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Bioecology of Kapingamarangi Atoll, Caroline Islands: Terrestrial aspects

by

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INTRODUCTION

The role of the land ecologist was to describe and to obtain a representative collection of the land biota. This was accompanied by observations and analyses of the interrelationships which exist between the plants and animals and their environment. Since man plays a dominant role in the environment, special emphasis was placed on human influences with respect to floristic utilization and vegetation management. It was anticipated that by this approach data would be obtained which would also be of value in guiding future administrative policies.

Kapingamarangi Atoll is located in the southern Caroline Islands 1° north of the equator (Fig. 1*). It is extremely isolated, the nearest atoll being Nukuoro 164 nautical miles northward. The pear-shaped atoll, approximately 5 by 6 miles in diameter comprises thirty-three islets all of which are located along the eastern reef (Fig. 3). The islets vary considerably in size. In length they range from 100 feet (Matukerekere) to one mile (Hare) while width ranges from 25 feet (Matukerekere) to 1200 feet (Werua). The total land area comprises approximately 276.4 acres or 0.42 square mile. The atoll is populated by 426 Polynesians (June 1954) who live primarily on two of the islets - Touhou and Werua. These as well as the outlying islets serve as their plantations.

Geologically the land area is composed of limestone bedrock, lime sands, and coarser coral and limestone fragments. On the ocean side the majority of the islets are formed of boulder conglomerate and/or coral rubble limestone which, except for occasional outcrops, is overlain with unconsolidated coral rubble and larger limestone fragments. Lagoonward the bedrock and rubble give way to beach sands. A few of the smaller islets located lagoonward on the reef are dominantly sand while others situated more oceanward are primarily limestone overlain with rubble and boulders. Two processes - erosion and deposition - play a major role in modifying the islets. Oceanward both processes are operative. Erosion occurs as undercutting especially along the channel margins. On the other hand as a result of deposition a beach ridge composed of rubble and boulders extends a few feet above sea level along the ocean and channel margins. Elevated reef rock areas frequently extend toward the ocean from the islets and probably represent remnants of a higher reef level that was possibly vegetated at one time. Dipping beach rock, apparently representing the former extension of the islet oceanward, is especially conspicuous on Torongahai. Lagoonward, depositional processes result in sandy beaches. Here sand bars commonly project from the ends of the islets. An exception occurs on Pumatahati where an extensive rubble beach extends inland for 50 feet. This may be correlated with severe storms in the past. In general, the islets are relatively flat with a rise of only a few feet above sea level. However, in the interior, banks of coral rubble reach a maximum of 14 feet above sea level as a result of puraka pit excavations. As a result of causeways constructed between the islets several have been completely connected. This accounts for the extensive length of Hare

*All figures will be found at the end of the report.

islet. The formation of Pepeio, 0.7 acre, was initiated by man through his construction of a coral boulder wall on the reef flat. (Data in part from E. McKee, 1956.)

The soils are relatively immature and consist largely of mixtures of lime grove or rubble, sand, and fine lime particles combined with varying amounts of humus. Throughout most of the smaller islets and oceanward on the larger ones rubble soils are most common. Here the surface rubble is typically gray as a result of the presence of blue-green algae, primarily Entophysalis crustacea, in the surface layer. The organic layer varies considerably but reaches its greatest development in these rubble areas where it ranges from 6-12 inches in depth. In two areas, depths of 18 inches and 30 inches were recorded (Tokongo and Rikumanu, respectively). On Pumatahati a dark brown humus layer 6-8 inches in depth, free of the usual sand and rubble, overlies a highly phosphatic cemented layer. The organic material is also phosphatic (100% apatite, McKee, 1956) and acidic (pH 4.5). The consolidated layer underlying the humus consists of light brown cemented sand with scattered rubble. Lighter cream-colored particles are scattered throughout this brownish matrix. The upper zone is cemented giving way to soft crumbly material below. With the limited data obtained from these two layers the profile resembles that described by Fosberg (1954) as the Jemo soil series (see section on Associated fauna, birds). Lagoonward, sandy soils are most conspicuous, especially on the larger islets. In these soils incorporation of organic material ranges from less than 2 inches to 6 inches in depth. This is correlated with the lagoonward migration of the islets and the extreme immaturity of these soils as compared with the rubble areas. In the rubble and sandy soils only the A and C horizons are represented. A darker surface layer gives way to a grayish transitional zone which in turn gives way to the parent material composed of cream and orange foraminiferal sands and/or whitish rubble. Buried profiles which occur on several islets are indicative of previous storms. In the puraka pits a poorly drained muck type soil occurs (Stone 1951). On the smaller islets the soils would probably be classified in the stony and very stony complex while on the larger wider islets they appear similar to the Shioya or Arno types (Stone 1951).

