked westward in the group. Typhoons have caused serious damage a number of times within this century.

C. Map Showing Climatic and Geologic Lines.

The accompanying map attempts to illustrate the basis for a possible division of Micronesia into something like natural regions, based principally on the general aspect of the vegetation and the basic geological features of rock types and volcanism. Regional boundaries are not drawn as in many respects the necessary information is lacking. At present the map is intended to be merely suggestive and to invite criticism and correction.

The climatic lines are based principally on vegetation and indicate a summation of effective climatic influences, rather than any one feature. In the future, when weather data become available for enough stations, the lines may be altered as necessary to fit such more objective criteria. The other lines indicate the distribution of such significant geological features as elevated limestone and recent and old volcanic rocks. Finally, a line is drawn to include areas characterized by sword-grass (Miscanthus floridulus), one of the most striking vegetation types in Micronesia.

D. Classification of Vegetation.

The subject of classification of vegetation is in such an unsatisfactory state, especially with regard to tropical vegetation, that it does not seem advisable to try to force the array of Micronesian types into any of the schemes in vogue. The classification outlined below and used as the framework of the treatment to follow is merely a briefly descriptive one that results obviously from the observation of the vegetation.

It is realized that it would be desirable to keep topographic features and other habitat factors out of such a classification, and to have a system based entirely on the plants present. However, more understanding and clarity can be reached by bringing in both plants and habitats as may seem necessary to describe actual situations.

E. Outline of Micronesian Vegetation.

A brief outline of the main vegetation situations of Micronesia, as known at the present time would be as follows:

1. Mangrove formation.

Mangrove swamps.

Sonneratia-Rhizophora type -- quite saline.

Bruguiera-Lumnitzera-Xylocarpus -- brackish.

Mangrove depressions -- rock bottom.

Nipa swamp.

Barringtonia racemosa swamp.

Acrostichum marsh.

2. Strand.

Vegetation of sandy beaches of high islands.

Volcanic beaches.

Calcareous beaches.

Vegetation of shingle beaches.

Vegetation of rocky coasts of high islands.

Volcanic coasts.

Coral limestone coasts.

Pemphis forest and scrub.

Vegetation of atolls and low islands.

Scaevola fringe.

Scaevola scrub.

Xerophytic openings.

Xerophytic forest.

Brushy sand spits.

Pemphis forest or scrub.

Mesophytic forest.

Mixed forest.

Pure stands.

Coconut-breadfruit forest.

Marshes and taro patches.

3. Vegetation of raised coral limestone.

Primary forest on smooth limestone with soil.

Primary forest on rough limestone, without soil.

Scrub on tops of bluffs.

Cliff vegetation.

Passiflora foetida-Ipomoea indica on smooth limestone

with no soil.

Thick mixed herbaceous weedy vegetation on denuded soil.

Brush, either mixed or pure stands of various pioneer shrubs.

Mixed secondary thickets and forest, and pure stands.

Casuarina

Leucaena

Macaranga

Pandanus tectorius

Acacia confusa

Albizzia lebbek

Macaranga-Pipturus-Abroma

4. Vegetation of rough lava flows.
5. Casuarina forest.
6. Coconut plantations.
7. Vegetation of coastal plains.
  - Primary forest.
  - Secondary thickets.
  - Swamps.
  - Metroxylon groves.
  - Reed brakes, with or without Pandanus.
  - Marshes.
  - Taro patches.
8. Lower primary forest.
9. Secondary forest on slopes.
  - Mixed secondary thickets.
  - Hibiscus tiliaceus.
  - Coconut plantations and coconut-breadfruit plantations.
  - Leucaena glauca thickets and forests.
10. Montane rain forest or cloud forest (mossy forest).
11. Dwarf vegetation on open crests.
12. Savanna or grassland vegetation.
  - Swordgrass
  - Dimeria

## Gleichenia

### Gleichenia-Nepenthes-Hedyotis

#### F. Vegetation Types as Practical Indicators.

Although 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 much less available than in 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. A certain amount of correlation was ascertained, on the basis both of recorded information and of new data collected in the field. In the general part of this report, 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.

It must be pointed out that much greater reliability may be gained in using vegetation as an indicator by taking into consideration such factors as topography, general climate, season, human influence, etc. Some of these very items are ascertainable from studying vegetation, and when established provide keys to further use of the vegetation as an indicator of other aspects of the environment.

### PART III. GENERAL DESCRIPTION OF VEGETATION TYPES

#### A. Mangrove Formation

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

Mangrove swamps (Figures 3-5) 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 forming 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 m 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 and pneumatophores (aerating organs) (Figure 5). 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 which 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 (Figure 5b), makes progress 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 as extensive or well-developed as those in the subcontinental region farther west. Considerable areas exist around all of 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 important 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. 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 conjugata 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 native have thrown Bruguiera seedlings.

The principal tree species found in the mangrove vegetation in Micronesia are Rhizophora mucronata (Figure 3b), R. apiculata, Bruguiera conjugata, B. sexangula, Sonneratia caseolaris, Xylocarpus granatum, Lumnitzera littorea, Barringtonia racemosa, Heritiera littoralis, and Excoecaria agallocha. Shrubs are Clerodendrum inerme, Acrostichum aureum, and Nipa fruticans (Figure 4), lianas Derris trifoliata, Smythea lanceolata, and Cassia sp., 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 conjugata, Xylocarpus moluccensis, Heritiera litoralis, and Lumnitzera littorea are found on Guam, and in Saipan the number has decreased to one, Bruguiera conjugata, but with the addition of two species of strand trees, 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, Bruguiera sexangula seems to go no further than Truk, and Xylocarpus granatum no further than Ponape. Other species stop at Kusaie, except Sonneratia caseolaris, Rhizophora mucronata, Bruguiera conjugata, and Lumnitzera littorea, which occur in the Marshalls, especially in the south. Bruguiera conjugata occurs very rarely in the northern Marshalls, but is known there as isolated individuals (Bikini).

Farther west, in the Malayan region, there is, according to various writers, a distinction between mangrove swamps and NIPA SWAMPS, the latter characterized by dominance of the stemless palm, Nipa fruticans (Figure 4). This is scarcely the case in Micronesia except in Guam, where extensive stands of Nipa, generally regarded as introduced, occur along some of the estuaries on the east coast. Elsewhere Nipa colonies 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.

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 bottom lands 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 between the root-masses of the trees. Since most of the Guam Barringtonia forest is in fresh water, this type will again be referred to in the section on the coastal plain.

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 sometimes fresh. It may form pure stands, but is frequently mixed with Clerodendrum inerme, and sometimes also with Hibiscus tiliaceus, as around Hagoi (Lake) Susupe, on Saipan.

Only a rough idea has been gained of the factors controlling the local distribution of the principal trees of the mangrove formation. A definite zonation is commonly observed, which may either be sharply defined or blending. It may be correlated with a gradient inland from sea water through brackish to fresh. In general, Sonneratia 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 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 as near to the open sea as the two foregoing but does go inland as far as any trace of mangrove swamps are found. It is one of the principal components of mangrove depression vegetation, and is found in pure stands in some of the land-locked ponds in the southern Palau Islands. It seems to favor brackish rather than very saline situations. Lumnitzera and Xylocarpus both seem to prefer similar habitats 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. Nipa patches 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 Nipa 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 places 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. Toward 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. 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 any 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 preference. The main types of this formation are best recognized by their aspect or physiognomy, their dense, fine-textured, usually dark green appearance, mostly with an even, compact surface (except where Sonneratia is common, with its turret-like habit), and the conspicuous pneumatophores. The boundaries between the mangrove and most dryland forest types are sharp and easily seen.

As an indicator the mangrove formation, in general, reveals a number of things. It dependably indicates level 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, Excoecaria, is likely to be present, whose latex (milky sap) 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 (Figures 3, 5b), it is likely to be nearly impassable to a man on foot, both because he will mire down in the mud and because of the densely interlocking aerial roots that form a tangle that is hard to cut one's way through even with machetes. Where Sonneratia is abundant, going in much better. The substratum is more likely to be firm coral silt or sand, though it may be mud. The roots form a firm platform only a few inches below the surface, and, though the erect, slender pneumatophores (Figure 5a) 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 it is hard going. A dense stand of Nipa 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. If logs are laid down as corduroy, after ways have been cut, men and light equipment can be moved across it, but this sort of operation will be very conspicuous from the air.

## B. Strand (Figures 6-9).

Normally the strand is that portion of the vegetation 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 those species with special adaptations for resistance to salt plants commonly termed halophytes. Fleshiness is the most common and obvious of these characteristics. The 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 coastline bounding the islands; this is because the vegetation of coral atolls is entirely of a strand character, 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 saline influence, both in spray blowing in from the ocean and in 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 toward 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 toward 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 will be 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 will be discussed separately (p. 31).

Normal strand vegetation exists on such portions of the coastline of all the high islands that are not occupied by mangrove swamps; even on some of the mangrove coasts there is a line of beach either outside or inside of the mangroves that is occupied by strand vegetation. The strand around high islands may be volcanic or coral sand or gravel beach, coral rocks or bluffs, or volcanic rocks or bluffs.

The vegetation of the strand will be discussed under four headings, followed by a concluding statement discussing strand vegetation types as indicators.

## 1. Vegetation of the beaches of high islands.

Beaches, and sand flats or small dunes immediately back of them, present even more rigorous conditions than other strand situations, because they are made up of loose, shifting sands. Rather few plants have developed adaptations to cope successfully with this factor, especially because 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 developed means of readily crossing large stretches of sea, either by floating or by sticking to birds' feet or feathers. 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 practically to high tide mark in places, is the beach morning-glory (*Ipomoea pes-caprae*\*). It is found throughout the tropics, wherever a beach vegetation develops, and is, in many places, 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.

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\* The Micronesian plant is *I. pes-caprae* subsp. *brasilienses* (L.) van Ooststroom, sometimes regarded as a species distinct from the Indian Ocean *I. pes-caprae*.

Because corals, calcareous algae, foraminifers, and mollusks live in such abundance in tropical waters, most beaches are of calcareous 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 usually principally 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 forest of Messerschmidia argentea, Hernandia sonora, Pandanus tectorius, Thespesia populnea, and Pisonia grandis, sometimes Calophyllum inophyllum, Casuarina equisetifolia, and Guetarda speciosa. The most important strand forest, the coconut plantation, will be described below in the section on atolls. 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 which 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 they can stand complete washings with storm waters). Such 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 (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, to be described next.

## 2. Vegetation of the 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, and Kusaie, and rocky headlands on Babelthup and Arakabesan (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 and will be described later.

Limestone rock strand is much more common in Micronesia than volcanic strands, 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 miscalled 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 (Figure 6), 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 or raised coral limestone, to be described later in this paper.

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. Hernandia trees and others were completely stripped of leaves and the young growth killed back. Areas of young Casuarina on sand flats were either 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 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. 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 rough idea of 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" which 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 those which never reach a large size but form food for the larger fish.

### 3. Vegetation of coral atolls and low islands (Figure 7-9).

By far the most important areas of strand vegetation are on the atolls and other low coral islands. These are bodies of level

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, foraminifers, 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. Commonly 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 back of it are sand; in the interior this develops a higher humus content, proportional to the rainfall, often with marshy spots, artificial depressions filled with muck for taro growing, or brackish ponds, sometimes rock bottomed; then as the outer beach is approached the material becomes coarser and more gravelly until 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 surfline and reef flat, which is a wave-cut platform a few to many meters wide 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 entirely of gravel or broken rock.

The vegetation varies in relation to the substratum and the history of human occupation. In many places, the original vegetation 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 to locate any small undisturbed fragments of vegetation and piece together information from them. Here, only a description of present conditions may be given, 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, or coconuts and breadfruit. Thus, the basic vegetation is a planted forest of Cocos nucifera (Figures 14, 15a) with usually a large admixture of Artocarpus altilis and some other trees. The coconut plantation extends to the inner beach, with a scattering of wild trees, such as Calophyllum inophyllum, Hernandia sonora, Pemphis acidula, Cordia subcordata, and Messerschmidia argentea, and some 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 (Figure 9b), Vigna marina, etc. form a dense ground cover. Commonly a sparse growth of Lepturus (Figure 15a), Ipomoea pes-caprae, Triumfetta procumbens, Thuarea, Fimbristylis cymosa, Cassytha filiformis, and weeds cover 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 Nonwin, 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, of small individuals of the second story trees plus Wedelia biflora, Polypodium scolopendria, Nephrolepis, Asplenium nidus, Tacca leontopetaloides; in the Carolines Piper is also found except in the most shaded parts of this forest. Controlling this undergrowth, particularly where it is made up of Wedelia (Figure 9b), and Premna, is one of the major problems of the native agriculturist.

In some places, especially on the wider islets, there are grassy openings with Thuarea, Paspalum conjugatum, Digitaria, Lepturus, etc. and marshes with Cyperus javanicus, Jussiaea, etc. 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, with Morinda, Messerschmidia, Soulamea amara, Pipturus argenteus, Terminalia samoensis, Pandanus, Cordia, Pisonia grandis, Guettarda, etc. 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 (Figures 7a, 8b) 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, sometimes covering whole islets. Scaevola is the most important constituent of this vegetation, with Pisonia assuming dominance toward 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, Cassipoua filiformis, Triumfetta procumbens, Ipomoea pes-caprae, and in the northern Marshalls at least, Boerhavia diffusa form a thin ground cover.

On sand spits, narrow end of islets, and other places more than usually exposed to salt spray, is a lower brushy vegetation of Scaevola sericea (Figure 7b), Suriana maritima, Euphorbia chamissonis, small plants of Messerschmidia and Pipturus, etc., 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 may be found in places, forming a dense fine-textured growth up to 6 meters tall. The tree trunks may be up to 25 centimeters 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 few as 10 years and may reach 5 meters 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 sand drifting 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 includes the great majority of atolls 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 exists here and there, especially in the northern Marshalls. It has largely been replaced by coconuts. Usually it is a mixed forest (Figure 9b), 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 species may be lacking, and the forest is quite varied 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 (Figure 9a) and Ochrosia oppositifolia. From old records as well as from modern indications it appears that pure forests of Pisonia 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 general rigorous nature of the salty atoll environment, as well as with the very small total number of plant species available.

In general, the pattern of vegetation on an atoll seems largely correlated 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 would suggest 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 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, Paspalum conjugatum, Eragrostis amabilis, Fleurya ruderalis, Portulaca oleracea, P. samoensis, Phyllanthus, various Euphorbia species, Centella asiatica, Hedyotis biflora, Eclipta alba, Vernonia cinerea, etc.

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 practically every atoll, even the 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 atolls. 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, sugarcane, 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 (Figure 8a) in many varieties is everywhere. 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 for something.

Certain islets were seriously denuded during the war, either by fighting or for other reasons, but early concern about the revegetation of these areas has proven 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, etc., tangled with Ipomoea tuba, Canavalia, etc. has promptly reestablished itself. In compacted areas pure stands of Ipomoea pes-caprae, Vigna marina, or Fimbrisylis 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 deep, of Wedelia biflora (Figure 9b). The factors influencing or causing the differences in these successions are not clear and the eventual course of these successions is not known. This problem deserves much more study.

#### 4. 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.

#### 5. Strand vegetation types as indicators.

Strand vegetation, in general of course, indicates salinity. Places along the seashore displaying any 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 especial 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 is 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 with easy trafficability. Taro patches indicate soft mud, though it 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 this is difficult because of the hardness of the wood. Beach forest of Pisonia, Hernandia, Casuarina, etc. usually has little undergrowth, and is easily traversed.

C. Vegetation of Raised Coral Limestone (Figures 10-13).

1. Primary vegetation.

One of the most important and extensive vegetation types in Micronesia is the forest found on limestone which 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 safely 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" (Figure 13b). 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 certain areas of comparatively level terrace. All except the last of these are easily understood. The last may be the result of internal drainage or some such cause. In many places a similar surface produced by different causes often exists on talus slopes and debris cones at the bases of cliffs. The distribution of these two surface types has been the determining factor in the pattern of present day vegetation and agricultural land. 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 does not have any obvious effect on the natural vegetation pattern. However, mining of

the phosphate rock for fertilizer destroys utterly the original forest and is followed eventually by 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 nonphosphatized 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 further along 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. 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 island or groups of islands. The highly developed forest on comparatively level land with some soil has mostly been 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, Aglaia, Fagraea, Pipturus, Cycas, Claoxylon, Boerlagiodendron, Laportea, Eugenia, Premna, Guamia, Hernandia, Pouteria, Erythrina, Randia, Melanolepis, Cynometra, Samecarpus, Meruta, Pongamia, Dracaena, etc. The undergrowth is of many genera, prominent among which are Psychotria, Clerodendrum, Morinda, Taranna, Polyscias, Maesa, Ficus, Eugenia, etc. The whole may be tangled with such vines as Canavalia, Mucuna, Opreculina, Caesalpinia, Gymnosporium, Freycinetia,

Schefflera, etc. Naturally, no single stand of this vegetation will have all of 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 (Figures 10, 13), while in the Marianas it is largely on level terraces (Figures 12, 13a) and cliffs. Also, in Palau, a characteristic feature is the abundance of tall, very slender palms, especially on the ridges. In Palau, also, many more species enter into the composition.

Epiphytes, especially ferns, are common in these forests, and in the wetter aspects of them, are abundant. Asplenium nidus, Polypodium scolopendria, Davallia solida, and Nephrolepis acutifolia are common, both epiphytic and terrestrial, 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 is particularly noticeable in Palau and Guam.

On bluffs and seaward slopes the forest is likely to be more brushy, with several additional genera, such as Ochrocarpus, Barringtonia, Cordia, Casuarina, etc. Some of the inland genera, as Artocarpus, Elaeocarpus, Boerlagiodendron, etc. 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, commonly 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, Pomphis, Myoporum, etc. In places of extreme exposure this scrub becomes prostrate or gives way to a herbaceous ground cover of Zoysia, Heliotropium anomalum, Hedyotis albido-punctata, Evolvulus alsinoides, etc.

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 limeberry (Triphasia), a viciously thorny shrub that is the scourge of travellers wherever it occurs, has, in many places, been able to invade the forest and form an impenetrable undergrowth. Among the trees which drop their leaves, at least facultatively, during dry seasons, are species of Ficus,

Erythrina, Laportea, Hernandia, Pisonia, etc. Because of the time at which these observations were made, it is not altogether certain that a certain proportion of the effects described are not due to the typhoon of November, 1949.

