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Author(s): William A. Niering
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TERRESTRIAL ECOLOGY OF KAPINGAMARANGI ATOLL, CAROLINE ISLANDS*

WILLIAM A. NIERING
Department of Botany, Connecticut College, New London, Connecticut

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INTRODUCTION

During World War II many of our operations in the Pacific Islands brought out a lack of information on atoll ecology. Therefore, an extensive series of environmental investigations was undertaken in Micronesia from 1950-1954 with teams of investigators studying various atolls—Arno in the Marshalls, Onotoa in the Gilberts, Ifaluk and Kapingamarangi in the Carolines and Raroia in the Tuamotu Archipelago (Polynesia). The aim of these studies was to analyze the physical and biological environment of different atolls and to assess their economic potential. This report presents one facet of these studies; namely the work of the land ecologist in describing and interpreting the vegetation and associated fauna on Kapingamarangi. It is considered a preliminary work which, it is hoped, may serve as background for more intensive studies on atolls. This atoll was selected because it is isolated, and because it represented a Polynesian outlier in Micronesia where previous anthropological studies had been undertaken (Eilers 1934, Buck 1950, Emory 1954). Previous ecological observations have been limited to those of Emory (1954) made in conjunction with a study of the people, Miller (1953) made during a survey of health conditions, and Fosberg (1946) made during a brief reconnaissance of the vegetation.

Kapingamarangi, also known as Greenwich Island, is located in the southeastern Caroline Islands just north of the equator (Lat. 1° 05′ N Long. 154° 45′E). The nearest land is Nukuoro, 164 nautical miles northward. The pear-shaped reef which encloses the lagoon, with the exception of a narrow pass, is 8 statute miles in a southeast to northwest direction and 6.3 mi. in width from north to south (Figs. 1, 2, 3). The 33 islands are all located along the eastern or windward side of the reef. Although the islands vary from .03 of an acre to 79.5 acres in size, over half of them are less than 3.5 acres. The smallest, Matukerekere, is 100 by 20 ft—a mere dot of sand and rubble, whereas the largest, Hare, is 1.29 mi. in length. In width the islands range from 20 to 1,000 ft (Werua). The total land area comprises approximately 276 acres or 0.42 sq mi.

* Study supported by funds from contract N7onr-29104 (NR388001) between the Office of Naval Research and the National Academy of Science. Preliminary Report (Niering 1956).

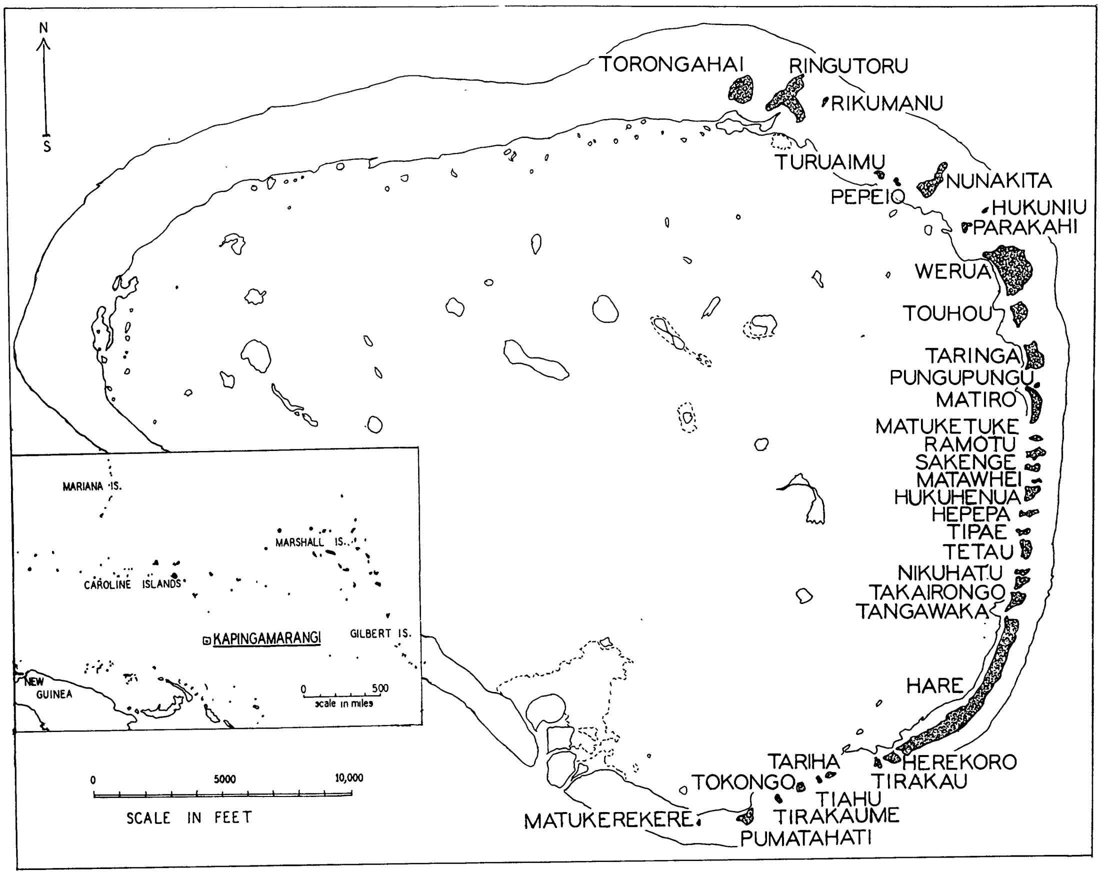

FIG. 1. Map of Kapingamarangi Atoll and insert map showing location of atoll in Micronesia. Based on aerial photography—Herold Wiens, 1945.

The land surface is relatively flat with a rise of only a few feet above sea level, except where excavations in the interior have resulted in rubble banks which reach 14 ft above sea level.

The atoll is inhabited by 426 Polynesians (June 1954). Although they live on only two of the islets, Touhou and Werua, they utilize the others for their plantations. Initial settlement of the atoll is obscure. Emory (1954) suggests that it may have been inhabited as early as 1200 A.D. Presumably the population has fluctuated considerably in the past, reaching a maximum of 500-600 prior to 1900. During World War II the area served as a Japanese weather and sea plane base which was bombed by U.S. forces in 1943-44. As a result, the vegetation was seriously disturbed or partly destroyed on the north-central part of Hare and on much of Nunakita. In 1945 the U.S. Navy took charge of the atoll as a part of the U.S. Trust Territory. By 1947 the population had reached 527 and at about this time some natives began to migrate to Ponape and other islands. This movement has continued to the present and indicates a growing pressure on the atoll's food resources.

As is typical of inhabited atolls in Micronesia, the islands are dominated by coconut plantations and breadfruit groves (Egler 1956; Fosberg 1956, 1960). Although originally covered by a mixed native forest or scrub, this vegetation has been greatly reduced and is often restricted to the marginal beach areas and plantation undergrowth as on Kapingamarangi. This strand type vegetation includes a limited halophytic flora.

The expedition was supported by the Pacific Science Board of the National Academy of Science and the Office of Naval Research. Harold Coolidge, Lenore Smith and the late Ernestine Akers assisted with preparations. The cooperation of my colleagues, Cadet Hand and Robert Rofen (marine biology), Jan Newhouse (non-vascular plants), Edwin McKee (geology) and Herold Wiens (geography) was indispensable, as was the continuous assistance of a native interpreter, Maea. I am especially indebted to Dr. F. Raymond Fosberg for his floristic briefing, aid in identification of the vascular plants and his many suggestions in the preparation of this paper. Miss Marie-Hélène Sachet, and Drs. Frank E. Egler and Richard H. Goodwin made many helpful comments on the manuscript.

Thanks are due to the following specialists who gave aid with identifications: Dr. W. C. Brown, reptiles; Dr. F. A. Chase, Jr., crustacea; Dr. G. E. Gates, annelids; Dr. J. L. Gressitt, insects; Dr. H. A. Miller, bryophytes; Dr. J. P. E. Morrison, gastro-

FIG. 2. Aerial view of southern arc of atoll. Breakers form white band oceanward and sandbars project irregularly lagoonward. Islands from right to left are Hare, Herekoro, Tirakau, Tariha, Tiahu, Tokongo, Tirakaume, Pumatahati, and barely visible Matukerekere. Beyond, navigation passage is evident by discontinuity of reef. On Hare marginal coconut belt oceanward is replaced by coconut-breadfruit plantations toward the interior. Smaller islands covered with coconut plantations. U.S. Navy photograph.

FIG. 3. Aerial view of northern arc of atoll. Breakers form relatively smooth white line oceanward. Sand bars form irregular shore line lagoonward. From left to right the islands are Werua, Parakahi, Hukuniu, Nunakita, Pepeio, Turuaimu, Rikumanu, Ringutoru, Torongahai. On Werua marginal coconut belt oceanward is replaced by coconut-breadfruit and breadfruit groves lagoonward. U.S. Navy photograph.

pods, mammals and birds; and the late Dr. H. Albert Herre, the lichens. The illustrations were done by Miss Vivian J. Andrist. Photographs are those of the author unless designated otherwise.

METHODS

Field observations were made on all islands of the atoll. On some, quantitative data on vegetation was obtained using quadrats and strip transects. Mapping of the vegetation was done in collaboration with the geographer. To estimate the number of coconut and breadfruit per acre, total tree counts were made on several of the smaller islands and quadrats were employed on the larger ones. A strip transect was used to analyze the crustacean population. Annelids were sampled in 0.5 m quadrats in the upper 15 cm of soil with mercuric chloride solution (4 g/gal) which brought the worms to the surface. Soils and ground water data were obtained from wells and Cyrtosperma marshes in collaboration with the team geologist. Ground water salinities were determined on 11 islands by the silver-nitrate titration method. Extensive collections of the terrestrial flora[1] and fauna were made and are on file at the United States National Museum. Native interpreters frequently assisted in taking data and they, along with older inhabitants, provided additional information concerning the biota. The field studies, approximately two months in duration, extended from 22 June to 31 August, 1954.

GEOGRAPHICAL SETTING

GEOLOGY

Geologically, atolls are relatively young, having been formed in post-glacial time. Those such as Kapingamarangi are essentially rims of inundated organic limestone set upon a mountain base which rises from the ocean floor. This limestone cap is known to reach a thousand or more feet on Eniwetok Atoll (Wiens 1959). It is formed primarily by lime-secreting organisms which form a ring-like reef around a lagoon. Scattered land masses frequently emerge above sea level as islands along the reef.

On Kapingamarangi, the islands are restricted to the east side of the reef and are composed of limestone bedrock, lime sands, coral rubble and limestone boulders. Oceanward, the larger islands are formed primarily of coral rubble, although occasional rock outcrops may occur. Lagoonward this pattern is replaced by more recently deposited beach sands. Many of the smaller islands, especially those located oceanward on the reef, are composed of coarse rubble and boulders, while those situated lagoonward are underlain by sand (McKee 1956, 1958).

Erosion and deposition play a major role in modifying the islands (McKee, Chronic, & Leopold 1951). Seaward and along the inter-islet channels, deposits of coarse limestone boulders form beach ridges or ramparts. In some situations undercutting of these deposits and of the associated bedrock occurs. During severe storms coral rubble and boulders are moved inland as much as 250 ft—a phenomenon which accounts for the characteristic rubble surface toward the oceanside of the islands. Elevated limestone areas frequently extend seaward onto the reef flat from the land surfaces and represent remnants of earlier island masses that were presumably vegetated at one time. On at least five islands, these remnants are highly phosphorized and thus indicate a considerable population of sea birds in the past. The role of birds in phosphate formation will be discussed in a later section.

Lagoonward, sand bars composed of clastic materials and foraminiferal sands project from the ends of the islands (McKee 1956, 1958). These unconsolidated beach deposits account for a considerable

[1] Nomenclature of the vascular plants follows that of Fosberg (1956).

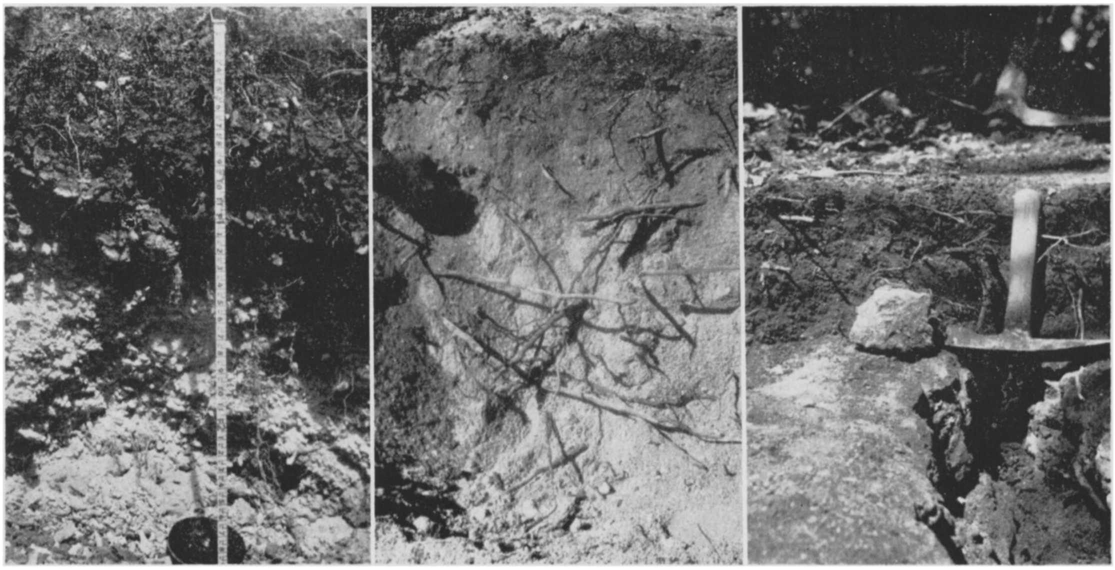

FIG. 4. Left—Coral rubble profile found typically from the center of the islands oceanward. Note extensive organic incorporation in upper 10 in. which gives way to grayish and finally whitish rubble beneath. Roots are concentrated in upper 12 in. but are present throughout the 2.5 ft profile. Center—Sandy soil profile typically found lagoonward. Organic staining evident at surface with gray staining to 10 in. in depth. Beneath, the parent material consists of orangish-pink foram sand. Coconut roots scattered throughout the profile. Right—Jemo soil type developed under former Pisonia forest on Pumatahati Islet. Humus layer 6-8 in. in depth overlies phosphate rock.

part of certain islands and furnish evidence that these islands are building into the lagoon. An exception to this pattern occurs on Pumatahati, where an extensive rubble beach occurs with coarse material extending 50 ft into the interior. Due to the proximity of the islands, narrow causeways of coral boulders have been constructed by the natives across the inter-islet channels to facilitate passage. As a result of these causeways, certain islands have been completely connected during severe storms. These connections account for the extensive length of Hare which actually represents three islets joined together in this manner. The islet of Pepeio, 0.7 of an acre, has been induced to form as a result of man's activities. A coral boulder wall was constructed in 1919 on the reef flat and subsequent deposition has resulted in its formation.

SOILS

The soils are relatively immature and consist largely of mixtures of lime rubble, sand, and fine lime particles combined with varying amounts of humus (Fig. 4). They are well drained, primarily alkaline and vary from black to gray-brown to creamy white. Throughout most of the smaller islets and oceanward on the larger ones, boulder or rubble soils are most common. The surface rubble is typically gray, stained by blue-green algae which may also be important in nitrogen fixation. The organic layer, a mixture of rubble and humus, varies from 6-12 in., although depths of 18 in. and 30 in. were recorded on Tokongo and Rikumanu, respectively. Lagoonward, the recently deposited sandy soils are extremely immature, the organic development ranging from 2-6 in. in depth. In both the rubble and sandy soils only the A and C horizons are represented—an upper darker layer of rubble and/or sand mixed with organic matter (A) which in turn is replaced by the parent material (C) composed of cream and orange foraminiferal sands and/or whitish rubble. Buried profiles which occur on several islets are indicative of previous storms which laid down rubble over an earlier profile. Following Stone (1951) the soils on the smaller islets would probably be classified in the Stony and Very Stony Complex, whereas those on larger ones appear similar to the Shioya or Arno types on Arno Atoll. Two other soil types occur: the poorly-drained, muck-type soil in the artificially formed Cyrtosperma marshes and a distinctive phosphate soil profile restricted to Pumatahati, which will be discussed later.