On the atoll, fresh water occurs in the form of a shallow Ghyben-Herzberg lens. Although its distance above sea level was not determined, it may be assumed to be about 10-12 inches, as found in the Marshalls (Cox 1951; Arnow 1954). The upper limits of the water table vary considerably from the lagoon to the ocean side. On the larger islets of Werua and Taringa, it averages $2\frac{1}{2}$-4 feet from the surface near the center and lagoonward, while on the ocean side it varies from 5-$5\frac{1}{2}$ feet. On the smaller islets the water table is nearer the surface and the degree of salinity is higher. Oceanward on the larger islets, the salinity ranges from 1,000 ppm. to 3,800 ppm. and lagoonward from 18 ppm. to 340 ppm. (Table II). On the lagoonside, wells furnish fresh water for bathing and washing. Although this water is potable the natives prefer rain water which is collected in cisterns. On one of the smaller islets, Hukuniu, 0.9 acre in area, the salinity is similar to that of the ocean, averaging 18,000 ppm. Throughout, the soils and underlying bedrock have a considerable influence on the degree of salinity.

Climatic data for Kapingamarangi is limited to the Sailing Directions for the Pacific Islands, 1952 and observations made during previous and current expeditions. As would be anticipated, within this equatorial region the temperature is relatively uniform throughout the year. Data taken during July and August 1954 indicated the average maximum to be 89.1° F; the average 74° F. The average daily relative humidity was 57.4% with the average daily maximum reaching 83.8%. Available estimates on average yearly precipitation range from 78-108 inches. The Sailing Directions for the Pacific Islands, 1952 indicate the greatest rainfall during May and June and October and November (12 inches) and relatively light precipitation from February to April and from July to September (7 inches). The average for December to January is 9 inches. In 1954 there was little rain during July and August - the average for the seven week period was only 4 inches. Previous expeditions also encountered dry summers which extended into the "fall". Within a region dependent upon squalls, the rainfall pattern is probably very erratic. Droughts occur, the most severe of which extended from 1916 to 1918 and cost the lives of ninety natives. Although the Sailing Directions for the Pacific Islands, 1952 indicate winds from varying directions throughout the year, during July and August they were primarily from the east. Although the area is outside the typhoon belt, severe storms frequently occur, usually from the southwest. Information was available from the native secretary Rikaneti on the damage caused by these storms as far back as 1858. The most recent and severest was in 1947. Specific damage resulting from these storms will be included under the section on Climatic Influences.

METHODS

The small size of the atoll and proximity of the islets facilitated field studies.* During the first few weeks a general reconnaissance was made of all islets either by foot or native outrigger canoe. This was followed by more detailed corroborative studies on specific islets. It included collecting both flora and fauna, laying out strip transects across representative islets, studying the various environmental influences and talking with the natives concerning their land management practices, past and present, as they related to better understanding of the atoll complex. Joint studies were carried on with the expedition geographer (Herold Wiens) in mapping shoreline features and general vegetation maps.

Native interpreters aided in mapping the coconut and breadfruit-coconut plantations. This involved measuring from the high tide mark to the outer edge of the breadfruit canopy at 100 foot intervals around the islets. In order to estimate the number of coconut and breadfruit per acre, total tree counts were made on several of the smaller islets and quadrats 52 by 52 feet and 104 by 104 feet were laid out in the various plantations types on the larger islets. Soil and ground water data were obtained from wells and puraka pits with the team geologist (Edwin McKee). In conjunction with the marine biologists (Cadet Hand, Robert Harry and Jan Newhouse) the land vegetation was mapped as a part of a continuous transect extending from the seaward reef margin across an islet into the lagoon.

