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Vegetation of Central Pacific Atolls, A Brief Summary

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VEGETATION OF CENTRAL PACIFIC ATOLLS, A BRIEF SUMMARY[1]

by
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[1] Publication authorized by the Director, U. S. Geological Survey.

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Contents

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Introduction

One of the primary purposes of the meeting on Atoll Soils and Vegetation, held in St. Louis in December, 1952, was to summarize the results, insofar as vegetation is concerned, of the three Pacific Science Board atoll investigations, undertaken on Arno, Onotoa, and Raroia atolls, along with results of recent expeditions to the Marshall Islands by William Randolph Taylor and F. R. Fosberg. Formal papers were not prepared for this meeting, nor was a verbatim record kept of the discussion. It seems worth-while to briefly summarize what is known of Pacific atoll vegetation in light of the results of the St. Louis meeting and of other significant studies that have been made. No attempt will be made, however, at this time to digest the complete literature on the subject. Work is being done on such a project, but it will require much more time.

Unfortunately the reports on the vegetation of Onotoa and Raroia have not yet been submitted, so that the greater part of the following summary is based on studies in the Marshall Islands. The vegetation of some of these islands has been observed by Bryan in 1944, Taylor in 1946, Stone and Anderson in 1950, Hatheway in 1952, and Fosberg in 1946, 1950, 1951, and 1952. Detailed notes are available for Arno, Bikini, Eniwetok, Rongerik, Rongelap, Pokak, Bikar, Utirik, Taka, Ailuk, Jemo, Likiep, Lae, Ujae, Wotho, Ujelang, and parts of Kwajalein, with less satisfactory observations on Majuro, Jaluit, and Ailinglapalap. Fairly good information is available on Nomwin, Kapingamarangi, Nukuoro, Satawan, and Lukunor in the Carolines, also some on Kayangel and Pingelap. The only comprehensive modern study of atoll vegetation, other than those mentioned above, whose results are available, is that of Christophersen on the Whippoorwill Expedition in 1924 (Christophersen 1927). Incidental to other work some notes on vegetation on the southeastern Pacific and a few central Pacific atolls were made by St. John and Fosberg in 1934 and on Christmas Island by Fosberg in 1936. Only a few of these are published (St. John and Fosberg 1937, Fosberg 1937, Fosberg and St. John 1952). Hatheway investigated Canton Island on short visits in 1950 and 1951 and prepared an account that is still unpublished.

The Atoll Habitat

Atolls are reefs of organic limestone that are partly, intermittently, or completely covered with water, and on which there are islets or islands made up of accumulations of limestone debris, loose or consolidated, and occasional remnants of former higher reef surfaces. These islets are usually not more than two or three meters above high-tide level, sometimes

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much less than this; occasionally storm-built rubble or boulder ridges and wind-deposited dunes rise to somewhat higher elevations. The highest of these wind-deposited features is Joe's Hill, a dune on Christmas Island, which is variously reported to be as much as fifteen meters. Where the surface of these islets is more than a few dm. above mean tide level the drainage is perfect, down to this level. From a few cm. above mean tide to somewhat below it, lens-shaped bodies of fresh to brackish ground water lie in the porous material of the islands, floating on the surface of the salt water which otherwise permeates these structures and held there in equilibrium by friction with the solid material.

Since the atolls are practically entirely within the tropics, and also are surrounded by water, there is not much temperature variation. Rainfall and winds, however, show quite a diversity. Rainfall ranges from extremely scanty in the belt of atolls along the equator and in the northern Marshalls and southern Gilberts to very heavy in the southern Marshalls and Caroline atolls. Most of the atolls, of course, have a moderately wet climate. In some, though the total average rainfall may be moderate, the erratic precipitation makes the total figures give a false impression. Also, the porous nature of the substratum makes comparison with regions of ordinary soil difficult. For example, Pokak Atoll, with rainfall comparable to that of parts of the eastern United States, has the aspect, vegetationally, of a semidesert. Winds are important in three main respects. The drying power of a steady fairly strong breeze, even after it has blown over the sea for great distances, is extreme, and the effects of wind on the vegetation in the trade wind belts are very obvious. It is never difficult to tell which side of an atoll islet is the windward side, as the vegetation is commonly "wind-sheared" (probably more correctly spray-sheared in many cases) in an inclined plane down to the top of the beach. On the leeward side the edge of the vegetation is usually perpendicular or rounded. The salt carried in spray by winds undoubtedly has a very important effect on the vegetation. There have been no actual measurements of this, either as to quantity or effects, however. The absence or rarity of certain species of plants on the windward sides of islets in windy belts may very well be due to this salt accumulation. The third climatic factor of great significan is the occurrence of typhoons or hurricanes. These powerful storms create and destroy land, drench the land with salt water, remove vegetation, modify it, and indirectly affect it through changing the human population. They create a type of long-term instability of the habitat that is reflected in the character of the vegetation in several ways which are apparent to the observer, but which must be studied more critically than they have yet been to be understood. In some of the Marshalls, considerable areas have been denuded of their vegetation or most of it by relatively recent typhoons.

The age of these islands is an important consideration, ecologically. It is possibly ascertainable, within certain limits, through knowledge of the relatively recent eustatic fluctuations of sea level, though there is some difference of opinion on both the time and nature of these fluctuations. The current idea seems to be that a period of higher levels, perhaps two meters above the present stand, occurred several thousand or up to five thousand years ago, during the so-called post-glacial "xerothermic period" or "climatic optimum." If such a higher sea level did exist, it might not

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be necessary to regard ecological reasons only, as responsible for the impoverished floras of coral atolls. It may well be that dry land did not exist on most atolls at that period, and that these floras have come into existence through accumulation of chance seaborne and airborne colonists in a period as short as five thousand years.

In the biotic environment, sea-birds, land-crustacea, and man are the three most conspicuous groups and probably the most important, ecologically. The birds played a most important part in making the habitat favorable for plants and in maintaining it so, by additions of phosphatic and nitrogenous material, until they were driven away from most places by man. Land crabs and hermit crabs, present in myriads on most atolls, promptly reduce organic matter of most sorts to soil, tending to make the habitat suitable for other than the most extreme pioneer species of plants. They must also play an important role in mixing soils, because of their burrowing habits, bringing up deposited and unaltered materials and burying vegetable debris (Wood-Jones, 1910). Dr. Otto Degener (conversation, 1950) contends, also, that the hermit crabs are important in devouring seedlings of plants and thus impoverishing the vegetation. This has not been noted by other investigators, though they have been seen occasionally eating leaves from living plants. Man has, ever since his arrival, been an extremely destructive agent, especially toward indigenous forest vegetation. He has, of course, replaced it with coconut and breadfruit plantations and their attendant weed species; he has contributed a host of exotic weeds; and he has upset the phosphate balance both by driving away the sea-birds and by exporting untold quantities of copra, which has a high phosphorous content. He also, in many places, burns the organic matter which would ordinarily go to build up the soil. Where he exists in large populations, he may reverse these processes to some extent by composting and fertilizing.

Colonization by Plants

Plant seeds may be brought to an atoll islet by water, wind, on the feet, plumage, or in the stomachs of birds, or by man, accidentally or deliberately. One case has been observed by Dr. Kenneth Emory on Kapingamarangi of a portion of a tree drifting ashore while still alive and taking root. An examination of the floras indicates that, before the coming of Europeans, the water was probably much the most effective means of transport. Most of the plants possess adaptations for floating their seeds across even large expanses of water.

The plants that make up almost the entire indigenous floras of atolls are those that constitute the strand floras of high islands, continents, and other coral islands, and they are mostly very widespread. There are very few species confined to or even principally found on atolls.