HYDROLOGY

The only source of fresh water on the atoll is from periodic showers or storms. Although some interception and evaporation occur, most of the rainfall penetrates the soil with little run-off. As this rainwater percolates downward, there builds up a shallow double-convex layer of fresh water, known as a Ghyben-Herzberg lens, which overlies the salt water. For this lens to develop, the permeability of the sediments must be great enough to permit sufficient infiltration to maintain a positive hydrostatic pressure. Although other factors may be involved, in general, sand and rubble soils of considerable depth are conducive to its establishment, whereas bedrock with many fissures is unfavorable. The lens is not developed on the smaller rocky islands. On the small rocky islands of Hukuniu, (0.9 acre) where the fresh water lens is absent, the ground water salinity is similar to that of the ocean. On the larger islands where the lens occurs, the water table lies from 2.5-4 ft below the soil surface lagoonward and 5-5.5 ft oceanward. Since the salinity ranges from 1,000 ppm-3,800 ppm seaward and only 18 ppm-340 ppm* lagoonward (Fig. 19) on the larger islets, the wells, which furnish fresh water for domestic use, are located toward the lagoon side. Although this water is potable, the natives prefer the cool fresh water from green coconuts. Cisterns also supply an additional source of fresh water.

CLIMATE

The climate of the Eastern Carolines is tropical with relatively uniform temperatures. Both temperatures and humidity are relatively high. Rainfall is erratic, occurring primarily as showers or squalls. Although periodic severe storms occur, the atoll lies outside the typhoon belt. Droughts have also been reported on the atoll.

Daily temperature and humidity data recorded during the survey are considered fairly representative of the general pattern throughout the year. The average maximum temperature was 89.1°F, average minimum 82.5°F, absolute maximum 94°F and absolute minimum 74° F (on a cloudy overcast day). The average daily maximum humidity reached 83.3%, usually from midnight to sunrise. During less than a quarter of the day the humidity reached 90%, although the average daily reading dropped to 57.4% between noon and late afternoon. The minimum during the survey was 48% (Wiens 1956).

According to the U.S. Hydrographic Office (1952) rainfall is greatest in May and June and again in October and November, averaging about 12 in. per month. Precipitation is light from February to April and July to September, averaging about 7 in. For the 7-week period from July to August 1954 only 4 in. were recorded. During the survey there was only one extended period of overcast skies which lasted for about 24 hrs during the latter part of July. Rainfall on Touhou was .74 in. during this time. Average annual rainfall estimates for the atoll range from 78 to 108 in. Two droughts are mentioned by Emory (1954): one in 1890 and another which extended from 1916-1918 when 80 to 90 people died directly or indirectly from the famine which resulted.

The Carolines lie within the belt of the northeast trade winds which prevail from November to April, although considerable variability occurs. During the current and previous surveys the winds on Kapingamarangi were primarily from the east. The severe storms that occasionally hit the area are 20-25 mi in diameter with winds averaging 15-25 knots, but occasionally reaching 40-50 knots. Thunderstorms may also occur. According to the community secretary on the atoll, numerous severe storms have hit the islands. In 1858 the small island of Matukerekere was destroyed and the storm in 1886 caused considerable damage to breadfruit and coconut. In 1896 a tidal wave hit the lagoon beaches from Werua to Ringutoru but did minor damage to the plantations. Around 1920 heavy waves during a thunderstorm damaged some coconut. In 1937 a storm blew down five breadfruit trees. The most recent storm in the late 1940's was one of the worst to hit the atoll. Estimates of the damage vary—Emory (1954) states that 201 productive breadfruit trees were destroyed, although the community secretary lists 67 breadfruit, 10 coconut and 30 houses destroyed. Six *Cyrtosperma chamissonis* marshes, mostly on Ringutoru, were also damaged by salt water.

* Water hardness: less than 50-60 ppm, soft; up to 200-300 ppm, hard (Arnow 1954).

FLORISTIC ASPECTS

A relatively limited vascular flora (99 species) occurs on Kapingamarangi, representing about one-tenth of the total flora of Micronesia (Kanehira 1933). It has been estimated that Pacific atolls may average less than 150 species (Fosberg, written communication), although reports range from 3 on Vostok Island (Christopherson 1931; Fosberg, 1937), 4 on Rose Atoll in the Samoan Islands (Pickering 1886; Sachet 1954) to over 300 on the Maldives in the Indian Ocean (Fosberg 1957c). Considering the broad moisture range encountered throughout the Pacific, such extreme variability is to be expected. On Pokak and Bikar, in the drier northern Marshalls, only 9 vascular species are reported, whereas on Arno in the wetter southern Marshalls, Hatheway (1953) estimates 125 species. On Onotoa in the Gilberts, Moul (1957) found only 60 species following a drought. Papers on various atolls of the Carolines report 58 vascular species on Ant (Glassman 1953), 73 on Mokil (Glassman 1953), 78 on Pingelap (St. John 1948; Glassman 1953) and 94 on Namonuito and the Hall Islands (Stone 1959) which are island groups floristically similar to Kapingamarangi. Some of the factors accounting for this floristic sparcity, as suggested by Fosberg (1953), include the distance from seed sources, the ocean barrier, lack of topographic relief, ground and aerial salinity, immature calcareous soils, precipitation regime, and shortness of the history of land availability to plant colonization.

Of the 99 vascular plants on Kapingamarangi, over one-half (56) have been introduced either as early aboriginal or more recent introductions (Figs. 5, 6, 8). Coconut (*Cocos nucifera*) and *Pandanus tectorius,* the most important trees, along with breadfruit (*Artocarpus altilis*) and the taro-like aroid *Cyrtosperma chamissonis,* are considered introduced, although *Pandanus* may also be indigenous. As assumed for other atolls in the Pacific, coconut was probably an aboriginal introduction, since nuts have limited viability following prolonged exposure to salt water. Breadfruit and the formerly abundant taro (*Colocasia esculenta*) were probably recent European introductions. The more vigorous Cyrtosperma was introduced even more recently.

The genus *Pandanus* shows much variation on

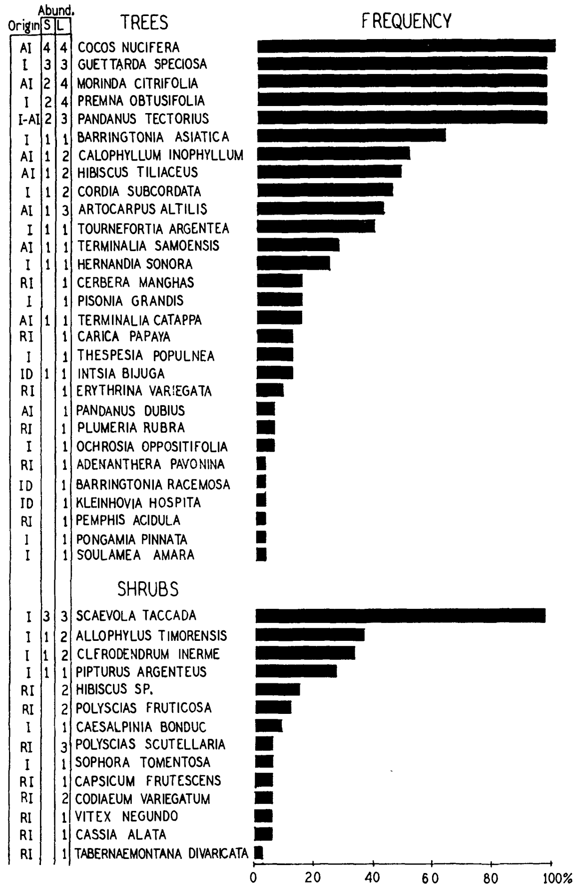

FIG. 5. Species list of trees and shrubs arranged according to their frequency of occurrence of various islets of atoll. For example, coconut with 100% frequency was found on all islets whereas *Soulamea amara* with 3% frequency occurred on only one island. Abundance of species on small (S) and large (L) islands indicated in left columns: abundant-(4), frequent-(3), occasional-(2), rare-(1). Probable origin of each species is also indicated by letters. (AI)-aboriginal introduction, (RI)-recent introduction, (I)-indigenous, and (ID)-indigenous drift, which includes a few species found only as seedlings in the beach drift.

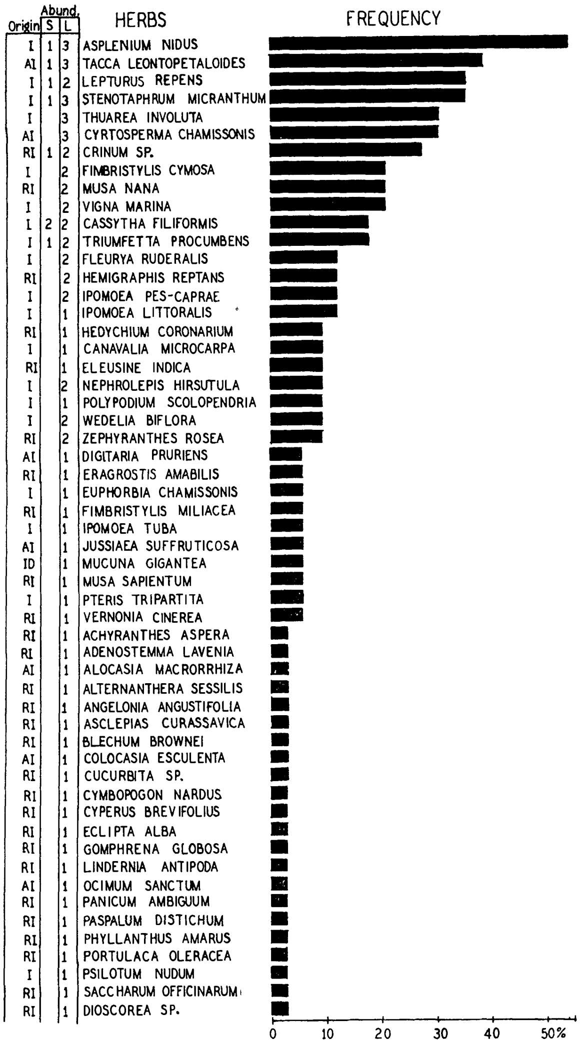

FIG. 6. Species list of herbs arranged according to their frequency of occurrence on various islands of atoll. For example, *Asplenium nidus* with 54% frequency was found on 18 of the 33 islands, whereas *Dioscorea* sp. with 3% frequency occurred on only one islet. Abundance of species on small (S) and large (L) islets indicated in left columns: frequent-(3), occasional-(2), rare-(1). Probable origin of each species is also indicated by letters: (AI)-aboriginal introduction, (RI)-recent introduction, (I)-indigenous, and (ID)-indigenous drift, which includes a few species found only as seedlings in the beach drift.

atolls and may well represent several species and possibly endemics (as reported on Eniwetok, St. John 1960a, b). At least six different kinds of Pandanus are recognized and named by the natives of Kapingamarangi. The most common, "pinu pinu," reproduces naturally in the plantations, but produces poor fruit. According to the natives, cuttings from only certain trees produce the best fruit and at least five different qualities are distinguished. A variegated leaf form also occurs on one island. Differences were also noted among the coconut and breadfruit populations. Three types of coconut are represented: the common type which dominates the plantations and the red and dwarf nut varieties recently introduced from Nukuoro. Several kinds of breadfruit are also named by the inhabitants: the Kapinga type, probably an aboriginal introduction, and others of more recent origin; the Nukuoro, which was originally introduced from Samoa circa 1922; and the Ponape variety brought in circa 1935. Although opinion varies as to which fruit is superior, Kapinga breadfruit is apparently preferred and most common throughout the plantations. The Kapinga and Nukuoro varieties are propagated by seed and the seedless Ponape trees by air grafting and suckers.

The most important native trees are *Morinda citrifolia, Premna obtusifolia* and *Guettarda speciosa* which occur on practically all the islets (Fig. 5, 6). Of the 29 tree species over one-third are rare, occurring on only one or two islands and two species are merely represented as drift seedlings on the beach. Among the shrubs, *Scaevola taccada* is most widely distributed, primarily along the beaches. In the herb stratum the fern *Asplenium nidus* occurs on over half of the islets, although herbaceous cover is rare or absent on most of the smaller islets. Along with *Asplenium,* certain other species such as *Tacca leontopetaloides, Lepturus repens, Stenotaphrum micranthum, Thuarea involuta* and *Crinum* sp. frequently occur on the larger islands. Of the 55 herbaceous species over half occur on only one or two of the islands and over one-third are present on only one. Many of these are recently introduced ornamentals restricted to the two inhabited islands. A single marine seed plant (*Thalassia hemphrichii*) is locally frequent in the shallow lagoon waters along Hare and Ringutoru.

The number of different species found on each island ranged from 5 on the smallest (Matukerekere) to 61 on inhabited Werua, the widest island in the atoll. When the total species per island are plotted logarithmically against island size two linear relationships result (Figs. 7, 8). One includes those islands less than 3.5 acres in size which fall along one line with little variation in number of species. The other includes the larger islands and shows more strikingly the direct relationship between island size and number of species. On the smaller islands there are from 5 to 16 species. However, as the islands increase in size the flora correspondingly tends to increase, which is apparently correlated with increased soil maturity, soil moisture and protection from salt spray resulting from a larger vegetated land mass. On the two inhabited islands, introduced ornamentals account for the larger number of species.

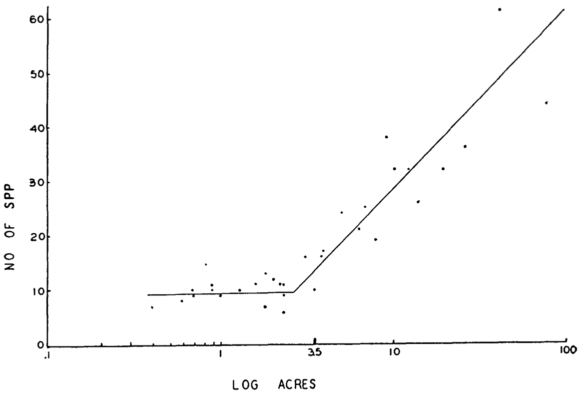

FIG. 7. Line graph showing number of species plotted against island size. Although the islands vary from .03 to 79.5 acres the smallest island was deleted since plotting was facilitated and no change in the relationship occurred. (See Fig. 8). Note the two linear relationships. On those islands 3.5 acres or less there is little variation in number of species per island. However, on those larger there is a continuous increase in number of species with increase in island size.

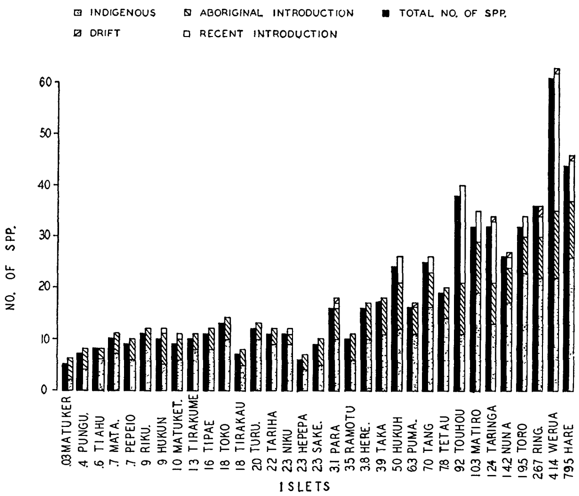

FIG. 8. Bar graph showing number of species found on each island and presumed origin. Solid bar refers to the total vascular flora with adjacent bar divided according to the origin of these species. Note continuous increase in number of species on islets over 3.5 acres. On the inhabited islets, Touhou and Werua, recent introductions account for the increase in species. Numbers adjacent the islands refer to size in acres. Drift refers to those few species found only as seedlings in the beach drift.