## 2. Secondary vegetation.

Disturbance and clearing bring out great differences between the rough and smooth types of substratum mentioned above. On all of 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 construction of military installations. On Guam large areas of the smooth type are in coconut plantations. In addition to this, there are other extensive areas now covered with almost pure stands of Pandanus tectorius (P. fragrans Gaud.) which are regarded as resulting from 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, practically all of the soil has been cleared off the limestone surface. On these places, very extensive 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 centimeters deep. 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 (Figure 12) which grow in great luxuriance. Among these are Cassia occidentalis, Malvastrum coroman-delianum, Sida, Crotalaria mucronata, Asclepias curassavica, Euphorbia heterophylla, E. hirta, E. hypericifolia, E. prostrata, E. thymifolia, Phyllanthus amarus, Cleome viscosa, Portulaca oleracea, Mitracarpum hirtum, Borreria laevis, Blechnum brownei, Sesbania sesban, Amaranthus spinosus, A. viridis, Emilia, Vermonia cinerea, Bidens pilosa, and a number of weedy grasses such as Eragrostis amabilis, E. pilosa, Eleusine indica, Cenchrus echinatus, Chloris inflata, C. radiata, etc. Later brushy patches appear with Melochia, Leucaena glauca, Morinda citrifolia, Carica papaya, Triphasia trifolia, etc., 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 appear, made up of Macaranga, Pipturus argenteus, Hibiscus tiliaceus, Casuarina, Abroma, Pithecellobium dulce, Pandanus, often with a dense undergrowth of shrubs such as Triphasia, Morinda, Melochia, etc. On Saipan, and to some extent other islands, Acacia confusa and Albizia lebbek form solid stands, either singly or together and quickly take over sizable areas. Casuarina equisetifolia also does this, 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-leafed vines. In the areas on Angaur and Peliliu 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 tall. In 1950, these same stands were from 10 to 15 meters tall, and still very dense.

### 3. As an indicator of environmental features.

As with the previously discussed types of vegetation, study of this type as an indicator of environment yields considerable information.

It can be taken as certain that there will be no surface supply of fresh water available on the limestone substratum of this vegetation type. 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 of the rain that falls on an area percolates into the ground to augment the lens-shaped body of ground water, none being lost by runoff. This porosity, however, also makes it necessary to be extremely careful to avoid pollution. Drainage from garbage disposal, sewage, waste oil, leakage from oil or gasoline storage, etc. are all certain to drain directly downward into the body of fresh water, and such pollution, once accomplished, is practically permanent. Foreknowledge of this characteristic can make it possible to avoid such mistakes.

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 U. S. forces in Micronesia, and a considerable number in Okinawa (Colwell, 1946) were built on this sort of substratum. Coral rubble for surfacing roads, air strips, etc. will also certainly be 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, because 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 need to 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 canopy of monsoon forest is important.

The effect of a limestone substratum on trafficability and equipment 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 in attempting it, or in attempting to clear 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.

Concealment in this type of forest is complete, except in the drier aspects of it, termed monsoon forest, where during the dry season there will be very poor shelter, though camouflage is not difficult.

In areas where Pandanus (Figure 12b) is common, mosquitoes of the genus Aedes may be very troublesome. In spite of the lack of standing water, they can breed in abundance in the water collected in the bases of the Pandanus leaves.

#### D. Vegetation of Rough Lava Flows (Figure 35).

In the northern Marianas are some fresh rough lava flows, usually originating somewhere on the sides of the volcanic cones and spreading fanwise to the coast, in many places making extensive, gently

sloping plains stretching down to the sea where they protrude as peninsulas. Practically always they end in low cliffs. Their surface is commonly 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 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 largely made up of Pipturus, Ficus, Melanolepis, Randia, Aglaia, Pandanus, Hibiscus tiliaceus, Morinda citrifolia, Psychotria mariana, with some Trema, Elaeocarpus, Guamia, Pouteria, Premna, etc., the last five especially toward 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 head 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 mentioned are all among those found on limestone in the southern Marianas, and the aspect of the vegetation is practically identical with that on limestone.

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

Much of this forest has been cleared and planted to coconuts (Figures 32-34), especially where soil has accumulated on the lava.

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.

#### E. Casuarina forest (Figures 10b, 30, 31)

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. 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 competition. Trees of all ages are very susceptible to fire. Casuarina is one of the most successful 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 this is owing 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, and cover is excellent in thick stands. Considered in relation to particular topographic features, there is little doubt that significant and useful correlations could be worked out.

#### F. Coconut plantations (Figures 14, 15).

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 lands, from level 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, cordlike roots 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 practically wiped out of Rota, Tinian, and Saipan by the attacks of a weevil (Brontispa). This weevil is now controlled by an introduced parasite, and coconut may be expected to reappear in those areas. In the Palaus, a rhinoceros beetle (Oryctes) has done great damage to coconuts, practically 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 indicated by coconut plantation. It is usually traversable, open, giving partial cover, 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 place. Food and potable drinking water, logs for temporary construction, and leaves for thatch are available wherever there are coconuts.

## G. Vegetation of Coastal Plains (Figures 16-19)

### 1. Geography.

In Micronesia the coastal plain is a strip, usually quite narrow, of level land back of the strand and back of 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. The substratum may be coral sand or rubble, or volcanic soil and debris from the slopes above and is often quite high in humus 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, Babelthuap, 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 is found on Yap, because the mangrove swamps commonly come right 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 calcareous, 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. When the land is too high for mangrove swamps, a coastal plain results. Also included here as coastal plain are lower areas where the water is fresh or almost so, with consequent distinction from mangrove vegetation.

### 2. Vegetation.

Probably the original vegetation on this level land was mostly tall primary rain forest, such as will be described in the next section. Some of this, not much modified, still exists on Babelthuap, and perhaps a little on Ponape. Most of the land of the coastal strip has, however, been cleared and occupied by human populations for so long as to have an entirely different character, showing little or nothing of what the original forest looked like.

The coastal plain is the area that is most favored as a place to live by the native populations of the high islands. The result is that it is mostly under cultivation. It may be roughly divided into two types or patterns of vegetation, depending on whether the

substratum is relatively dry firm ground, or marsh and swamp.

The dry ground (Figure 16), where the villages are situated, is largely dominated by coconut and breadfruit plantings, which are the most important agricultural crops. Terminalia, Calophyllum, Ficus, Casuarina, mango, and other large trees are common, also in the Carolines, Parinari glaberrimum. 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, Alocasia, bananas, 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 reed, Phragmites karka, (Figure 19) or with dense patches of Scleria (Figure 18b), Scirpus, Paspalum, Panicum Saccharum (Figure 18a), or other sedges and grasses. On Saipan, Guam, and Truk are large areas of pure stands of Phragmites, a cane-like grass 2 to 3 meters tall. Scattered in these brakes may be some Pandanus trees. Cyrtosperma and Colocasia are extensively cultivated in marshy places (Figure 17), 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. Metroxylon amicarum groves occur in swampy places on Truk.

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

### 3. Environment.

On the dryer parts, conditions of penetrability, substratum, etc. are such as might be expected from a mixture of habitations, cultivation, tree agriculture, and thicket. Concealment is good, and 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 cane is so dense as to require constant cutting and pushing aside, and the effort will wear a man out in a short time especially in hot weather, when the windless atmosphere is damp and steamy. Mosquitoes are abundant. Concealment is good for single men or small parties, but the disturbance made by a large party is conspicuous. It is impossible to see more than a yard or two ahead.

#### H. Lower Primary Forest.

##### 1. Vegetation.

There seems little doubt that the coastal plain and the slopes up to about 300 meters altitude of 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 wet coast of Babelthuap and the north coast of Arakabesan (Ngarakabesang) in the Palaus, on the tops of some of the mountains in Truk, and on the slopes of Kusaie are areas of various 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 Babelthuap, a spectacular type of jungle is to be seen, similar to the imaginative jungle pictures often seen in books. Large-leaved 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 on 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 down 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 constant aid of a machete.

As with most primary tropical forests, the composition of this type is exceedingly varied, especially so in Palau. The trees are so large as to necessitate cutting or climbing to secure any material, both of which processes are laborious and time-consuming. Consequently, only a suggestion of the great number of genera represented may be

given here. Parinari, Camposperma, 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 Ipomoea species form tangles around the edges and in the canopy.

This vegetation is one of the two 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, a great amount of 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 if this forest and that on the raised limestone on the north end of Guam were managed properly they would be capable of supplying the lumber needs of Micronesia. For this reason it is imperative that no more of them 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 forest, as has been done in so many parts of the world. Proper utilization for lumber is also entirely consistent with watershed protection, except perhaps on very steep slopes.

## 2. Environment.

This type of forest indicates slopes of volcanic soil, often well weathered, largely clay in nature. There are usually streams of fresh water. Wherever the canopy has not been destroyed, the lack of undergrowth makes traverse easy, except for fallen trees and some thorny vines. 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, and cover is perfect. The ground underfoot may be very slippery because of the clay present. Semecarpus is a tree in this forest that causes severe contact dermatitis in some people. The sap or latex is especially dangerous.

### I. Secondary Forest on Slopes (Figure 21).

#### 1. 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 meter altitude. Above this, 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 well suited to such terrain. This is mixed planted forest of coconuts and breadfruit (Figure 21a). From a distance this looks like natural forest rather than like planting. Spacing and arrangement are not at all regular, but more suited to the terrain. Bananas, citrus, papayas, dryland, 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 sometimes Cyrtosperma. In general the ravines seem to be planted more completely to breadfruit while the ridges are given over more to coconuts. The slopes between the two average about equal proportions. In Ponape and Palau there are some slopes planted to pure stands of coconuts.

On some of these slopes are thickets of native shrubs and trees (Figures 20, 22a). 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, etc. If not burned over 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 Canvalia, Ipomoea, Merremia, Cayratia, etc.

On Ponape and Kusaie most of the slopes of secondary vegetation, except those under active cultivation, have been taken over by stands of one species, Hibiscus tiliaceus (Figure 27b). This, in many places forms an impenetrable tangle, so dense as to exclude most other plants. These plants are scarcely to be considered trees. They are coarse, extensive tangled shrub-like plants with springy trunks and branches as much as 10 centimeters or more thick, rather low, presenting an unbroken surface of large dark green leaves to the light. This vegetation type 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 repeatedly that the forest has been replaced by coarse grassland, a type which will be discussed below. However, thickets and tangled forests of Macaranga, Glochidion, Parinari, Pandanus, Dracaena, Symplocos, etc. are common enough. Leucaena glauca (Figure 23b) also, in certain localities, forms dense pure stands, tolerating 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 cathecu, the betel palm. This forest is quite varied in composition. In many places it includes coconut palms and even bamboo clumps. It may be much overgrown by vines and commonly has a spiny undergrowth of Triphasia. It is termed "ravine forest" from its common occurrence in ravines and on steep slopes (Figure 48b).

## 2. Environment.

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, because the undergrowth is shaded out, and becomes similar in its environmental aspects to primary forest in the same locations.

## J. Montane Rain Forest and Cloud Forest .

### 1. Characteristics.

Botanically, perhaps the most interesting type of vegetation on tropical islands or tropical mountains is the scrubby, wet, dripping, 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 a few level places, the trees have a low bushy growth habit, in many places with bare branched trunks, and broomlike tufted tops. On the crests they are even more gnarled and dwarfed. Moss 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 every step with a machete when traversing this forest.

There is no definite correlation with altitude in the distribution of the cloud forest. It may be found above 500 meters in one island, down almost to sea level in 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, may be recognized. In the Andes a great belt of forest of these types extends from about 1000 to 3500 meters elevation. The determining factors seem to be mainly rugged topography and a cloudy climate with almost continuous rain. In Micronesia these conditions are met only on Ponape and Kusaie and two belts can scarcely be distinguished.

Although cloud forest is a definite forest type found in the tropics wherever the conditions are right, 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.

Relatively little is known about this interesting part of the vegetation in Micronesia, because of the comparative paucity in economic species and the fact that in Micronesia, this forest is uninhabited. Consequently the information available as to the local diversity in physiognomy and the actual floral composition is meager. Prominent genera of trees are Macaranga, Alseodaphne, Alseodaphne, Astronidium, Clinostigma, Cyathea, Claoxylon, Eurya, Alseodaphne, 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 true home of the 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 amount 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. This is so much more important than any other economic factor in an island that it is unthinkable for this area to be used as anything else than watershed.

The native population 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. It should be discouraged. Hunting or any other means of reducing populations of wild hogs, deer, cattle, or other introduced large animal that happens to gain a foothold should be given every sort of encouragement. This type of forest, at least on islands, is rapidly broken down by trampling, rooting, or browsing of large animals, as it originated in the absence of such, and the component trees are not able to withstand these disturbances.

## 2. Environment.

The cloud forest indicates a continuous humidity of almost saturation, a very high rainfall, little sunlight, cool temperatures and often high winds. The slopes are steep, ridges narrow, footing insecure and slippery, and undergrowth is so dense as to be a continuous obstruction. On the ridges the vegetation may be dwarfed and scrublike, and practically impossible even to cut one's way through. The leaves and moss cushions are likely to be so wet as to saturate clothing in a few moments. Water supply is usually no problem,

but campsites are sometimes very hard to find and water-proof camping equipment is essential. Dry wood is scarce. Trails in this type of forest become canals of mud after very little use.

#### K. Dwarf Vegetation on Open Crests.

On summits or high slopes of many tropical mountains appears a vegetation characterized by its dwarf stature and dense, wet tussocky nature. This, as is the cloud forest, is dependent on high rain-fall, but with the additional factor of high winds and extreme exposure. The paramos of the Andes and the "open bogs" of the Hawaiian Islands are good examples.

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 found great numbers of very restricted endemic species. The plants found are commonly dwarfed specimens of the components of the forests below with a liberal admixture of others characteristic of such exposed areas.

If this type were not of such extreme scientific interest, it would be scarcely worth mentioning in a report on Micronesia, as it only occurs on the summits of a few peaks on Kusaie and Ponape. On these peaks the dwarf vegetation is mainly of ferns--Nephrolepis, Gleichenia, Davallia, Lycopodium, etc., with great banks of mosses and liverworts. A few trees of Elaeocarpus have gained a foothold, 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.

#### L. "Savanna" or Grassland Vegetation

(Figures 24-27, 30-31, 32, 34, 45b, 46-49, 53a).

##### 1. 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, where Safford has called them "savannas" (although they are not level, nor do they always have scattered trees, as the word suggests), and where 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 peculiar 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, various other small grasses, many sedges, principally species of Fimbristylis, Scleria and Rhynchospora, Geniostoma, Eurya, Melastoma malabathricum, Pandanus, Gleichenia linearis, Lycopodium cernuum, Cheilanthes tenuifolium, Lygodium scandens, Blechnum orientale, Myrtella benningseniana, 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, 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, (Figure 49b) though it is normally a good indicator of volcanic soil. In these spots, swordgrass 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 many 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 varied in aspect, because of the varied dominance of several of its principal components, and the varied composition from island to island. In its most extensive form it is dominated by swordgrass (Miscanthus floridulus) (Figures 24, 46a, 47b) 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 (Figure 48a). Scattered bushes occur, and often seedlings and small trees of ironwood, Casuarina equisetifolia (Figures 46a, 47a, 48a). 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 tall. 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, as they had other things to do during their short administration there. 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, observing almost fifty years ago, 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 (Figure 26), and Pandanus (Figure 25b). In others there are mixed grasses and Pandanus, and in still others, almost solid stands of Gleichenia (Figure 27). It is interesting to note that, whereas Miscanthus dominates large areas in the Marianas, in the Carolines it has been found only on Ponape, though there are apparently plenty of suitable habitats for it on the other islands. Saccharum spontaneum (Figure 18a) has been occasionally mistaken for Miscanthus.

## 2. Origin and development.

There seems little doubt that the Micronesian islands were, before the advent of man, almost entirely forested except, perhaps, the fresh volcanic slopes of the northern Marianas. The forest types have been summarized 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 manmade 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 are 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 exceedingly 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 get started where they never could have in the original forest. In the absence of fire, the normal succession would soon lead, in a naturally forested region, to typical secondary forest. However, if the area is burned over this succession is altered. Some plants, particularly tree seedlings, are killed out. 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 will be gradually crowded out by the normal secondary flora. However, if fires continue, those plants which are more capable of surviving it, having deep-seated rhizomes, or other persistent parts, will tend to become more and more dominant. The forest succession is further retarded and the association of pioneer species is encouraged by 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 same problem from a slightly different viewpoint with emphasis on similar vegetation in the vicinity of Manila, Philippines. His conclusion is that grassland in these parts 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 swordgrass and encourage better forage species. There is, of course, no better way to perpetuate swordgrass. On Saipan less than a year after a forest fire had burned off a forest of Acacia, killing every tree, swordgrass, which had existed in poor condition under this forest, had produced a solid stand up to 2 meters tall.

On practically every island in the Carolines and southern Marianas on which savanna vegetation of any sort is encountered it is possible to 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, there are small open areas, dominated by Gleichenia linearis, where there are found some of the plants characterizing savanna elsewhere. Here the natives said that there were frequent fires, set, in this case, just for amusement. Glassman ( conversation 1950 ) said that he saw an area of Gleichenia on Ponape, well up in the rain forest, which had been burned several weeks previously. This is by no means unlikely, as herbaceous vegetation in well drained situations, even in wet climatic areas, dries out rather quickly during a series of 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 schist. 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.

It is interesting that, in the northern Marianas, extensive areas of swordgrass savanna lie on slopes of unconsolidated ash and cinders (Figures 30-32), where there does not seem to be evidences of recent burning. On steeper slopes, primarily of lava, Casuarina is one of earliest invaders (Figure 31), and forests are formed, but there is little evidence even that Casuarina commonly invades the main ash slopes of these volcanic cones. There seems to be a striking correlation between grassland and slopes that are more or less at the angle of rest 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 swordgrass type of vegetation.

Dr. 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 (Figures 26, 27). 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 Witipon Hill (Figure 20b), where there is a significant amount of bauxite in the residual soil. If an area of bauxite could be protected from fire for some years, the questions of whether this material could support forest might be settled.

One of the interesting problems connected with this type of vegetation is that of the origin of its flora. Many of the species are scattered through the Indo-Pacific region. Some of these might have followed man in his early migrations, or might 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, Ischaemum longisetum, Dimeria chloridiformis, Hedyotis tomentosa, Hedyotis korrensis, Geniostoma micranthum, etc. 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 in the condition of the bare northern Marianas at present, 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 these 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 flammable. There is also the fact that many of the limestone areas are so rough that they are seldom cleared; this applies to some of the driest of them. It is certainly a fact that the secondary growth on limestone, as on Peliliu, Angaur, and on the low islands, very rapidly produces a dense and complete cover. On Truk, Ponape, and Kusaie, where, even on volcanic soil, the revegetation is rapid and the results are very dense, areas of savanna are small or almost absent.

A comparison of the pH 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, whereas soil on volcanic material is usually pH 6 or below, more commonly around pH 5, or even lower especially when the top soil has been eroded away. This may very well be the answer - if savanna plants cannot stand the high alkalinity or cannot stand 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 cut down 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 any great success. Fire will destroy deliberately planted tree seedlings just as readily as those planted by natural agencies. Since 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, and 1954, however, show that in spite of laws against burning, fires are becoming again of frequent occurrence.