Contrasted with the probable situation on high islands, successful establishment of transported plants on atoll islands is a very frequent affair. Abundant seedlings from drift seeds may be seen during almost any walk along the beaches of an atoll. These are, of course, mainly the same series of pioneer species, over and over again. The following species were seen as drift seedlings in the northern Marshalls:

Abundantly establishing themselves in drift:

Messerschmidia argentea
Scaevola frutescens
Lepturus repens
Guettarda speciosa

Rather frequently seen:

Pandanus tectorius
Portulaca lutea (in drift situations but not positively of drift origin)
Triumfetta procumbens
Vigna marina

Rarely seen in drift:

Cocos nucifera
Ipomoea pes-caprae
Hernandia sonora
Calophyllum inophyllum
Intsia bijuga
Morinda citrifolia
Barringtonia asiatica
Suriana maritima
Terminalia samoensis
Wedelia biflora
Ipomoea tuba

Seen as seedlings, once each, but never seen to persist:

Caesalpinia majus
Caesalpinia crista

A number of kinds of seeds frequently drift ashore but were not seen germinating. Among these were Entada and several species of Mucuna.

Although not directly observed, colonization by many other species unquestionably takes place. Many species do not seem to be able to survive on open beaches and bars, but need either the protection from wind and salt or shade from the sun provided by already established vegetation or the presence of at least a small amount of humus in the soil. Some deeprooted species doubtless require a certain degree of freshness in the ground water. The species that require the presence or influence of other plants, as well as those that need fresh ground water, are commonly found in the interior of islets, though they often may be much nearer the lagoon than the seaward beaches.

How their seeds are carried to such situations is not always apparent. Unquestionably Pisonia is carried around by birds. Its fruits are exceedingly sticky and a noddy (Anous) was seen on Wotho literally plastered with them. Several species of birds seem to prefer to roost and nest in Pisonia trees. Boerhavia and Peperomia, as well as Adenostemma, also have sticky fruits and may be transported by birds. Cassytha and Pipturus have small fleshy fruits, which doubtless are eaten by birds and the stones transported in birds' stomachs. Which birds would do this is not demonstrated. Scaevola is, without question, carried around in this way in addition to floating, as the droppings of curlews were seen to be commonly packed with the stones of this plant. Ximenia might be carried in the same way, though its fleshy fruits ./

are quite large, resembling small plums. Another aspect of this, not previously suspected, was discovered on Arno by Marshall (1951). He found in the stomach of a fairy tern (Gygis) the seed of Ipomoea pes-caprae, a plant not even growing on Arno, but common on Majuro, a few miles away. Why the bird had eaten this is not apparent, as terns are fish-eaters. Perhaps the seed was picked up to serve as a gizzard-stone. Wind doubtless accounts for some small-seeded species, but there are few indigenous atoll plants that seem especially adapted for this method of transport, except the ferns, mosses, and other cryptogams. Plants with floating fruits or seeds, such as Ochrosia, Thuarea, Cordia, and the ones mentioned above as pioneer species, since they may be found growing back of or far from the beach, must sometimes be carried inland by storm waves, as is the occasional pumice found scattered on the ground surface far inside the beach. Man must not be disregarded as an agent of distribution, even of apparently indigenous plants, as well as of his cultivated ones and camp-followers. Sida fallax is planted about houses in the Marshalls and Carolines, as well as growing wild. Evidence seems to be accumulating that the mangroves, at least Bruguiera, found in landlocked pools and muddy depressions have been deliberately introduced and planted by the Marshallese. And in addition to planting the various obviously useful and ornamental plants, the Gilbertese, at least, (Luomala m.s.) pick up and plant any seeds that happen to be cast up on the beach. A further influence is exerted by man in the creation of habitats for species which otherwise might seldom find a place to get a foothold. Such are especially the taro-pits, dug down to ground water and filled with vegetable muck. Several weeds, such as Eleocharis, Cyperus, Jussiaea, and a number of ferns are found only or usually in such situations. The coconut plantation is also a rather special habitat and may, at least, give some plants enormously more opportunities or "lebensraum" than they normally would have. Willis and Gardner (1901) give a much more comprehensive discussion of these matters for the Indian Ocean atolls.

Little is known about the reasons for the small numbers of species in atoll floras. These range from three (Christophersen 1931, Fosberg 1937) to perhaps 150 in Pacific atolls and as many as 284 (Willis and Gardner 1901) in those close to continents as the Maldives in the Indian Ocean. Distance from sources of colonists and the effectiveness of the ocean as a barrier are obviously of primary importance. Shortness of the history of land availability on atolls may well be another consideration. The scarcity of endemic species results from this. Lack of topographic or altitudinal diversity is another obvious factor. However, the difficulty in getting many of the commonly tried cultivated species to grow in these islands and the large number that simply will not grow there, at all, point to the importance of edaphic considerations, though these have not been much analyzed as yet. Salinity and the highly calcareous nature of the soils are two unquestionably controlling factors. Such observations as the distribution of species in relation to ground and aerial salinity, the death of breadfruit trees where washed by typhoon waves or where the ground water becomes saline (Cloud 1952), and the native practice of leaving a protective strip of forest on the windward sides of coconut plantations are at least indicative in this direction, though systematic studies remain to be done. Certainly one of the most striking systematic variations observed is the increase in number of species from atolls with a dry climate to those with a wet climate. Pokak and Bikar,

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in the dry extreme north of the Marshalls, have 9 species of vascular plants each, while from Arno, in the wet south of the same group are recorded 129 species (Anderson 1951, Stone 1951). This discrepancy is not due to inadequate collecting, as Pokak and Bikar have been very thoroughly examined. Any further collecting may result in increasing the difference, as more plants may possibly be found on Arno while this is not likely on the others. There are doubtless other limiting or controlling factors and combinations of factors influencing the sizes and compositions of atoll floras, but to discover and understand them will require further study and further correlation of available information.

Succession or Vegetational Change

No coral atoll has had sufficient study for even the principal vegetational successions to be well known. No single succession, from bare ground to a relatively stable vegetation, can be described in anything like a complete fashion. Only locally are relatively stable (climax) vegetation types known with certainty. But it is possible to outline, however roughly, some probable successional trends, and to point out with some confidence certain successional relationships that are more than accidental. In this paper any change in vegetation that seems to proceed in a definite direction is regarded as a succession. This is in contrast with fluctuations around a point of equilibrium. And if the latter, over a period of time, result in a directional change in the equilibrium, that also is regarded as a succession. Such changes as are known or suspected are described below under several categories.

1. Usual development of vegetation:

As noted above, under Colonization, bare sand and gravel bars are soon covered by seedlings of a small number of pioneer species. These are able to stand full and very bright sun and high salinity, also considerable dryness. Of these, a large proportion are tree species, and, in an ordinary mixed stand of pioneer species, many will be trees. In most sites scrub is the first vegetation to appear, and if tree seedlings form an important component, these soon overtop the others, developing a low forest. Growth, even under quite dry conditions, is extremely rapid. On Wake Island, with an annual rainfall of 650-1370 mm., *Messerschmidia* has been observed to grow almost two meters in a year. The simplest forests thus formed are pure stands of *Messerschmidia*, mixtures of *Messerschmidia* and *Guettarda* alone, or with *Pandanus tectorius* and a varying smaller proportion of a number of other trees. *Terminalia samoensis*, *Intsia bijuga*, *Barringtonia asiatica*, and possibly *Cordia subcordata* are pioneer species and may make up a part of the original composition of such a stand. There is no doubt, however, that they, as well as *Guettarda* and *Pandanus* are also capable of increasing in number in mixed stands. *Pisonia grandis*, *Allophylus timorensis*, *Pipturus argenteus*, *Soulamea amara*, *Ochrosia oppositifolia*, and other species are, so far as known, added only after the original stand has become established and usually after it has assumed the character of forest. The resulting mixed forest is the commonest type of native forest existing in the Marshalls today. The same type apparently develops following clearing by man. In the northern Marshalls there is no particular pattern in the arrangement of

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species in this type of forest, but Hatheway (1953) reports that in the southern Marshalls the trees commonly occur in small clumps or groves of a single species.

The shrub and herb species present in the original stand persist for a long time in these forests as undergrowth and ground cover. Eventually, however, they may be almost entirely eliminated. Lepturus, curiously enough one of the first and most abundant pioneers to appear, often persists longest, forming a thin grass ground cover in all but the most dense mixed forests. With it is usually Thuarea, which was not seen as a true pioneer on new habitats in the northern Marshalls. Fimbristylis, also one of the pioneers, often persists a long time, especially if the canopy is not too dense. Wedelia and Ipomoea tuba may persist a long time, the latter probably becoming more abundant as time goes on. It is an important part of the canopy in many mixed forests. In rocky places Fleurya ruderalis persists a long time if the canopy is at all thin.