The entry of the native flora onto the atoll has probably been by water, wind and birds. The fruit and seeds of Scaevola, Guettarda, Pandanus, *Tournefortia argentea, Barringtonia asiatica, Cordia subcordata, Ochrosia oppositifolia* and grasses such as Lepturus, are primarily adapted to floating; and seedlings of certain of these were encountered in the beach drift. In fact, 4 species, *Mucuna gigantea, Intsia bijuga, Barringtonia racemosa* and *Kleinhovia hospita* were found only as drift seedlings, thus indicating their recent entry by water transport. Other species with sticky seeds or fruits, such as *Pisonia grandis,* are probably carried on the feet or feathers of birds. The fruits of some others may be eaten, as with *Cassytha filiformis, Pipturus argenteus, Morinda* and *Premna,* and the seeds transported internally. The ferns Asplenium, *Nephrolepis hirsutula, Polypodium scolopendria, Pteris tripartita,* and the spore-bearing *Psilotum nudum* have probably reached the atoll by wind-blown spores. On Kapingamarangi, Emory (1954) also observed that entire plants, such as *Sophora tomentosa* and *Hernandia sonora* can float onto the beach and become established. The floristic spectrum includes a wide-ranging Indo-Pacific flora some elements of which may have come from the scattered volcanic islands in Micronesia, while other species may have originated from New Guinea which lies south of the atoll.

The bryophyte flora on the atoll includes 7 species of mosses and 6 of liverworts (Miller 1956) and their ecology and phytogeography have been published (Niering & Miller 1956). One new species of liverwort, *Cololejeunea kapingaensis* Miller, was

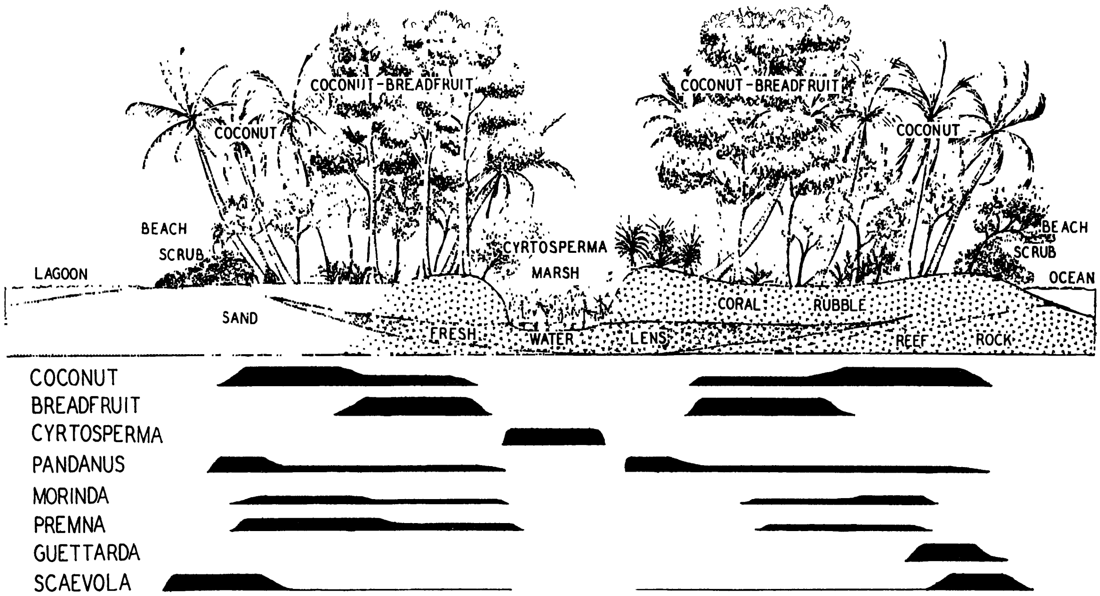

FIG. 9. Generalized bisect of large island from ocean to lagoon showing vegetation belts, soils and fresh water lens. Oceanward, beach-scrub of *Scaevola taccada* and *Guettarda speciosa* is replaced by coconut. Coconut-breadfruit type dominates the interior surrounding *Cyrtosperma chamissonis* marsh. Young *Pandanus tectorius* planting on rubble bank. Lagoonward Scaevola is a pioneer on sand bar. Abundance of dominant species on various sites indicated by width of bars.

collected and described (Miller 1956). The lichen flora comprises 19 species (Herre 1955) including a new species, *Bacidia Nieringi* Herre. Identifications of the algae and fungi were unavailable at this writing. Studies of the fungi on 8 atolls and a single island in the Marshalls reveal 34 species including two new forms (Rogers 1947).

VEGETATION

Coconut plantations comprise the dominant vegetation, often in mixture with breadfruit. On the smaller islands coconut covers the entire land area, whereas coconut and coconut-breadfruit groves dominate the larger land masses. In a typical transect across a larger island, from the ocean side to the lagoon, the initial vegetation on the beach rampart is a marginal beach-scrub belt of Scaevola and Guettarda (Figs. 9, 17). Towering above this belt and extending into the interior, coconut forms an outer band of varying width which is replaced toward the center of the island by a mixture of coconut and breadfruit within which occur excavated swampy areas planted to Cyrtosperma. Toward the lagoon there is again a narrower belt of coconut which continues to a more open beach vegetation along the lagoon shore (Fig. 18). On Werua, in addition to the other types, large breadfruit groves also occur in the interior. The village areas which occupy all of Touhou and the lagoon shore of Werua occur primarily within the coconut-breadfruit type. In addition to an abundance of Pandanus around the villages, recently introduced ornamentals are common. Since the total land area is essentially under cultivation, the spontaneous vegetation is restricted to the plantation undergrowth, and to a narrow belt along the beaches. Because the plantations are periodically cleared, there is considerable variability in the undergrowth. In the coconut, coconut-breadfruit and breadfruit groves repeated clearing keeps understory vegetation in a constant state of change. At any one time there may be 20-50% woody growth composed of resurge 2-5 ft high and scattered understory trees 10-20 ft in height. Within these vegetation types the herb layer usually represents less than 25% cover consisting primarily of grasses or, less frequently, ferns where the cover may be continuous. On the smaller drier islands both woody and herbaceous ground cover decreases markedly. On all islands one can walk throughout the plantations without being impeded by the undergrowth.

This highly manipulated vegetation has been arbitrarily divided into six types: namely, coconut plantations, coconut-breadfruit plantations, breadfruit groves, Cyrtosperma marshes, beach-scrub and village vegetation.

VEGETATION TYPES

COCONUT PLANTATIONS

Although coconut plantations completely cover the smaller islands, on the larger ones they form marginal belts ranging in width from 100-150 ft oceanward and 60-100 ft lagoonward. As shown by the vegetation mapping, these plantations cover about one-half of the total land area on the atoll (157 acres). From the quadrat data it was estimated that there are 116.5 coconut trees per acre, which form a relatively continuous canopy with considerable overlapping of fronds. Mature trees are irregularly spaced on an average of 21 ft between trees. This, compared to the recommended 27-34 ft (Menon & Pandalai 1958) would suggest considerable overcrowding on Kapingamarangi. Since the islands are under such intensive management and the coconuts judicially harvested, natural reproduction was observed only on Pumatahati, one of the two community islands, where the coconuts are not harvested as often as on those owned by individual families.

Indigenous trees such as Guettarda, Pandanus, Morinda and Premna comprise the important undergrowth. On the smaller islands Guettarda and Pandanus are most common, while on the larger ones the latter, along with Morinda and Premna, increases in abundance. Herbaceous cover is sparse or wanting on the smaller boulder strewn islands but increases in diversity with island size. Coconut stumps are relatively common and often covered with cushion-like mats of *Leucophanes smaragdinum,* a moss which resembles *Leucobryum glaucum* of North America.

Since the plantations differ considerably with island size the pattern encountered on the small and large islands will be discussed.

SMALL ISLANDS: These 19 islands, 3.5 acres or less in extent, tend to be elongated in an oceanward to lagoonward direction (Figs. 1, 8). They vary from 25-350 ft in width and 100-500 ft in length. The coarse bouldery rubble or sandy soils are extremely immature. Although coconuts completely cover these islands, they reach only 55-65 ft in height and are the least productive plantations on the atoll (Fig. 10). On the recently formed sandy artificial

FIG. 10. Oceanward view of coconut covered island from reef at low tide showing raised reef rock platform. *Scaevola taccada* shrub cover relatively continuous oceanward (right) and less continuous with taller *Guettarda speciosa* along the more exposed southeastern windward side of the islet.

island of Pepeio the trees are only 35-40 ft in height and extremely chlorotic in appearance. · Only one breadfruit was found on these islands. The open understory with often less than 25% cover is characterized by scattered trees of Guettarda 25-30 ft in height along with transitional stages of resurge depending upon the recency of clearing (Fig. 11).

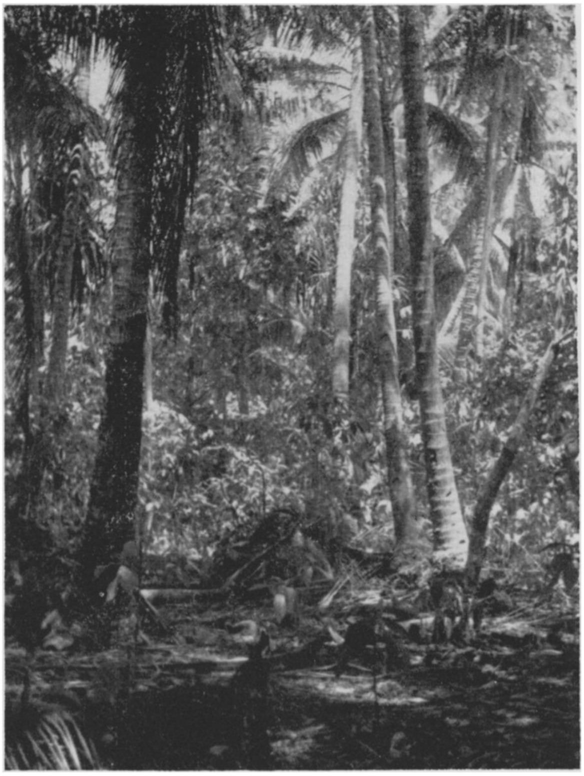

FIG. 11. Differential clearing of indigenous undergrowth within coconut plantations. Recently cleared in foreground, uncleared beyond comprising a mixture of *Guettarda speciosa, Premna obtusifolia, Morinda citrifolia* and *Pandanus tectorius.* Hepepa Islet.

Morinda and Premna are rare and Scaevola occurs only sporadically in the interior except on the very narrow islet of Rikumanu where it forms a continuous shrub layer under the coconut. On two other narrow islands (Matuketuke and Matawhei), which are covered by coarse coral boulders, the undergrowth is absent oceanward but reappears on the finer soils lagoonward (Fig. 12). The presence of

FIG. 12. Interior of small island dominated by coconut and scattered *Pandanus tectorius.* Sparse undergrowth oceanward (foreground) increasing lagoonward. Ground littered with leaf debris. Matuketuke Islet.

stumps on such islands would suggest a former understory which may have been cut or killed by salt spray or salt water inundation, or a combination of these factors.

The herbaceous layer is either absent or, where present, comprises less than 10% cover including such genera as *Tacca, Asplenium, Crinum, Lepturus,* and *Cassytha,* a parasite. In openings on sandy Turuaimu island, *Triumfetta procumbens* forms a relatively continuous ground cover. The sparse undergrowth and paucity of species on these smaller islands is related to a complex of environmental extremes including the bouldery substrate and limited soil development, severe effect of salt-laden winds accentuated by the narrow shape of the islets, the absence of protective marginal beach vegetation and the lack of a fresh water lens. Apparently a certain minimum area, somewhat over 3.5 acres, with sufficient soil development, is required for undergrowth development which, in turn, tends to ameliorate the environment and favor the establishment of additional species.

LARGE ISLANDS: The remaining 14 islands (3.5 acres or larger in extent) are elongated along the reef and range from 800 ft to 1 mi in length and 500-1,200 ft in width (Figs. 1, 8).

As on the smaller islands, coconut plantations tend to dominate most of the land surface on those up to 10 acres in size. However, on the largest ones, coconut-breadfruit plantations increase toward the interior and frequently equal the area occupied by coconut (Figs. 14, 15). On these 14 islands the plantations are taller (75-85 ft average) and more productive. In the disturbed areas on Hare the postwar trees, which are approximately 10 yrs old, are already productive, although they have not attained the height of the surrounding older trees. In contrast, recovery has been slower on Nunakita where scattered tall pre-war palms stand out conspicuously. This poorer development appears to be correlated with greater disturbance and a thinner soil overlying the bedrock on Nunakita. As on the smaller land areas, Pandanus is an important associate, the larger trees entering the main canopy, while recent localized plantings form a part of the understory.

The understory aspect differs markedly from that of the smaller islands. Although Guettarda is present, Premna and Morinda comprise 50-75% of the understory. Trees frequently reach 5-7 in. dbh and attain 25-30 ft or more in height. Other associates include Pisonia, *Hibiscus tiliaceus* and a variety of other native species of minor importance (Fig. 5). A relatively mature stand of Pisonia formerly occurred on Pumatahati, but it has since been cleared and planted to coconut. Here Pisonia sprouts are frequent in the understory, although the larger stems reach 12 in. in diameter. On the various islets, shrubby growth includes sprouts and suckers from Morinda and Premna mixed with such shrubs as *Allophylus timorensis* and *Clerodendrum inerme.* The undergrowth may be continuous in some areas and relatively sparse in others, depending upon the stage of development following clearing.

Herbaceous cover, which increases markedly on these islands, is better developed on the rubbly-humus soils than on the less humified sandy soils. Grasses, especially Stenotaphrum and Thuarea, form carpet-like coverings in the more open situations, with the epiphytic fern Asplenium occurring either on coconut stumps or on old coconut husks on the ground. Other herbs comprising the ground cover are shown in Fig. 6. On the wider islands, such as Torongahai and Ringutoru, at the northern end of the atoll, a luxuriant growth of ferns, especially Nephrolepis and Asplenium, forms a dense continuous cover 2-3 ft in height between clearing operations (Fig. 13).

FIG. 13. Dense ground cover of fern, *Nephrolepis hirsutula* within coconut plantation. *Pandanus tectorius* conspicuous in understory.

The restricted distribution of Nephrolepis to the wider, possibly more mesophytic, islands of the atoll is of interest. It would appear that the increased protection from salt spray afforded by a larger, more continuously vegetation-covered land area may be an important factor in accounting for this distributional pattern. Moisture differences between these islands and others nearly as large were not superficially evident from the soil profiles. However, soil moisture studies would be of interest in this relation.

Tree reproduction was limited to Pandanus and *Soulamea amara,* the latter restricted to a small area on Nunakita. Reproduction of other species appeared primarily vegetative, although sprouting following clearing operations has undoubtedly obscured this point. The pattern of undergrowth described is periodically modified as a result of selective clearing, but at any one time the pattern described may be evident.

Local variants occur in the undergrowth on the relatively recently formed sandy lobes which project lagoonward from the ends of the islands and on the channels between the islets that have been filled in during severe storms. Since these sandy lobes are increasing in size as a result of deposition lagoonward, a developmental trend is evident in the understory from the lagoon beach to the interior. On Ringutoru lagoonward migration of the land is so rapid that the typical beach-scrub vegetation, including Guettarda, Scaevola and Tournefortia, persists inland where it forms an open understory. On these relatively unaltered sands the ground cover is sparse with only scattered patches of Lepturus and occasional seedlings and saplings of Morinda and Premna. Back from the beach 100 ft or more this pioneer vegetation is replaced by the typical Premna-Morinda understory along with a ground cover of ferns. On these sandy lobes there appears to be a developmental trend toward an increase in Premna and Morinda.