*Field work lasted from 22 June to 31 August 1954.

THE LAND BIOTA AND ASSOCIATED INFLUENCES

As a result of man's activities the entire land area is dominated by coconut (*Cocos nucifera*), breadfruit (*Artocarpus altilis*), pandanus (*Pandanus tectorius*) and *puraka** (*Cyrtosperma chamissonis*). On the smaller islets coconut dominates completely. However, on the larger ones a typical zonation is evident (Figs. 10, 15, 30). Here the pure coconut plantations form an outer band and are replaced toward the interior by a mixture of breadfruit and coconut or pure breadfruit around the puraka pits. On the beach ridge a mixture of *Guettarda speciosa* and *Scaevola sericea* forms the outermost zone under the leaning coconut palms. The variety of vegetation types frequently encountered on atolls is absent (Fosberg 1953; Hatheway 1953). The typical strand vegetation, restricted primarily to the undergrowth and marginal areas, consists mainly of indigenous species.

As is typical of most atolls, Kapingamarangi is represented by a relatively sparse flora and fauna. Of the ninety-eight vascular plants found on the atoll it is estimated that thirty-eight are indigenous and fifty-eight introduced (Figs. 28, 29, 31). Of those introduced, sixteen are possibly of aboriginal origin (early introductions by man) and forty-two of more recent origin. Another category includes four species potentially indigenous but not found as mature specimens. These were found on the beach as drift seedlings. Since two species are considered to have more than one means of entry, the various categories, when totaled, slightly exceed the actual flora.

Since the total land area was sufficiently small a relatively complete floristic list was made for each islet (Figs. 28, 29). The number of species per islet varied from seven on the smallest islet (Matukerekere 0.03 acre) to sixty-one species on one of the larger inhabited islets (Werua). When the total number of species per islet is plotted logarithmically against islet size two linear relationships are evident (Fig. 32). Those islets less than 3.5 acres fall along one line with little variation in number of species. The other relationship includes those islets 3.5 acres and over and shows more strikingly the direct relationship between islet size and number of species.

Of the limited fauna, land and hermit crabs, insects, skinks, geckos, and birds are most abundant. The only mammal besides the pig and cat is a small rat which is locally abundant.

In order to adequately describe the land biota the vegetation has been arbitrarily divided into several types or areas: coconut plantations, breadfruit-coconut plantations including a breadfruit grove, puraka pits, marginal vegetation and inhabited areas. Since the faunistic aspects are generally similar throughout, a section on Associated Fauna follows the description of the vegetation. This is followed by sections on other environmental influences.

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*Native name.

I Coconut plantations (Figs. 10-27)

Although coconut plantations dominate the smaller islets, on the larger ones they usually occur as marginal bands 100-150 feet in width oceanward and 60-100 feet lagoonward. According to the most recent survey of the Trust Territory these plantations occupy 320 of the 332.8 acres* of land area. This survey revealed by a reportedly actual count that there were 44,752 mature coconut and 22,213 immature coconut (Trust Territory Statistical Requirements, 1954). However, during the present survey it was found that only 157.03 acres are covered by coconut plantations. When the total number of trees is estimated in the coconut as well as breadfruit-coconut plantations only 22,174 coconut are present, i.e. about one-third the number previously reported (Wiens, Table III). It is obvious that the "320 acres" in plantations listed by the Trust Territory Statistical Requirements has not discriminated between coconut and breadfruit-coconut plantations. The validity of this lower figure (22,174) for the total number of coconut trees is accounted for by Wiens in calculating the tree density from close-up aerial photographs of other atolls and comparing them with Kapingamarangi. From these it is obvious that the estimated 116.5 coconut trees per acre on Kapingamarangi already represent overcrowding and that the census by the natives for the Ponape District Administration was much too high.

The plantations are dominated by relatively mature trees spaced on an average of 21 feet apart. Of course some variation occurs depending upon the age of the stand and the necessity to plant new trees in order to replace the older less productive ones. The most desirable plantation, according to Rikaneti, is planted so that the fronds merely touch to form a closed canopy. On Kapingamarangi there is considerable overlapping of the fronds, which would further substantiate the overcrowded aspect of the plantations.