Whether this mixed forest ever reaches stability is not known. Its widespread occurrence suggests that it may, as does the structure of the most mature and well-developed stands, with large trunks, dense canopy, thin or absent undergrowth, and seedlings of some of the dominant species. It seems certain that Messerschmidia, one of the most abundant early constituents, drops out after one generation. Healthy seedlings of it are never seen in full shade, and when it is present in a very well developed mixed forest the trees are all old and very large. Messerschmidia logs are often seen lying in this type of forest where there are no living trees. Observation of Pisonia, with its habit of sending up root sprouts and of usually taking root wherever it touches the ground when blown down, suggests that it may gradually take over mixed forest if left long enough. Common occurrence of pure stands of Pisonia may be due to this process. These may, however, result also from colonization of Pisonia in Lepturus grassland, as seen on Pokak Atoll. This might more commonly be the case on drier islands, where stands of Lepturus, or Lepturus and Sida fallax often persist for a long time.

There seems little question that, at least under conditions of moderate rainfall, such as in the central Marshalls, Ochrosia oppositifolia may eventually dominate mixed forest once it gets started, and often will take over completely, forming extensive pure stands. The best areas seen of this type are on Wotho Atoll, but it is a common occurrence on Lae, Ujae, Kwajalein, and Erikub, at least. There is good evidence that it will eventually crowd out even Pisonia. Pure stands of Ochrosia are relatively permanent and stable as shown by the normal occurrence of a dense ground cover of seedlings several dm. tall, which shoot right up if even a little light is available. One puzzling circumstance about these stands of Ochrosia is the presence of persistent yellow spots, seen in the same locations on photos taken in 1944 and on the ground in 1951. The trees are chlorotic and in some cases there are a few dead ones, and in these places Allophylus and even other trees seem able to come in. There is no obvious difference in soil or other environmental factors in these spots.

Frequency of pure stands of various species is a peculiarity of atoll vegetation, at least in the northern Marshalls; pure stands of Pandanus and Pisonia and perhaps others are also found in central and southeastern Polynesia. How this is related to the general successional picture is not

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apparent, except perhaps in the cases of Pisonia and Ochrosia. These and at least some of the other pure stand types may very possibly be end stages of successions under certain conditions. This is certainly not the case, though, with such pure stands as those of Lepturus, Portulaca, Scaevola, Messerschmidia, Pemphis, and other strictly pioneer plants. Pure Pandanus forests, while rare in the Marshalls, seem to occur more commonly in the Tuamotus, also on Maria Atoll, Austral Group. Their origin is a matter of great interest and curiosity.

On bare rock, especially rough conglomerate or pitted beach rock, Pemphis acidula is ordinarily the first plant to appear, though actual seedlings colonizing such habitats have seldom been observed. Hatheway (1953) says that small pockets of sand on such rock surfaces are the seed beds for this species. Once established on rocky places, these trees persist, often or usually in pure stands, even where their roots are bathed in pure sea water at high tide. Such stands were not observed to be succeeded by anything else.

2. Effects of catastrophe and instability:

Natural catastrophes on coral atolls are mainly of two sorts, typhoons (hurricanes) and tsunamis (so-called tidal waves). The former are, of course, much more frequent than the latter, and their frequency varies much more in different parts of the world. Typhoons are almost unknown, for example, in the Gilberts, somewhat more frequent in the Marshalls, and common in the western Carolines. Statistics on typhoon incidence would be very valuable in interpreting vegetation differences.

Both typhoons and tsunamis are capable of sending salt water completely over atoll islets. There are apparently no actual records of the effects of tsunamis on atolls, but they have poured water onto high island shores to a much greater height than the total altitude of most atolls. Certain plants would undoubtedly be killed by this, but few facts are available. Breadfruit, at least, has been observed to be so killed by salt storm waves (Cloud 1952).

Typhoons, in addition, commonly uproot trees of all sizes. They defoliate trees both by actually tearing the leaves off and by "burning" them off by driven salt spray, and perhaps by drying at the same time. They profoundly alter both the character and topography of the substratum, and change the actual outline of islands. Large areas of land surface on Arno Atoll were actually removed during the typhoons of 1905 and 1918, vegetation and all. Some of these places have been extremely slow to becoming revegetated. In others Pemphis has taken over effectively. There is no doubt that, in many areas, instability of substratum owing to typhoons is a major ecological factor in the determination of the character of the vegetation. Even where trees are not actually blown down, soil may be removed from around their roots, or rubble or sand may be piled up around the bases, smothering smaller vegetation and possibly eliminating certain larger species. Trees blown down make openings in the canopy in which species may appear that cannot establish themselves in its shade when unbroken. Defoliation of the canopy may allow temporary undergrowth to come in.

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Effects of typhoons on the vegetation are quite evident to the observer on most atolls, but a careful assessment of these effects has not been attempted, at least in recent times. Considerable information is recorded, but most of it by casual and nonbotanical observers. The thing that is most lacking is an actual eye-witness account, by a botanist, of a severe typhoon on an atoll. Accounts by others are usually conflicting and show evidence of very unreliable observation.

Effects on the vegetation maintained by man are sometimes recorded. The coconut trees were removed, along with the rest of the vegetation, on Arno in the typhoons mentioned above. Hundreds of coconut trees were blown down on Utirik, and many on some of the other atolls in the Marshalls, especially Aur and Maloelap, by "Typhoon Georgia" in March 1951. Likiep was completely devastated and apparently rendered temporarily unfit for human habitation by a typhoon sometime after the middle of the nineteenth century. In German colonial literature are many accounts of natives on the Caroline atolls being moved because their islands were rendered temporarily unable to support them by typhoons. One of the important effects was the filling in of taro pits with sand and salt water. Many accounts of hurricanes in the Tuamotus exist, but they give very little information on the effects on the vegetation. In places, however, the coconut groves were actually swept away.

3. Effects of climatic fluctuations:

Although there are atolls with the same annual rainfall with and without pronounced yearly dry seasons, no comparisons have been made of their vegetation. So the effect of simple annual fluctuation is not known. It would probably result, at least, in less epiphytes and a smaller total flora, probably in less overall luxuriance. Pisonia and possibly some other trees would show brief defoliation during the dry season. A strong dry season in 1951 in the northern Marshalls showed in some places partial defoliation of some other trees, such as Cordia and Terminalia. Whether this was normal or only the result of an extreme fluctuation is not known. The general aspect of the more northern atolls during this particular season became quite drab, where a few months earlier it was green.

In many atolls, especially those just south of the equator--the southern Gilberts, Phoenix, Howland and Baker, Jarvis, and Malden--one of the most potent factors influencing the vegetation is the extreme fluctuation in rainfall from year to year. Sometimes more than a year may elapse with no rain at all. In other times, more than the annual average may fall in one month. Under such conditions the general aspect is much drier than the average annual rainfall would suggest. And the luxuriance may vary so much from time to time that descriptions written several years apart scarcely sound as though the same island were described. Canton Island, in the Phoenix Group, has been described as having a general growth, principally Sida fallax, up to two m. tall during a wet period, but when visited in 1949, seven or eight years later, it had the aspect of a desert. On islands with large populations of sea-birds the injurious effects of high concentrations of guano seem to be greatly accentuated by these severe dry periods. Trees may be severely damaged or even killed. This has been seen on Pokak, in the Marshalls, Canton, in the Phoenix, and Christmas Island.

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The theory, advanced by Hutchinson (1950) that phosphate deposits on islands that are at present wooded indicate a major shifting of climatic belts in the recent geologic past, so that these islands would have formerly been barren, does not seem in any way justified by the facts. Phosphate is formed on these islands at present under forest conditions, and only under such.

4. Changes caused by Man:

Alterations by Man's activities have affected the vegetation far more profoundly than typhoons, droughts, or any other natural phenomena. These have occurred in the Marshall Islands in three stages, the pre-European Marshallese period, the copra commerce period, and the Second World War. Comparable periods, or variations of them, have occurred on many other atolls. On some of the drier ones the copra commerce period has been replaced by a guano-digging period. On many the war had little or no effect. On a few, such as the Line Islands, the pre-European period was omitted, as the atolls were not inhabited when discovered by Europeans.