As a result of channel filling, the physiognomy of the atoll has been modified over the years. As previously mentioned, Hare island, 1 mi in length, originally represented 3 separate islands which have been joined together by deposition during storms, one channel having closed about 1865, another in 1942. They are clearly demarcated by the nature of the parent material, the presence of old beach ramparts lined with Guettarda trees crossing the interior, and the chlorotic appearance of the palms on the channel most recently formed. These areas are of particular interest in that they give some indication of the rate of organic matter accumulation and subsequent influence on the vegetation. Just how soon coconuts were planted after closing is not known, but it can be assumed that with such a limited land area for food and copra production it occurred quite soon. After 12 yrs on the unaltered sands of the most recently closed channel, the largest palms are just becoming productive. Pioneer undergrowth, such as Scaevola, is scattered and seedlings of Morinda and Premna are rare. On the older channel, the soil development shows an organic layer 1 in. in depth which is replaced by gray-stained foraminiferal sands to a depth of 6 in. beneath which is unaltered parent material. Here the vegetation resembles that typical of the smaller more xeric islands: Guettarda typifies the understory, grasses the sparse ground cover, and there appears to be little evidence of vegetational change.

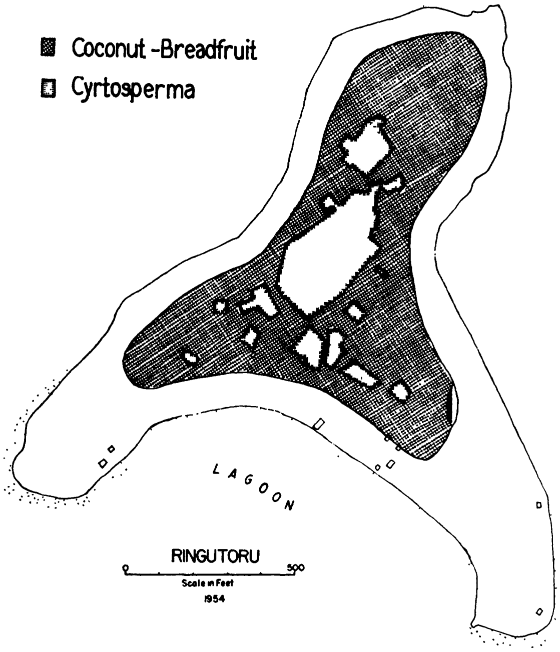

FIG. 14. Three major vegetation types on Ringutoru. Coconut plantations dominate unshaded band surrounding coconut-breadfruit type. Lobes projecting lagoonward on Ringutoru are sand bars. Rubble soil covered land area represented by single lobe projecting oceanward. Map taken from Wiens (1956).

COCONUT-BREADFRUIT PLANTATIONS

On 13 of the larger islands the coconut plantations are replaced in the interior by the coconut-breadfruit type (Figs. 14, 15). These plantations cover about one-third of the total land area (76 acres) and extend to within 60-100 ft of the lagoon beach, except on the slightly more elevated islet of Touhou where trees occur within 40 ft of the ocean and only 18 ft from the lagoon. This restricted distribution of breadfruit to the interior is correlated with its sensitivity to ground water salinity and salt spray, as will be discussed later. Although breadfruit has a dominant aspect throughout, forming a canopy 15-20 ft above the coconuts, an aspect especially conspicuous from offshore, the actual number of coconut trees is more than double that of breadfruit per acre (47 coconut: 19 breadfruit—Werua island). The straight fluted breadfruit trunks, free of branches for the first 25 ft or more, average 1-2 ft in diameter, with occasional larger trees. They are interspersed among the coconut about every 50 ft and together form a relatively closed canopy 90-100 ft in height. Openings in the canopy are due primarily to dead or partly defoliated breadfruit branches resulting from storms, ground water salinity or heavy breeding bird populations. These branches are the preferred nesting site of the gregarious white-capped noddy tern.

The understory vegetational pattern is similar to that found in the coconut plantations on the larger islands, except for a more open aspect due to the denser overstory. Local variations occur on the excavated rubble banks surrounding the Cyrtosperma marshes. On the older more stable banks, young Pandanus plantings are common with the trees spaced 3-5 ft apart and ranging from 6-12 ft in

FIG. 15. Coconut-breadfruit type in interior of Hare Islet. *Pandanus tectorius* is a conspicuous associate. Scattered indigenous undergrowth includes young Pandanus (foreground).

height. Their generally small and uniform size suggests post-war planting, probably resulting from the recent demand for mats and other handicrafts which are made from the leaves. Shrubby undergrowth includes thickets of Clerodendrum and sprouts of Morinda and Premna. Scattered *Hibiscus tiliaceus* frequently lean out over the sunken Cyrtosperma marshes. On the rubble banks Thuarea and Stenotaphrum form continuous carpet-like patches and *Vigna marina* and *Wedelia biflora* may form a continuous layer 1-2 ft in height. Locally on Ringutoru there occur small plantings of banana (*Musa sapientum*) and papaya (*Carica papaya*).

Natural reproduction of breadfruit was evident on only one island and here the seedlings were nipped off, presumably by crabs. According to the inhabitants, breadfruit was more abundant prior to the 1947 storm. Young trees 8-12 in. dbh are frequently found in the surrounding coconut plantations, which is indicative of an expansion of this coconut-breadfruit type as a result of planting.

BREADFRUIT GROVES

On Werua, the widest island in the atoll, the coconut-breadfruit type is replaced by a relatively pure breadfruit grove covering 10 acres. The breadfruit density increases to an average of 50 trees per acre as contrasted to only 28 for coconut. The massive breadfruit canopies tower over 100 ft in height and so dominate the area that even mature coconut are relatively inconspicuous. This is the most mature forest encountered on the atoll, with trees reaching 2-4 ft in diameter. The largest breadfruit tree observed on the atoll was 77 in. in diameter. Computing the quadrat data on an acreage basis the following number of trees in the various size classes was recorded: 1-6 in., 6 trees; 6-12 in., 6.5 trees; 12-24 in., 13 trees; 24-38 in., 24 trees; over 38 in., 2 trees. Pandanus forms an important associate with coconut in the second story and also occurs as pure stands which have been planted on the open rubble banks surrounding the Cyrtosperma marshes.

Natural undergrowth, although very restricted except on the rubble banks above the Cyrtosperma, is similar to that described in the coconut-breadfruit type. Natural reproduction of breadfruit was not observed within the grove and young trees were uncommon, as was noted by Hatheway (1953) in the Marshalls.

CYRTOSPERMA MARSHES

On 11 of the larger islands, artificially formed marshes, which cover 25 acres, are located near the center or slightly lagoonward within the breadfruit or coconut-breadfruit groves (Figs. 14, 16). These

FIG. 16. Artificially created marsh planted to *Cyrtosperma chamissonis* on Werua surrounded by breadfruit grove. *Morinda citrifolia, Premna obtusifolia* and banana along margin of marsh. Werua Islet.

areas, which vary from a few square feet to several acres (Werua) in extent have been formed by excavating to slightly below the top of the fresh water lens and filling with a layer of organic matter. Banks of rubble usually 3-5 ft high, but sometimes reaching 15 ft above the adjacent land, surround the marshes. Cyrtosperma is planted 8-12 in. apart and eventually grows to 2-6 ft in height. In shaded situations the plants are taller and more vigorous than in the center of the marshes where they are frequently small with yellowish-brown leaves. Although Cyrtosperma is presently dominant, taro was more important in the past. Since only scattered specimens of the latter occur, it is assumed that taro has been replaced due to competition from the more vigorous Cyrtosperma.

Scattered banana, ornamental *Hibiscus* sp. and *Cassia alata,* a recent introduction for medicinal purposes, occur within the marshes. Weedy herbaceous growth includes *Jussiaea suffruticosa,* which is most frequent and grows 2-3 ft in height. Other plants occasionally associated are *Angelonia angustifolia, Lindernia antipoda, Ipomoea littoralis, Cyperus brevifolius, Hedychium coronarium,* and *Fimbristylis miliacea.* Along the slightly elevated paths one finds *Alternanthera sessilis, Digitaria pruriens* var. *microbachne* and *Paspalum distichum.*

As evidenced by a few new excavations, the acreage of Cyrtosperma will probably increase slightly in the future. Only one small abandoned marsh (12 x 15 ft) was found on Werua where the natives were unable to grow Cyrtosperma, possibly due to salt water penetration. The restriction of Cyrtosperma to the interiors of the larger islets is correlated with its dependence upon a fresh water lens, which will be discussed in a later section.

BEACH-SCRUB VEGETATION

Seaward and along the inter-island channels a border of beach-scrub vegetation has developed under relatively natural conditions (Figs. 17, 20). Here on the coarse rubble ramparts or beach ridges, Scaevola and Guettarda form a two-layered border varying from 15 to 30 ft in width. The taller growing Guettarda occurs either as low trees up to 12-15 in. in diameter and 20-25 ft in height or as numerous stump sprouts of smaller size. In front of or under the Guettarda, Scaevola forms a sloping fringe 5-15 ft high. Species occasionally associated include

FIG. 17. Beach-scrub vegetation on beach rampart oceanward. *Scaevola taccada* forms outer shrub border. Sakenge Islet.

Cordia, *Terminalia samoensis* and Clerodendrum. Tournefortia, an important shrubby beach tree on other atolls, was infrequent. Guettarda and Scaevola tend to be associated, although where erosion is severe, the latter decreases in importance (Fig. 10). Therefore, along the east-southeast windward exposures, Guettarda dominates the border, whereas on the more protected leeward sites both species are present. On the other hand, wherever Scaevola is conspicuous on the windward side there is some protection such as raised beach rock off shore or fish traps constructed of coral boulders in the channels. Where erosion is severe the shallow-rooted Scaevola is either partly or completely washed out. Large coconut palms were also frequently eroded out and strewn along the windward beaches (Fig. 20). Herbaceous cover is lacking except for occasional clumps of Asplenium, established on coconut husks.

Along the sandy lagoon shores, except on the sand bars which project lagoonward, the Scaevola-Guettarda belt is absent or poorly developed. Along the lagoon beach, coconut and Pandanus are planted to the edge (Fig. 18). In addition, large trees of *Calophyllum inophyllum* (1-2 ft dbh) are scattered and primarily restricted to the lagoon side. Only two specimens were seen elsewhere, one vigorous tree in the interior and the other, severely damaged by insects and salt spray, toward the ocean.

FIG. 18. Coconut palms line the sandy lagoon beach adjacent village on Werua Islet.

Herbaceous cover encountered along the lagoon beach includes Vigna, a locally abundant pioneer vine which forms dense tangles over the adjacent marginal species. It sometimes becomes so dense that trees such as Pandanus must be periodically cleared of it. Other frequent herbs include *Ipomoea pes-caprae* and Triumfetta.

Along the lagoon beach, seedlings readily become established, most of which are of drift origin. On the back shore of 7 islands observations were made regarding their frequency and abundance. Of the 7 important species found, 6 occurred on over two-thirds of the islands surveyed and are arranged according to their abundance: Scaevola, Guettarda, Pandanus, Tournefortia, *Barringtonia asiatica,* and

Hibiscus. Seedlings of Barringtonia were present on all 7 islands but only one mature tree was found along the beach on the atoll. Less common were seedlings of Morinda, Calophyllum, Premna, and Hernandia. Many of the seedlings, especially of Barringtonia, were damaged, presumably by crabs. On the sand bars, Scaevola is a typical pioneer, frequently forming open thickets. On Pumatahati the lagoon beach is formed of coral rubble which extends for 50 ft back from the beach. This site was covered by a low gnarled pure stand of Cordia, 35 ft high, which presumably represents a remnant of the indigenous vegetation.

VILLAGE VEGETATION

The majority of the people live either on Touhou, which is completely inhabited, or along the lagoon shores of Werua. Only a few families live on the outlying islands. Throughout the villages, coconut or coconut-breadfruit plantations form the conspicuous cover. The undergrowth is characterized by an abundance of Pandanus and recently introduced species. Even on Touhou where the houses are closely spaced each family owns sufficient land to support several Pandanus. Scattered specimens of Morinda, Pisonia, Premna, Guettarda, banana, and papaya occur throughout the village. Most conspicuous are the recently introduced ornamentals which include *Codiaeum variegatum, Plumeria rubra, Zephyranthes rosea, Polyscias scutellaria, Polyscias fruticosa, Crinum* sp., Hibiscus hybrids and others. These ornamentals are especially common around the houses and cemeteries. Along the streets and to demarcate property lines, *Polyscias scutellaria* is frequently used as a shrub border.

Although the natives weed and clean up fallen leaf debris, a few scattered introduced weeds persist in the gray coral rubble. These include *Adenostemma lavenia, Eclipta alba, Phyllanthus amarus, Portulaca oleracea* and *Hemigraphis reptans,* as well as scattered patches of grasses and sedges. On the bare rubble Premna and Morinda seedlings are locally abundant under Pandanus and other trees which are visited by starlings, although there is little evidence that these seedlings survive. Around some of the houses small nurseries of breadfruit, Calophyllum, and recently introduced species are encountered. Seed coconuts are frequently placed on the roofs of the houses to protect the germinating nuts from crabs. Here they are allowed to sprout prior to planting. Seedlings of drift origin, such as Calophyllum, are likewise protected from crabs in these nurseries until large enough to plant along the lagoon shore.

ECOLOGIC INFLUENCES

THE ROLE OF MAN

Man has had a profound influence on the vegetation of atolls, and his role in the dispersion and introduction of species is well documented (Fosberg 1949a, 1959; Merrill 1954; Egler 1956; Dawson 1959). On inhabited islands, the dominant vegetational pattern is a result of his activities in the introduction, propagation, manipulation and utilization of plants. It is from this terrestrial phase of the atoll ecosystem that the inhabitants derive their basic needs for life, supplemented by the rich marine resources of the surrounding aquatic environment.

The inhabitants have introduced over half the vascular plants on the atoll, only a few of which dominate the vegetational pattern. During the past decade introduced ornamentals have increased markedly and this trend may even accelerate with inter-island travel now facilitated by trading ships. The lack of greater diversity in the native floristic spectrum is partly due to geographic isolation but it may also be reflected in the fact that the Kapingans are not sea-faring people as are many others in Micronesia.

The important plants propagated by the natives include coconut, breadfruit, Pandanus and Cyrtosperma, and to a lesser degree, banana and papaya. In the villages the conspicuous planted ornamentals include Hibiscus and Plumeria, and a variety of other species. Calophyllum, a native species, is propagated by the inhabitants to a limited extent and Hibiscus trees are tipped so that lateral branches will grow tall and straight for use as yards on outriggers.

The manipulation of the vegetation involves selective clearing of the native undergrowth since many of the species are used in construction and in making utensils and handicrafts. Periodic clearing of the woody resurge and herbaceous cover decreases competition with the coconut and breadfruit and permits greater ease of access throughout the plantations. It may be an annual operation; but is usually done more often, especially on the larger islands. As a result of differential clearing by adjacent plantation owners, sharp lines of demarcation are often evident (Fig. 11). Burning is practiced only to a very limited extent. The marginal beach-scrub vegetation is usually preserved since its value in erosion control and salt spray interception is recognized.

The dependence of the native population upon the vegetation is impressively presented by Buck (1950) in his study of the material culture of the atoll. The most valuable single species is coconut which provides a source of water, food and shelter. The green or immature nut furnishes the primary source of drinking water and a palatable soft food for infants, the mature nut—fresh coconut, and the sprouted nut a spongy sweet pulp. Coconut husks are used in making rope and also provide an important source of fuel. The fronds are utilized in making thatch, mats, baskets, brooms, and as fishing torches, while from the flower buds a sweet exudate is tapped and drunk fresh, or occasionally, fermented into toddy. Coconut logs are invaluable in house construction. In addition, copra (dried coconut) has played an important role in the atoll economy. This trade reached its peak during the Japanese period when 300 metric tons were exported annually. In recent years copra production has decreased with shipments ranging anywhere from 3 to 30 tons. In July 1954, the trading ship picked up 15 tons. This decrease is probably correlated with lower prices, gradual population increase, abundance of older less productive trees and the competitive demand for Pandanus mats and other native handicrafts which are an equally good source of income.