### 3. Variations.

In the ravine bottoms in savanna areas, there usually develops a certain amount of thicket or gallery forest (Figure 48b), 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 damage to assure that the forests will commonly be secondary in nature.

If the ravines are shallow and quite wet, the vegetation may be a dense stand of reeds (Phragmites karka) (Figure 53a), which stand out as a somewhat greener band against the brownish or grayish-yellow-green of the swordgrass. The reed stands may commonly be tall enough to be almost level with the swordgrass on higher land, concealing the ravine from view except for the difference in color.

### 4. Environmental significance of "Savanna".

This readily identifiable type of vegetation practically always indicates a volcanic substratum. Excepting in the northern Marianas, this substratum is a weathered volcanic material; the slopes are generally less steep than on limestone; there are few extensive level areas; surface drainage is usual because of 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.

Concealment is very poor on any variation of this type, but is available to some extent to men on foot in the swordgrass phase. Swordgrass, however, is almost completely impenetrable 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 ridgecrests is, however, commonly 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, Hedvotis, etc. is usually sparser and much more low growing, and offers little obstacle to traverse; also it offers no concealment.

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

#### PART IV. VEGETATION OF THE MARIANA ISLANDS

The Mariana 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 144°35' E. and 146°4' E. The regional climate is a tropical one; temperatures show relatively little seasonal variation, with monthly averages between 24° C. and 27° C., and extremes of 18° C. and 35° C.; precipitation between 2,000 and 2,500 mm., decreasing somewhat northward, is strongly seasonal with rainy season 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 and some of them are very destructive. Their effect on the vegetation is hard to estimate but must be considerable. 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 not totalling more than 500 species.

A number of sketches of the vegetation of the Marianas have been published beginning with that of Gaudichaud (1826) and including those of Marche (1891), Prowazek (1913), Kanehira (1934), Hosokawa (1934), U. S. Geological Survey (1944), and Gressitt (1954), as well as descriptions of a number of individual islands, notably Guam, by various authors. Most of these are superficial or highly generalized. This reflects a paucity of reliable information. With the exception of Safford (1905) the writers only made 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 Mariana archipelago may be divided 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, whereas 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 amounts of forest. That of the southern islands is predominantly forest with some grassland, the greater part of this of secondary origin resulting from human activity.

Man has been a factor influencing the vegetation of the Marianas, especially the southern Marianas, for at least 3,500 years. Alexander Spoehr (1955) reports a radiocarbon date indicating about that age for archeological remains found on Saipan and allows 4,000 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. Their profound effect on the vegetation cannot be doubted, considering the abundance of archeological remains and the plantings of bamboo, coconuts, and other economic plants in remote inland localities far from present-day habitations. Very little, however, 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 will be treated in such detail as is feasible with present knowledge in the descriptions of individual islands. Their general nature may be summarized.

On old volcanic soils clearing and burning of forest has 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 has 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 shallow soils and the deep red soil on hard limestone the forest has generally persisted, except where cleared for military installations or for 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 has rapidly grown to a tangled second growth where left alone. In many areas such introduced woody species as Triphasia trifolia, Jatropha gossypifolia, Pithecellobium dulce, Muntingia calabura, Nipa fruticans, Cananga odorata, and especially Leucaena glauca, have largely occupied certain habitats, changing the aspect of the vegetation conspicuously. Many of these plants were introduced very early during the Spanish occupation. Some are principally confined 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 which is similar in aspect and even to some extent in composition to that on rough limestone in the southern Marianas. This 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.

#### A. The Northern Marianas - General.

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 vegetation survey 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 have been examined on short visits by the writer in 1950. Some information has been gleaned from photographs taken in 1945, loaned by A. H. Banner, and some of a very general character from aerial kodachromes made by J. I. Tracey, Jr., David B. Doan, and S. L. Schlanger, and from photo-mosaics lithographed by the 64th Engineer Battalion, USAFFE.

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 are covered by coconut plantations. Recent volcanic material, if loose and fine grained, is gradually colonized by grasses and grasslike 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.

##### 1. Individual Northern Islands.

Nine islands are discussed in order from north to south.

a. Farallon de Pájaros Uracas (Figure 28) -- Neither field data nor published information are available on the vegetation of this active volcano except for a brief account by Fritz (1902, p. 116). One species of sedge, Fimbristylis urakasiana Kuk., has been described from it. Excellent aerial kodachrome photos taken in 1952 by the members of the Guam Party of the U. S. Geological Survey suggest that the greater part of the island is covered by fresh volcanic material, lava and ash, which apparently supports no macroscopic vegetation whatever.

Two lighter colored rocks of older material protrude from this (Figure 28), and show a thin grassy vegetation, possibly Miscanthus floridulus. No woody plants can be discerned. These facts accord with the observations of Fritz who speaks of 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 modern photos.

b. Maug Islands -- These are 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 any collections. Fritz wrote a brief account, republished by Prowazek. Notes have been taken, also, from photos taken in 1954 loaned 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, has some trees, including coconuts, Terminalia, Pandanus, Boehmeria, Hernandia, and fago (Ochrosia, according to Safford and modern Guamanians, but Prowazek 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 U. S. Hydrographic Office Sailing Directions 1:337, 1952, report that higher slopes of East Island are covered with trees. Modern air photos show patches of forest on the higher slopes and dense scrub below the grassy slopes along the shore and running up ravines.

c. Asuncion (Assongsong) -- This island is a steep volcanic cone still showing occasional signs of activity. Here again there is a dearth of information. Beechey (1831, p. 438) writes, "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.

Judging from the photos, 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 forest and coconut plantations, the forest covering these slopes irregularly over half way to the top.

Woody vegetation runs farther up the ravines. Cocos, Carica, Morinda, and Musa are identifiable from the photos, while Prowazek adds Terminalia, Pandanus, Hibiscus, and breadfruit 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, even though according to Safford (1905, p. 216) the natives at least of Guam, do not care much for its fruit.

d. Agrihan (Agrigan) -- This island is a recently active (1917) volcanic cone 965 meters high, largely composed of beds of loose ash with some interbedded basaltic flows. Its flora is reasonably well known through the collections of Kanehira, Hosokawa, and myself, 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, since he records the altitude of the central peak as only 750 meters (Fritz 1902). His brief characterization of the vegetation, however, is not discrepant from the account below, summarized from personal observations and notes published by Kanehira and Hosokawa.

The vegetation, though locally complex, is separable into two main provinces. The steep ash slopes covering the greater part of the island are clothed with dense swordgrass (Miscanthus) and cut by ravines which are wooded well up toward 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 (Plate 27a) where the terrain is too steep or rough to plant 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 making allowances for the effects of the extremely rapid drainage through the coarse volcanic ash. Epiphytes are not common on the trees and leaf epiphytes are absent altogether. The increasing abundance of ferns which is found toward the upper parts of the wooded ravines shows that the humidity, at least, is greater there. This may well be because of the cloud cap which often covers the upper part of the mountain. Surface water seems to be absent except during rainy weather when apparently there is some runoff in the ravine bottoms.

c. Pagan (Figures 29b, 30, 31) -- Pagan 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 northern one of these, Mt. Pagan, 570 meters high, has been recently active and minor activity such as warm springs and emissions of steam and hot gases may 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 small 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 catalog of the vascular flora has been prepared on the basis of these (Fosberg, 1958). A small fossil flora has also been found and is reported on by Fosberg and Corwin (1958). The geology was thoroughly studied in 1954 by Corwin, Bonham, Terman, and Veale in an extensive report (U. S. Geological Survey, 1957). Notes on the vegetation were made in connection with the geological study by Bonham. Brief notes were published on the vegetation by Marche, Fritz, Kanehira, Hosokawa, and Fosberg. From these sources the following summary has been written.

The present-day vegetation of Pagan gives a general impression of semiaridity; 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 (Inner lake), thickets of broad-leaved trees are luxuriant enough, 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, extending up its lower slopes in places and on steep slopes on the west shore of the isthmus, as well as choking numerous ravines throughout the island. There has been no investigation 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 parkland 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 largely vegetated by an almost pure stand of swordgrass, Miscanthus floridulus (Figure 30). This forms a coarse, harsh, brake-like grassland, the grass 1 to 3 meters tall and in places very dense. On the steepest slopes and above 250 meters elevation

this grass tends to be shorter and the clumps more widely spaced. Above 450 meters it is sparse to absent.

Lava flows may be practically bare (Figure 31), 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. 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 lava 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 with scattered trees or clumps of trees. The trees may be Pandanus, Casuarina, or any of a number of broad-leaved 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. On the gently sloping northwest part of the island is a large coconut plantation (Figure 31). 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 swordgrass has been burned over large areas, but this does not seem to be much of a deterrent to Miscanthus itself. After burning in 1954 the grass in favorable places grew to waist-high 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, have 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 are being gradually reoccupied at present. The coconut plantations were not changed except to be choked with weeds and young coconut seedlings.

f. Alamagan (Figures 32-35) -- This island is a dormant volcano in many respects similar to Agrihan. Plant collections and notes on the vegetation have been made to about the same extent and by the same people as those on Agrihan. 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 Agrihan, surface water is absent except during rainy weather.

The dominant vegetational feature, as on the other northern Marianas, is the swordgrass on the ash slopes (Figure 32). These slopes are cut, well toward the top, by deep ravines which are densely wooded with mixed broad leafed forest made up of many species. The upper middle slopes have a sparse scattering of woody vegetation, which Kanehira describes as a continuous stand of tree ferns, branched at the base, the bases not less than 1 meter in diameter. This tree fern is a species of Cyathea not found elsewhere. The uppermost slopes are thickly covered by swordgrass. 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 (Figures 33-34). In places however, they are exceedingly rough and covered by a type of forest resembling that on the rough limestone in the southern Marianas (Figure 35). The forests are made up of Ficus prolixa, F. tinctoria, Pipturus, Pouteria, Hibiscus tiliaceus, Elaeocarpus ioga, Melanolepis, Premna, Morinda citrifolia, Guamia, Psychotria mariana, Trema orientalis var. argentea, Randia cochinchinensis, and other tree species. Undergrowth is generally very sparse, the two most important components being the ferns Polypodium scolopendria and Asplenium nidus. Toward 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 only seen 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 Agrihan, where conditions of substratum are similar.

g. 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 fifty 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 photos the interior is largely covered by barren black lava, with some grass visible near the edges.

h. Sarigan -- This is a dormant or extinct volcano, conical in shape and just over 550 meters high. 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 thickets also run 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 treeferns.

i. 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.

## B. The Southern Marianas: General.

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 as well.

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 varied 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 plantation, 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, land surface has possibly been continuously available since 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 Aguija (Aguiguan) and Farallon de Medinilla; topographically they are generally sharply dissected and characterized by abundant surface drainage and complicated drainage patterns. Remnants of gentler 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 surfaces, characterized by knobs and sinks, which have generally been worn down to a rounded but very complicated topography of rather low relief. There are locally great thicknesses of soil and in the filled sinkholes, marshy places. Finally there are areas of limesand forming flat low terraces near the coasts, in places mixed 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 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 largely been planted 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.

#### 1. Individual Southern Islands.

The vegetation of six islands is described in order, north to south.

a. 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 photos taken by geologists of the U. S. Geological Survey Guam party in 1952 and a photo mosaic map. The island has been frequently used as a bombing target and the vegetation has apparently suffered from this, though in the photos it does not appear too different from what Fritz described.

Even the size of this island seems to have 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 Sailing Directions give its height 266 feet but are noncommittal as to its other dimensions from a photo mosaic map by the U. S. 64th Engineer Battalion, 1952, its greatest length is determined as about 2.75 kilometers and its greatest width as 0.5 kilometers. Its shores are steep cliffs and great blocks are said to be loosened from the mainland. It is apparently entirely limestone. Fritz says the plateau is covered by brush about 4 meters high 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 any of them survived. No coconuts are apparent on the photographs. Part of the island still seems to be grassy or almost bare.

b. Saipan (Figures 36-39) — The second largest of the Marianas and about 474 meters in altitude, Saipan has a complicated geological structure and great topographic diversity. Added to this in its effects on the vegetation in a history of human occupation of at least 3,500 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 elongate 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 Kalaha (Mt. Marpi), 256 meters high. The highest peaks are of limestone (notwithstanding statements that Mt. Tapochau is an extinct volcano), 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 of somewhat elevated relatively level limestone. Similar slightly elevated 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 level 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.

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, Ervthrina, or by a mixture of trees. Pandanus tectorius and P. dubius are generally common with Pisonia grandis on lower sites, P. umbellifera on higher, 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, 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. 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 albidopunctata, Myoporum, Phyllanthus mariana, and other plants. At times the spray blowing up over these cliffs is so thick that visibility at several miles distance 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 of the level land was put into sugarcane by the Japanese. There is no record of what was there before, though some of it must have been mixed forest, either primary or secondary. Since 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 (Figure 38a). Sugar growing was not resumed after the war and the cane fields (Figure 37a) 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, quickly covering any open land. On some level areas in the south part Saccharum spontaneum has in a short time formed a thick brakelike growth. Whether this wild cane is descended from Saccharum spontaneum cultivated in the Japanese experimental plots or whether it is progeny of cultivated sugarcane which 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 the war or during Japanese time by pure or mixed stands of Albizia lebbek and Acacia confusa, (Figure 37b) and others by Casuarina equisetifolia. The first two were said to have been planted by the Japanese for charcoal. All of 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 likely 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 tanning 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 (Figure 39), with a scrubby vegetation of Hibiscus tiliaceus, Clerodendrum inerme, Acrostichum aureum, scattered Casuarina trees, and patches of Paspalum vaginatum. Some low places and roadsides are occupied by Panicum purpurascens.

The volcanic areas, such as the "sabanans" south of Laderan Tagpochau, and Ogso Talofoto (Densinyama Ridge) to the north, and part of the hills around Fanunchuluyan 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, causing it to become very loose and elongate. 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 scarabeoides, Scaevola sericea, Desmodium unbellatum, and many less common species make up the vegetation. The first pioneers on this bare clay are Sphenocmeris 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 thick, underlain by hard coral limestone. In at least two places (the north slope of the peak of Ogo Tagpochau and the pass in the center of the island south west of Bahia Fañunchuluyan, 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.

The strand zone is mostly made up 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, Pisonia grandis as the most important trees and with Thuarea involuta and Ipomoea pes-caprae beneath, running out onto the beach. 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 conjugata, 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, many areas had changed almost beyond recognition. These disturbed areas can be expected to come gradually back to a forested condition in most parts. The level parts 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.

c. Tinian (Figure 40) -- This island is essentially a terraced platform of elevated reef limestone with the locally irregular surface mostly varying between 50 and 100 meters in elevation. 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 generally limestone environment. The topography varies, including level plains on the more extensive terraces, long irregular lines of cliffs bounding 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. Elsewhere the internal drainage is very effective, as would be expected in limestone country. There are no surface streams, the only permanent surface water being the pond mentioned above, called Hagoi (Lake Hagoya), in the north end of the island. Excepting a stretch of the southeast coast, the island is surrounded by low cliffs, in places 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 18th and 19th centuries. Marche (1891) briefly refers to it, as does Alvarez Guerra (1887). Fritz (1901, 1906) and Prowazek (1913) give brief accounts during the German occupation, and Kanohira (1937), Hosokawa (1934), and Matsue (1932) during the Japanese period. All together these give only the sketchiest idea of the vegetation and the change it has undergone. During the Economic Survey in 1946 several days were spent on Tinian and the observations made then by Fosberg are the principal basis for the present account.

Nothing but conjecture is possible about the original vegetation of Tinian. When discovered 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 18th century. Unquestionably the intensive occupation by the aborigines largely altered or destroyed the original forest which must have completely covered the island. During the 18th and 19th centuries the Spanish governors maintained the island in a depopulated state as a pasture for great herds of wild cattle which supplied meat to the garrison on Guam. The early visitors mentioned thousand of cattle, hog, 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 parklike landscape so enthusiastically described by Anson. He reports (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 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 nowhere lower than our middles, which continually entangled our legs, and cut us like whipcord ..."

Wallis (1773) described the island as one continuous thicket, with the cattle not nearly as abundant as Anson had described. Gilbert (1789) found things essentially as Wallis had.

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

Marche (1891) merely noted that the vegetation was very poor, with the coconuts the only tall trees.

Fritz (1901) says the vegetation is not especially luxuriant. He mentions a forest zone in the south, the trees 10 to 15 meters tall, passing gradually to a scrub 4 meters tall of guava, lemon, orange, and Annona trees. This passes in turn to a savanna which covers by far the greater portion of the island. But, instead of grass, this is 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 says that in especially dry seasons the entire plant cover of the savanna dies, but in the rainy season it comes back to life.

By Fritz' time the number of wild cattle had apparently diminished greatly. His native informants said there were 600 to 700. It may well be that they had been largely starved out by 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 dominant suggests that this may well have happened. Von Prowazek, the other German writer who treated Tinian to any extent, contributes very little more information.

During the 1920's the Japanese cleared every square foot of Tinian that had level soil. In Matsue's book describing this (1932) are colored panorama views showing the landscape before the forest had been cleared and after the clearing. At least the part shown in the first panorama 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, though Hosokawa (1935) does mention mixed forests on limestone and almost pure stands of Guamia.

When visited by the Micronesian 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 airbase, with two large airfields and a network of roads. The cane plantations had been abandoned for at least two years, though some of them had been used for farms and gardens to produce vegetables and other food plants, both by the Japanese and American forces. The following two paragraphs are practically quoted from the description of the vegetation written at that time, except for corrections in the names of the plants.

The vegetation of the cliffs separating the terraces (Figure 40), 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. The same is true of the sea cliffs, but on the west side more moisture than usual seems available and this 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 only support 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 than Wake Island. On exposed headlands there is an interesting transition of the vegetation from low forest down to brush, mainly Scaevola, this becoming lower and lower, changing 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 sugarcane or other crops every patch of arable soil (Figure 40). This area was in 1946 mostly very weedy open ground with large patches of sugarcane and Napier grass (rennisetum purpureum) persisting in it. Different parts had been abandoned for different lengths of time and consequently showed a different weed flora, but none had come back to any sort of secondary forest as yet. 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 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 elevation, 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 two meters high. It was introduced by the Japanese as an ornamental (T. Tuzama, unpublished information, 1953) and in 1937 was only seen as a short hedge. In less than ten years it had spread and dominated large areas.

Conspicuous in the landscape on the level parts of the island in 1946 were dense windbreaks of Casuarina equisetifolia and of a 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 which were open in 1946 had so grown up to thickets as to seriously impede the surveys.