The undergrowth varies considerably due to the recency of clearing, protective marginal vegetation, and islet size. On the smaller islets it is usually sparse or practically absent, while on the larger ones it has the potential of forming a continuous understory and dense ground cover. In general, Guettarda is most conspicuous on the smaller islets and gives way to Morinda citrifolia and Premna obtusifolia on the larger ones. Pandanus is common either as scattered mature trees or as immature localized stands. Numerous native varieties of it occur. Although seedlings are often abundant under some trees, most of them are propagated by burying the cut end of a branch from a known productive variety.

The shrub layer consists primarily of sprouts and suckers of Guettarda, Morinda, and Premna. Scaevola, although a common marginal shrub, is unimportant in the interior. Other shrubs contributing sporadic cover include Allophylus timorensis, Clerodendrum inerme and Pipturus argenteus.

On the smaller islets herbaceous cover may be absent or consist of scattered specimens of Asplenium nidus, Tacca leontopetaloides and Crinum sp.

*Wiens' mapped land surface indicates only 276.43 acres.

On the larger islets these species as well as Stenotaphrum micranthum, Thuarea involuta, Nephrolepis hirsutula, Wedelia biflora and others are most conspicuous.

Sharp lines of demarcation in the undergrowth are evident between recently cleared and uncleared areas. The ground is littered with coconut and pandanus leaf debris and occasional coconut logs. Coconut stumps, which are relatively common, are often covered with Leucophanes smaragdinum, a moss which forms cushion-like mats. Old stumps of Guettarda and Premna are also present.

Since considerable variation occurs within this type, depending upon islet size, the islets have been divided into three groups: islets 3.5 acres or less, islets 3.5-9.5 acres and islets over 9.5 acres (Fig. 31). The first category includes the smaller islets characterized for the most part by a Guettarda understory, a general uniformity in number of species and a sparsity of herbaceous cover. In the second and third categories the coconut plantations usually occur as a band surrounding the interior breadfruit-coconut type. Here the understory is primarily Premna and Morinda accompanied by an increase in herbaceous cover, especially grasses. The second and third categories are separated chiefly by the more mesophytic aspects of the latter. These variants closely resemble those described by Hatheway (1953) on Arno Atoll in the Marshalls.

A. Smaller islets (3.5 acres or less)

Most of the nineteen islets in this group are elongated in an ocean to lagoon direction across the reef. They vary in size from 25-350 feet in width and 100-500 feet in length. Due to the severe environmental conditions they support an extremely sparse flora comprising 5-16 species.

Coconut trees completely dominate these smaller islets and average 55-65 feet in height. On the immature sandy soils chlorotic palms are very conspicuous. For example, on Pepeio, a recently formed sandy islet, the trees, which are only 35-40 feet in height, are extremely yellow. According to the natives the trees are less productive on these islets than on the larger ones. Breadfruit is virtually absent: only one tree was observed.

The understory development varies considerably. In general, Guettarda is most characteristic with scattered Morinda and Premna. The former occurs as scattered trees 25-30 feet in height with various transitional stages, primarily stump sprouts or root suckers, as a result of continuous cutting in the past. Periodic clearing of the undergrowth leaves only occasional taller Guettarda and Pandanus scattered throughout the understory. In the interior lagoonward Scaevola occurs only sporadically although Rikumanu islet is an exception where it forms a continuous shrub layer. On two of the very narrow islets (Matuketuke and Matawhei), which are covered with coarse coral boulders seaward, the understory is practically wanting except for an occasional Pandanus. From the ocean margin these areas extend into the interior for 100 feet or more and give way to scattered low undergrowth lagoonward. In such areas lacking an understory old stumps indicate previous vegetation which has either been cut during clearing operations or killed by salt spray or salt water inundation.

In general, the herbaceous cover is absent or comprises scattered specimens of Tacca, Asplenium, Crinum and Lepturus repens. Cassytha filiformis occurs as a parasite. Only on one islet, Turuaimu, which is extremely sandy and open, is herbaceous cover abundant. Here Triumfetta procumbens occurs as an important ground cover.