After the arrival of aboriginal man, the process of clearing the forests began. It could never have been very extensive, on most atolls, because of the lack of metal for clearing tools. It is probable that *Pisonia* forest may have been the principal type cleared, as the wood of *Pisonia* is soft enough to be cut by shell or stone implements. It is also possible that there was actually not much clearing, because coconut and breadfruit trees could be grown in the forests without clearing. In the case of the coconuts, at least, it might take longer for them to reach bearing age. Breadfruit, in wet climates, can shade out practically anything else likely to be found on atolls. In any event, there were probably over the centuries, fairly substantial areas dominated by coconut and breadfruit groves. Hatheway (1953) has estimated that in pre-European times perhaps fifteen percent of the land area was given over to agriculture. A part of this, on most Micronesian atolls except the driest, was used for taro pits. Marshy and swampy places were probably used for this purpose at first, then enlarged and enriched by addition of vegetable refuse. A few weeds probably came with the aborigines, as well as ornamental, medicinal, and food plants. The principal food plants brought along were coconut, breadfruit, several taro-like plants, possibly *Tacca*, and possibly *Pandanus*, though it is probable that at least some varieties of *Pandanus* were on most atolls already.

The drier atolls were probably mostly never permanently inhabited. Most of them were not when discovered by Europeans, though some showed signs of former habitations. Populations on the more favorable atolls varied, and the intensity of utilization of the land fluctuated accordingly. Typhoons, warfare, and losses at sea probably prevented overpopulation. If these failed, migration solved the problem. The more resistent types of forest and the less productive parts of the islands were probably not much disturbed.

With the coming of the Europeans this changed drastically. The demand for copra and the introduction of axes and machetes of steel caused the rapid replacement of the larger part of the native vegetation by coconut plantations, except on the driest atolls. And on these, enormous quantities of guano were dug up and exported, altering the vegetation, though it is

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not easy to know how much. On the wetter atolls coconut plantations so completely dominate the vegetational picture that, ordinarily, coconut forest is regarded as the natural vegetation of such islands. It is, indeed, hard to dispel the idea that the coconut is indigenous and the dominant tree in the natural vegetation of these South Sea Islands. Now it is mostly the smallest islets, the exposed or very narrow ends of islets, and the seaward strip on the windward islets which show any native vegetation at all.

This change vastly increased the available habitat for some native plant species, however. Some of the undergrowth and ground cover plants, such as Euphorbia chamissonis, Clerodendrum inerme, Thuarea involuta, Fimbristylis cymosa, and Wedelia biflora, as well as such second-story trees as Pipturus argenteus, Morinda citrifolia, and Pandanus tectorius found this new habitat much to their liking and are now characteristic of such situations. Now, on fairly moist to wet atolls, dense undergrowth soon develops into thickets that choke the plantation. Keeping the plantations free from undergrowth is a major item of labor in this form of agriculture, even greater in places than harvesting the crop. Many new weeds and a few new cultivated plants, mostly ornamentals, came during this period. Papayas and bananas existed in many atolls previous to extensive coconut plantation, and were brought to others subsequently. Papayas, of course, are American in origin and did not exist in the Pacific prior to early European voyages. Most of the weeds are commonest around villages and paths, but some are ubiquitous, especially in plantations.

Long-continued harvest and export of large quantities of copra are beginning to show their effects. One of these seems to be phosphate deficiency, probably the cause of the gradual dying out of sizable areas of coconut plantation in the Marshalls. Similar symptoms are found in other regions.

Another effect of copra economy in some areas, notably the northern Marshalls, has been the abandonment of taro culture. Throughout the northern Marshalls there are extensive evidences of former taro pits that have not been used for many years. This phenomenon is most marked in what were probably the marginal areas of taro culture but is becoming evident also in the southern Marshalls, where both Colocasia and Cyrtosperma, the two taro-type plants grow very well. The culture and utilization of Tacca, also, has been almost abandoned in many islands, except when, after a typhoon, there is no copra to trade for rice or flour. Tacca, however, is still abundant as a spontaneous plant in the coconut groves in many atolls.

The war profoundly affected many of the atolls, especially in the Marshalls, Gilberts, and the central Pacific. Actual war, with the complete or partial destruction of the existing vegetation, took place on some islets of such atolls as Tarawa, Funafuti, Majuro, Kwajalein, Eniwetok, Wotje, and Wake Island. Here, in many places, were produced completely bare areas. These were soon covered by a blanket of Ipomoea pes-caprae, Vigna marina, Wedelia biflora, Pluchea odorata, Cenchrus echinatus, and other weeds. The Ipomoea and Wedelia in many places formed such a heavy mat that little else was able to gain a foothold, and many of the other weeds were smothered out. In other places Messerschmidia, Scaevola, and other pioneer woody plants

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quickly became dominant. Only in relatively dry islands, such as Wake, has anything like the original vegetation come back. There Messerschmidia, Pemphis, and Cordia were the principal original woody plants, and in 1951 these dominated the scene again, in spite of almost complete obliteration in 1941-1945.

Another effect of the war was the construction of huge military establishments, especially air fields, on many atolls, even completely outside the area of actual military activity. This commonly involved complete destruction of vegetation. The bulldozer scraped the land clean, destroyed what soil had been developed, and smoothed down all topographic irregularities. Afterward, when the absolute desolation of such establishments became apparent, attempts were made to reestablish vegetation and to landscape these bases. Many of these have since been abandoned, but some are maintained and have even been extended and developed.

A further effect, though localized, has been the utilization of the atolls of Eniwetok and Bikini for testing atomic weapons. The effects of this were undoubtedly both destructive and otherwise. Although the bombs destroyed some areas of vegetation, these atolls had their native populations removed, and revegetation and succession have been able to proceed in most areas undisturbed. Some studies of these effects have been made, but no results have, as yet, been released, subsequent to the publication of the surveys made prior to the tests.

A great number of additional weeds have been introduced and spread during and since the War. Some of them, such as Pluchea odorata, Pluchea indica, Paspalum conjugatum, and Chloris inflata have been very aggressive, and have covered large areas in a short time. But over a period of a few years it has become evident that Wedelia biflora and Ipomoea pes-caprae will in most situations dominate and probably eventually smother out all of these, if disturbance is not continued. Another interesting point is that evidence points to the probability that Ipomoea pes-caprae is an introduced plant, at least in the Marshall Islands. Previous to the war it was only known from Jaluit, the headquarters of German and Japanese occupations. Now it is abundant in Kwajalein, Majuro, and Eniwetok, all sites of extensive military activity. This point has not yet been investigated for other Pacific atolls, though much evidence is available.

Probable future effects of man on the vegetation are hard to predict accurately. Undoubtedly populations will increase, and any available land will be planted to coconuts. This will not be much, however, as most of it is used at present--if it will raise even poor crops of nuts. Programs for economic development of coral atolls are under way and will unquestionably take the form of attempts to improve and extend agriculture. Attempts will likely be made to introduce new agricultural and horticultural plants, some of which might possibly be successful. New weeds will doubtless come in. There will unquestionably be further and accelerated vegetational change, most of it destructive to what little native vegetation is left. It is important that sample areas of all existing types be set aside for continued study. It is also very important that much more extensive general surveys be carried out to describe what is left before it is too late.

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Principal Types of Vegetation and their Variations.

Short descriptions of the principal vegetation types that have been recognized as occurring repeatedly or over large areas on Pacific atolls follow. The account is based again largely on studies in the Marshall Islands, but with the little available information from other areas brought in wherever possible. Some types that are conspicuous are treated here as variants of a widespread Mixed Forest type, as they really seem to be extremes of a rather continuously varying association of trees that characterize ordinary atoll habitats. Some of the kinds of vegetation described below have definite habitat relations and also successional relations with other types. These relationships are pointed out briefly and brought out again in the following section, where the pattern is integrated as far as is possible with present knowledge.