In 1946 a narrow strip of trees lined the edges of the depression of Hagoi ( 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 swordgrass (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 entirely 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 this and some characterized it as the worst climate that they had met. 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 (occasional, 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, Geniostoma, Piper, and large ferns. Toward the edges of cliffs and on high summits the forest was probably dwarfed and similar to that existing in such situations now. The vegetation of the actual cliffs and strand situations also was probably very similar to what is there now. In some ravines and broken terrain there still exist traces of a taller forest, but in it the introduced Delonix regia is conspicuous.

d. Aguijan (Aguiguan) (Figures 41-43) -- This small island is just south of Tinian and is in its geological structure essentially similar to it, being a limestone platform with several level terraces. Little if anything has been written on its vegetation, and, except from the air, it has not been studied with this in mind. As with Tinian, the Japanese cleared the level places for sugarcane 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. The other parts are wooded, but the undergrowth, at least, has been largely 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, and the same Jatropha gossypifolia as on Tinian is also locally common here, apparently being unpalatable to the goats.

e. Rota (Figures 44-45) -- Although many earlier botanists have visited Rota, 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 mentioning vegetational features, but from all of these no clear idea of either the character or the pattern of the vegetation may be gained. Seidel (1915, opposite 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 are very convincing, and the paper which 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 photos and a published photomosaic.

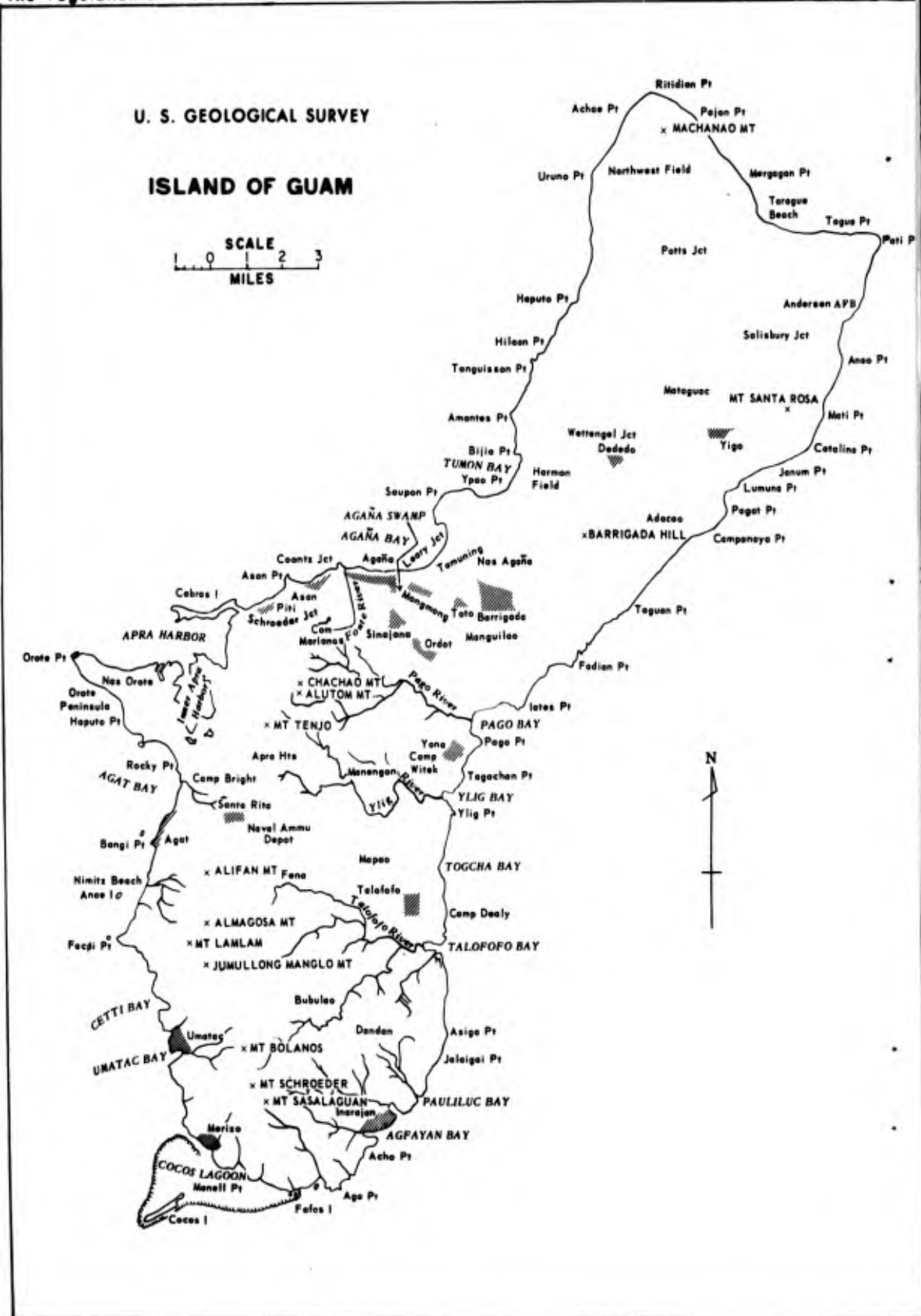
This is quite inadequate for an exact description, but makes possible a generalized account. Rota has an area of 85 square kilometers. It is principally a series of limestone terraces rising one above the other, surrounding a volcanic core which protrudes slightly through the topmost plateau (to an elevation 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 there appear to be from 5 to 11 terraces. They seem to slope mostly gently toward the sea but this is imperceptible in many places when actually on the ground. 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 fairly smooth and covered by a thick 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 (Figure 45b), cut by small streams which issue from the base of the limestone cliff above. These have eroded small ravines in large parts of the surface, but 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 18th century. The rougher parts of the island were probably not cleared by the aborigines and during the period between the depopulation and the Japanese occupation 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 even be traversed 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 sugarcane but were then abandoned and in places were growing up to second-growth scrub and forest (Figure 44). Areas still under cultivation by the natives were rather insignificant in size, although scattered in various sections of the island. An aerial photograph mosaic prepared from photos taken in 1946 shows that about one-fourth of the total area was covered by well-developed forest, but this was much cut up into 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, though scarcely a true rain forest, on the highest terraces. The best parts of this forest were undoubtedly cut, 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 species such as Cycas circinalis, Terminalia catappa, Laportea, Macaranga, Ochrocarpos, 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 terrible thickets of Triphasia trifolia to make penetration difficult. Much of this forest has been cut, and weed patches and thickets remain. Coconut trees were formerly abundant but are gone now, because of the ravages of the Brontispa weevil. Ferns are common in the shade at the bases of the cliffs, and on open vertical 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 following the contours, exposing the bedrock between the rows, in order to obtain sufficient depth of soil to plant anything. On many of the thin-soil areas on these and more elevated terraces the soil has 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 (Figure 44). The most extensive terrace is a gently sloping one between 150 and 200 meters on which the airstrip and the ruins of Shinaparu (Shimaparu) are located. Here the original forest had been mostly cleared. Even in 1946 secondary thickets were occupying many areas, but cultivation was carried on 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 marianensis, 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 clearing 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 (Figure 45b) contrasts conspicuously with that of the rest of the island. It is typical swordgrass 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 shows conspicuous erosion scars cut into the very acid, bright red, or where deeper, 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. On the gentler slopes are prosperous-looking little farms with breadfruit and mango trees, maize patches, and gardens with various cultivated plants. In marshy areas along the streams which 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 dryland 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.

f. Guam (Figures 46-54) -- Guam is the largest and southernmost of the Marianas (see Figure 2. Island of Guam). It is almost 30 miles long and from 4 to 9 miles wide. The highest point, Mt. Lamlam, is 406 meters high. The northern half is mostly limestone, with three small volcanic hills protruding through it. The largest part of this, to the north, is a level plateau of hard limestone. This plain slopes gently to the southward from about 200 to about 100 meters at the narrow waist of the island which is an old karst surface

of argillaceous limestone, worn down into rounded hills and marshy-bottomed sinks. There is no surface water in the northern part except several springs. The southern half contrasts sharply with this. It is of ancient, deeply weathered volcanic material, plastered here and there with patches of limestone, the largest of which is the Lamlam-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 Talofofo. The mouths of the valleys hold small estuaries surrounded by a certain amount of level land. Higher up there are level or gently rolling areas as well as rugged terrain. Small remnants sometimes termed "mesitas", 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, and in its broadest part extending halfway across the island and including 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, in a few places 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 account for present conditions. Safford spent a year on Guam as a government official just after its transfer to United States jurisdiction in 1899. His book (1905) and several other works (1902-1904) give a very interesting and comprehensive account of the plants and an account of the vegetation. Merrill (1914, 1919, 1946) provided a rather complete listing of the flora, but without much information on the vegetation. During World War II a number of United States 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 to that time. The present study is based on observations made on six

visits, aggregating somewhat more than three months, in 1946, 1950, 1952, 1953-54, 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. Future work might well take the direction of establishment of successional trends, more critical correlation of variations in the vegetation with those in the environment, and detailed phytosociological studies.

### C. General Picture of Guam Vegetation.

The greater part of Guam is forested, but substantial areas, especially in the southern half, are covered by coarse grass (Figures 46-49) 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 thickets, generally dense, tangled, and in many places with spiny undergrowth.

Limestone areas are usually wooded (Figures 51, 52a), 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, have 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 relatively bare of vegetation, others 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 much longer subject to disturbance. 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 (Figures 46a, 48b). Lowlands in the

valleys of the Talofofo river drainage and of some of the other rivers are occupied by extensive swamp forests and a few 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 of the volcanic soils are mostly, but not all, believed to be the result of extensive and repeated burning over many years. Much of the grass is tall, harsh swordgrass, with sharp-edged leaves, forming a very dense growth, especially on slopes. Ravines in these areas are filled with thick growth of coarse reeds, standing out from the rather similar swordgrass by their brighter green color. Level areas are more usually covered by a softer, bluish green low grass. Erosion scars are grown over by small bushes and tangled ferns.

When left unburned for a few years the grasslands may be abundantly invaded by Casuarina trees (Figure 48a), 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 only grown up since the Japanese invasion in 1941. They are now being destroyed again 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 brushy, and characterized by betel-nut palms. The forests 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.

#### 1. Detailed Consideration of Principal Vegetation Types.

##### a. The forest of elevated hard limestones

- 1) Artocarpus forest
- 2) Mixed moist forest
- 3) Ochrocarpos type
- 4) Cordia type
- 5) Merilliodendron forest
- 6) Pandanus forest
- 7) Halophytic and xerophytic scrub

##### b. Ravine forest of southern Guam

- c. Swamps and marshes
  - 1) Marshes
    - a) Reed marsh
    - b) Scirpus marsh
    - c) Shallow water with Cyperus
    - d) Paspalum flats
    - e) Panicum flats
    - f) Rice and taro patches
    - g) Miscellaneous other marshy vegetation
  - 2) Swamps
    - a) Mangrove swamp
    - b) Nipa swamp
    - c) Barringtonia swamp
    - d) Hibiscus tiliaceus swamp
    - e) Hibiscus-Pandanus swamp
- d. Strand vegetation
- e. Grassland or savanna vegetation of volcanic soil areas
  - 1) Miscanthus community
  - 2) Dimeria community
  - 3) Erosion scar community
  - 4) Phragmites community
  - 5) Weed communities
- f. Vegetation of the argillaceous limestone area
- g. Coconut groves and plantations
- h. Ruderal or weedy plant communities

- 1) Mixed herb type
- 2) Pennisetum polystachyum community
- 3) Pennisetum purpureum type
- 4) Tripsacum latifolium type
- 5) Panicum purpurascens type
- 6) Mixed grass community
- 7) Nephrolepis hirsutula type
- 8) Carica papaya type
- 9) Passiflora foetida-Ipomoea indica community
- 10) Operculina ventricosa type
- 11) Ipomoea pes-caprae type
- 12) Mixed shrub community
- 13) Leucaena glauca thicket

The significant vegetation types found on Guam and some of their variants are described below, grouped ecologically. It is probable that few or none of these exactly represent any of the original vegetation of the island, but are more the results of modification by man. In many of them 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 type described first are the most stable and perhaps are nearest the original, while those resulting from recent disturbance and still changing rapidly, are treated last.

## 2. The forests of elevated hard limestone.

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 a couple of 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 Lamlam-Alifan ridge and the hill west of the Fonte River are also of this rock. These areas were, and partly still are, covered by a tall dense mixed forest (Figures 12, 13a, 51a), mainly of evergreen dicotyledonous trees. In the central part of the island the agrillaceous limestone may have borne the same sort

of forest, but because it was the most suitable agricultural land on the island, the original vegetation of this area has been completely altered. Its secondary vegetation will be treated in a separate section.

It is difficult to be certain of the character of the original vegetation, even in the hard limestone areas. Guam has been inhabited by man for possibly several thousand years, but of this practically nothing is known except for the last 430 years. Until 1941 the total population has not been large, but at the time of Magellan's visit in 1521 there were at least many tens of thousands of aborigines. The influence of these on the vegetation is hard to estimate, but could not have been negligible. Since Magellan's time, though 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 brought about 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 Guam's vegetation types 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 will be discussed farther on in a section on weedy vegetation. In the following paragraphs the main present-day aspects of this forest will be discussed.

Because of the presence, practically everywhere, of species that generally occur in secondary vegetation and even of introduced plants, as Triphasia, Cestrum, and Carica, and because of the uneven, brushy nature of almost all of the remaining forests, it seems best to regard the present-day forests on the plateaus and terraces as secondary. 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 secondary forest.

Generally, this secondary limestone forest 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 this 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 may be 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 half-dead. Several reasons are advanced for this--insect damage, typhoon damage, damage from military activities especially 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. Possibly all of the above-mentioned factors and still others may together be responsible for this condition. Examples may 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 numerous aspects occur. These are described below and where possible localized and correlated with topography and other features. It must be remembered, though, that in a continuously varying vegetation by no means all examples will fit any of the described categories.

a. Artocarpus forest -- The most widespread aspect of the limestone forest is dominated by large trees of the wild breadfruit or "dugdug" (Figure 12a). 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, finer-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, 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 (Figure 51a), Intsia, Pisonia, Claoxylon, and Pandanus as fairly large trees, and smaller plants of all of these, as well as Guamia, Cycas, Morinda, and Triphasia as 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 tall, 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 tall or even taller. Locally these two may be as much as a meter in diameter, the Ficus even more, but most of the Artocarpus are much less. The understory and shrub layers are not sharply separate. 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 stand 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 Talofofu Bay, and on the Lamlam-Alifan ridge. It is no longer continuous over extensive areas because of the widespread military activities of the past ten 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 leaving some large trees, these usually become unhealthy and die in a few years. The Artocarpus seems to stand the exposure resulting from clearing longer than most other species.

b. Mixed moist forest -- East of Mt. Santa Rosa and for an undetermined distance north and south along the strip just back of the edge of the cliff, there is a type of forest 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. Ochrocarpos 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 of large trees of secondary species such as Macaranga in this area, growing with the other trees enumerated under the Artocarpus type.

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

c. Ochrocarpos type -- On the eastern escarpment of the plateau, as at Anao, excepting where it is vertical, the dominant tree is Ochrocarpos odoratus, 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 uneven to uniformly dense, with a smooth canopy as seen from the air. It is usually of medium height and with a well-developed undergrowth. Aglaia, Guettarda, Cynometra, Bleekeria, Guamia, Ochrosia, and Ficus are generally numerous, and on the gentler slopes and terraces below the cliffs, Pisonia grandis is common in places. Here Hibiscus tiliaceus is an important component, and, locally, Barringtonia asiatica.

d. Cordia type -- On the steep slopes and cliffs back of 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, 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.

e. 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 50 meters high, dominated by trees of Merrilliodendron megacarpum and Ficus prolixa, the latter less abundant but taller. The second story, only about 4 meters tall, is of saplings of Merrilliodendron and the lowest layer, from 0.5 to 1 meter tall 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" commonly applied to such species.

f. Pandanus forest -- Common on interior areas on the plateau are forests made up of an almost pure stand of Pandanus tectorius (Figure 12b), the screw pine or "kafu." The trees in any one stand appear to be about the same age, 10 to 15 meters tall, the trunks 10 to 20 centimeters in diameter, with a thick undergrowth. The prominent stiltroots of the Pandanus add to the Flagellaria, Cestrum, Triphasia, and Nephrolepis and other components of the undergrowth in making walking difficult.

Pandanus forest 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.

g. Halophytic and xerophytic scrub -- On terraces and cliff edges not too far above the sea on the east and north coasts and on vertical limestone cliffs and their tops is a scrub of varied height and density that may be a response either to extreme salt spray, to dryness resulting from too good drainage, or 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 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, Ochrocarpos, 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, Ochrocarpos, 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, 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.

### 3. Ravine forest of southern Guam.

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. Since its floristic composition is rather variable it may conveniently be termed ravine forest (Figure 48b). Good examples may 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 soil, this type or variants of it occurs on outcrops of Bonya and Maemong limestones (Doan, personal communication) in the Talofoto drainage. The south side of the Talofoto valley is largely forested with this type, which also alternates with swamp forest in the valley bottom. Where the valley bottom is level there is generally swamp, but 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 its characteristic occurrence 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 may usually be distinguished in the deeper parts of the ravine, but, toward the edges, these merge and become indistinguishable.

This forest type is varied in composition from place to place but generally much poorer than the forests on the limestone plateau. The inclusion of the lowland limestone hills of the Talofoto 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 is 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 cathaca, 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 which most generally sets this forest off from the plateau forest is the betel palm, Areca cathecu. 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 commoner 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 cathecu, coconuts, Triphasia and even bamboo, that this type is secondary. The abundance of artifacts, broken pottery, etc. as well as scanty historical evidence, shows that these parts of Guam were densely populated in pre-Spanish times, and undoubtedly the ravines were largely used 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 descendents 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 Pena River area. These species may possibly all 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.

#### 4. Swamps and marshes.

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 the vegetation present. Marshes are wet areas dominated by herbaceous, or non-woody, plants, frequently grasses and sedges. Swamps are dominated by woody plants,—shrubs and trees. Several types of each exist on Guam. Bogs do not exist on the island and are rare in all lowland tropics, unless peat swamps are considered bogs.

Marshes may be found in low places along the coast, along streams, in depressions and sinkholes 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 mostly found 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 Ylig. The drainage in the limestone is too nearly perfect.

The wet areas of Guam are mostly occupied 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 this was recorded.

The ground in all of 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.

The principal types represented in these categories may be outlined as follows, and then briefly discussed separately.

#### Marshes.

- 1) Reed marsh
- 2) Scirpus marsh
- 3) Shallow water with Cyperus
- 4) Paspalum flats
- 5) Panicum flats
- 6) Rice and taro patches
- 7) Miscellaneous other marshy vegetation.