B. Intermediate islets (3.5-9.5 acres)

In contrast to the smaller islets, these seven tend to be more or less elongated parallel with the ocean and lagoon or along the reef. In size, they attain a maximum of 500 feet in width and 800 feet in length. A slightly more favorable environment exists and therefore a slightly larger number of species occurs. Although coconut plantations are dominant, on a few islets they give way to the breadfruit-coconut type.

On these islets the coconut are somewhat taller, ranging from 75-85 feet in height. Sprouted coconuts are usually not found in the plantations. However, on one islet, Pumatahati, they are relatively common. Since this is one of the two islets owned by the community it is apparently not managed as judicially as those privately owned.

The most striking change occurs in the understory. Although Guettarda still occurs as scattered trees Premna and Morinda, 5-7 inches in diameter or larger and 25-30 feet in height, predominate. In addition, Pisonia grandis is locally abundant, especially on Pumatahati, which was formerly covered by a Pisonia forest. Pandanus is scattered or localized. Sucker and sprout growth of Morinda and Premna often form a shrub layer 3-4 feet in height. Again land management practices account for the variation from a relatively open shrub layer with scattered larger Morinda and Premna to a relatively dense undergrowth.

Herb cover increases compared to that of the smaller islets. In addition to those species found on the smaller islets the two grasses Stenotaphrum and Thuarea are most frequent, especially in the openings. Other species which appear for the first time include Fimbristylis spathacea, Ipomoea littoralis and Ipomoea pes caprae.

C. Larger islets (over 9.5 acres)

These seven islets attain a maximum of one mile in length (Hare) and 1200 feet in width (Werua). Although the coconut plantations reach their maximum development on these larger islets the breadfruit-coconut type approaches, or may actually exceed, the area occupied by coconut. With the exception of bombed areas on two islets and causeways on Hare, the coconut form a relatively uniform closed canopy 85-95 feet in height. In the bombed sites on Hare the post-war trees are already productive, although they have not attained the height of the surrounding pre-war trees. This is especially evident over a wide strip through the middle of the islet. In contrast, recovery has been considerably slower on Nunakita where scattered tall pre-war palms stand out conspicuously. This may also be correlated with greater disturbance and the abundance of bedrock outcrops.

As on the previous islets, Premna, Morinda and Pandanus are the typical understory species, although variants occur. Occasional associates include Pisonia and Hibiscus tiliaceus. Others such as Hernandia sonora, Cerbera manghas, Thespesia populnea and Ochrosia oppositifolia usually occur as scattered isolated trees. A small pure stand of Soulamea amara, 50 by 50 feet occurs on Nunakita. These trees are 6 inches in diameter or less and seedling reproduction is abundant. As on the smaller islets Premna and Morinda sprouts and suckers are common.

The herbaceous cover increases markedly compared to the smaller islets. Considerable variation also occurs especially between the wide and narrow islets. On the latter, such as Matiro, Hare, and Nunakita the two grasses Stenotaphrum and Thuarea, Wedelia, Vigna marina, and occasional ferns are most typical. On the wider more mesic islets, Ringutoru and Torongahai, ferns attain a lush development in the more shaded plantations with scattered grasses in the openings. The ferns Nephrolepis and Asplenium, form a continuous ground cover 2-3 feet in height. Further variation occurs from the ocean to lagoon side. Herbaceous cover is usually less continuous on the recently deposited sandy areas, in contrast to the highly organic rubble areas oceanward. In openings around abandoned house sites, now within the plantations, Vigna frequently forms dense tangles which completely engulf the other vegetation. The two most troublesome weeds are Wedelia and Vigna. Throughout, this pattern is modified periodically by complete clearing.

1. Sandy lobes

On the sandy lobes forming lagoonward a successional trend is evident in the understory. This is most striking as one progresses from the lagoon beach into the interior. On Ringutoru the lagoonward migration is so rapid that the typical marginal species - Guettarda, Scaevola and Messerschmidia argentea persist inland where they form an open sporadic 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. At 100 feet or more from the margin this pioneer undergrowth gives way to a Premna-Morinda understory typical of the interior regions. Here Asplenium, Nephrolepis and Stenotaphrum form a continuous ground cover. These areas indicate a successional trend in the undergrowth from the early beach pioneers to a Premna-Morinda type.