1. Coconut groves and plantations:

These are artificial forests of coconut palms planted, often in geometrical arrangement, five to six meters or less apart. In moist areas the crowns touch and interlace, forming a rather complete canopy; in drier places, they are well separated. In height an old plantation may reach an average of 25 m. The ground cover is varied, usually Lepturus, Thuarea, and Fimbristylis are fairly general in pure stands or mixtures, with Polypodium scolopendria, Tacca, Cassytha, Boerhavia, Fleurya, and other herbs locally common, extensive patches of Euphorbia chamissonis, Clerodendrum inerme, and Triumfetta procumbens, as well as mats of Wedelia biflora, Ipomoea tuba, Vigna marina, and Canavalia microcarpa. Pandanus, Morinda, Premna, Pipturus, Guettarda, and other trees may form a scattered understory, or, if clearing out of the undergrowth has not been kept up, these with Wedelia, Ipomoea, and Canavalia may form a dense tangled thicket, in which seedling coconut trees are likely to be quite abundant, making walking almost impossible. Breadfruit trees are often scattered through parts of the plantation near villages.

2. Breadfruit groves:

Although breadfruit (Artocarpus altilis) trees are commonly seen around villages and scattered in coconut plantations, in the wetter atolls especially in the Carolines and southern Marshalls are areas completely dominated by them. These groves are commonly made up of enormous trees, towering even above the coconut palms and with dense crowns that form a complete canopy through which very little light penetrates. On the floor of such a forest few other plants can survive. Seedlings of Morinda citrifolia occasionally maintain themselves where conditions are not too extreme, and in the Carolines an as yet undetermined species of Piper may form a mat on the ground. Several ferns are also occasional in such situations. Varieties of breadfruit both with and without seeds are present in these forests, the latter being undoubtedly originally planted by man. Both may increase by root sprouts, but the seeded varieties spread very readily by seed. Seedlings may be abundant beneath the parent trees if the light is not too scanty. The possibility should be investigated that these may occasionally be pollinated by seedless trees, and that some seedless ones may be offspring in this way of the seeded varieties. The trunks of large breadfruit trees may be two or three meters in diameter and unbranched to a height of 10 or 15 meters.

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3. Mixed forest:

The most generally distributed native forest on coral islands is a variable mixture that, in one place or another, may include practically all tree species found on atolls. It is, in fact, so diversified that its principal common feature is that it is a mixture. It usually includes, among its components, Pandanus, Guettarda, Pisonia, Messerschmidia, Intsia, Cordia, and Ochrosia, frequently, also, Terminalia, Allophylus, Soulamea, Hernandia, Barringtonia, Pipturus, and Ficus. This I have called Mixed Forest. Hatheway 1953 calls it Scrub Forest, which term is often appropriate, as its stature varies from scrub to tall forest 25 m. high. In density it varies from close enough to form a complete canopy to sparse and open. If sparse, there is ordinarily a tangled scrubby undergrowth, which, with low branches of the trees, makes it almost impenetrable. The undergrowth consists of seedlings of the trees, with Scaevola, Suriana, Achyranthes, Wedelia, Clerodendrum, and Ximenia, the whole tangled and laced with lianas of Ipomoea tuba and Canavalia. On rocky places there may be Pemphis acidula. Coconuts may be scattered here and there from nuts planted by the natives or dropped by accident.

In the northern Marshalls there is no particular organization to this mixture, except that when tall and dense, there is little or no undergrowth. In the southern Marshalls, Hatheway reports that the trees usually occur in small groups of one species, rather than mixed as individuals. What seems essentially the same forest may result from second growth after clearing and from new colonization on new land. There seems to be no special correlation with any of the several types of substratum. On the seaward sides, if they are to the windward, there is a transition to a dense scrub. In the interior of well developed Mixed Forest, Messerschmidia tends to drop out gradually, not reproducing itself in the shade.

Most of the recognizable forest types on atolls seem to be extreme variations of Mixed Forest consisting principally or entirely of one of the component species of this forest. Because the intergradation between all of these types and Mixed Forest seems to be complete, and since their actual developmental relations are not fully understood, they are, for the purposes of this review and to emphasize their lack of sharp limits, here regarded simply as variants. The principal ones are as follows:

a. Pisonia Forest--Pure stands of Pisonia grandis are a very common and widespread phenomenon on coral islands throughout the Indo-Pacific region. The distribution and some data on the occurrence of this species has been reviewed, recently, both by St. John (1951) and by Shaw (1952). Shaw suggests that bird guano may be required for the growth of this species, or at least for germination and establishment of its seedlings. However, healthy trees have been observed in absence of any noticeable guano. Germination of seeds must be a rather infrequent occurrence, as no seedlings of this species were seen in the northern Marshalls investigation.

A characteristic of many or most of these groves or forests is a layer of highly acid raw humus on the surface of the ground, and often, just beneath this, a layer of phosphatic sandstone or hardpan. There seems little doubt that this is a phenomenon dependent upon the presence of the Pisonia

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(together with sea-birds), rather than controlling the distribution of the Pisonia. This relationship will be discussed in detail elsewhere. It has already been touched upon by Hatheway 1953.

This forest, up to 25-30 m. tall, commonly has a dense canopy, elephantine white trunks, spreading at the base into twisted root platforms, and little or no undergrowth except for Pisonia root sprouts. These are of quite irregular distribution, some trees having them, others not, even in the same grove. Fallen trees usually, but not always, take root wherever they touch ground, sending up a number of erect branches that become trunks. In dry regions Pisonia is more or less deciduous in the dry season, allowing more than usual light to enter. Birds tend to favor this forest for roosting and nesting; there are often hundreds or thousands of fairy terns, noddies of two kinds, red-footed boobies, and frigate birds nesting in the branches of a grove, and white-tailed tropic birds have been found nesting in cavities.

b. Ochrosia forest: One of the most striking atoll forest types is a pure dense stand of Ochrosia oppositifolia. These trees are up to 20-25 m. tall, with clean slender trunks, seldom more than 3 dm. through, and umbrella-shaped crowns of broad dark green leaves. These grow in contact, forming a canopy so dense that there is perpetual twilight beneath it. There are few seedlings of any other species on the ground, but those of Ochrosia are there in millions. The egg-like bristly fruits form a continuous layer on the ground, and the seedlings are of more or less even height, usually 3-4 dm., evidently reaching this height, dying and being replaced or not growing much further. If an opening of any kind is formed in the canopy, the seedlings beneath quickly grow up and fill it.

This forest does not seem to be found especially on any one type of substratum, being seen on sand, gravel, or broken coral rock. It has been observed particularly, as a continuous stand, in islands with a moderate rainfall. Apparently, once started, Ochrosia is able to replace most, if not all other species, at least in the moderate rainfall belt in the northern Marshalls. It has not been described from anywhere outside the Marshall Islands, though the tree is widely distributed in the Pacific.

c. Pandanus forest: In the Marshalls pure stands of Pandanus tectorius are uncommon and not of large extent. A solid stand was seen on Maria Atoll, Austral Islands, that covered an entire islet. Such stands have also been reported from the uninhabited atolls of the Tuamotus. Though Pandanus commonly branches toward the base, in dense forests the trunks are usually rather tall and straight before branching, with conspicuous prop roots holding up the bases and making walking difficult where the trees are close together. The crowns are pyramidal in shape, composed of enormously long sword-like leaves imbricated on the stem in three close spirals which give the tree one of its common names, "screw-pine." These leaves are provided with a row of stiff spines on the midrib and others along the margins. The leaves form a loose accumulation on the ground beneath the trees, where they retard the appearance of seedlings or herbaceous plants. Pandanus seedlings are able to start in denser shade than in Pandanus forest, but are not common in this type of forest, though they often form a carpet under isolated trees where leaves have not accumulated. Pandanus seems equally at home in almost any atoll habitat.