## Swamps.

- 1) Mangrove swamp
- 2) Nipa swamp
- 3) Barringtonia swamp
- 4) Hibiscus tiliaceus swamp
- 5) Hibiscus-Pandanus swamp

a. Marshes -- It is almost certain that on Guam as in most wet tropical areas, herbaceous marshes are memely stages in successions leading to woody vegetation, usually of a swamp character. In some of them 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 war.

1) Reed marsh (Figure 53) is by far the most frequent type of marsh vegetation. It is dominated, often in pure stands, by the tall tropical reed, Phragmites karka. This plant forms hollow canes the thickness of a man's thumb and 6 to 12 or even 15 feet tall. Ordinarily a stand of these canes is so dense as to make penetration by a man of foot difficult. Stands are seen in which the canes may average 3 inches 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 either from volcanic or calcareous materials but are confined to areas which are wet with seepage, standing or running water for the greater part of the year, and which 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, since 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 swordgrass 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 some feet in relief, and be as different as rough rock and soft mud.

2) Scirpus marsh (Figure 54b), actually submerged ground covered by bullrushes, Scirpus erectus, exists in small areas around the base of Orote Peninsula. These bullrushes are naked green stems the size of a finger and rising 3 to 6 or even 8 ft from a mat of prostrate rootstocks 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.

Pure dense 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.

3) Cyperus marsh is uncommon and not at all uniform. Shallow ponds occur with scattered tufts of Cyperus, usually Cyperus polystachyus but in places C. odoratus or C. javanicus. Rhynchospora corymbosa is in a few places found with them. Cyperus odoratus and, less commonly, C. javanicus also occur in local stands in ordinary low wet ground. In all of these types, the dominant plant is a tufted grasslike 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 may be seen at the base of Orote Peninsula.

4) Paspalum flats (Figure 54) are lawnlike areas usually wet and usually brackish, covered by a dense stand of Paspalum vaginatum. This is a wiry, creeping, mat-forming grass growing no more than a foot, usually only a few inches high. Though this grass may grow on mud as well as sand, and commonly in shallow standing water, it usually provides a safe enough footing for walking. The tough mat of roots will normally 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 commonly 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 back of beach ridges as at Umatac.

5) Panicum flats (Figure 53b) are similar in superficial appearance to Paspalum flats, but dominated by Panicum purpurascens. The mass of vegetation is much deeper, in many places 3 or 4 feet thick, 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, both on dry and wet ground. On wet ground what are here termed Panicum flats, possibly better called wet meadows, have resulted. One such may be seen along the road at the north side of the base of Orote Peninsula.

6) Rice and taro patches are at present uncommon on Guam, though during the war they were much more important. Rice is now only grown on 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.

7) Miscellaneous marshy vegetation that does not fit any of the common types may also be found in some 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. In a very few places, 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.

b. Swamps — Almost any of the above marsh types tend to develop into swamps as shrubs and trees invade them. The brackish marshes are invaded by mangrove swamp plants, especially Avicennia (Figure 54a). 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 a patch of mixed marsh and swamp just east of the high ridge of Mt. Lamlam.

Five types of swamp are recognized, but it should not be thought that the actual stands may all be sharply separated into one or another. They tend to grade into each other 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 of the alluvium filling the valley floor is swampy.

1) Mangrove swamps (Figure 3a) are very poorly represented, indeed, in Guam, in comparison with those of islands and coasts to the south and west. Around the base of Orote Peninsula, 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, Bruguiera conjugata, Avicennia sp., Xylocarpus moluccensis, Lumnitzera coccinea, Heritiera littoralis, Hibiscus tiliaceus, Acrostichum aureum, Nipa fruticans.

2) Nipa swamps are even more feebly represented. There are a few patches of Nipa 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.

3) Barringtonia swamp is a striking swamp forest type known in Guam only from the Talofoto River. Where best developed it is a pure stand of Barringtonia racemosa 10 to 15 meters tall, close set, and with a dense complete canopy. The tree trunks are seldom more than 20 centimeters thick. There is no undergrowth whatever, and the trees grow on conspicuous hummocks with muddy channels between them. Water may be standing in these channels, or they may be almost dry, in areas near the sea fluctuating 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.

4) Hibiscus tiliaceus swamp 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.

5) Hibiscus-Pandanus swamp. Both types 4 and 5 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, in few or no places proper trees with trunks. They are tangled together into an intricate mass of stems of all sizes, commonly 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 fairly firm, to soupy mud.

## 5. Strand vegetation.

There are, on Guam, three basic types of shore line. The most extensive is 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 (Figure 6) which has been described earlier. It is of gnarled, twisted hardwood bushes with small fleshy leaves with a slightly astringent taste. The mangrove vegetation of low swampy coasts has also been described above.

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 centimeters thick and 20 meters tall. They do not form dense stands, but few other plants grow with them. This homogeneity may be the result from the ability of few plants to establish themselves in the layer of dried branchlets or "needles" that accumulates beneath Casuarina trees except under very wet conditions. Since 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, Guettarda speciosa, Messerschmidia argentea, Scaevola sericea, Hernandia sonera, and, of course, Coccoloba 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 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 has something to do with 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, Lantana repens, and Pimbristylis 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.

#### 6. Grassland or savanna vegetation of volcanic soil areas.

Volcanic soil in the Marianas is generally thought of as covered by a dense stand of swordgrass, 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 (Figures 24, 46a) (2) the Dimeria community (Figure 25a), (3) the erosion scar community (Figures 46b, 47, 48a), (4) the Phragmites or reed community (Figure 53a), and (5) the weed communities which follow disturbance. The first four form, at the present time, a natural mosaic over a large part of the volcanic part of Guam, with the fifth added where clearing and scraping of the soil has 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 to again dominate and slowly shade out the new pioneers.

a. Miscanthus community — In its best development this is an almost pure stand of Miscanthus floridulus (Figures 24, 46a), a coarse, sharp-edged cane-like grass. It grows to a height of 2 or even 2 meters, the clumps so close together that it is very difficult to push through them. The color varies with the season and local moisture conditions 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, there are usually small Casuarina trees scattered unevenly through this grassland.

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.

In few places they are completely absent, however. Almost any of a large number of accessory species may be found in this community, but any great abundance of them suggests recent burning, recent erosion, or a transition toward 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 may 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, because the fires travel rapidly and it is not easy to move fast through swordgrass. A rocky or open place in the grass is the safest spot to weather a fire, if a bare erosion scar or road cannot be reached.

Foot travel in a dense stand of swordgrass, except on trails or ridge tops, is slow and at times almost impossible for any distance. The clumps of finger-size canes are springy and tangled, and the leaf blades can cut the skin like knives 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.

b. Dimeria community -- This low grassland is dominated by Dimeria chloridiformis (Figure 25a), a tufted soft hairy grass of a bluish green color, the flowering stems up to half a meter tall or even more. Even when very well developed the tufts are far enough apart for many accessory species to be present in practically all stands, but in a well developed undisturbed area they generally make up less than ten percent 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. Large numbers of other native species indicate an erosion scar recently healed over, whereas 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 the low elevations that swordgrass 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 jeeps or other motorized transport, providing the ground is not eroded in a rough fashion. It is, however, likely to alternate with Miscanthus patches and to be discontinuous 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, because the dominant species is not a first-choice forage. The stock tend to pass it by and to search out several minor species in the community.

c. Erosion scar community -- 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 which 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, may be found a characteristic assemblage of species (Figures 46b, 47, 48a) 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 will dominate and produce one or the other of the two grass communities described above. For a long time, however, traces of the erosion scar will remain in the unusual abundance of the species characteristic of such areas.

d. Phragmites community -- Reed brakes, pure stands of Phragmites karka, are so commonly found in wet ravine bottoms (Figure 53a) 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 tall, 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 completely cover the ground, the canes from 5 to 20 centimeters apart. Since 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, make it desirable to avoid this sort of ground.

e. Weed communities -- A varied assortment of pioneers or weeds, practically 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 indica, Elephantopus mollis, Hyptis capitata, Hyptis suaveolens, Mitracarpum hirtum, and Chrysopogon aciculatus. These may occur in mixtures, or, more usually, one 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 toward 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.

#### Swordgrass on limestone soil.

For some years the idea has been current that swordgrass, Miscanthus foridulus, is a reliable indication 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 east side of the summit of Mt. Tapochau, the other to the north in the Magazine area. Two peculiarities were noticed in observing these stand -- 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 swordgrass 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 (Figure 49b) 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 as follows: Piti, just above Marine Drive; 2.5 kilometers north northeast of Sinajana; Agriculture Farm Dairy; Agriculture Farm at Manguilao; small hill just south of Pago River bridge; bluffs south Ylig River bridge; top of hill south of Talofoto 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 even 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 2; one 3; one 5; one 13; and one with 15.

The last is a very small spot surrounded by savanna, whereas 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 swordgrass, but this is manifestly not the case, as there are any number of argillaceous localities where swordgrass is lacking.

Of the Guam localities listed above, half were being actively invaded by Leucaena and the swordgrass showed the effects of shading in long spindly growth habit, sparseness, and in some cases, dead clumps. In the areas where swordgrass 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 seem adequate to account for the distribution of this species. The best explanation that has suggested itself 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 although Miscanthus is generally an indication of a volcanic substratum, it must not be regarded as a completely reliable one, for at least 14 exceptions are known where it

grows on limestone.

#### 7. 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, not 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 sink holes plugged by clay soils, and drainage patterns produced containing intermittent streams. A deep brown soil, as much as 10 meters more in depth, covers even some of the ridges, though the underlying limestone crops out here and there, and in places loose limestone fragments litter the surface.

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, mostly in a very bad state of repair. The result is that there is none of the original vegetation left; and it is impossible to say what this original plant cover may have been.

At present the vegetation is an intricate mosaic of small areas of different types and 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 numerous. These are dense growths with fine feathery foliage, the individual plants up to 5 or 6 meters tall, with smooth stems seldom more than 5 centimeters in diameter. They usually grow only a foot or two apart, so that in many places a man cannot walk between them with comfort. The ground may be covered with seedlings of the same plant which quickly grow up and fill any gaps in the continuous canopy of foliage above. In stands of this nature there are few other plants, except that around the edges, thorny bushes of Triphasia trifolia may in places be found, seriously impeding penetration.

In areas of relatively low relief may be large patches of mixed scrubby thicket 3 to 4 meters tall, the trees usually contiguous, but with some 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, Annona sp., in varied proportions, with local patches of Moghania strobilifera. Morning-glory vines of several kinds are tangled in these trees and bushes. 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 centimeters or more thick, 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 high, not forming any sort of complete canopy. The second story, 3 to 10 meters high, 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-leaved 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 are 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 marshy lowlying spots occupying 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 swordgrass, 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 only be characterized as a complex unit whose local characteristics are completely dependent upon the activities of its human inhabitants.

#### 8. Coconut groves and plantations.

Large or small areas throughout the island are occupied by more or less pure stands of coconut palms. These have mostly been planted 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 back of beaches, as at Tarague Beach, on level 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 Talofofo 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 tall, 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 two or more meters high, 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 production in these plantations is at present nonexistent. Labor costs are so high that the copra produced would 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.

#### 9. Ruderal or weedy plant communities.

Most of the vegetation types on 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 secondary, 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 introduced species, many of the plants are from the nearby natural savanna areas. The assemblages to be noted below however, are almost exclusively made up of exotic weedy plants. The vegetation described above on the argillaceous limestone might be included here, but since it forms a quite distinctive and recognizable mosaic, it has been 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, 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 although at least one of them, the Leucaena glauca thicket, may persist indefinitely so far as present observations show. These vegetation types may be only roughly classified. As with most vegetation situations, especially those where active succession is taking place, varying mixtures occur which defy classification and which may largely result 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 weedy plant communities that are reasonably distinctive and that occur repeatedly enough to be more than merely accidental.

a. Mixed herb type — On cleared land, fills, roadsides, and burned areas, the first colonists are normally a mixture of many nonwoody 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 a large 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 numerous 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 in determining what species are abundant, as does season and the degree of consolidation of the vegetation. These combinations are too numerous to be described conveniently. However, several striking aspects repeat themselves enough to be pointed out, mostly where they are completely dominated by one species.

Most conspicuous and common of the aspects of the mixed herb community is that dominated by Stachytarpheta indica. This herb growing to about 1 meter in height, with purplish blue flowers, completely dominates much ground both volcanic and limestone soil that has been relatively recently cleared of vegetation. This is a vegetation of short duration and is 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 over. Where savanna dominated by swordgrass, Miscanthus floridulus, has been burned and replaced by Elephantopus, the resulting herb vegetation is likely to be short lived, because the Miscanthus root

crowns are not killed by fire. Within a short time the Elephantopus will be crowded out. On burned-over weedy land this rapid succession will not take place, and the Elephantopus communities may last until further fire, 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.

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 ground.

b. 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 tall, 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.

c. 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 reedlike grass up to 3 to 4 meters tall, and after the first year it forms dense tangles. The canes are up to 1 centimeter 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.

d. 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 looks much like a very dark-green maize plant and forms dense pure stands up to 3 meters tall. It produces horizontal rhizomes, which, matted in the surface of the ground, enable it to exclude other plants.

e. 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.

f. 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 will take place rapidly.

g. 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 to 1.5 meters tall, 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.

h. Carica papaya type -- Along roadsides newly bulldozed 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 postlike trunk topped by a crown of great palmately divided leaves. These are as much as half a meter in diameter on long petioles. The trunk is not very woody but rather pulpy and soft. When cut, leaves and stems exude an abundant white latex. This may be irritating to tender skins because of its protein-digesting properties.

i. Passiflora foetida-Ipomoea indica community -- On bare limestone that has at some time been scraped clear of vegetation and soil, is commonly 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 few inches.

j. Operculina ventricosa type -- Around Northwest Field Operculina ventricosa forms huge dense mats of coarse vines. These may be actually a meter deep 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.

k. Ipomoea pes-caprae type -- In clearings on sand flats back of 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.

1. Mixed shrub community -- On cleared limestone or limestone soil, various secondary herbaceous vegetation types are in many places, succeeded by shrubby vegetation of varied 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 of 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 introduction, as Psidium guajava, Carica papaya, and Lantana camara.

The density and stature of this scrub is 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 major (Figure 52b) 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 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 to indicate any real successional relations to forest types.

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 will be 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 tall. 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 dangerously spiny. The wood is hard but not too 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 makes up a large part of a thicket, it is simpler to go around it 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 intricate 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. The 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 of 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.

m. 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 centimeters thick and grow so close together that they must be pushed 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 cut down 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 strongly. 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. Others, who have tried to get rid of it or check its invasion of an area, regret its being brought to Guam. It is probably the most widely used tree for firewood 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 8 years. In fact, the local Department of Agriculture, under the Navy

Administration, caused large quantities of Leucaena seed to be broadcast from planes, especially on the volcanic southern half of the island. It is now very abundant on roadsides and over vast areas of former open field 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 which 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.

Figure 3. Mangrove vegetation.



Figure 3a. Guam: Rhizophora in edge of harbor at base of Orote Peninsula (Fosberg, Jan. 1954).



Figure 3b. Truk, Dublon I. Mangrove swamp, principally Rhizophora, (Fosberg, May 1946).

Figure 4. Mangrove vegetation.



Figure 4a. Small patch of Nipa fruticans along channel in mangrove swamp north of Lele Harbor, Kusale. (Fosberg, Aug. 1946).



Figure 4b. Nipa fruticans showing buried stem exposed on edge of estuary of Ngarumiscang River, west side of Babeldaob, Palau. (Fosberg, June 1946).

Figure 5. Mangrove vegetation.



Figure 5a. Vertical aerating organs ascending from roots of Sonneratia caseolaris in mangrove swamp north of Lele Harbor, Kusaie. (Fosberg, Aug. 1946).



Figure 5b. Aerial prop roots of Rhizophora mucronata in mangrove swamp, Babeldaob, Palau. (Fosberg, Feb. 1950).

Figure 6. Strand vegetation.



Figure 6a. Limestone terrace above sea, showing Pemphis acidula and other shrubs dwarfed by exposure to salt-spray and winds, south of Campanaya Point, east coast of Guam. (Fosberg, Jan. 1954).



Figure 6b. Same location, close-up of dwarfed prostrate Pemphis shrub. (Fosberg, Jan. 1954).

Figure 7. Strand vegetation.



Figure 7a. Compact fringe of Scaevola sericea in front of coconut plantation at top of pebble beach on seaward (south) side of Kalo Islet, Ujelang Atoll, Marshall Is. (Fosberg, Feb. 1952).



Figure 7b. Scaevola sericea colonizing sand flat at north end of Taka Islet, Taka Atoll; Lojrong Island (Lojiron Islet) in background. (Fosberg, Dec. 1951).

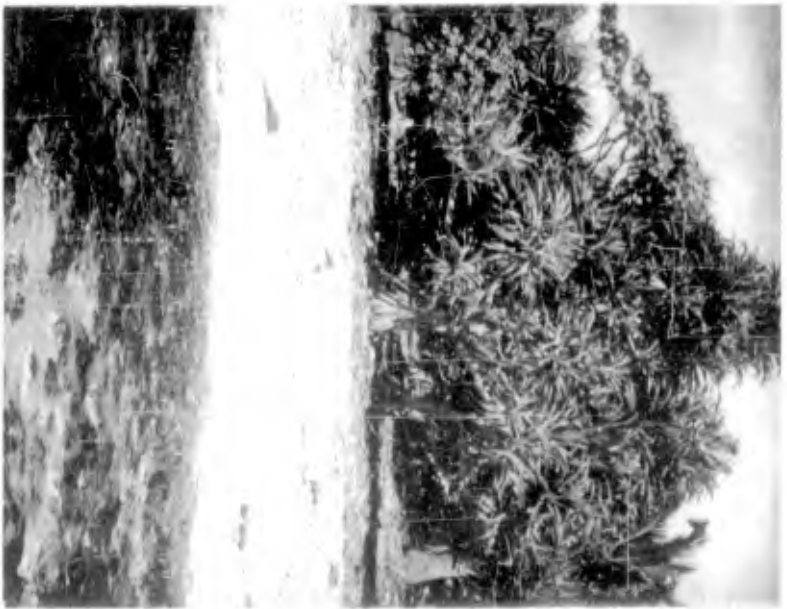


Figure 8a. Pandanus trees at top of seaward beach, Normin Islet, Norwin Atoll, Caroline Is. (Fosberg, May 1946).