2. Filled channels

These areas have formed as a result of deposition occurring between the islets to the point of connecting them. This accounts for the extreme length of Hare islet which actually consists of three islets that have been joined together in the past by severe storms (Fig. 23). The older

Rawa-Hare channel closed around 1865 and the more recent Herengaua around 1942. The former is clearly demarcated by the old inter-islet beach ridges which occur diagonally across the islet. The latter is delimited by the unaltered sandy soil and low yellowish palms. These areas are of particular interest in that they give some indication of the rate of organic accumulation and subsequent influence on the vegetation (see section on Biotic Influences). Just how soon coconut were planted on the older causeway is unknown. However, it may be assumed that planting occurred soon after it closed since the total land area of the atoll is so limited. On the more recent filled channel they were planted soon after its formation.

On the recently closed Herengaua channel the sandy soil shows no organic development. The larger palms 35-45 feet in height are just becoming productive while the smaller immature trees are extremely chlorotic. This area is in sharp contrast to the more recently bombed and replanted areas on Hare where the trees are already taller, more vigorous and more productive. In the sparsely developed understory scattered stump sprouts of Guettarda, Scaevola and Messerschmidia occur. Herbaceous cover is wanting. Morinda and Premna seedlings are rare and the trend toward such an understory is not as yet evident.

On the older channel a layer of dark organic matter 1 inch in depth has developed. It is intermixed with grass roots and gives way to a 6 inch layer of gray stained foraminiferal sands which in turn give way to unaltered parent material. The vegetation differs considerably from the surrounding areas. Coconut dominates across the entire channel in contrast to breadfruit-coconut plantations on both sides of the channel. The understory, where present, is dominated by Guettarda which occurs either as sporadic trees or stump sprouts. Large shrub clumps of Scaevola which have been cut many times also occur. Grasses such as Stenotaphrum, Lepturus and others form a continuous ground cover. Some areas are extremely savanna-like, i.e. relatively open with scattered palms and grasses. Asplenium occurs only locally. In the adjacent areas on either side of the causeway Morinda, Premna and Pandanus dominate and form a dense understory. Here Asplenium is more common with grasses forming a less continuous aspect. In contrast to the sandy lobes, there is little evidence of vegetational change even on this older filled channel.

On the coarse coral boulders of the relict beach ridges crossing the islets, Guettarda forms a conspicuous band along with Asplenium. One of the tall leaning coconut palms on the ridge, which is highly scarred by innumerable knife cuts, was said to have been planted when the causeway closed.

II Breadfruit-coconut plantations (Figs. 10, 11, 15-18, 20-23)

On thirteen of the larger islets coconut plantations give way in the interior to a mixture of coconut and breadfruit occurring on, but also beyond, the rubble banks surrounding the puraka pits. From the lagoon the breadfruit stand out conspicuously with their dark green canopies which tower 15-20 feet above the coconut. This type extends to within 100-150 feet of the high tide mark on the ocean side and 60-100 feet on the lagoon side. An exception occurs on Touhou islet where this admixture dominates the entire islet and occurs to within 35-45 feet of the ocean shore and 12-25 feet of the lagoon shore (see section on Inhabited Areas). On the smaller islets only a few scattered breadfruit occur while on the larger ones the breadfruit-coconut type may equal, or exceed, the area occupied by coconut plantations. It reaches its maximum development from the center of the larger islets lagoonward. Oceanward the breadfruit decreases in abundance until only scattered recently planted small trees demarcate this type from the pure coconut. This restriction to the larger islets is apparently correlated with the greater protection afforded from adverse saline effects.