Breadfruit, another important tree, provides an edible fruit similar to sweet potato when ripe, and, from the larger trees, logs are derived for making the hulls of outrigger canoes. The wood is also used in making coconut graters and the green leaves for wrapping food in ground oven cooking.

Pandanus also provides an edible pulp from its fruit and the leaves are highly valued for plaiting mats. The current demand for Pandanus floor mats, involving a 100,000 sq ft contract, has stimulated extensive plantings. Dead leaves are gathered from the trees for roofing houses and the prop roots provide a source of string.

Cyrtosperma, the fourth food source, produces a large starchy tuber which must be cooked but can be stored as an emergency food. Other foods less commonly available include banana, papaya, and Tacca, also a source of starch. The leaves of banana are frequently used in ground oven cooking.

Most of the native species are important in house or canoe construction and in the making of utensils, implements and handicraft articles. For example, the hard wood of Premna is used for canoe poles and paddles, and Calophyllum for making coconut graters. The flexible twigs of Clerodendrum are utilized in making fish traps and the inner bark of *Hibiscus tiliaceus* was formerly woven into bark cloth for clothing. Flowers from the ornamentals, especially Plumeria, are used in making flower headbands or leis. The inhabitants appear extremely aware of their dependence upon the vegetation. This is evidenced by their selective management policies and further emphasized by their reluctance to sell canoes to outsiders since it would mean the loss of another large productive breadfruit tree.

EFFECTS OF SALINITY AND STORMS

In addition to man, aerial and ground salinity and periodic storms are important factors in determining the vegetational pattern. Although salt spray and ground water salinity constantly condition the vegetation, their effects are greatly accentuated during storms, as well as droughts. Most of the vegetation is dependent upon soil water held in the upper strata, although certain species such as breadfruit and Cyrtosperma utilize the ground water reserves (Fosberg 1949b; Cox 1951; Stone 1951; Arnow 1954, 1955; Mason 1960). During severe storms ground water salinity and salt spray increase and during prolonged droughts salt water may penetrate by capillarity into the soil water above and adversely affect the vegetation.

These various influences act as an interacting complex whose separate effects are often not readily discernible. This discussion will consider the effect of salt spray, ground water salinity and storms and attempt to interrelate their effects.

AERIAL SALINITY

In the beach-scrub belt the importance of Guettarda and Scaevola attests to their extreme tolerance of salt spray. Scaevola showed no marked damage, although the foliage was occasionally chlorotic and some severely eroded shrubs exhibited dwarfed leaf rosettes which may be the result of either salinity or a mineral deficiency. On the windward side of the islands the leaves of Guettarda occasionally showed marginal browning and die-back of twigs which was not evident on the lagoon side. Associated trees such as Cordia and Terminalia are more adversely affected, which may account for their minor importance in this belt. All Terminalia were extremely depauperate with only a few leaves at the ends of branches and Cordia showed spray-sheared effects with many stems killed back 6-12 in. or more within the time of the survey. This kill-back may be related to the lack of precipitation during the two-month period.

Coconut and Pandanus are extremely salt-tolerant and showed no adverse salinity effects. However, Morinda and Premna, typically restricted to the undergrowth in these plantations on the larger islands, exhibited severe salt spray damage where trees were situated in exposed sites near the beach. Further inland, the upper branches of breadfruit, which project above the surrounding coconut, are frequently defoliated or dead. According to the natives the upper branches lose their leaves following severe storms and new ones appear later. In this situation salt spray and ground water salinity are probably both involved and, in certain situations, the concentrated breeding bird populations may also be a contributing factor (Fig. 23). Another sensitive tree is Calophyllum which is essentially restricted to the lagoon shore. Specimens observed oceanward showed both severe salt spray and insect damage.

To summarize the relative tolerance of the more common species to salt spray the following groups are listed beginning with the most tolerant.

Cocos nucifera
Pandanus tectorius
Tournefortia argentea
Scaevola taccada
Guettarda speciosa
    Cordia subcordata
    Clerodendrum inerme
        Terminalia samoensis
            Premna obtusifolia
            Pisonia grandis
            Morinda citrifolia
                Calophyllum inophyllum
                    Artocarpus altilis
                    Cyrtosperma chamissonis

The pattern of distribution among the more important native species is apparently related to salinity. Guettarda, more tolerant of salt spray than Morinda and Premna, dominates the undergrowth on the smaller more exposed islands, whereas the more sensitive Morinda and Premna are restricted to the understory on the larger more protected islands. The absence of other species on these smaller islands may also be related to salinity.

GROUND WATER SALINITY

In studying ground water salinity in relation to breadfruit distribution, water samples were analyzed from Cyrtosperma marshes and wells on 11 islands. Some islands were sampled only once; others several times during the survey. On the larger islands, salinities were highest oceanward, decreasing to a minimum toward the lagoon (Fig. 19). Where breadfruit occurred, the extremes ranged from 3,840 ppm toward the ocean on Nunakita to 18 ppm on the lagoon side of Torongahai. In the breadfruit grove on Werua where some of the largest trees occur, salinities varied from 28 to 46 ppm. In general, the larger and more productive trees occurred in the center of large islands and lagoonward where the salinity was less than 350 ppm, which compares favorably with the 200 to 400 ppm reported from the Marshalls (Cox 1951). On small rocky islands no fresh water lens occurs, whereas it may develop on the sandy islands.

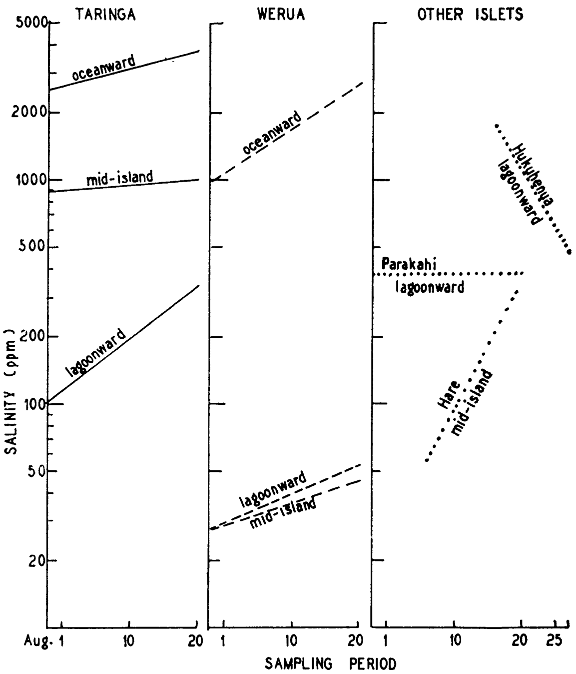

FIG. 19. Salinity data from various islets taken during survey. On Taringa and Werua samples were taken oceanward, mid-island and lagoonward. Locations for other islets indicated. The salinity decreases from the oceanward to lagoonward sides of the larger islets. During the survey the salinity increased at most stations except for Hukuhenua where it declined and Parakahi where it remained the same.

The decrease in salinity from the ocean to the lagoon is related to the underlying parent materials. The seaward shores are composed of stratified rocks and rubble boulder ramparts, whereas the lagoon shores consist of beach sands. On the larger islands the fine-grained sandy sediments of the lagoon side are much less permeable than the coarse rubble materials and cavernous limestone. Although breadfruit had not been planted on the small sandy island of Parakahi (3 acres), located lagoonward on the reef, the ground water was relatively fresh—350 ppm at three different sampling periods. In contrast, on the larger islet of Hukuhenua (5 acres), underlain by a course rubble, the salinity ranged from 480 ppm to 1,740 ppm within a 10-day period. Here the breadfruit trees were in poor condition with many dead or defoliated branches. One might assume that the coarse rubble more readily permits the penetration of salt water and therefore, the fresh water lens is poorly developed. Under such circumstances, light showers or minor tidal changes might result in marked fluctuations. On Nunakita which is underlain by considerable cavernous bedrock, the salinity, as previously mentioned, was also high. However, the scattered immature breadfruit (10-12 in.) were vigorous, which would suggest that they may not be as dependent upon the ground water as are the larger trees.

Cyrtosperma is another species dependent upon relatively fresh ground water. The following salinities were recorded in marshes located toward the center of the islands or lagoonward: Torongahai 18 ppm; Werua 28 ppm; Hare 56 and 310 ppm; Takairongo 140 ppm; Hukuhenua 480 and 1,740 ppm. It can apparently tolerate a relatively wide range of salinity, although the most extensive areas of Cyrtosperma occurred where the salinity was less than 30 ppm. This compares closely with findings where the freshest ground water, containing 20 ppm and as low as 5 ppm, occurred in the Cyrtosperma marshes on Arno and Ifaluk Atolls, respectively (Cox 1951; Arnow 1955). As previously mentioned, small areas had been abandoned from Cyrtosperma culture, presumably due to saline contamination.

Other species such as coconut and Pandanus are not dependent upon a fresh water lens and, therefore, predominate on the smaller islands where the ground water is extremely saline. On Hukuniu, which is covered with coconut and scattered Pandanus, ground water salinities ranged close to that of the surrounding ocean.

During the survey the salinities on all the larger islands increased, except on Hukuhenua. Increases were more pronounced oceanward but were also recorded lagoonward. The community well on Touhou, sampled 4 times over the 2-month period, rose from 202 ppm to 286 ppm and other changes are shown in Fig. 19. This general increase may be related to the scant rainfall of 4 in. during the survey period. With prolonged aridity one can visualize the potential adverse effects which these extremes might have in certain sites throughout the atoll. On Hukuhenua the erratic fluctuations suggest a poorly developed ground water lens.

STORMS

Periodic storms which hit the atoll tend to accentuate the effects of both salt spray and ground water salinity. In addition, they can affect the vegetation by causing blow-downs. However, since the atoll lies outside the typhoon belt this type of disturbance is less serious compared to other atolls (Blumenstock 1961). Following storms the breadfruit and possibly other trees lose their leaves, according to the natives, but usually a new set develops if the salinities effects have not been sufficiently extreme to kill the trees. Although no storms occurred during the survey, a strong wind backed up considerable salt water against one of the causeways connecting two islands and the water rose to within 50 ft of a small breadfruit (5 in dbh). The tree turned brown and a month later 4 branches were dead and some brown leaves still persisted. This was caused presumably by ground water salinity and suggests that the periodic extremes of salinity may be of greater significance than the so-called average which one is likely to sample during a given period.

Within the last 100 yrs severe storms, and probably many of lesser magnitude, have hit the atoll (see Climate). During the most recent storm estimates of trees, primarily breadfruit, destroyed by wind and salt water, range from 80-200, in addition to several Cyrtosperma marshes destroyed by salt water inundation. Although some of these trees still stand, most have been utilized by the natives. An incident on Hare island during the most recent storm emphasizes the influence of salt water and the significance of minor differences in topography on breadfruit trees. Prior to the storm two large breadfruit over 12 in. in diameter grew practically equally distant from the lagoon beach. The tree still living is on a bank of rubble and the adjacent one, which is now dead, was growing at the normal ground level several feet below. This suggests that the elevated banks around the Cyrtosperma marshes have been a favorable factor accounting for the survival of the breadfruit during storms. This may also account for the presence of large productive breadfruit on the higher islet of Touhou where the trees also extend closer to the water's edge than on any of the other islets.

What then is limiting the survival of breadfruit? It appears to be a combination of aerial and ground water salinity; not necessarily the daily norms sampled, but the periodic catastrophic extremes often unmeasured by the instruments of the ecologist. In certain instances the adverse effects of excessive guano from sea birds must also be added as a contributing factor (see Birds—Effects on Vegetation). Could breadfruit be grown on the small sandy island of Parakahi where a favorable salinity was recorded during the brief sampling period? Possibly it would survive until a storm hit at which time the salinity might soar to toxic extremes. The absence of breadfruit there may be a result of past experience by the natives.

EDAPHIC INFLUENCES

Along with salinity, the coarse-textured soils, lacking in organic matter limit vegetation development. The density of the herbaceous layer is directly related to organic accumulation since ground cover is generally greater on the more mature rubble soils than on the poorly humified sandy sites. In fact, ground cover tends to increase with organic accumulation regardless of soil texture. This may be related to increased water-holding capacity and a higher nitrogen level since soil nitrogen is directly correlated with organic development (Stone 1951).

The organic content of the soil is also important in regard to coconut productivity. On Hare, trees planted around 1943 on the immature, sandy soils resulting from channel filling average 40 ft in height and are just becoming productive while those planted several years later on more highly organic sites which were bombed during World War II average 60 ft and are already productive. Another instance where organic accumulation appears significant is on Tokongo. This island, with an 18 in. humus layer, has a greater number of species (16) for its size (1.8 acres) than any other, and the undergrowth, which is characterized by Morinda and Premna, is typical of that found on larger islands. This extreme development may also be correlated with its greater age, as will be discussed later.

In the interior of the smaller islands and along the beach rampart Guettarda and Scaevola can withstand the high salinity and the extremely bouldery condition. Herbaceous cover is usually absent on such sites except for clumps of Asplenium which become established on the scattered coconut husks. In more favorable sites this fern is typically found on tree trunks and old coconut stumps, which is indicative of its dependence upon such organic substrates. On sandy sites Scaevola and, to a lesser extent, Tournefortia are found along with such herbaceous species as *Triumfetta procumbens, Ipomoea pes-caprae, Vigna marina, Lepturus repens* and *Fimbristylis cymosa.* In the poorly-drained muck-type soils one or both of the aroids may be expected. Coconut and breadfruit were found on all soil types, although the latter was restricted to the interior of the larger islands where a fresh water lens occurs.

Although no striking mineral deficiencies were evident, chlorotic coconut, Scaevola, and banana were observed. Such young coconut were restricted to the immature sandy soils with little organic matter, which suggests a lack of nitrogen. On one island a few large chlorotic palms were found situated on a narrow rubble bank between two Cyrtosperma marshes. Here root restriction rather than a mineral deficiency may be the causal factor. No poor coconuts of low productivity were seen, such as the two types reported from Arno, where presumably low phosphorus and nitrogen were involved, although salinity may have also been a contributing factor (Hatheway 1957). Occasional eroded Scaevola along the beach show a more pronounced yellow-green foliage than normal, and banana with similar symptoms are scattered throughout the villages.

Considering the immaturity of the soils throughout the atoll, the lack of more evident mineral deficiencies is of interest. It may be that the mineral cycling by sea birds from the surrounding waters onto the land and the nitrogen-fixing role of the rubble covered by blue-green algae are important factors. This problem is worthy of further investigation.

Island Migration and Vegetation Change

Migration of the islands lagoonward is a major phenomenon inducing vegetational change. On the rapidly forming sand bars plant colonization is occurring; whereas oceanward, coconut and Scaevola are constantly being eroded away (Figs. 20, 21). On the bars projecting into the lagoon Scaevola is the conspicuous pioneer (Fig. 21). In certain situations where the process is most rapid, concentric belts occur in a step-like sequence. Rows of Scaevola seedlings along the back shore are replaced by shrubby cover 3-4 ft in height which is backed by taller Scaevola and, finally, by Guettarda.

FIG. 20. Windward beach-scrub vegetation and eroded coconut. *Scaevola taccada* and *Pandanus tectorius* (foreground), *Guettarda speciosa* beyond leaning palms.

FIG. 21. On newly-formed sand bar lagoonward *Scaevola taccada* is typical pioneer. Seedlings in foreground.

This lagoonward migration appears to be taking place at a relatively rapid rate. On Ringutoru, the lagoon beach between the sand bars is building radially at an estimated rate of 1 ft per yr. This figure was derived from data furnished by the inhabitants regarding the change in position of former marginal trees. The contiguous sand bars are probably building at an even more rapid rate. As a result of this migration, the newly formed sandy areas are gradually planted to coconut, thereby increasing the acreage of these plantations. As the palms mature, pioneer species such as Scaevola, Tournefortia and Guettarda persist in the undergrowth, although the trend is toward an increase in Morinda and Premna. On some islands, relict beach ramparts lined with old Guettarda trees can be recognized in the interior, thus providing further evidence of this lagoonward migration.