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d. Messerschmidia forest: On some of the drier atolls, such as Pokak and Wake, low forest of *Messerschmidia argentea* is the dominant vegetation. The trees are not very close together and commonly preserve their perfect hemispherical shape. Their silvery gray-green leaves are fleshy and in extreme dry weather all but the youngest on the twigs drop off. Pure stands of this species often colonize new islets and may remain uninvaded by other species for a long time. On some islands a strip of this type, but of very much taller trees, closer together, and open beneath, may occur just back of the beach scrub. The trees sometimes, but rarely, reach 20 m. tall. Their trunks are twisted and freely branched. They are seldom dense enough to exclude a ground cover, which may be of grass (*Lepturus*, *Thuarea*, *Stenotaphrum*), *Triumfetta procumbens*, or *Boerhavia*, or, on rocky substrata, *Fleurya*. Underbrush is not so common in this type, though *Scaevola frutescens* may be present, or *Sida fallax*. *Ipomoea tuba* lianas are frequently tangled abundantly in this forest, even in its driest manifestations. This type, also, seems to have little or no preference in substratum, but it is a pioneer type and will only persist under conditions which do not favor its more mesophytic competitors.

e. Cordia forest: In drier atolls *Cordia subcordata* often forms pure forests, though not of large extent. The trees may be close set and reasonably tall, but are commonly farther apart, at least the trunks, and with low, long widespreading branches that drag on the ground, become tangled and entwined, and make an impenetrable thicket. Often there is no undergrowth or ground cover at all. In the dry season this species may be briefly deciduous.

f. Barringtonia forest: Only one area of this has been observed, on Lae Islet, Lae Atoll, but it is such a striking type that it is worth looking for elsewhere. The trees were of enormous diameter, massive, 20-25 m. tall, canopy complete and dense, nothing on the ground except a colony of *Peperomia*. The ground in this forest had been covered, subsequent to the trees reaching a large size, by a deposit of large boulders to a depth of up to a meter. This should be looked for elsewhere, as the species is found everywhere in the tropical Pacific and Indonesia.

4. Pemphis forest:

On rock at or above high tide level, whether elevated reef rock, coral conglomerate, or beachrock, pure stands of *Pemphis acidula*, a densely branched small-leafed tree, are common. The trees are able to grow where pure sea water wets their roots at high tide. They reach 6-8 m. tall, are commonly gnarled and twisted, with trunks up to 2-3 dm. thick, rarely much more, of extremely hard and heavy wood. The lower branches, even though dead, are persistent and rigid, and as the trees grow very closely, the stand may be fairly impenetrable. Usually nothing grows beneath it. The general color of this forest, from a distance, is a soft bluish green, and the texture of the trees leads persons unfamiliar with *Pemphis* to describe it as looking like a conifer. This type is a fairly reliable indicator of rock substratum, but occasionally may be found on sand. Possibly these cases have rock at shallow depths, but this has not been investigated thoroughly.

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5. Mangrove Forest:

Mangroves of a number of kinds may be found in shallow lagoon margins, in tidal ponds or swamps with outlets, and in depressions with no outlets. In open lagoons Sonneratia or Rhizophora are found, rarely Bruguiera conjugata. The latter is much more common in the depressions, either mud bottomed or rock bottomed, where it may be accompanied by Lumnitzera, Intsia, or Pemphis. The latter two are usually found on rock bottoms. In the ponds with outlets Rhizophora is commonest. In the Marshalls, where the depressions without outlets are commonest, there is some evidence that Bruguiera may have been placed there deliberately by man. This is certainly true in some cases (Schnee 1904). The fruits are used in making a dye.

6. Beach Scrub:

Generally along the seaward sides of islets, especially on the windward sides, on the ends, and to a lesser extent along the lagoon beaches, beach scrub may be found on scrub vegetation. This is usually preponderantly Scaevola frutescens, but with varying admixtures of small bushy specimens of Messerschmidia, Guettarda, Terminalia, Suriana, Pemphis, and, on lagoon beaches, sometimes Cordia, Sophora tomentosa, and Allophylus. In different situations this has a vastly different appearance. On both beaches it commonly forms a fringe, principally Scaevola, along the edge of the forest at the top of the beach, merging with the forest on the landward side. If this is a lagoon beach or seaward beach on the leeward side its margin is abrupt, vertical or rounded, and it may be several meters tall. On the windward outer beaches, especially in the trade-wind belts, the top surface of the scrub slopes down in an inclined plane, continuous with the similarly "wind-sheared" top of the forest, to the top of the beach. Occasionally the edge of this has a scalloped appearance and the upper surface is grooved in the direction of the prevailing wind, the groves gradually disappearing landward. Depending on the physiography of the ends of the islands, the scrub found there may be merely a continuation of the fringe on the seaward side if it is a boulder beach, or, if it is a sand or gravel spit, a scattered to dense growth, principally Scaevola may be quite extensive, resulting from original colonization. On the lagoon side of such a spit, or lagoonward of the forest, a row of Scaevola or mixed scrub may catch windblown sand and form a low dune ridge.

7. Miscellaneous scrub types:

In the interiors of islands, especially of drier ones, different sorts of scrub vegetation may occasionally be found. On Pokak Atoll are areas of Scaevola 1-2 m. tall, often on exposed rock substratum. Such areas, on most atolls, would probably be occupied by Pemphis scrub or forest, but this plant does not occur on Pokak. A similar inland scrub has been reported by Christophersen (1927) from Christmas Island.

A thin scrub of Sida fallax, usually with Lepturus and other herbs, occurs in fairly large areas on Pokak and on Christmas Island, Canton, and other dry central Pacific atolls. This seems to fluctuate a great deal with wet and dry periods, the individual bushes partially dying during dry cycles, but with some branches continuing to flower. In some favorable localities this may reach almost 2 m. in height and be so dense as to somewhat impede walking. Small patches of this are found on dry islets in other atolls of

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the northern Marshalls, often surrounded by forest. In places, as on Christmas Island, Messerschmidia trees, perfectly rounded on top, are more or less thickly scattered in the Sida scrub to form a park-land or savanna.

Hedyotis romanzoffiensis and Heliotropium anomalum form a dwarf scrub, usually rather sparse, on Christmas Island. In places Sida and Suriana may be added to this to form a mixed dwarf scrub. Herbs, such as Lepturus, Portulaca, and Boerhavia are commonly associated with this. It is usually not more than about 0.5 m. tall. Something similar occurs in openings in the Tuamotus, but little is known about it.

On Christmas Island, and perhaps, Jarvis, are small areas of loose scrub made up of Abutilon indicum. The bushes grow to 1-2 m. tall.

8. Lepturus Grassland:

On most of the drier atolls are patches, and on Pokak and Christmas large areas, of a bunchgrass vegetation of Lepturus repens, sometimes with admixtures of Heliotropium anomalum, Portulaca, Boerhavia, and other herbs. These seem, invariably, to have sand or fine gravel as a substratum, either pure or between the rocks. The bunches may be so close together as to form a continuous cover or may be widely separated, and may be very small to as much as 3-4 dm. tall. On Pokak this type of area is invariably undermined by the burrows of enormous numbers of wedge-tailed shearwaters. On Christmas Island there may be a scattering of Messerschmidia trees, giving a savanna effect. This is also somewhat true on Pokak. On some atolls, these Lepturus patches are often extensively parasitized by mats of Cassytha filiformis. On Christmas Island Lepturus is locally mixed with Tribulus cistoides or with Heliotropium anomalum.

9. Other Natural Herb Types:

On some atolls, as Taka, Bikar, Jarvis, and other rather dry ones, are areas where Portulaca lutea is dominant or in pure stands. The cover is ordinarily not complete. These are usually on rather freshly formed sand or gravel surfaces, and are probably short-lived, being invaded by other species rather promptly.

Mixtures of Portulaca, Boerhavia, and Lepturus may cover the ground sparsely to rather densely. On Christmas Island Christophersen (1927) described, also, areas of a pure stand of Boerhavia, which he said had grown over and killed the other plants.

On highly saline flats, usually near the lagoon, at practically high tide level, the vegetation is of scattered mats of Sesuvium portulacastrum. This vegetation has been noted on Wake Island, Canton Island, and Christmas Island, and probably occurs more widely, at least in the dry Pacific Equatorial and Phoenix groups.

10. Secondary Herbaceous Types:

During the war large areas on such atolls as Kwajalein, Eniwetok, Wotje, Jaluit, and others were denuded of their vegetation. Most of these

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have scarcely been studied, but on Kwajalein and to a much lesser extent, Jaluit and Eniwetok, observations have been made. These areas seem, usually, to be occupied by mats of Ipomoea pes-caprae, Wedelia biflora, or Vigna marina. These may become so dense that invasion by woody species is greatly retarded. Wedelia tends to dominate in many such occurrences, and may form a dense mat one or even two m. thick, sometimes mixed with Ipomoea. On Lae Islet, Lae Atoll, a similar mat of pure Wedelia occupies an open meadow-like place of unknown origin in the forest. This did not change significantly between 1944 and 1952. The substratum was fine broken coral.