The presence of breadfruit in this type contributes to a more dense and mesophytic aspect. The breadfruit occur fifty or more feet apart interspersed with coconut and together they form a relatively closed canopy. Although there are fewer breadfruit than coconut the large crowns of the former contribute considerably greater cover. The trunks average 2-3 feet in diameter although occasional trees reach 6 feet in diameter and often attain a height of 90-100 feet or over. The straight fluted trunks are usually devoid of branches for the first 25 feet or more. In some areas the recent planting of breadfruit in the coconut type is evident by the generally smaller trees, 8-12 inches in diameter. Openings that occur in the canopy are due primarily to dead or partly defoliated branches as a result of storms. On two islets, Hukuhenua and Ringutoru, damaged trees are especially common. In the upper canopy large branches are frequently devoid of leaves or the foliage is dwarfed. These branches are the favorite nesting site of the gregarious white-capped tern (see section on Associated Fauna). Under the breadfruit, seedling reproduction is evident only on Hare islet. Here the seedlings are often nipped off, probably by hermit crabs.

The understory varies considerably from the rubble banks to the area beyond. On the banks the recency of excavation results in diverse patterns. On those more recently disturbed, Thuarea, and occasionally Lepturus, are typical pioneers. These species, especially the latter, are important in stabilizing the sloughing of the banks caused by crab activity.

On the older more stable banks Pandanus plantings are common. The trees are spaced 3-5 feet apart and range from 6-12 feet in height. Their generally small and uniform size suggests post-war planting, probably resulting from the recent demand for mats and other handicrafts. Since they provide an important source of leaves used in mat making, many of the lower ones have already been cut off close to the stem. Shrubby undergrowth includes thickets of Clerodendrum and sprouts and suckers of Morinda and Premna. Scattered Hibiscus tiliaceus frequently lean out over the puraka pits. In the more shaded areas Thuarea and Stenotaphrum form continuous carpet-like patches over the rubble. They are occasionally intermixed but more commonly occur as pure grassy areas. On the more open banks Vigna and Wedelia sometimes form a continuous cover 1-2 feet in height.

Beyond the banks the undergrowth pattern is quite similar to that found in the coconut plantations on the larger islets, except for a less profuse growth due to the dense shade produced by the breadfruit. Variation in this pattern occurs on Ringutoru where a small area 100 by 150 feet is planted to banana (Musa sapientum) and papaya (Carica papaya). Although some bananas are produced, they are considered a luxury. In contrast, few of the papaya trees appeared very productive.

On Werua, the widest islet, this mixed type gives way to a relatively large area dominated exclusively by breadfruit which occurs on the rubble banks surrounding the puraka patches (Fig. 15). These trees are occasionally larger in diameter and form a denser canopy. The paucity of trees in the smaller size classes is similar to that reported from the Marshalls (Hatheway 1953). The undergrowth here is similar to that found in the breadfruit-coconut plantations but is less dense. In the openings extensive pandanus plantings occur.

Within the plantations there are several kinds of breadfruit: the Kapinga type, probably an aboriginal introduction, and those of more recent origin: the Nukuoro, which was originally introduced from Samoa circa 1922 and the Ponape brought in circa 1935. Although opinion varies as to which fruit is best, the Kapinga type is apparently preferred and dominant throughout the plantations. This is followed by Nukuoro and Ponape types in preference and abundance. The Kapinga and Nukuoro varieties are propagated by seed and the seedless Ponape trees by air grafting and suckers. According to the natives, all trees are productive two to four times per year depending upon rainfall.

Although they report that there was more breadfruit in the past, today there is little evidence of this. On the contrary, the lack of old stumps in the breadfruit-coconut type is suggestive of relatively recent expansion of this type into areas formerly dominated by pure coconut. Today the presence of young trees in the marginal areas is also indicative that the mixed plantations are still increasing in area. On the other hand, in the pure breadfruit grove, the large cut stumps would suggest that this area has probably been producing breadfruit longer than any other area on the atoll.

III Puraka pits (Figs. 10, 11, 13, 15, 17, 18, 20-24, 30)

Puraka pits occur on eleven of the larger islets. They are located near the center or slightly lagoonward and are surrounded by breadfruit and coconut. The pits, which vary in size from a few square feet to one extensive area of eleven acres on Werua, are formed by excavating the rubble to slightly below the fresh water level and then adding organic matter in which puraka (Cyrtosperma chamissonis) is subsequently planted. A muck type soil eventually develops, the upper 6 inches of which consist of a fibrous network of roots with an algal covering over the surface layer. Since this soil is usually saturated, narrow elevated paths traverse the pits. Although the banks are generally 3-5 feet in height above the floors of the pits larger ones on Werua attain a height of 10-15 feet or more.