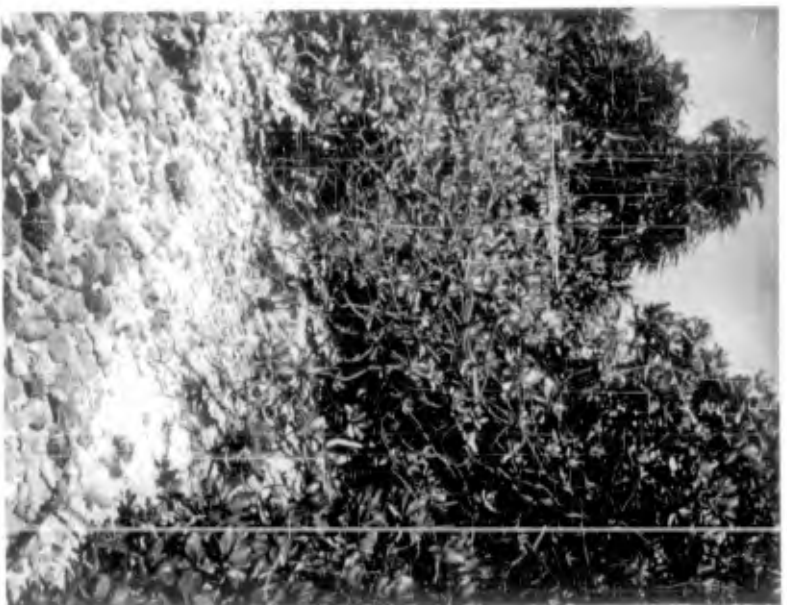


Figure 8b. Tangle of Scaevola sericea and Pandanus at top of seaward beach, Normin Islet, Norwin Atoll, Caroline Is. (Fosberg, May 1946).

Figure 9. Strand vegetation.



Figure 9a. Interior of *Pisonia grandis* forest, showing root sprouts of *Pisonia*, otherwise bare forest floor covered with twigs, leaves and raw humus, Almani Island (Almeni Islet), Bikar Atoll, Marshall Is. (Fosberg, Aug. 1952).



Figure 9b. Opening in mixed forest on rocky ground, occupied by a blanket of *Wedelia biflora*, Lae Islet, Marshall Is. (Fosberg, Jan. 1952).

Figure 10. Forest on elevated coral limestone.



Figure 10a. Undisturbed forest with native palms (Gulubia), Pandanus and many other trees, small islands west of Urukthapel, Palau. (Bridge, June 1947).



Figure 10b. Southwest peninsula of Urukthapel Island, with Casuarina equisetifolia forest on cliffs on right. (Fosberg, Feb. 1950).

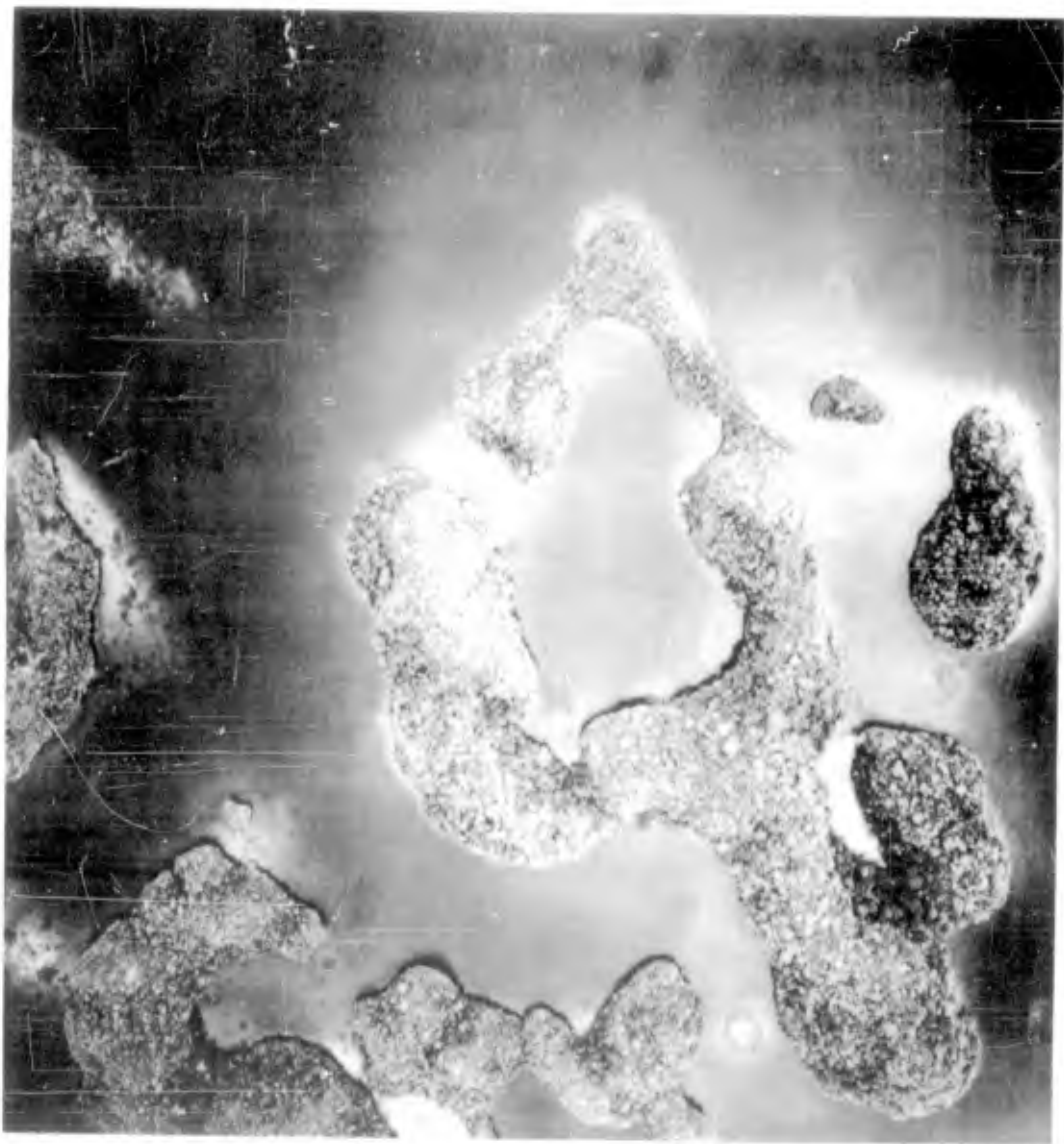


Figure 11. Vertical aerial photo of small limestone islands near Urukthapel Island, Palau, showing mixed character of forest on steep rough elevated coral limestone. (U. S. Navy).

Figure 12. Forest on elevated coral limestone.



Figure 12a. Bushy clearing in mixed forest, central part of north Guam near Ipapao, east of Dededo. (Fosberg, March 1950).



Figure 12b. Bushy clearing in Pandanus forest, near Ipapao. (Fosberg, March 1950).

Figure 13. Vegetation of elevated coral limestone.



Figure 13a. Mixed forest on hard limestone, top of Mt. Alifan, Guam. (Fosberg, Jan. 1954).



Figure 13b. Rough limestone formerly covered by Pemphis acidula but denuded by typhoon, showing character of limestone surface, Inarajan, Guam. (Fosberg, Jan. 1950).

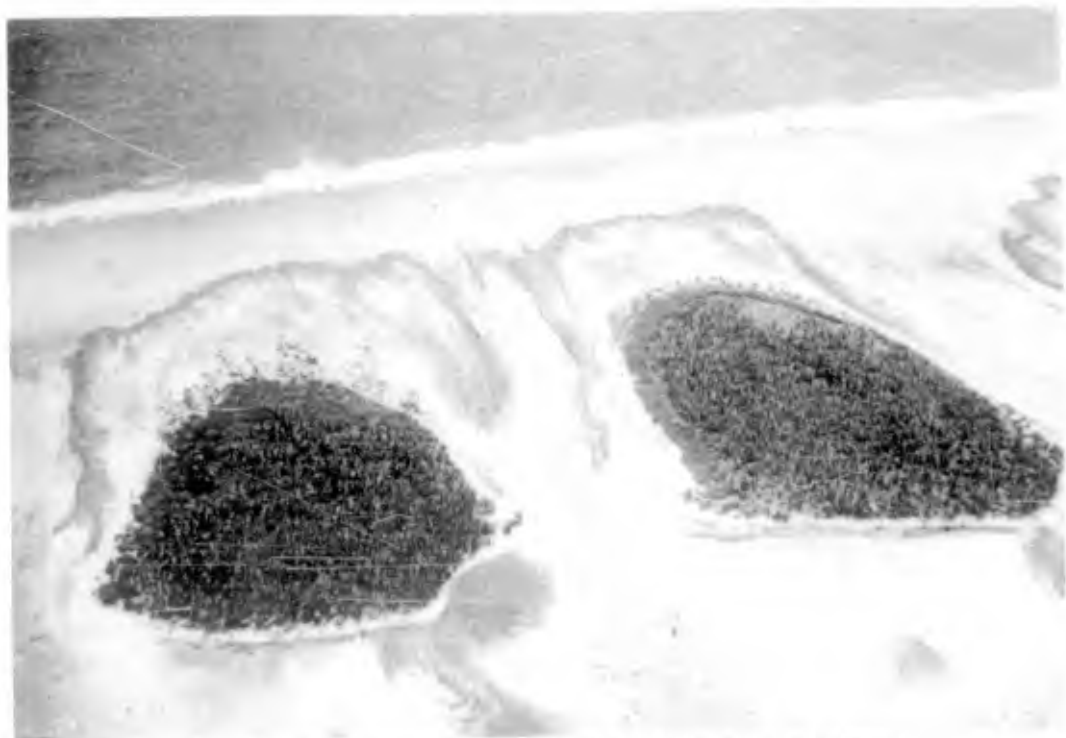


Figure 14. Aerial view of coconut plantations in windward islets of Ailuk Atoll, Marshall Is., showing crescent shaped strips of strand scrub and scrub forest left on windward sides to protect plantations from wind and salt spray. (Fosberg, Feb. 1952).

Figure 15. Coconut plantations.



Figure 15a. Opening in coconut grove, Pandanus on left, ground cover of Lepturus repens, Utirik Islet, Utirik Atoll, Marshall Is. (Fosberg, Nov. 1951).



Figure 15b. Coconut plantations battered by typhoon, soil washed away from roots of trees, east of Merizo, Guam. (Fosberg, Jan. 1950).

Figure 16. Coastal Plain complex.



Figure 16a. Home site with coconuts, breadfruit, and bananas, Ulalu I., Truk Group. (Hay, Dec. 1954).



Figure 16b. Typical scene in coastal plain thickets, bare tree in center is kapok (Ceiba pentandra). (Hay, Feb. 1955).

Figure 17. Taro marshes on coastal plain.



Figure 17a. Bushy coastal plain with taro marsh in left foreground, reeds in middle distance, and coconut and mango trees in background, Uman I., Truk Group. (Hay, Dec. 1954).



Figure 17b. Taro pit with Cyrtosperma, Ulalu I., Truk group. (Hay, Dec. 1954).

Figure 18. Coastal plain complex.



Figure 18a. Saccharum spontaneum forming dense brakes between coconut trees, Uman I., Truk Group. (Hay, Dec. 1954).



Figure 18b. Dense tangle of Scleria, with cutting edges, in thicket, Moen I., Truk Group. (Hay, Nov. 1954).

Figure 19. Reed marshes on coastal plain.



Figure 19a. Road through dense Phragmites karka on wet ground, Udot I., Truk Group.



Figure 19b. Close up view in Phragmites marsh Param I., Truk Group. (Hay, Dec. 1954).

Figure 20. Secondary Vegetation.



Figure 20a. Denuded slope covered by grass and scattered bushes and trees, south slopes of Witipan Hill, Moen I., Truk. (Hay, Mar. 1955).



Figure 20b. Denuded grassy summit of Witipan Hill, with scattered bushes and thicket. (Hay, 1954-1955).

Figure 21. Secondary Vegetation.



Figure 21a. Lower slopes with secondary thickets, middle with coconut plantations with some breadfruit, upper slopes at foot of bluffs with secondary forest, some primary forest on top, Mt. Tolomen, Dublin I., Truk. (Hay, Dec. 1954).

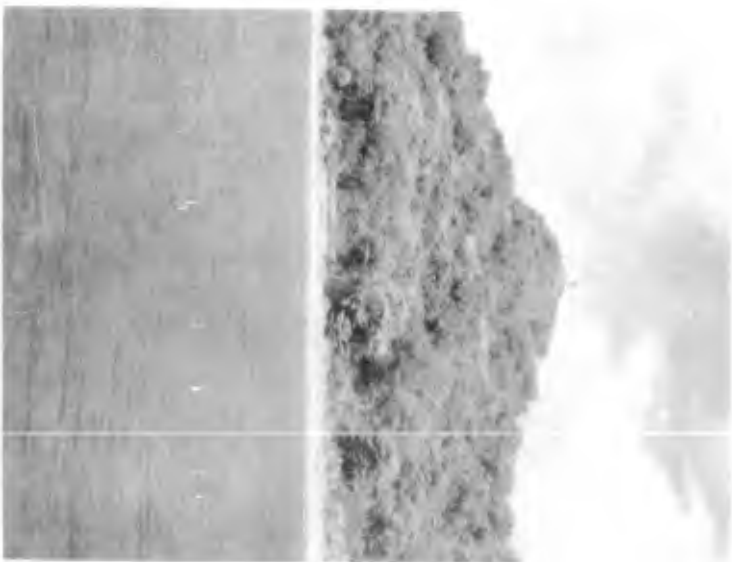


Figure 21b. Secondary forest on volcanic soil, Malakal I., Palau. (Bridge, Mar. 1947).

Figure 22. Secondary Vegetation.



Figure 22a. Secondary thickets and scattered bushes, Moen I., Truk. (Hay, 1954 or 1955).



Figure 22b. Abandoned installations covered by a thick mat of Wedelia biflora and Ipomoea per-caprae, abandoned for about 4 years, Enebu I., Kwajalein Atoll, Marshall Is., (Fosberg, Jan. 1952).

Figure 23. Secondary Vegetation.



Figure 23a. Scrubby second - growth after clearing, north plateau of Guam near Campanaya Point. (Fosberg, Jan. 1954).

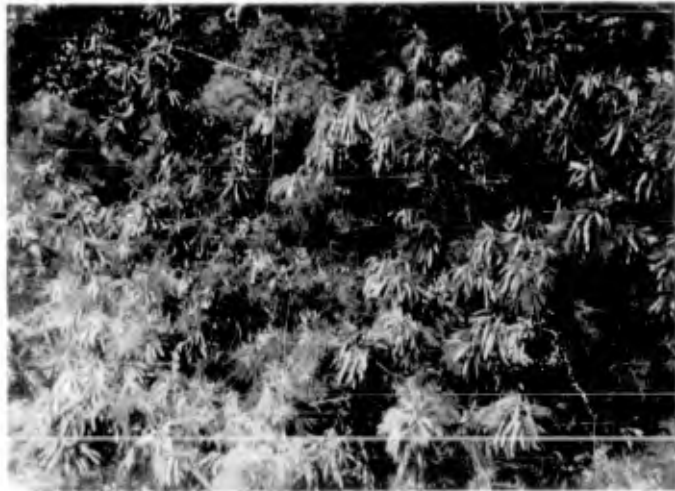


Figure 23b. Leucaena glauca thicket, Ngerebed, Koror I., Palau. (Fosberg, Mar. 1950).

Figure 24. Swordgrass.

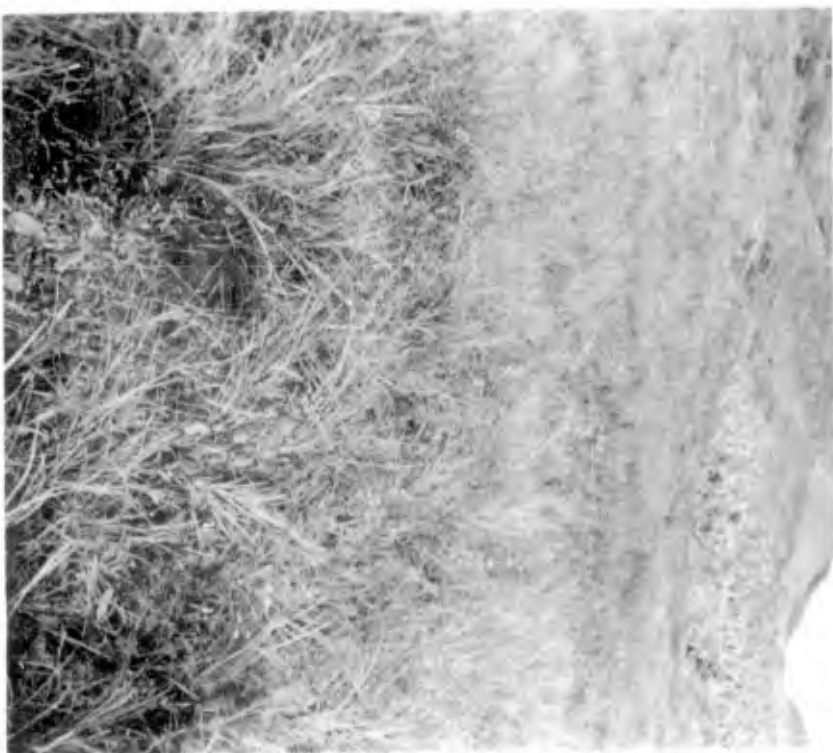


Figure 24a. Swordgrass (Miscanthus floridulus) with Hypoxis and other weeds, near base of Mt. Schroeder above Merizo, Guam. (Fosberg, Jan. 1954).



Figure 24b. Slope with Dimeria and clumps of Miscanthus, Casuarina sapling, volcanic soil, cross Island Road east of Apra Heights, Guam. (Fosberg, Jan. 1954).

Figure 25. Savanna.



Figure 25a. Dimeria grassland with scattered small Pandanus and Casuarina trees. Mt. Schroeder with patches of ravine forest in background, Merizo, Guam. (Fosberg, Jan. 1954).



Figure 25b. Ischaemum grassland with Pandanus trees, northeast of Cakip, Babelthuap I., Palau. (Bridge, April 1947).

Figure 26. Savannas in Bauxite areas.



Figure 26a. Typical savanna landscape, Ngardmau, Babelthuap, Palau. (Bridge, May 1947).



Figure 26b. Pandanus savanna, burned not long previously, Ngeremtengel, Babelthuap, Palau. (Fosberg, Feb. 1950).

Figure 27. Fern savanna.



Figure 27a. Gentle slope dominated by Gleichenia linearis with some Merremia, between Nanepil and Palikir, Ponape I. (Fosberg, July 1946).



Figure 27b. Same, with secondary Hibiscus tiliaceus forest in background, Cynthea sp. in center, same location. (Fosberg, July 1946).