On abandoned compacted coral air strips, Fimbristylis cymosa (or atollensis) may get started as a pure stand and persist for some time, as on Bikej Islet, Kwajalein.

In 1945 an attempt was made to revegetate Kwajalein Islet and some others that were being used as active military establishments, by planting Cynodon dactylon. This has persisted in some places, but soon became invaded by other species, especially by Paspalum vaginatum, a similar sod-forming grass. The latter is now the commonest grass on Kwajalein Islet. Heavy traffic tends to discourage such plants as Wedelia and to favor such temporary weeds as the obnoxious Cenchrus echinatus, Eragrostis amabilis, Eleusine indica, and several species of Euphorbia. The weedy vegetation around such establishments is complicated by the great influx of new weeds brought in accidentally. Pluchea odorata and P. indica have become very abundant around most military bases, and for a while there seemed a probability that they would dominate the vegetation. However, where left reasonably undisturbed, Wedelia seems very able to smother them out.

11. Bogs and Marshes:

For present purposes bogs and marshes may be distinguished by defining the former as having a substratum of a spongy peat, the latter a substratum of soft muck.

Pits, artificially established for cultivation of taro-like plants, usually Cyrtosperma and Colocasia, occasionally sugar cane and other things, even ornamentals such as Hibiscus rosa-sinensis, are the commonest kind of marshes found on atolls. These are essentially pits dug down to below the water table in the centers of islets, then filled in up to the surface of the fresh or brackish water with vegetable refuse or compost, which rots and forms the muck substratum. Such pits vary from a few square meters to many hectares in extent. Cyrtosperma, a gigantic herb with great arrow-shaped leaves up to three meters or more tall, usually dominates these pits. This tends to crowd out Colocasia, which is often preferred as food. The starchy corms of these plants are the parts utilized, the tops of these being broken off and replanted. Many weeds occur in such places, the most aggressive being Alocasia, a giant aroid similar in appearance to Cyrtosperma but inedible, and Paspalum vaginatum. The latter, introduced recently in the northern Marshalls, has completely taken possession of many of these pits on Likiep and Ailuk. Other common weeds are Cyperus odoratus, Eleocharis geniculata, Jussiaea suffruticosa, Polygonum sp., and Athyrium sp.

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Natural marshes occur on many atolls, being places where, for one or another reason, the ground surface dips beneath the water table. The bottom is a soft mud whose composition has not been investigated. Cyperus javanicus, Jussiaea, and various weeds are commonly found here.

On Washington Island, at one end of the freshwater lake, is a peat bog of some extent. The vegetation of this is a solid stand of Scirpus riparius, invaded around the edges by Cyrtosperma and Polypodium scolopendria. This is a rather rare or possibly unique occurrence on an atoll and has been well described by Wentworth (1931) and Christophersen (1927).

12. Terrestrial algal vegetation:

The land algae have been little investigated on atolls. There are, of course, the usual epiphytic unicellular green and blue-green algae on tree trunks and in lichen association with fungi, and microscopic algae on moist ground. There are algal mats in pools, both blue-green and green. On the wet bottom of a depression on Wake Island was noted a luxuriant fur-like growth of Enteromorpha. Almost nothing is known of the composition of most of the algal vegetation. Two physiognomic types are apparently so widespread as to be almost universal in their respective habitats. These have attracted some attention from other than vegetation students. They are as follows:

a. Surface discoloration on limestone rocks: Rocks exposed above high-tide level, whether consolidated material or loose boulders and cobbles, though white, pinkish, or very pale brown in color within, are ordinarily colored from a blue-gray to black. On close examination this is found to result from a layer as much as several mm. thick in which the rock is green in freshly broken cross section. Often the inner margin of this layer is more strongly colored than the intermediate depths, while the outer surface seems black. When the limestone is dissolved away in acid this color is found to be due to unicellular blue-green algae belonging to the Chroococcales. There have been various observations on its effect on the hardness and decomposition of the surface layers of the limestone, but no one, as yet, has separated out the effects which are due to the algae from those with other causes. Also, nothing is definitely known as to the origin and differences in intensity of color. It has been suggested by Teichert (1947) that the color is in proportion to the age of exposure, and that this might be a means of dating, relatively, the shingle deposits. Not enough is understood about this, as yet, to make any such conclusions dependable. It has been noticed, on Pokak Atoll, that where there is much abrasion by rolling around of loose material the algal layer is kept worn thin or is absent.

b. Algal crust on coral sand: On most areas where there is open sand, either with no other vegetation or between bushes of sparse scrub or tufts of sparse bunch grass, the surface of the sand for the first few millimeters is caked into a crust, held together by gelatinous blue-green algae. The general color is gray to blackish, but appears greenish when moist. When very dry such a crust, if well developed, may crack and curl up or wrinkle. The algae forming this crust are, so far as known, principally, Hassallia byssoidea, Scytomema ocellatum, and Porphyrosiphon fuscus, all filamentous Myxophycae, and Gloeocapsa alpicola, a gelatinous colonial form (Taylor 1950).

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This crust has attracted some attention as a possible source of fixed nitrogen in atoll soils, since it has been demonstrated that certain blue-green algae are able to fix atmospheric nitrogen. A limited amount of work has been done toward finding out if this is actually the case, but not enough has been done to yield any definite results. The crust undoubtedly serves an important function in retarding wind drift of find sand.

13. Marine Seed-plant Vegetation:

On sandy, quiet-water shores in the western Pacific, Indian Ocean, and Caribbean Sea several genera of marine spermatophytes, commonly called "sea-grasses" tend to form a sod-like vegetation, holding the surface layers of sand in place by their entangled rhizomes. This type of vegetation is probably not unusual in the lagoons of atolls, but has scarcely been reported from them. Two occurrences are known. One is a tiny patch of Thalassea hemprichii at the outlet of a mangrove swamp on Ailinglapalap Atoll; the other is a long strip of sod of the same species at low tide level on the lagoon beach of Ujelang Islet, Ujelang Atoll, both in the Marshalls. Undoubtedly this will be found to be more widespread, especially in the Caroline atolls when they are more adequately investigated. It is a common feature of barrier reef lagoons around high islands in Micronesia.

This vegetation is often referred to as "turtle-grass" and is said to be the principal food of the green turtle. It is rather difficult to account for the abundance of turtles in the northern Marshalls when there is so little "turtle-grass" without assuming either other foods or extensive migrations. Such migrations are known in the western Indian Ocean, where the turtles breed on some of the atolls, but migrate to the Mozambique Channel, hundreds of kilometers away, to feed during a part of the year. Their stored fat apparently keeps them alive during the breeding season. It would be very interesting to know if there are such migrations of turtles in the Pacific.

14. Marine Algal Vegetation:

The actual algal communities of atolls have not been sufficiently studied to enable a very significant summary to be made. A zonation is observed, even by the casual collector, which will be outlined below, beginning with the outer edge of the reef. The problem is complicated by the fact that the zonation is by no means the same on windward and leeward sides, by seasonal fluctuations in abundance of species, and by fluctuations in response to available nutrient material dissolved in the water. An excellent example of this is given by Taylor (1950), when he notes that Enteromorpha was scarcely seen when he arrived on Bikini in 1946 but had become very abundant during the time the party spent there, presumably in response to the pollution of the lagoon by sewage and refuse from the large establishment set up there for the atomic-bomb tests. There is also much difference in algal floras, at least as to relative abundance of species, from atoll to atoll.

a. Algal ridge (Lithothamnion ridge of most authors): At the outer edge of the seaward reef, especially on the windward side, calcareous red algae of the genus Porolithon and possibly other genera form a massive accumulation

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of limestone that is generally built up several feet above the general level of the reef flat. It is of a bright pink color, rough to rather smooth, and is very resistent to the pounding of the waves. Many people believe that the strength of this indurated edge of the reef protects the whole structure from pulverization by the breakers. The height to which this ridge is developed is more or less in proportion to the constancy and roughness with which waves break against it. Frequently it is entirely absent on the leeward sides of atolls. On the leeward sides, also, there may occasionally be a small such ridge developed on the edge of the lagoon reef, in response to lagoon waves.