Although island migration is occurring throughout the atoll, it is most pronounced on the northern islands. On Ringutoru lagoonward deposited sands represent about three-fourths the total land area and on Torongahai one-third of the island is underlain by sandy sediments. Oceanward from the islets there occur bevelled remnants of stratified bedrock or beach rock extending 400-600 ft outward from the present seaward beaches and these mark the original boundaries of the island which are now eroded away (Fig. 22). Presumably such areas were formerly vegetated and supported a nesting bird population, as indicated by the phosphorite incorporated in certain bedrock remnants (McKee 1956, 1958). A similar condition occurs on Nunakita. Although the construction of causeways between a few of the islands has arrested this migration to some extent, there is every evidence that this geomorphic process will continue as an important force in modifying the land and vegetative cover.

FIG. 22. Eroded beach and reef rock remnants indicating former extension of islet oceanward on the reef. *Guettarda speciosa* foreground. Torongahai Islet.

Vegetational changes are also occurring on the smaller islands, especially as a result of storms. The changes which have occurred on the small island of Matukerekere are of interest. Around 1858 the island (0.7 acre) and its vegetation were completely destroyed by a severe storm. Rebuilding occurred until 1947 when it supported 10 coconut, at which time another storm destroyed 9 of the coconut and most of the land area. Upon our arrival the island and its meager vegetation—one mature coconut, 5 small chlorotic palms and many drift seedlings, were mapped. A resurvey after 7 weeks showed that 25% of the land surface had disappeared including one palm and most of the seedlings. However, during this period no storms occurred, which illustrates the ease with which change can occur on these smaller islands.

On Kapingamarangi, vegetation change appears to be limited to primary vegetation development on the continuously depositing sands. Changes within the plantation undergrowth may be occurring but periodic clearing tends to obscure possible trends. The natural vegetation development which can occur on atolls is often limited by the salinity, immaturity of the soils, the moisture regime and the floristic spectrum which can become established on a given islet by overseas transport. Therefore, herb and shrub communities (Fosberg 1953, 1956) may represent relatively stable types in drier sites whereas a forest vegetation may be expected to develop eventually under more mesophytic conditions.

RELATION OF SOIL DEVELOPMENT TO AGE OF ISLETS

It is recognized that atolls such as Kapingamarangi are geologically young—the land masses having formed from an already existing submarine platform in late post-Pleistocene time. Sea level fluctuations in the past, which have been documented, have obviously been critical to islet formation. During the Climatic Optimum which ended 6,000 yrs ago the atoll would have been totally submerged and also 3,900-3,400 B.P. (Before Present) when there was a brief 10-ft rise in the sea level (Younger Peron terrace) recorded in western Australia, the western Pacific and other parts of the world (Fairbridge 1958). Since this last rise there has been a general emergence which has occurred to the present except for two minor sea level rises 2,300 B.P. and 1,200-1,000 B.P. (Fairbridge 1958).

Evidence regarding the time at which the land masses on Kapingamarangi rose above sea level is presented here based on the rate of organic accumulation in certain soil profiles. Throughout the atoll the organic development averages 6-8 in. in the rubble soils and much less in the more recently deposited sandy types. However, on two islands extreme organic accumulations were encountered. On Tokongo this layer was continuous with the rubble to a depth of 18 in., whereas on elevated Rikumanu it extended to the unusual depth of 30 in. If it can be assumed that the degree of organic accumulation is proportional to the length of time the area has been vegetated without disturbance, it would appear that these two islands have had the least surficial disturbance by storm deposits or other influences since their origin. This appears to be the situation, especially on Rikumanu which is situated on a limestone pedestal 5 or more ft above present sea level. Since it stands considerably higher than the other islands it may not have been subjected to the usual storm erosion or deposition which has occurred on certain less elevated islets during past storms. At least no evidence of such disturbance or buried profiles was observed. The island of Tokongo was not as noticeably elevated and in this situation the greater organic accumulation may merely indicate the chance of less surficial disturbance in the past. However, it is of interest that Tokongo has the largest number of species for its size and is dominated by a Prema-Morinda understory similar to that found on the larger islands. This may also reflect its longer existence.

The rate of organic accumulation was investigated on the Rawa-Hare causeway which filled in about 1865 and is now part of the island of Hare. In several samples the accumulation of organic material was 1 in. in approximately 100 yrs. If one assumes that the causeway was planted to coconut soon after filling, which is usually the practice, this provides a rate for organic development which can be applied to these profiles. If one applies this figure of 1 in. per century to the 30 in. of organic accumulation from Rikumanu the length of time involved would be about 3,000 yrs. This would suggest that certain of the land surfaces may have been formed at least some 3,000 yrs ago. Since the atoll has been emerging from the last rise in sea level, 3,900-3,400 B.P., this figure of 3,000 yrs for the period during which the atoll has been covered with vegetation seems reasonable. This figure would allow several hundred years for the entry of plant propagules to vegetate the newly formed islets.

The 18 in. Tokongo profile which suggests 1,800 yrs accumulation, may be contemporaneous with the Rikumanu, but merely truncated by storm erosion or it may mean a more recent origin of certain of the atoll's land masses. This would suggest that some of the islands originated since the more recent minor sea level rise 2,300 B.P. These preliminary observations warrant further investigation involving radiocarbon dating of the organic material.

VEGETATION COMPARED TO THAT OF OTHER ATOLLS

Since Kapingamarangi is relatively isolated and its vegetation highly manipulated, it is of interest to compare it with other inhabited atolls in the Carolines, as well as the Gilbert and Marshall Islands to the southeast and northeast respectively.

Studies from other island groups indicate that the general vegetational pattern is similar to that on Kapingamarangi. Coconut plantations dominate, with breadfruit frequently mixed with the coconut or occurring in pure groves. In addition, one or both of the aroids, Colocasia and Cyrtosperma, are cultivated in excavated swampy areas (Caroline Islands: Nukuoro & Puluwat, author's observations 1954; Ifaluk Atoll, Bates & Abbott 1958; Namonuito & Hall Islands, Stone 1959. Gilbert Islands: Catala 1957; Onotoa Atoll, Moul 1957. Marshall Islands: Taylor 1950; Arno Atoll, Hatheway 1953; Fosberg 1956).

Variants within the plantations occur on other atolls, depending upon intensity of land use and moisture regime. On Kapingamarangi the trees, especially coconut, are closely spaced, which restricts the native flora to the undergrowth. Although this pattern occurs on other atolls, widely spaced plantations, such as were observed on Puluwat Atoll in the Carolines by the author, are equally common and here indigenous species increase in importance and form pure stands locally (Catala 1957; Moul 1957). Mixed stands of native and cultivated species can also develop under natural conditions, as reported on Ifaluk (Bates & Abbott 1958). A comparable type (referred to as secondary vegetation) occurs on Arno and apparently develops naturally on sites formerly cleared by the natives but since abandoned (Hatheway 1953).

Variations in precipitation throughout Micronesia also account for vegetation differences. On Nukuoro, a wetter atoll just north of Kapingamarangi, islands of comparable size exhibit a much more luxuriant vegetation. Mammoth breadfruit (15 ft dbh), which approach the maximum size found on atolls, are covered with epiphytic ferns and a dense ground cover of ferns develops so rapidly that the plantations are cleared monthly. On Kapingamarangi, two islands, Ringutoru and Torongahai, exhibit a comparable but less well-developed fern stratum, although epiphytic ferns are rare. Within the Marshalls dryness increases northward until islands are reached where coconut does not apparently survive even if planted (Fosberg 1956). In the Gilberts periodic droughts have been reported during which the coconuts have been killed or productivity greatly reduced (Catala 1957; Moul 1957; Mason 1960). On Kapingamarangi, a drought early in the century resulted in a decreased coconut yield and produced a famine.

The most striking difference between Kapingamarangi and most other atolls is the occurrence on the latter of indigenous vegetation types which have remained where the land was not cleared for plantations. On such atolls a mixed forest (Fosberg 1956) is recognized which presumably represents a vegetation more wide-spread prior to habitation. Hatheway (1953) refers to this mixed type on Arno as a scrub forest, whereas on Namonuito and Hall Islands, Stone (1959) designates it as an intermediate forest. These stands include 10 or more species comprising many of the native trees found on Kapingamarangi (excepting Morinda and Premna). In stature they vary from a low impenetrable shrubby phase to a large forest, although highly variable in that no two stands are quite similar. Variants result where pure stands of certain species occur such as Cordia, Pandanus, Tournefortia, Barringtonia, Ochrosia (Fosberg 1953, 1956) and Pisonia (Hatheway 1953; Fosberg 1956; Catala 1957; Moul 1957; Stone 1959). Under the most mesophytic conditions Ochrosia, once established, tends to dominate (Fosberg 1953). It will be recalled that Pisonia formerly occurred on Kapingamarangi but has since been cleared and planted to coconut. On Pumatahati, the small stand of Cordia along the lagoon beach may also represent an aspect of the primeval vegetation. Otherwise the plantations have replaced these original types.

On the smaller drier islands of other atolls there are shrub communities of Scaevola and Tournefortia (Hatheway 1953; Catala 1957; Moul 1957). Although many small islands occur on this atoll, the possible shrub nature of their original vegetation has been greatly obscured by the plantations. However, on Rikumanu the undergrowth is predominately Scaevola, which is typical of the natural vegetation on such small islands. As previously mentioned, Tournefortia is not common on the atoll. Another shrub community of *Pemphis acidula* is widely distributed on atolls and usually occurs on reef rock at or above high tide. A single shrub was found on Kapingamarangi, presumably introduced, since the wood is especially hard and valuable for coconut husking sticks. On the more xeric islands in the Marshalls, herbaceous communities occur which are not represented on Kapingamarangi. These shrub and herb types are pioneer communities which are essentially stable under the rigorously arid climate and immature soil conditions.

Saline and fresh water swamps, absent on Kapingamarangi, occur on other atolls. Mangrove swamps may fringe islands or occupy muddy embayments (Fosberg 1953; Catala 1957; Moul 1957), or invade aroid marshes once they are contaminated with salt, as was observed on Nukuoro. Fresh water swamps or bogs are rare but they have been reported from three islands on Arno (Hatheway 1953). Those of presumably natural origin are covered with Pandanus and underlain by peat, which would be worthy of palynological investigation. On Namonuito and the Hall Islands (Stone 1959) the fresh water swamps are dominated by ferns and sedges. In the shallow lagoon waters a turtle grass community occurs in the fine sandy sediments on Kapingamarangi and similar vegetation is reported from other island groups (Glassman 1953; Fosberg 1956; Catala 1957; Moul 1957; Stone 1959).

In conclusion, it is evident that Kapingamarangi lacks the vegetational diversity found on some other atolls, a condition which is partly related to its geographical isolation but primarily correlated with the intensity of land use.

PRE-POLYNESIAN VEGETATION

A reconstruction of the vegetation prior to arrival of the Kapingan voyagers must be considered hypothetical in that remnants of the original vegetation are practically non-existent. Indigenous species now occur only along the beaches and in plantation undergrowth. From these clues and the evidence from other atolls it would appear that the original vegetation probably consisted of a highly variable mixed forest on the larger islands with a transition to a low shrubby vegetation on the smaller land masses. As evident today there was probably a zonation with the more salt tolerant species forming a marginal belt which was replaced in the interior by less tolerant species. Along the lagoon shore another belt may have existed.

Oceanward, Scaevola, Pandanus, Guettarda and Tournefortia, may have comprised the dominant marginal belt with Terminalia and Cordia of lesser importance. Tournefortia may have been more important in the past and its rarity today may be related to the demand for it in handicrafts. Toward the interior, Pandanus, Terminalia and Cordia may have extended inland and mingled with a mixed forest of Barringtonia, Hernandia, Ochrosia, Pisonia, Soulamea and others. Locally, pure stands probably occurred as the former Pisonia forest and the Cordia stand still present on Pumatahati. In the understory Premna may have been a distinctive species along with shrubby growths of Allophylus, Clerodendrum and Pipturus. Herbaceous cover included grasses and certain broad-leaved plants with ferns locally abundant. Along the lagoon beaches, Calophyllum, Pandanus and possibly Scaevola together with vines such as *Ipomoea* spp. may have formed a distinctive band. On the smaller islets a low scrub forest of Scaevola, along with Guettarda, Tournefortia and Pandanus, probably formed the conspicuous vegetation. Although periodic storms may have caused some damage, the lack of typhoons would have added to the stability and maturity of the vegetation. In the Marshalls, Hatheway (1953) has hypothesized a somewhat similar pattern but with a greater diversity of vegetation types than on Kapingamarangi, which is considerably more isolated geographically.

ASSOCIATED ANIMAL POPULATIONS

A relatively sparse land fauna inhabits the atoll. The most conspicuous animals are the birds, skinks and land crustacea, although insects and associated small arthropods are obviously the most abundant. Other animal life includes a few species of mammals, snails and annelids. Ecologically, the birds and land crabs are probably the most important: the former contributing nitrogenous and phosphatic nutrients and the latter serving to incorporate organic matter into the immature soils. Man also plays an important ecological role, as has been discussed. With the exception of certain insects and breeding birds, the animal populations tend to be dispersed throughout the various upland vegetation types previously discussed.

BIRDS

Of the over 200 species of birds in Micronesia (Baker 1951) only 14 species were observed on the atoll during the survey. Sea and migratory birds are most abundant, whereas true land birds are rare, especially the small singing species so typical of higher islands and continental land masses.

Among the sea birds inhabiting the atoll, the white-capped noddy tern (*Anoüs tenuirostris*) is most common, noddy tern (*Anoüs stolidus pileatus*) somewhat less frequent and the white tern (*Gygis alba candida*) rarely seen. Flocks of frigate birds (*Fregata* sp.) were occasionally observed and several immature birds were kept as pets in the village. These were presumably brought in from other islands, since, according to the natives, frigate birds do not breed on the atoll, but merely roost on one of the islands. The brown booby (*Sula leucogaster plotus*) and the crested tern (*Thalasseus bergii pelecanoides*) were recorded as transients. Although boobies and frigate birds do not presently nest on the atoll, according to the inhabitants they once did on Pumatahati when it was covered with a Pisonia forest.

Among the migratory shore birds the Pacific golden plover (*Pluvialis dominica fulva*), turnstone (*Arenaria interpres interpres*) and curlew or whimbrel (*Numenius* sp.) were commonly observed feeding along the beaches. Of the land birds only the Micronesian starling (*Aplonis opacus*) was represented by a breeding population. Another land species, the elusive long-tailed New Zealand cuckoo (*Eudynamis taitensis*), which breeds in the southern hemisphere, was observed several times gliding secretively through the coconut-breadfruit canopy. The introduced fowl (*Gallus gallus*) occasionally escapes from captivity and seeks refuge in the surrounding plantations. One other bird, the reef heron (*Demigretta sacra sacra*) was often seen feeding on the reef flat at low tide. Two color phases, white and mottled gray, were recognized.

Within the plantations, starlings, reef herons and noddy and white terns nest in the coconut or Pandanus trees, whereas the white-capped noddy tern nests primarily in the large breadfruit. Starlings and chickens depend exclusively on the land for food, while the others feed on marine organisms in the surrounding waters. Large flocks of terns are a common sight circling low and feeding around the coral patches in the lagoon. In contrast, the solitary reef heron wades over the reef flats at low tide searching for marine life, whereas on land it may consume insects, worms and skinks (Child 1960).

The bird population on Kapingamarangi is quite similar to that on Onotoa in the Gilberts where Moul (1954) reports 15 species during a comparable period. Over a period of several years Child (1960) observed over 40 species in the Gilbert and Ellice Island colony. Inhabited atolls such as Kapingamarangi lack the large breeding populations of sea birds reported on Canton Island (Murphy et al 1954), Midway, and Laysan Islands (Fisher 1949; Bailey 1956), Pokak in the Marshalls (Fosberg 1957b) and Gaferut in the Carolines (Niering 1961). The entry of man into the atoll environment has resulted in a decrease in the bird population on many atolls such as Kapingamarangi.