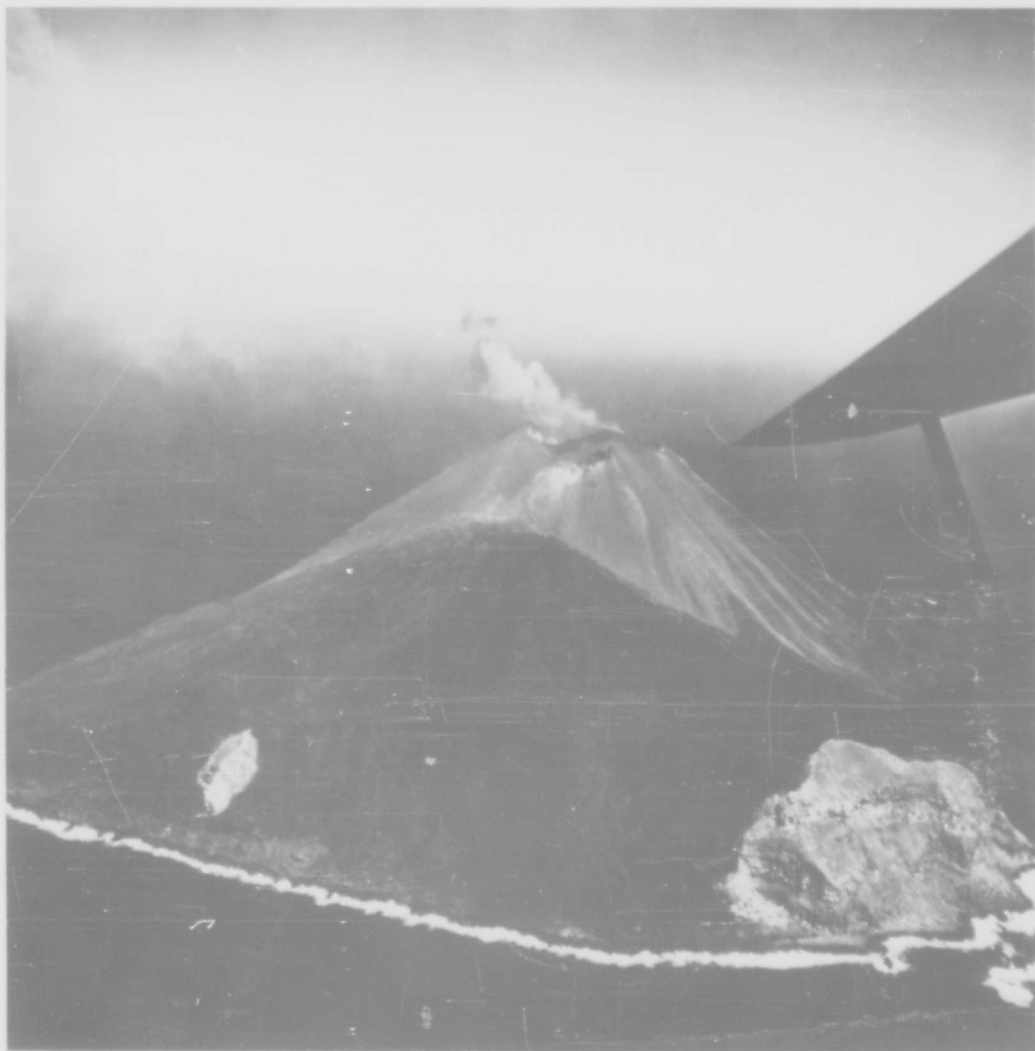


Figure 28. Uracas Island (Farallon de Pajaros), northern Marianas, showing fresh ash and lava slopes, two exposures in the foreground of older rocks which bear the only vegetation on the island, thin grass and sedges. (U. S. Navy Photo, Mar. 1953).

Figure 29. Northern Marianas.



Figure 29a. Secondary vegetation south of village, Agrihan (Agrigan) I. (Fosberg, Jan. 1950).



Figure 29b. Short grass on flat back of shore, coconut plantation in background, north end of Pagan I. (Bonham, 1954).

Figure 30. Pagan, northern Mariams.



Figure 30a. "Freshwater Lake," lined with Casuarina, ash slopes above with Miscanthus, cliffs with thicket. (Fosberg, Jan. 1950).



Figure 30b. Patch of young Casuarina on lava flow surrounded by ash beds with Miscanthus, caldera floor near "Freshwater Lake". (Fosberg, Jan. 1950).

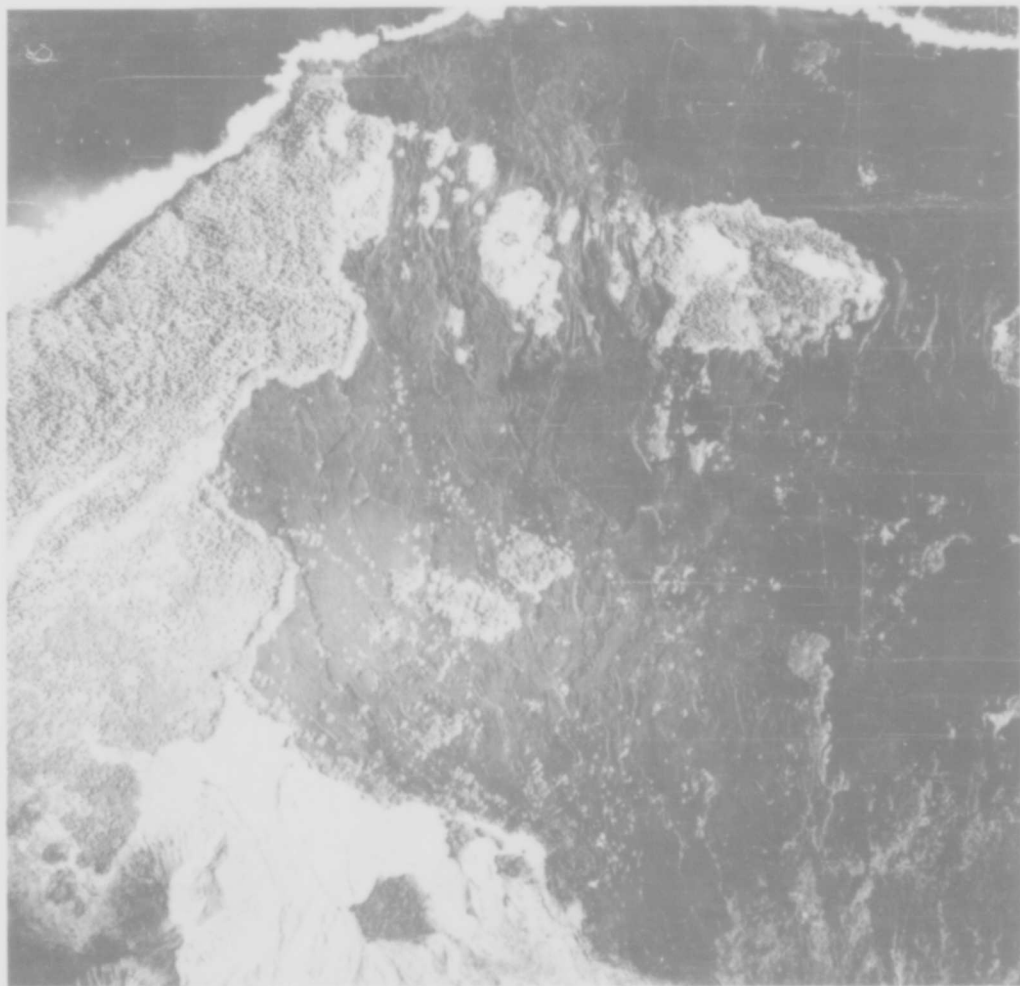


Figure 31. Vertical aerial photo of Pagan I. showing lava flow being invaded by Casuarina. The dark areas are bare lava; the lightest are Miscanthus, usually on ash beds; medium dark is forest; medium light gray secondary scrub; the strongly speckled gray with regular arrangement is coconut plantation; light gray spots on lava and border around lava are Casuarina. (U. S. Navy).

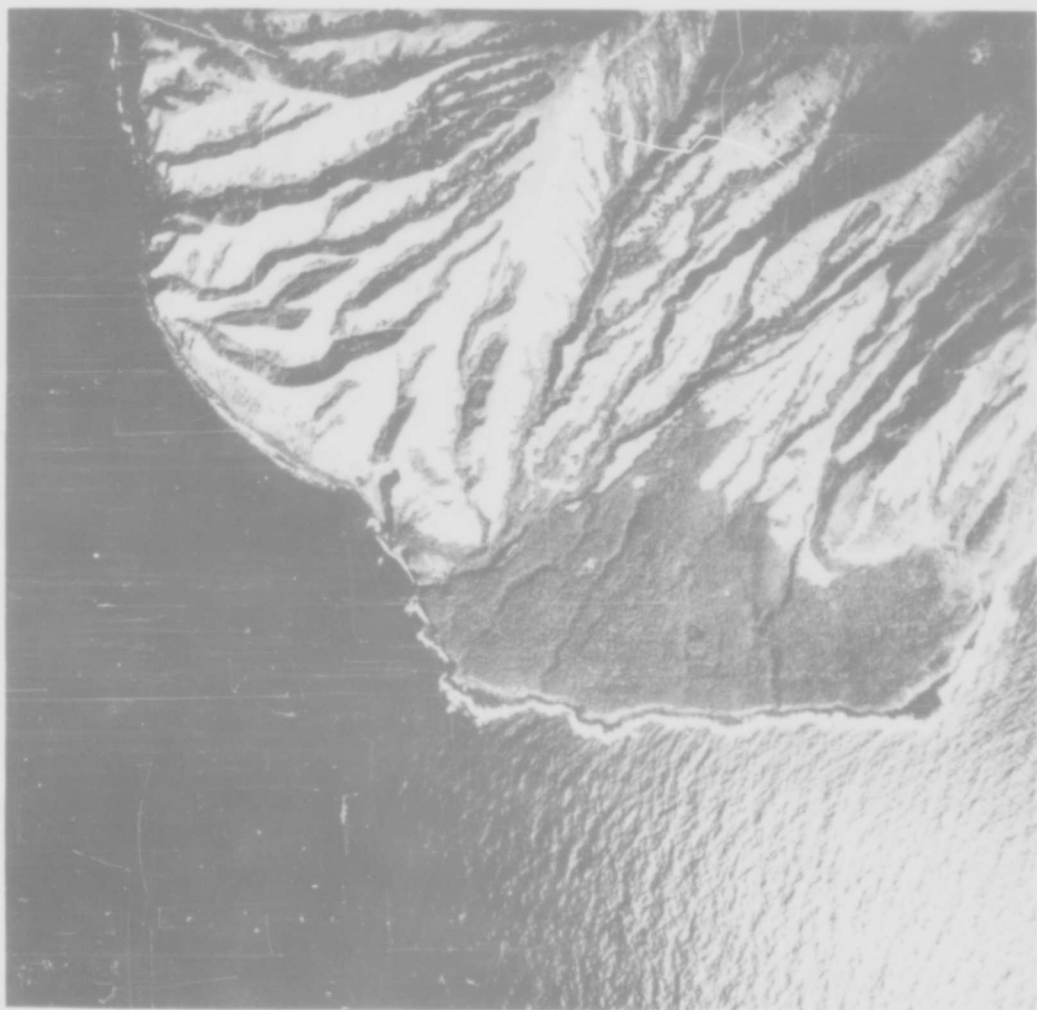


Figure 32. Vertical aerial view of south side of Alamagan I., showing coconut plantation, Miscanthus-covered ash slopes, and wooded ravines. (U. S. Navy, Jan. 1952).

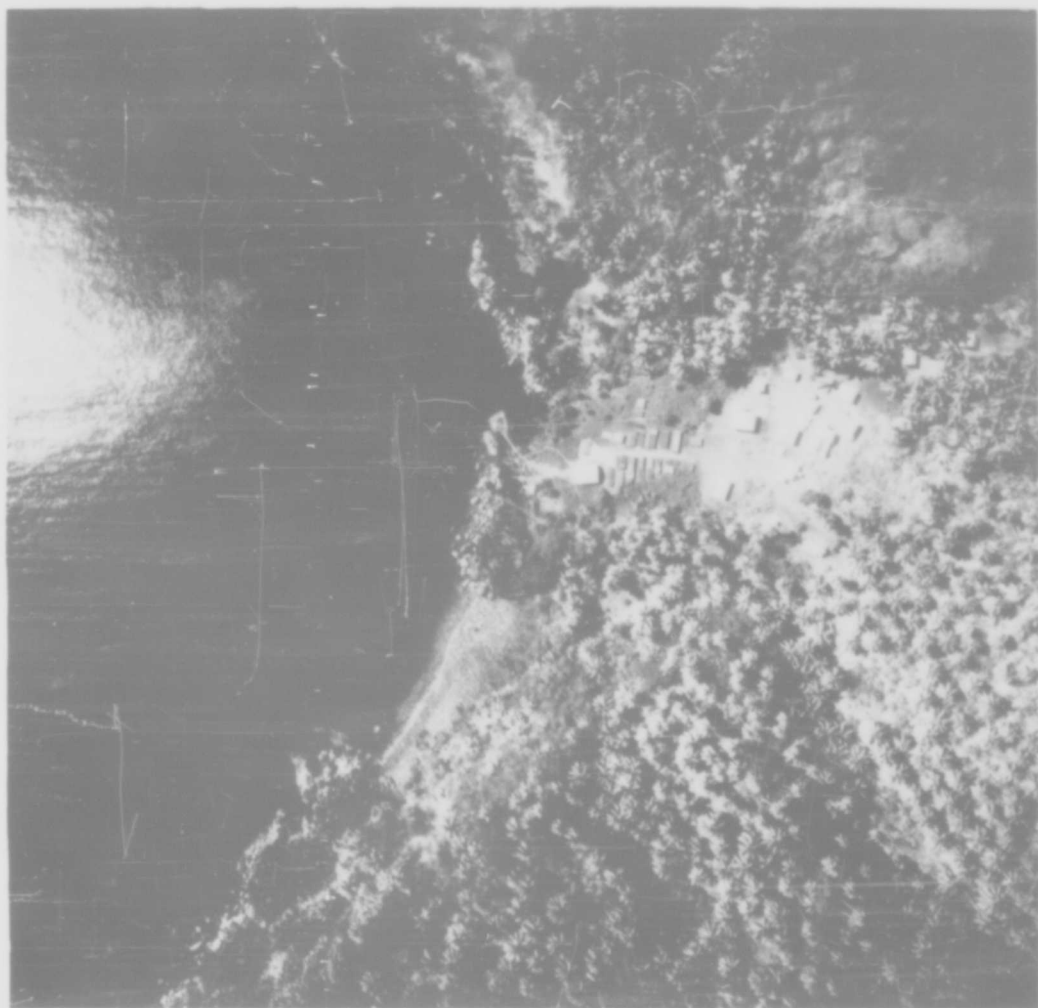


Figure 33. Northwest Village, Alamagan I., with coconut plantation, bananas in openings, and between coconut trees, scrub on cliffs, and mixed forest on rough lava to right. (U. S. Navy, June 1952).

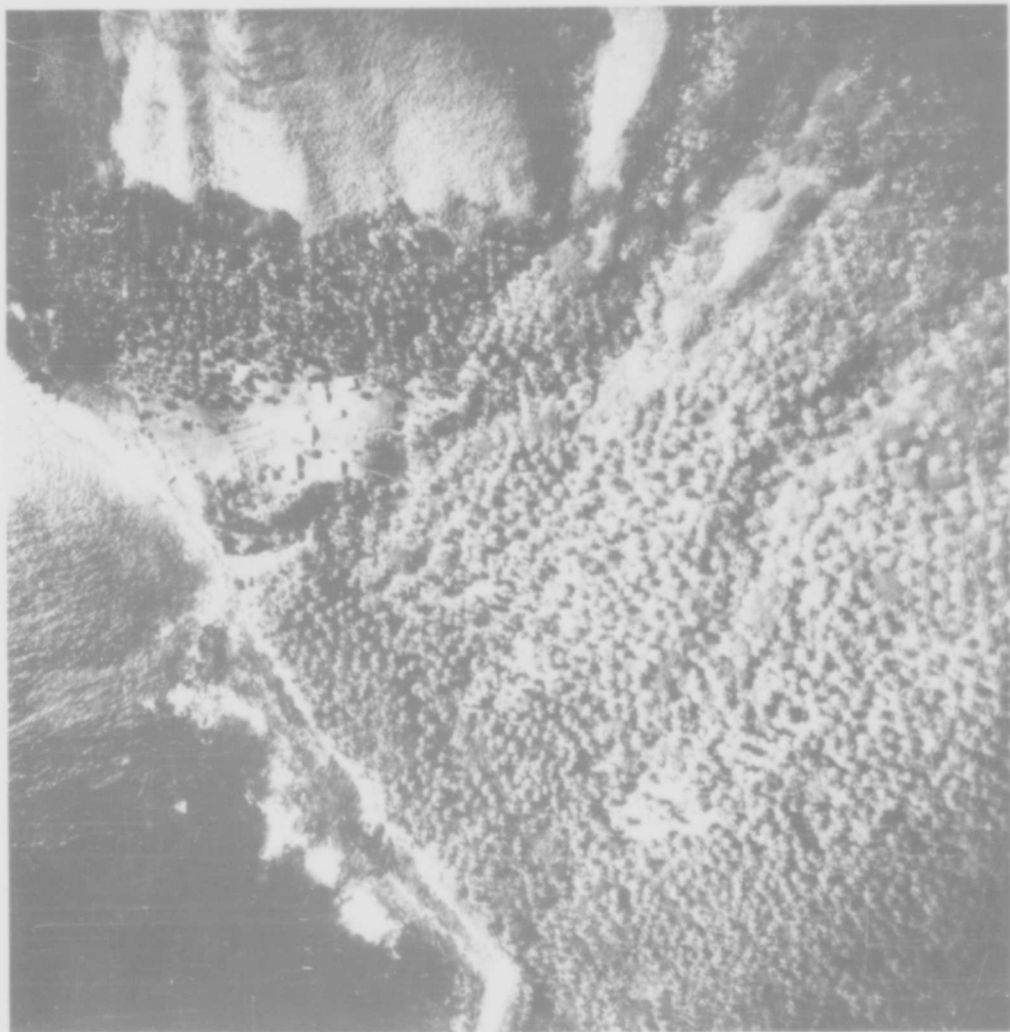


Figure 34. Southwest Village, Alamagan Island, showing coconut plantation, coconuts mixed in forest. Forest in ravines, Miscanthus on slopes. (U. S. Navy, June 1952).

Figure 35. Alamagan Island.



Figure 35a. Mixed forest on lava flow, north side. (Fosberg, Jan. 1950).