b. The moat: The depressed area or trough dipping below low tide level just behind the algal ridge, landward, sometimes represented by numerous tidepools, is usually filled with corals and has a considerable diversity of algae. There may be Laurencia in abundance, Liagora, Avrainvillea, Codium, Halimeda, and many other genera. They do not, however, form a continuous layer, except sometimes in the case of Codium.

c. The reef flat: This relatively smooth, gently sloping area, sometimes very broad, extending from high-tide level to low-tide level, is mostly covered by a continuous layer of algae, sometimes very thin, and little else. Over large areas Cladophoropsis is dominant, forming a dense felt which catches fine calcareous sand. Over other areas this is replaced by a fur of Jania, also a collector of sand. Padina is common in other places, though not very frequent in the northern Marshalls. In more restricted areas, near high-tide level, may be putty-like masses of silt held together by the very fine filamentous Schizothrix. In still other places there is only a slimy film of microscopic algae of several sorts. On the under sides of boulders strewn on this flat Microdictyon is common, and there is some Dictyosphaeria. In certain places the bottom is covered by a crust of a thin encrusting calcareous red algae, or by small pebbles so encrusted (nodular). There may be a rough correlation in the distribution of these communities with the duration of exposure above water, but it has not been worked out very well, as yet.

d. The lagoon reef flat: The lagoon reef flat, the shallow shelf extending out a short distance from the inner shore of the islets, is not generally a region of abundant algae. It is usually either sandy or covered by rubble. In the northern Marshalls, Halimeda stuposa and a species of Udotea of similar habit grow in sandy places as scattered tufts, with their curious "pseudostipes" buried in the sand. Between the boulders of rubble deposits a little Caulerpa may be found. Tiny tufts of small filamentous red algae also grow here, sometimes on the sea anemones that are common here.

e. The passage between islets: Here water is usually flowing in one direction or another. Luxuriant colonies of Halimeda, several species of Caulerpa, and, rarely, Turbinaria ornata grows at or below low tide level. The rocks, both above and below low-tide level are slippery with a film of very small algae.

f. The leeward reef where there are no islands: Where this is not exposed at low tide, except for coral heads and boulders, coral is very abundant and algae are scarce. On Ailuk only a species of Liagora seemed to be common in such a place, forming scattered tufts growing on the coral and boulders. Where the leeward reef is exactly at low-tide level or slightly

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above it, it is often covered by a platform of Porolithon, bordered by a slight Lithothamnion ridge. In cavities in this are Halimeda and Caulerpa.

g. The lagoon bottom: This has not been studied much, but in the northern Marshalls it is known to be covered at least in some areas, by a stand of Halimeda growing in such abundance that the lagoon bottom sediments are in places almost entirely made up of its calcareous skeletons. In Ailuk a species of Caulerpa was snagged from the lagoon bottom by a fishline, so there may be some areas where it is abundant.

Vegetational Patterns

The original arrangement of the various types of vegetation on atolls has been very largely obscured because coconuts have been planted indiscriminately almost everywhere. The present pattern is for the greater part of the larger islets to be covered by coconut plantations, leaving a belt of scrub and scrub forest on the windward sides of islets on the windward sides of atolls. This protects the coconut trees from excess wind and salt spray. The outer edge of this belt is usually a fringe of Scaevola, which gradually merges with the mixed forest which lines the coconut groves. Very narrow islets and parts of islets, such as sand spits on their ends, seldom have coconuts, but usually have mixed scrub, usually dominantly Scaevola and Messerschmidia, or if the narrow place is rock, the vegetation may be Pemphis scrub. Along the lagoon sides of the coconut groves, there is usually a thin line of scrub or a row of trees.

From the remnants of native forest remaining here and there, and from a consideration of the present distribution of trees on the islets mostly occupied by coconut groves (Hatheway 1953), some idea may be obtained of the original patterns. It is apparent that some species of plants--and consequently, where there are so many types dominated by single species--some vegetation types are less halophytic than others. Such are Ochrosia, Pisonia, and mixtures of these with Intsia, Allophylus, Pandanus, Pipturus, Guettarda, and others, but lacking Messerschmidia. These types tend to be toward the interior of islets, and surrounded by more halophytic and scrubby forest and beach scrub, dominated by Messerschmidia, Scaevola, Pandanus, Terminalia, and Guettarda. The width of this more halophytic belt, especially of the outer beach scrub, is greater on the seaward and especially the windward sides. In the wetter atolls, after they are largely in coconuts, breadfruit groves and solid breadfruit forest seem to coincide in distribution with those parts of the islets where the more mesophytic forests formerly occurred. It has been suggested (Fosberg 1948, 1949) that the distribution of the more mesophytic types might be correlated with a lens of relatively fresh ground water, better developed on the wider islets. The existence of such a lens and its correlation with the distribution of some plants, such as breadfruit, has been amply demonstrated since, though there seems reason to think that the influence of salt spray and wind is much greater than previously suspected. And too little is yet known about the seasonal fluctuation in salinity in these shallow ground water lenses.

On very dry islands the occurrence of Lepturus grassland seems to coincide somewhat with sandy areas, completely rocky places being more likely to be occupied by scrubby forest of Messerschmidia, or, in places, Cordia or Pisonia.

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Pemphis forest or scrub is practically always found on rock surfaces at or above high-tide level. *Suriana*, which sometimes forms a rather pure scrub, but more often is a component of mixed beach scrub, has only once or twice been seen or recorded from anything but sand. *Sophora tomentosa* is usually found on sandy lagoon beach ridges.

Entirely too few atolls have been at all carefully studied to make more than the roughest generalizations possible. The only vegetation maps of atolls that exist are those of Arno (Hatheway 1953). Without such maps, similarities in distribution patterns are hard to see.

Most needed future studies

The most urgent need is for information on the few remaining bits of native vegetation on atolls in various parts of the world. Such studies of the more remote atolls in the northern Marshalls during 1951 and 1952, though very brief, yielded a great deal of information. And remnants of original vegetation will disappear extremely rapidly.

All opportunities should be taken advantage of to look into the salinity relations of the different vegetation types and of individual species of plants. Any ground water study should be accompanied by careful notes on the vegetation. Information is especially desired on the effects of seasonal fluctuations in salinity.

Anything contributing to an understanding of successional relations of these vegetation types will also be important. Observations as to what species can establish themselves in the shade of what others, as to what common species are seen dying out or lacking in some types, and as to changes taking place over the years in areas completely devastated during the war, are all especial *desiderata*.

Whether or not the prominence of types consisting of single species is a general atoll phenomenon or only characteristic of the relatively dry northern Marshalls is not known. And in any event, the explanation for this is of great interest. Whether it is a function of the extreme habitat, or of the very small floras, or of both should be looked into.

The cause for the areas of unhealthy or dying coconut plantations in the Marshalls, and whether such a phenomenon is found elsewhere, are matters of more than academic importance.

Whether pure *Ochrosia* forest is found elsewhere than in the northern Marshalls is not known. The nature of the yellow patches in this forest, also, seems of fundamental importance. This is especially so if it can be shown that it is an effect of the vegetation on the habitat.

Any influence exerted by the vegetation on the habitat is of great interest. The only clear-cut case familiar at present is the formation of phosphate rock under the influence of *Pisonia* forest. Phosphate exhaustion in coconut groves is suspected. Influence of beach scrub in the piling up of sand dunes is also probable. Protection of the land surface against mild typhoons is another possibility. Binding of sand by blue-green algae against

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wind erosion is still another. The effect, if any, of algae, in the formation of beach or reef sandstone needs to be determined. There are many others, but most studies have been so hurried that it was not possible to gain more than an inkling that something was happening. The careful study of any ecological process is one of the most important things that can be done to gain the understanding of atoll ecology. The student must, however, be cautioned against the tendency to explain everything in terms of the one process intensively studied. The vegetation is an expression of the interaction of many such processes, and the unraveling of their effects is the ultimate, though probably unattainable objective of the study of vegetation.

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