EFFECTS ON VEGETATION

The importance of sea birds in contributing certain basic nutrients to the land is well recognized. However, their gregarious nesting habits can also result in such concentrations of guano that the surrounding vegetation may be seriously injured or actually killed (Christophersen 1927; Fosberg 1953; Degener & Gillaspy 1955; Hatheway 1955). In the temperate region this has also resulted from concentrations of starlings in white pine plantations (Stewart 1933; Young 1936).

On Kapingamarangi the gregarious habits of the white-capped noddy tern are reported by the natives to have killed breadfruit in the past and from the numbers of nests in certain trees this seems reasonable (Fig. 23). At least 80 nests, 1-2 ft apart, were counted in the upper 30 ft of one large breadfruit. Where the nests are this abundant the branches are completely covered with fecal matter, a rank odor prevails and on the ground the undergrowth is turning brown and dying.

FIG. 23. Breadfruit branches defoliated and branches dead or dying. White-capped noddy terns and nests on the exposed branches. Ringutoru Islet.

The actual role of the birds presents a real dilemma. Do they prefer those branches partially defoliated, possibly by salt spray or high ground water salinity, as previously discussed; or has this condition resulted solely from the activities of the birds? They occasionally nest in other more vigorous trees, but the concentrated populations are in those partly defoliated. Since the appearance of the branches where the nests are most concentrated is similar to that resulting from saline effects, salinity may be the initial factor followed by the avian influence. If the birds prefer these partially defoliated limbs as nesting sites, their continuous fecal, deposits may further accentuate the effect, resulting in the death of the tree. Although recently killed specimens were not found, the natives periodically destroy the nests and, therefore, judicious care of the plantations today may account for the absence of dead trees.

On Tirakaume large flocks of frigate birds roost in the coconut palms. Although an unpleasant odor prevails, no adverse effects are evident on the vegetation. However, the small size of the island, sparsity of vegetation and recent clearing make interpretation difficult.

The influence of the Micronesian starling on certain species is worthy of comment. The ripe fruit of the breadfruit is one of the preferred foods of the starlings, which makes it necessary for the natives to pick the fruit while still immature, or otherwise suffer considerable loss. Starlings also disperse seeds of Morinda and Premna. Under Pandanus frequently visited by these birds, seedlings of those species were locally abundant on Touhou, although their survival here, as well as in the plantations, is questionable considering the periodic clearing operations and the possibility of crab damage.

BIRDS, PISONIA AND PHOSPHATE FORMATION

The widespread occurrence of phosphate rock as a result of guano deposits has long been recognized and extensively surveyed on Pacific atolls (Aso 1940; Hutchinson 1950). Recently a new hypothesis accounting for the formation of certain of these deposits has been proposed (Fosberg 1954, 1957a). It involves a particular forest type, *Pisonia grandis,* formerly more prevalent on such atolls, which produces an acid humus and shelters dense breeding populations of sea birds. Under these conditions a distinctive soil profile results consisting of a dark, spongy or peaty organic layer overlying phosphatic hardpan, itself underlain by loose, essentially unaltered or somewhat darkened lime sand or gravel. Although this soil type was recognized earlier (Hutchinson 1950), Fosberg (1954) has named it the Jemo series from the island in the Marshalls where it was first described (Fig. 4). Both a Pisonia forest and sea birds depositing guano under the trees are apparently prerequisites for its development. The humus from Pisonia leaf litter is highly acidic and the calcium phosphate in the guano deposits on the litter by the nesting or roosting birds is carried down into the humus by rain water. The calcium phosphate dissolves because of the acid reaction of the organic matter. However, when the solution reaches an unconsolidated calcium carbonate layer beneath the humus, it turns alkaline and the phosphate precipitates out, cementing the sand and gravel particles together into hardpan. With further bathing by this solution the calcium carbonate may also become partially or wholly replaced by calcium phosphate forming a phosphate rock (Fosberg 1954, 1957a).

On Pumatahati, this Jemo soil type was encountered where a Pisonia forest dominated until about 1920, when it was cut and the area planted to coconut. Presently there is a distinctive soil profile under the coconut unlike that on any of the other islets. A highly acidic (pH 4.5) and phosphatic (100% apatite) humus layer 6-8 in. in depth is underlain by a light brownish cemented layer interspersed with cream-colored particles containing pure apatite. This cemented layer gives way to a soft crumbly material characteristic of the parent material. This soil profile may represent a "relict" of the Jemo series formed in the past when Pisonia dominated the area.

Although this phenomenon has also been reported from other atolls (Hatheway 1953; Fosberg 1955, 1957a; Moul 1957) it has not been accepted by everyone as an explanation for phosphate rock formation. Critics have suggested that the presence of the phosphate may favor the entry of Pisonia. However, the widespread occurrence of Pisonia on atolls where no guano occurs should invalidate this conclusion. The best evidence that this formation occurs after the establishment of Pisonia is presented by Hatheway (1953) for the Marshalls where the rock was observed forming around a root 2 in. in diameter, suggesting that the process can occur rather rapidly, perhaps within less than a century.

Alternative theories for phosphate rock formation include the direct reaction between guano and limestone regardless of type of vegetation. Hutchinson's (1950) hypothesis for this and other types of phosphate formations is based on the premise that the climatic belts may have shifted, producing a drier climate and subsequently a more xeric open vegetation where large rookeries could become established such as are still found on Laysan, Midway and Canton Islands. Fosberg (1957a) failed to find phosphate rock currently forming under guano deposits on dry openly vegetated islands, and no evidence was found of this process occurring on xeric Gaferut, which is covered with a low scrubby forest of Tournefortia, and which has a large sea bird population (Niering 1961). One might conclude that the climatic regime was just the reverse—more mesic in the past, thus favoring a widespread development of Pisonia forests and subsequent phosphate formation. On the other hand, possibly no climatic change was needed at all, in that Pisonia was more widely distributed prior to the entry of man, but was cleared following colonization. The relict profile on Kapingamarangi would add supporting evidence to the fact that on other atolls man may well have removed the Pisonia from areas where phosphate rock presently occurs. The presence of this type of bedded phosphate rock on uninhabited islands where no Pisonia presently occurs is initially perplexing, but, considering the susceptibility of these forests to storms, they may have been destroyed by typhoons. This appears to be true on Gaferut where evidence of such a storm has been documented (Niering 1961).

LAND CRUSTACEA

Land and hermit crabs, which spend most of their life cycle on land, are abundant throughout the plantations (Fig. 24). As scavengers they are important in breaking down organic matter and incorporating it into the soil by means of their many burrows. Land crabs (*Cardisoma rotundum, Gecarcoidea lalandei, Geograpsus crinipes, G. grayi, Metasesarma aubryi, Sesarma rotundatum*) and hermit crabs (*Coenobita brevimanus, C. perlatus*) are found under piles of coconut husks or other debris on the forest floor. Small cavernous openings in the limestone bedrock also provide a natural habitat for them and for coconut crabs (*Birgus latro*). In the loose sandy rubble soils, land crab burrows are numerous, reaching a depth of 18 in. or more. One of the greatest concentrations of burrows was recorded within a coconut plantation where 15 openings occurred within a 10 x 10 ft area. They also honeycomb the rubble banks surrounding the Cyrtosperma marshes.

FIG. 24. Two land crabs and a hermit crab (lower center) exposed from beneath coconut husks on typical coral rubble surface within coconut plantations. Pumatahati Islet.

The crab population consumes large quantities of surface litter, including twigs, leaves of Pandanus and breadfruit, and coconut husks, which are taken underground by the land crabs, especially at night when they are most active and literally overrun the plantations. The abundance of hermit crabs is especially evident. A recently fallen Pandanus fruit literally swarms with the creatures.

A survey of the crab population was made during the day along a strip transect across Torongahai (Fig. 25). A total of 515 individuals including 201 land, 309 hermit and 5 coconut crabs was recorded under debris in approximately one acre (40,560 sq ft). Projected for the atoll this could mean an estimated 118,450 crabs within the 230 acres of plantations. Their occurrence is correlated with soil friability and surface debris rather than any specific

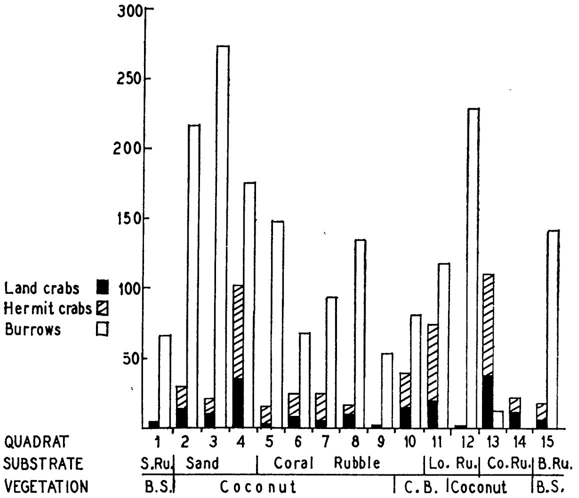

FIG. 25. Bar graph showing the number of land and hermit crabs as well as burrows found along a lagoon to ocean transect (left to right). Substrate indicated along the transect: (S.Ru.)—beach, sandy-rubble, (L.Ru.)—loose rubble, (Co.Ru.)—compact rubble, (B.Ru.)—coarse beach rubble. Vegetation also indicated: (B.S.)—beach-scrub, (C.B.)—coconut-breadfruit. Greatest number of burrows in loose textured sandy or rubbly soils (Quad. 2, 3, 12), whereas few or no burrows occur in compact rubble areas (13, 14). Crab population found above ground during the day is correlated primarily with the degree of surface debris which provides important cover (4, 11, 13). Crustacean count based on actual number of individuals per 52 x 52 ft quardat, whereas burrows were counted in a portion of quadrat and calculated for comparable area.

vegetation type. Those areas with loose rubble or sandy soils or localized concentrations of debris, especially piles of coconut husks left by the natives, support the largest populations. As would be expected, the burrows are especially numerous in the loose sandy and rubble soils lagoonward (Quadrats 2, 3, 4, 5) and in the rubble banks (11,12) surrounding the Cyrtosperma marshes. Burrows are also frequent in the coarse bouldery rubble-beach rampart oceanward. In the very compact rubble soils (13, 14) few burrows occur. In fact, in one quadrat (14) no holes were found. In such sites the crab population is correlated with surface debris which provides an important niche above ground. Based on the number of burrows, there is a heavy concentration of crabs lagoonward, especially in the more recently deposited immature sandy soils where their activities are especially important in increasing the organic content.

In contrast to their beneficial role, hermit crabs are destructive of seedlings and propagules. Seedlings of Barringtonia were severely damaged, which may account for the rarity of saplings and larger trees on the atoll. On Canton Island it has been noted that these crabs can climb Cordia trees and eat the bark from the young twigs (Degener & Gillaspy 1955). In fact, their destruction of Cordia propagules and seedlings was so great that there was no survival. On Kapingamarangi this action may well account for the absence of seedlings throughout the plantations, but their local occurrence in the inhabited areas where crabs are rare.

A further role of these crustaceans may be the transport of drift propagules from the beach into the interior of the islands. In the Bahamas, Howard (1950) placed fruits of 30 different land plants on the ground near the runways or holes of the land crabs. Fifty percent of the fruits, including Morinda and Scaevola, common to Kapingamarangi, disappeared and were later found scattered in the burrows and not eaten. As Howard suggests, crabs may play a major role in transporting propagules inland to favorable habitats. Further observations are needed from other atolls.

Since coconut crabs are considered a delicacy, they are relatively rare, as also observed by Moul (1954) in the Gilberts. However, on certain uninhabited islands this crab, which can reach 12 in. in length, is abundant and very destructive to coconut propagules. They can climb trees and take nuts, which they open with their powerful claws (Menon & Pandalei 1958). They are known to consume two nuts per day. On Gaferut (Niering 1961) coconut seedlings were severely damaged under the few scattered coconut trees, presumably planted when phosphate was being mined. The absence of coconut palms on uninhabited atolls throughout the Pacific may, in part, be correlated with their destruction by coconut crabs. It is worthy of note that on Kapingamarangi the natives germinate their coconuts by tying them to tree branches or laying them on the roofs as a means of preventing crab damage.

REPTILES

Only 7 species of reptiles were found on the atoll. These included 6 species of lizards and the green turtle (*Chelone mydas*), a marine species which comes onto land to lay its eggs.

The small, golden-striped, azure-tailed skink (*Emoia cyanura cyanura*) is the most abundant vertebrate and during the day it is found almost everywhere in the plantations moving rapidly over the debris on the ground. Its food includes insects, earthworms and, perhaps, geckos, since one was observed with a live gecko in its mouth. It in turn may be eaten by herons, chickens and land crabs (Marshall 1951), although its great abundance on Kapingamarangi would indicate limited predation. This species is widely distributed on other atolls throughout the Pacific (Schmidt 1932; Fisher 1948; Marshall 1951; Moul 1954; Fosberg 1956; Bates & Abbott 1958; Hill & Stone 1961).

The less common moth skink (*Lygosoma noctua*) was observed only twice. One specimen was collected on a small coconut and the other in a native house. This species was not found by the investigators mentioned above.

Geckos are relatively common, but they are most active at night. In the inhabited areas around the houses the small mourning gecko (*Lepidodactylus* *lugubris*) is frequently observed, especially in the evening when it is attracted to lights in search of insects. It also occurs, though less frequently, in the plantations. On Onotoa the mourning gecko was very abundant at night around Scaevola flowers, presumably in search of night-flying insects (Moul 1954). Its food consists of ants, termites, Drosophila, sand flies and winged-ants (Marshall 1951). Along with the predators previously mentioned, the large crab spider (Huntsman spider) has also been observed preying on this species (Moul 1954). On Kapingamarangi a land crab was also observed with a dead gecko. Like the azure-tailed skink, this gecko has a relatively widespread distribution in the Pacific (Loveridge 1946; Marshall 1951; Fosberg 1956; Bates & Abbott 1958). In the plantations, the big tree gecko (*Gehyra oceanica*), reaching 6 in. in length, was frequently observed on coconut palms, although it was also collected under debris and in the villages. Marshall (1951) observed hundreds in trees on Arno, but saw none on the ground. Studies of stomach contents revealed its own skin, along with crickets, ants, crane flies and other insects (Marshall 1951). This species is also widely distributed on atolls (Fisher 1948; Marshall 1951; Moul 1954). The four-fingered gecko (*Perochirus articulatus*), the largest found during this survey reaching 9 in. in length, is rare and restricted to the plantations. Also rare is the stump-toed gecko (*Gehyra mutilata*) collected around the village. The four-fingered gecko has been reported from Arno (Marshall 1951) and the stump-toed gecko from Yap and the Hawaiian Islands (Fisher 1948).

The large western Pacific monitor lizard (*Varanus indicus*), reaching 5 ft in length and introduced on some atolls by the Japanese to control the rat population (Fosberg 1956; Bates & Abbott 1958) was absent on Kapingamarangi.

The high lizard population of Kapingamarangi is probably correlated with the comparatively few predators and in turn may well account for the few destructive and annoying insects. The entry of this reptilian fauna onto the atoll may have been by accidental transport of living specimens on native boats or, in the case of geckos, by eggs, which were found attached inside the hollow stems of Scaevola.

During the survey a green turtle, about 3 ft in length, was caught by the natives. Although these turtles live in the surrounding waters they lay their eggs on the sandy beaches of atolls. Formerly an important source of food, they are now rare on most atolls, although on uninhabited islands, such as Bikar and Jemo in the Marshalls, they can still be observed (Fosberg 1956). Often the young fall prey to hermit crabs and rats before they reach the water after hatching.