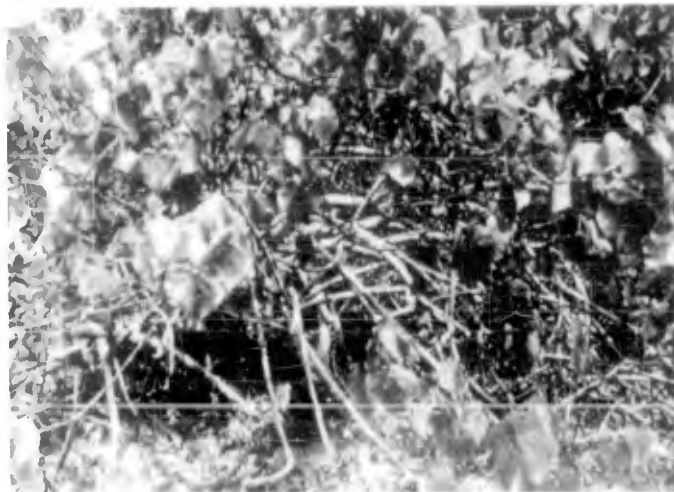


Figure 35b. Hibiscus tiliaceus tangle on lava flow, north side. (Fosberg, Jan. 1950).

Figure 36. Saipan Island.



Figure 36a. Beach forest with creepers running out on beach scrub on limestone cliffs in background, Fañuchuluyan Bay (Fañuchulyan). (Fosberg, Jan. 1950).



Figure 36b. Weedy secondary vegetation along road north of Tanapag. (Fosberg, Jan. 1950).

Figure 37. Saipan Island.



Figure 37a. Forest and thickets on limestone, with an abandoned patch of sugar cane, north of Mt. Tapochau. (Fosberg, Jan. 1950).



Figure 37b. Patch of Acacia confusa forest on limestone. (Fosberg, Jan. 1950).

Figure 38. Saipan Island.



Figure 38a. Operculina ventricosa forming thick mat, Hagman peninsula. (Fosberg, Jan. 1950).



Figure 38b. Scrub on rough limestone, Hagman peninsula. (Fosberg, Jan. 1950).

Figure 39. Lake Susupe, Chalan Kanoa, Saipan Island.



Figure 39a. Casuarina trees, Scirpus in water.



Figure 39b. Casuarina trees, Hibiscus tiliaceus scrub, and Paspalum vaginatum grass.

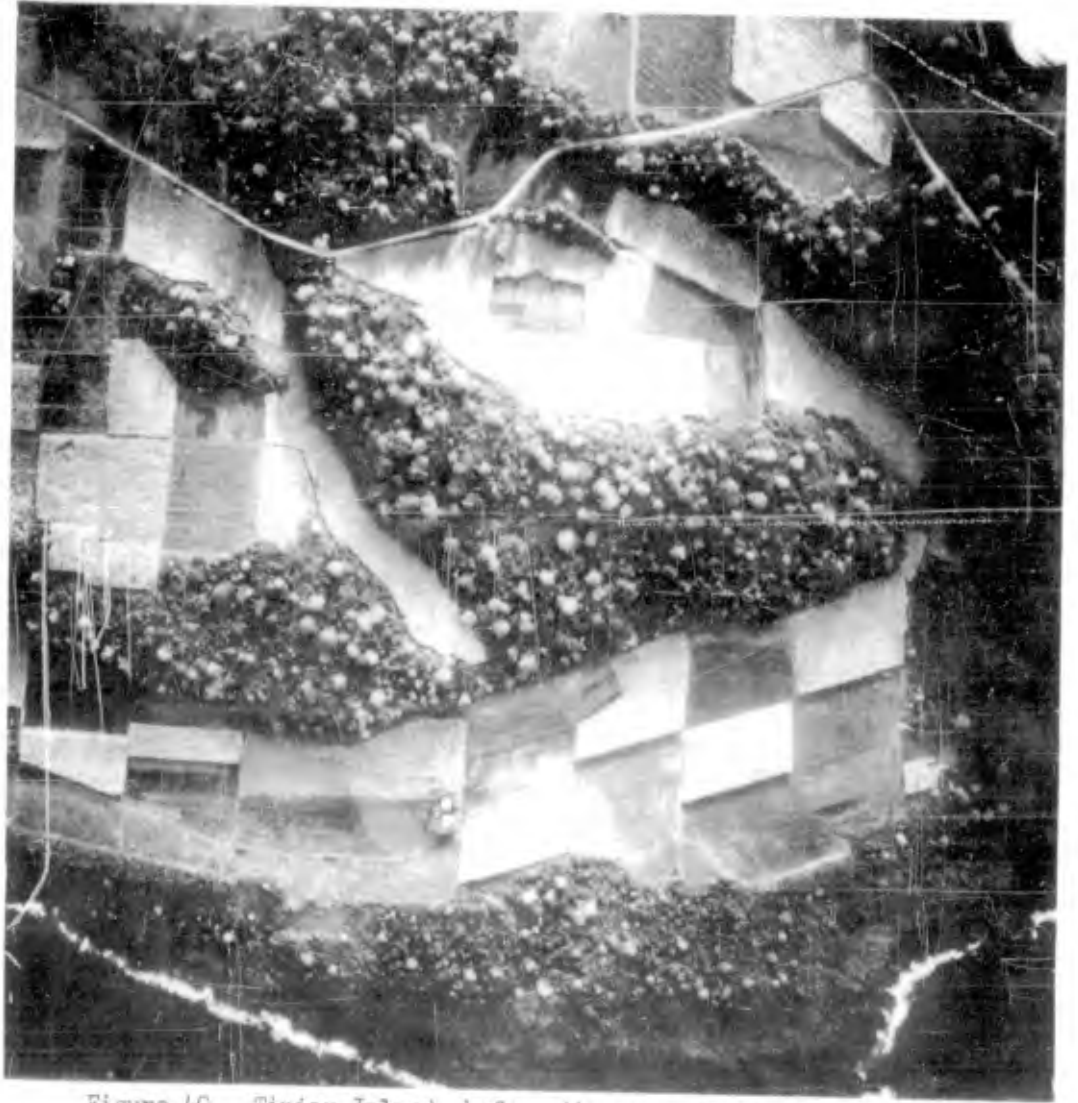


Figure 40. Tinian Island, before the war, showing terraces planted to sugar cane, with the bluffs of rough limestone between densely forested. (U. S. Navy?).

Figure 4l. Aguijan (Aguiguan) Island.



Figure 4la. Forest on lower limestone terrace.  
(C. J. Davis, Nov. 1955).



Figure 4lb. Pemberton's Peak from west end,  
forest on rough limestone. (C. J.  
Davis, July-Aug. 1954).

Figure 42. Aguijan (Aguiguan) Island.



Figure 42a. Aerial view toward southeast showing abandoned sugar cane fields, wind breaks, former Japanese village in trees to right, on top plateau of island. (C. J. Davis, Nov. 1955).



Figure 42b. South end of terrace showing dead sugar cane with *Cassia* coming up in it, trees on former Japanese village site, *Acacia confusa* on left, *Casuarina* on right. (C. J. Davis, Nov. 1955).

Figure 43. Aguijan (Aguijuan) Island.



Figure 43a. Grassy vegetation and goat eaten trees on top terrace. (C. J. Davis, July-Aug. 1954).



Figure 43b. Open forest, badly damaged by goats, lowest terrace on southwest side of island. (C. J. Davis, July-Aug. 1954).

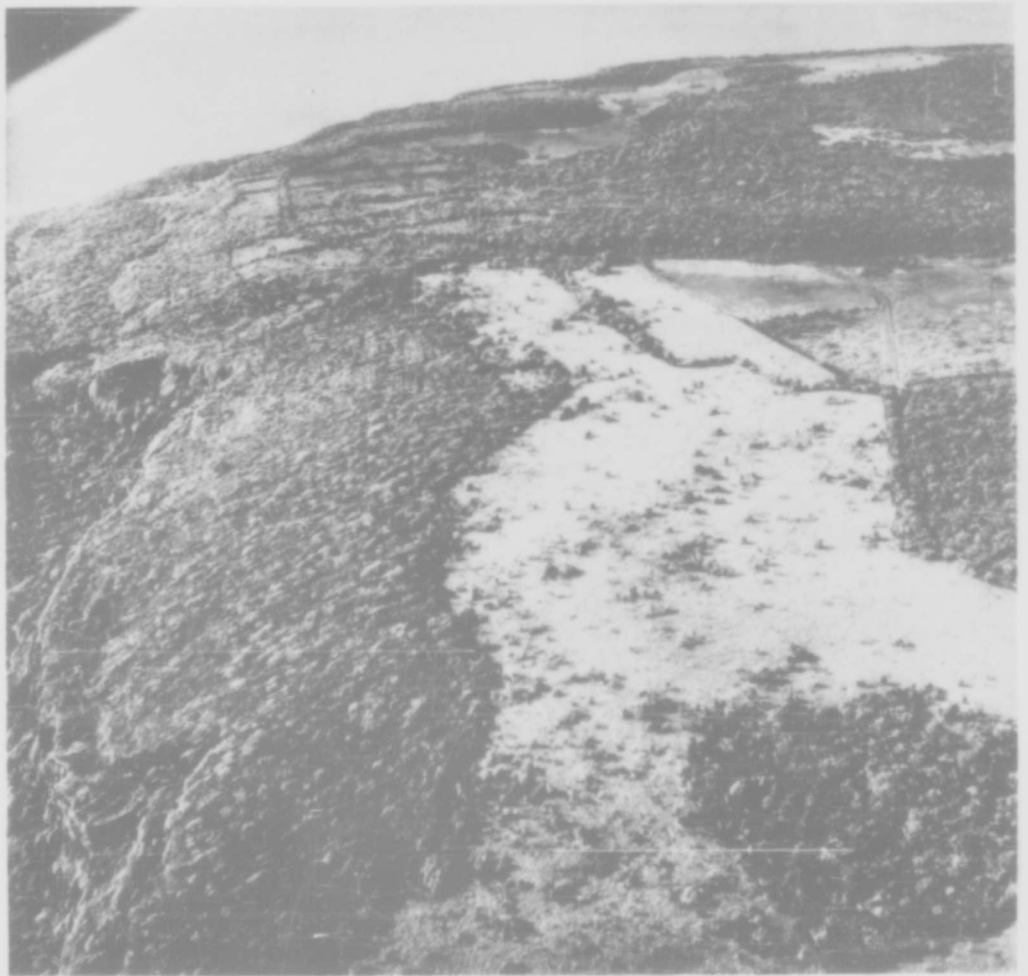


Figure 44. Oblique aerial view of Rota showing flat terrace, formerly cultivated covered by a mat of Passiflora foetida and Ipomoea indica, being invaded by shrubs, and secondary forest trees, forest on rough limestone and on cliffs, cultivated land and wind breaks in the distance. (U. S. Navy?).

Figure 45. Rota Island.



Figure 45a. Mt. Taipingot, southwest peninsula, showing limestone terraces, scrubby secondary vegetation on abandoned field in foreground. (Schlanger, 1952).



Figure 45b. South slopes, limestone above, densely forested, deeply weathered volcanic soil, grassy with wooded ravine. (Schlanger, 1952).



Figure 46a. Hills with Miscanthus, scattered Casuarina, patches of ravine forest, above Merizo. (Fosberg, Sept. 1956).



Figure 46b. Erosion scars at Dandan, being revegetated by Gleichenia and other pioneer plants. (Fosberg, Jan. 1954).



Figure 47a. Active erosion scar in deep red clay soil, scattered small Casuarina trees, some skeletons of Casuarina persisting in eroded areas, east of Apra Heights. (Fosberg, Sept. 1956).



Figure 47b. Miscanthus floridulus and Phyllanthus saffordii at edge of erosion scar, above Merizo. (Fosberg, Sept. 1956). 151

Figure 48. Guam.



Figure 48a. Savanna with Dimeria, Miscanthus, Scaevola, and Casuarina, east of Apra Heights. (Fosberg, Sept. 1956).



Figure 48b. Patch of ravine forest, mostly Pandanus, with coconut palms, weedy Miscanthus with Hyptis in foreground. (Fosberg, Jan. 1954).

Figure 49. Guam



Figure 49a. Pandanus savanna above Merizo.  
(Fosberg, Sept. 1956).



Figure 49b. Miscanthus growing on limestone, east slope  
of Mt. Almagosa. (Fosberg, Jan. 1954).

Figure 50. Guam.



Figure 50a. Pandanus tectorius with fruit, Merizo. (Fosberg, Sept. 1956).



Figure 50b. Pandanus tectorius with staminate inflorescence, Merizo. (Fosberg, Sept. 1956).

Figure 51. Guam.

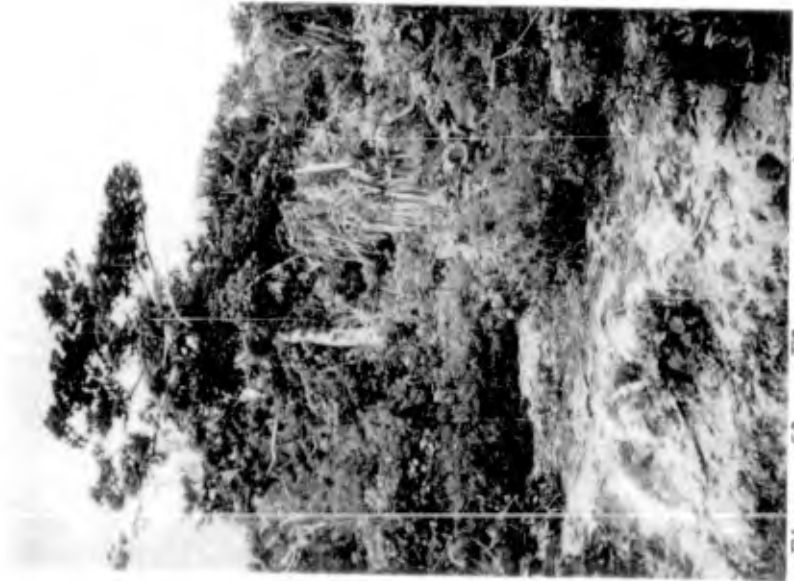


Figure 51a. Elaeocarpus toga in forest on limestone near Yigo. (Fosberg, Jan. 1954).

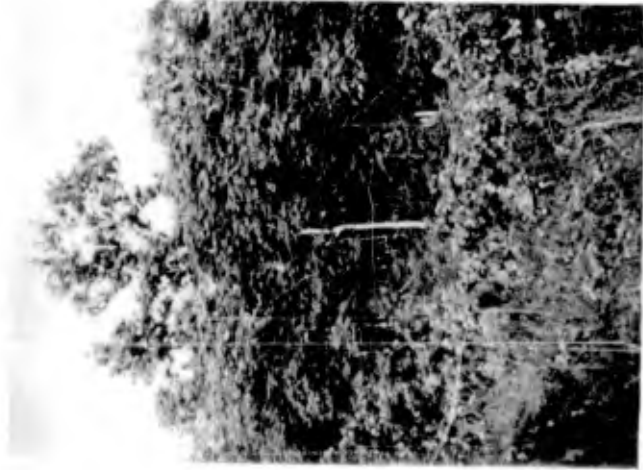


Figure 51b. Cananga odorata forest above Fena Dam. (Fosberg, March 1950).

Figure 52. Guam.



Figure 52a. Mixed forest on rough limestone with Heberospathe elata palms and Artocarpus, Fonte River. (Fosberg, Jan. 1950).

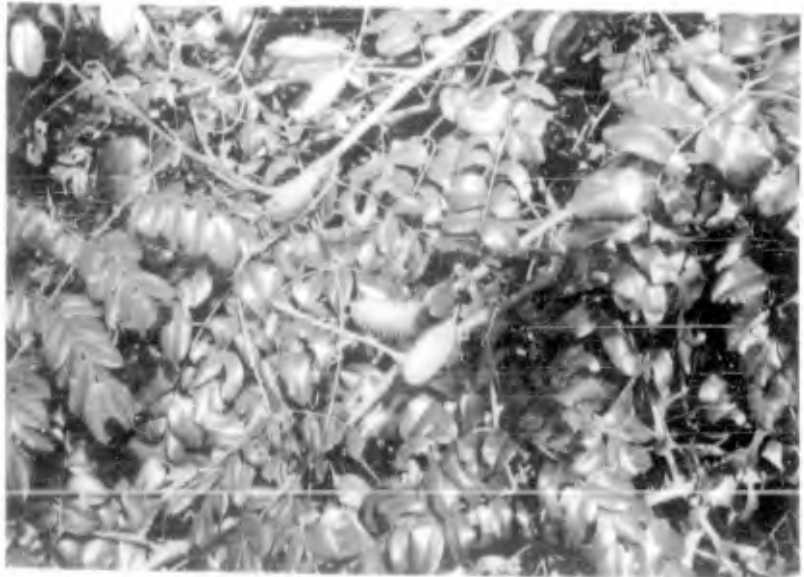


Figure 52b. Caesalpinia major, prickly vine, near Agafa Guras. (Fosberg, Jan. 1950).

Figure 53. Guam.



Figure 53a. Ravine in savanna filled by Phragmites karka, Pandanus in foreground, Casuarina in back, east of Apra Heights. (Fosberg, Jan. 1954).



Figure 53b. Panicum marsh surrounded by reeds (Phragmites karka), base of Orote Peninsula. (Fosberg, Jan. 1954).

Figure 54. Guam.

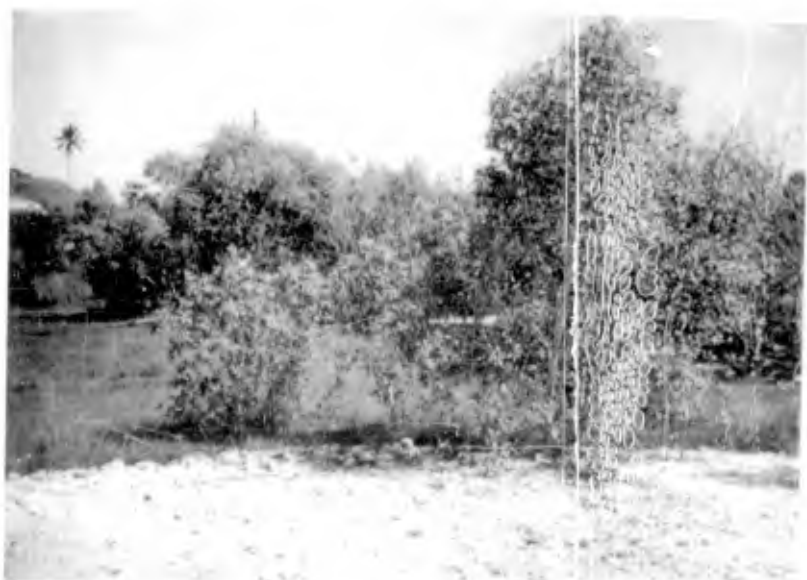


Figure 54a. Brackish marsh with Paspalum vaginatum and Avicennia trees, near Camp Bright, south of Orote Peninsula. (Fosberg, Jan. 1954).



Figure 54b. Brackish marsh with Paspalum vaginatum and patches of Scirpus. Gravel in foreground thrown into marsh by storm. Near Camp Bright. (Fosberg, Jan. 1954).