INSECTS

Insects and associated arthropods are the most abundant land animals, as would be expected. On Arno, Usinger & La Rivers (1953) estimated a total of 500 species which they compared with 96 species on drier Canton Island, 80 species on drought-stricken Onotoa (Moul 1954) and around 1,000 species on the moist volcanic island of Guam. Since a small percentage of the Kapingamarangi species have been identified and determinations will appear in a series of publications on the insects of Micronesia, this discussion will be limited to general groups of insects and their ecological role, based on studies from Arno in the Marshalls (Usinger & La Rivers 1953) and on Gressitt's (1954) monograph.

On atolls, as elsewhere, insects serve as primary and secondary consumers, as well as scavengers. On Arno at least one-quarter of the insects were considered predators, including the various parasites. In addition, two-thirds or more of the flowers are dependent upon insects for pollination. Marine insects are absent, which may be correlated with the great depths of the ocean and, possibly, to better adaptations to terrestrial conditions.

In the beach-scrub vegetation, dominated by Scaevola, Guettarda and occasionally Tournefortia, distinctive insect populations are associated with each species. On Scaevola, a leaf mining fly which forms the usual gallery patterns is common and on Tournefortia the caterpillar of the day-flying moth, Utetheisa, causes considerable damage. These were observed on Kapingamarangi and, in addition, ants were especially common on fragrant flowers such as Guettarda where they may also aid in pollination.

In the dense grassy cover of the plantations grasshoppers, butterflies and leaf hoppers are abundant. Under piles of coconut husks or other decomposing debris, there are considerable numbers of earwigs, ants, cockroaches, scorpions, spiders, and sow bugs. In the understory, Premna leaves are severely scalloped by leaf eating or cutting insects, possibly the leaf-cutting bee. Two large specimens of the Phasmidae, seldom seen by the natives, were also collected from the understory vegetation. In the plantations on Onotoa, Moul (1954) found many of the same groups of insects.

In the inhabited areas, insects are uncommon during the day, except for flies which quickly become abundant where fish are being handled or dried. Occasionally they are a troublesome pest in the plantations, especially on the leeward side of the islands. Mosquitoes were uncommon and no problem on Kapingamarangi in 1954, although Miller (1953) reported that in 1950 they were a nuisance at night on the outer islands. No ticks or chiggers were seen, and spiders and small scorpions are not known to cause casualties. In the evening, small moths and beetles are occasionally observed around the lights. Lice are found on birds and rats, as well as on the natives. Specific evidence of human disease due to parasites is lacking (Miller 1953).

Factors presumably involved in the dispersion of this insect population include wind, birds, rafts of debris carried by currents, native outriggers and, more recently, trading ships. Insects associated with man came with him; others attached to certain fruits may have also been introduced by the natives.

The small-sized herbivores are most abundant followed by the scavengers and then succesive groups of predators—the food chain terminating with the skinks, geckos, reef herons and cuckoos. The high skink population may account for the scarcity of annoying insects, as well as of economic pests in the plantations.

A partial list of the insects which have been identified from Kapingamarangi follows: *Aedes hensilli; Caccodes marquesanus; Chrysopa ramburi; Chrysopa megacephala; Dasyhelea esakii; Dihammus fasciatus; Exitianus fusconervosus; Forcipomyia fuscimanus; Melanoxanthus comptus; Mimegralla albimana; Pachybrachius chinai; Parasarcophaga misera; Simodactylus fasciolatus; Telostylinus longicoxa; Tomosvaryella micronesiae.*

Mammals

Mammals, other than man, are restricted to the indigenous Polynesian rat (*Rattus exulans*) and the domestic pig and cat. The small nocturnal rats are locally frequent on certain of the outlying islands and uncommon on the inhabited islands where cats are supposedly keeping them under control. Miller (1953), who visited the atoll 4 yrs earlier, reports that they live in trees, shrubbery or under organic debris, although none was observed in the plantations during the current survey and no rodent damage was reported. The only specimens found were those few trapped during the day in a boat house on Hare. Likewise in the Gilberts, Moul (1954) did not find this species sufficiently abundant to be a pest. In the northern Marshalls, Fosberg (1956) reports that they feed mostly on coconuts, taking a considerable toll of drying copra. He also observed them feeding on newly hatched sea turtles. This species is widely found on other atolls or island groups (Arno, Marshall 1951; Raroia, Morrison 1952; Truk, Mokil, Ant, Pingelap, Ponape and Kusaie, Marshall 1957). Their dispersion throughout the islands has probably occurred primarily by stowing away on native canoes or larger boats.

Although absent on Kapingamarangi, a far more serious pest is the larger house rat (*Rattus rattus*) found in the Marshalls and other atolls (Marshall 1951, 1957). On some islands in the south Pacific it is estimated that 75-100% of the coconut crop is destroyed (Dumbleton 1955) and in Polynesia copra exports might be doubled if rats were controlled (Lassalle-Sere 1955). The house rat cuts into and eats the green nuts and also causes considerable damage to stored copra and food (Marshall 1951). On Nukuoro the writer encountered similar damage to green and mature nuts. According to natives, copra production has dropped 50% since Japanese occupation, primarily due to these rodents. Uncontrolled, these small animals can seriously reduce coconut productivity and, indirectly, the prosperity of the native population.

Of the domestic animals, cats are restricted to the living areas and serve to keep the rat population under control. No dogs were observed, although they occur on other atolls. The pigs, small and inbred, are not allowed to roam wild but are tied or penned. The natives are cognizant of the fact that if they were not restricted considerable damage would result. Since there is essentially no refuse, the pigs must be fed coconut or other foods suitable for human consumption. Therefore, pork is considered a luxury item and is reserved for festive occasions.

Other Land Animals

Other land animals observed on the atoll were earthworms and snails. Annelids included the common peregrine (*Pheretima upolvensis*) of the Pacific (Gates 1954) and three other species, one yet undescribed (*Pheretima bicincta, Dichogaster* sp. and *Pheretima* sp.). As observed in the Marshalls (Fosberg 1956) earthworms are locally abundant wherever there is considerable moisture and organic matter in the process of decomposition. In the plantations they are found in the moist humus, especially under piles of coconut husks. In one such area 101 specimens were collected in a sample plot (0.5 sq m x 15 cm in depth) treated with mercuric chloride. They also occur under logs, fern clumps and other organic debris. Locally they are important in accelerating the incorporation of organic matter, as well as loosening and aerating the soil.

The snail population can be divided into three major groups: marginal marine species (*Truncatella striata, Nerita polita*), true land forms (*Pupinea brenchleyi, Opeas gracilis junceus*) and fresh water types (*Melanoides oualanensis*). The marginal marine species are typically found along the beaches usually under stones or logs (Truncatella) or buried in intertidal sand (Nerita). The latter is normally nocturnal and active only at low tide. It has also been reported as a conspicuous form on Raroia in the Tuamotus (Morrison 1952). The pulmonate land species (Opeas), widely distributed in the Pacific (Moul 1954) was collected under decomposing vegetable debris. Pupinea, another land operculate was found in decaying plant material.

The fresh water species *Melanoides oualanensis* occurred intermixed with green algae in Cyrtosperma marshes and was exceedingly abundant in a small well situated in one of these marshes. Also reported from other atolls (Moul 1954), it is presumably introduced accidentally with water supplies or on the roots of aquatic plants.

MAN'S FUTURE IN THE ATOLL MICROCOSM

As one views man as a part of the atoll ecosystem, it is strikingly evident that he is dependent upon both the terrestrial and marine environments for his survival and that these two environments are therefore intricately interrelated (Fig. 26). This discussion of the terrestrial environment has stressed the important influence that man has had on the biota since his entry onto the atoll. However, there is an even more significant aspect which involves the human carrying capacity of the atoll ecosystem. There is a limited population which the atoll can support. It has already been noted that the population is not static but on the increase, especially in

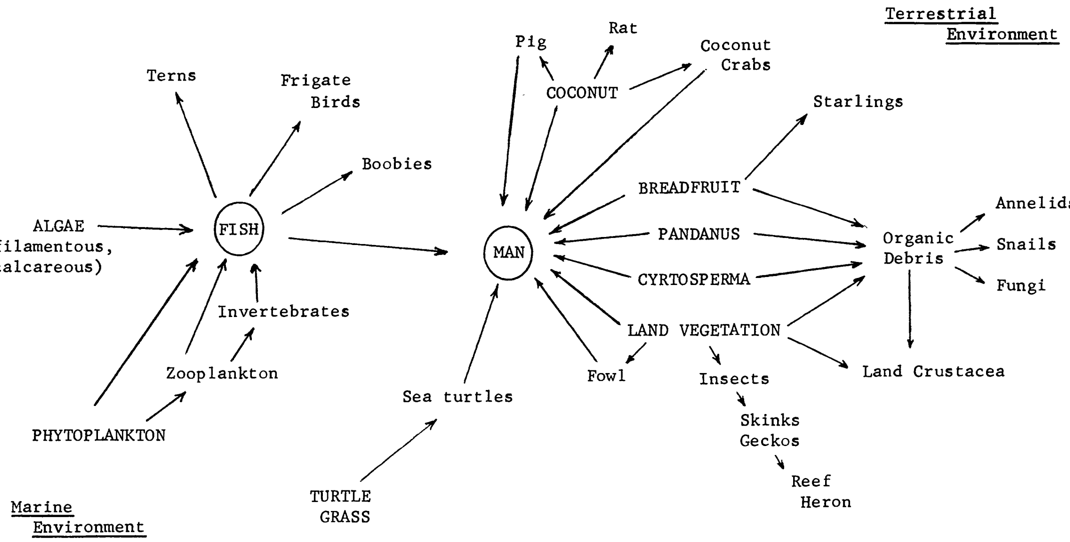

FIG. 26. Energy flow pattern in the Kapingamarangi Atoll ecosystem.

recent times. In the past, catastrophies such as the famine earlier in the century and, before that, inter-island warfare have tended to keep the population at a favorable level. Recently, migrations to other atolls have occurred. In 1947 the population reached a peak of 527 at which time migration to Ponape and other atolls took place. Therefore, by 1954 the population had decreased to a favorable level—426, a figure which the atoll can adequately support. Supporting more people than the natural environment will handle would, of course, necessitate the importation of food—a pattern occurring on other atolls. One of the inherent dangers of food importation is that there usually follows a decrease in the consumption of local native foods and a reduction in fishing (Anonymous 1951; Fosberg 1953; Danielsson 1954; Catala 1957). This can lead to the dislocation of a self-sufficient economy. On Kapingamarangi the people exhibit a high degree of adaptation to their salubrious environment (Miller 1953) and show no signs of malnutrition. Their needs from the outside world are a few trade items which make life easier and yet do not disrupt the ecological balance. However, in recent years there has been a tendency to make available, via trading ships, unnecessary imported items. In addition, there is often the desire to introduce other aspects of Western culture which the existing system cannot absorb without unfortunate repercussions. The introduction of goats on Kapingamarangi has been suggested as a source of milk. Not only is this commodity not needed, but the unselective browsing by such animals throughout the plantations would be most likely to have disastrous effects.

What then should be the fate of the few remaining microcosms in the Pacific? Should acculturation continue its inroads and give these people the attributes of Western culture or is it more desirable to assist them in a limited way in maintaining a favorable population level and in continuing the way of life they have known for centuries? By maintaining the population around 450, 0.64 of an acre of land is required to support each inhabitant plus access to the resources of the marine environment. As the rising population problem increases throughout the world it would be biologically and sociologically sound to assist these people in maintaining their present self-sufficient economy. This is also the opinion of Te Rangi Hiroa (Peter H. Buck 1950) an ethnologist who lived with the Kapingans while studying their material culture. ". . . they have nothing to gain from the outside world. They are self-supporting, healthy, and happy. They have created their adjustment with life from within and every effort should be directed toward avoiding any undue disturbance of that balance by influences from without."

SUMMARY

(1) Kapingamarangi Atoll, inhabited by over 400 Polynesians, is dominated by a strand type vegetation and limited land fauna. The flora includes 99 vascular plants over half of which (56) are either aboriginal or recent introductions. Among the most conspicuous animals are the sea birds, land crustacea and skinks.

(2) The dominant vegetational pattern is a result of man's activities and is divided into six types: namely, coconut plantations, coconut-breadfruit plantations, breadfruit groves, Cyrtosperma marshes, beach-scrub and village vegetation. Coconut plantations completely cover the smaller islands and form an outer belt around the larger ones. In the interior, coconut and breadfruit plantations surround the artificially created marshes planted to Cyrtosperma. A single breadfruit grove occurs on one of the larger islands. The native beach-scrub vegetation is limited to a marginal fringe along the oceanward and inter-islet beach ramparts. Recent introductions are especially conspicuous within the village areas.

(3) Within the plantations, the natural vegetation is restricted to the undergrowth. On the smaller islands *Guettarda speciosa* is dominant, whereas on the larger ones *Morinda citrifolia* and *Premna obtusifolia* are predominant. Herbaceous cover is sparse or wanting on the small islands with such grasses as *Stenotaphrum micranthum* and *Thuarea involuta* forming the conspicuous ground cover on the larger islands. Locally, ferns (*Nephrolepis hirsutula*) form a continuous ground cover.

(4) The Polynesian population is dependent upon coconut, breadfruit, Pandanus and Cyrtosperma as sources of food. Breadfruit is also important in canoe construction and other trees, both native and introduced, are used in house construction and in making implements and handicraft articles. Periodically the natives selectively clear the plantation undergrowth.

(5) The vegetation is modified by the average aerial and ground water salinity, as well as the extremes encountered during storms and droughts. Belting of the vegetation is correlated in part with man's planting regime, but this pattern is conditioned by aerial and ground water salinity. Breadfruit and Cyrtosperma are restricted to the interior of the larger islands where a fresh water lens develops. Breadfruit reaches its maximum development where the salinity is normally less than 350 ppm. In addition to ground water salinity, its survival appears to be related to salt spray intensity and also to the effects of concentrated breeding bird populations.

(6) Vegetation development is also limited by the immature rocky soils, especially on the smaller islands. Coconut palms planted on recently deposited sandy soils are chlorotic but otherwise mineral deficiencies are not evident. Herbaceous cover tends to increase with organic development. Species indicative of sandy soils are *Scaevola taccada, Lepturus repens, Ipomoea pes-caprae, Triumfetta procumbens* and *Vigna marina.*

(7) As a result of island migration lagoonward, primary vegetation development is occurring on the recently exposed sand bars where Scaevola is the conspicuous pioneer. The presence of old island remnants oceanward on the reef flat indicates considerable migration in the past. In the interior, vegetation change is difficult to detect, due to the periodic clearing.

(8) Based on the rate of organic accumulation in a well-developed undisturbed soil profile, it has been estimated that certain of the land areas on the atoll formed at least 3,000 yrs ago.

(9) The pre-Polynesian vegetation covering the atoll was probably a mixed forest of indigenous trees most of which are represented in the present flora. On the smaller islands a low scrub vegetation may have been the predominant pattern.

(10) Sea birds are frequent and serve an important role in the cycling of nitrogenous and phosphatic nutrients from the sea to the land. The gregarious nesting habits of the white-capped noddy terns in breadfruit trees may have deleterious effects upon them, actually killing them if the nests are not periodically removed. The biotic interaction of guano from large populations of sea birds roosting or nesting in a Pisonia forest formerly present on one of the islets appears to have resulted in the formation of phosphate rock. This interaction may account for many such deposits on other atolls throughout the Pacific.

(11) Land crustacea play an important role in the incorporation of organic matter into the immature soils. They may also destroy seedlings and propagules. Coconut crabs, potentially destructive to coconut, are rare since they are considered a delicacy by the natives. Skinks are the most abundant vertebrates on the atoll, possibly due to the lack of heavy predation.

(12) The inhabitants are dependent upon both the terrestrial and marine phases of the atoll environment which are intricately interrelated. The pattern of energy flow is toward man as a primary and secondary consumer. His main source of protein comes from fish and marine invertebrates, whereas land plants furnish his source of carbohydrates, in addition to other necessities of life. The atoll is an essentially self-sufficient microcosm in which man is a key component in balance with his environment. It is recommended that administrators assist in maintaining this present self-supporting ecosystem.

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