The puraka is planted 8-12 inches apart and varies in height from 2-6 feet or over, depending upon the stage of maturity and light intensity. In the more shaded situations the plants are taller and more vigorous. Those in the center of the larger patches are frequently smaller and the leaves are yellowish-brown, which may be caused by the intense insolation. According to Lia, one of the native women, the marginal areas are most productive. This would suggest that intermediate light intensity is most favorable.

Banana (Musa sp.) and ornamental hibiscus (Hibiscus sp.) are scattered throughout the patches. Cassia alata, a recently introduced shrub, used for medicinal purposes, is rare. In a few of the older patches rows of Premna, 6-8 inches in diameter, still persist and demarcate previous property boundaries.

The most abundant and troublesome weed is Jussiaea suffruticosa which grows 2-3 feet in height. Other herbs occasionally found include Angelonia angustifolia, Lindernia antipoda, Ipomoea littoralis, Cyperus brevifolius, Hedychium coronarium, and Fimbristylis miliacea. Along the paths one finds Alternanthera sessilis, Digitaria microbachne and Paspalum vaginatum.

Puraka is planted, cultivated, and harvested by the native women. Weeding of the above species, especially Jussiaea, is one of the major jobs. Periodic mulching involves adding banana and breadfruit leaves.

Only one small abandoned pit was noted where the natives indicated that they were unable to grow puraka. Since the water was slightly saline to the taste this may account for their failure.

Over the years the number of puraka pits has increased with the increase in population and in several areas expansion is still under way. One landowner killed a large breadfruit by fire in order to enlarge his puraka holdings. Although Cyrtosperma is most common now, taro (Colocasia esculenta) was dominant in the past. Apparently the more vigorous drought-resistant puraka crowded out the less successful taro. Today the latter occurs only as scattered isolated specimens.

IV Marginal vegetation

The marginal vegetation includes a relatively conspicuous border beneath the leaning coconut (Fig. 33). It is best developed on the oceanward and inter-islet beach ridges. Lagoonward the border is interrupted by native structures and finally gives way to sand bars at the ends of the islets.

Along these marginal areas two geological processes are operative: seaward, severe erosion and deposition and lagoonward, primarily deposition. As a result of the differential influences of these factors diverse patterns result. Therefore the discussion will be divided into Oceanward and Lagoonward aspects.

A. Oceanward

Tall leaning palms are typical along the beach ridge. They are generally planted to within a few meters of the edge and with subsequent erosion mature trees are found growing at the high tide mark. Under these palms, Guettarda and Scaevola form a two layered border on the beach ridge. The former occurs either as low trees, 12-15 inches in diameter and 18-25 feet in height, or as numerous stump sprouts of varying size. The latter grows in front of or under the Guettarda as a narrow often discontinuous shrub layer 5-12 feet in height. The width of the band varies from 15-30 feet with the Guettarda canopy projecting 15-20 feet out over the water. These species occur either together or in nearly pure stands depending upon the prevailing winds and erosion. Scaevola tends to increase in importance where erosion is least severe while Guettarda is common in the more severely eroded sectors.

On the seaward points of the smaller islets, where raised reef rock extends oceanward beyond the high tide mark, small thickets of Scaevola backed by Guettarda are extremely characteristic. The persistence of the former here is apparently correlated with the protection afforded by the reef rock. On the larger islets the pattern is more heterogeneous, but again dependent upon the severity of erosion and deposition.

Along the inter-islet channels, where erosion is most severe, a striking pattern is evident between the windward and leeward sides. On the east-southeast windward sides Guettarda is dominant and forms a continuous border. On the slightly more protected leeward margins the two species nearly share dominance. Where Scaevola occurs in abundance on the windward side there is usually some protection such as raised reef rock or beach rock off shore. Even fish traps constructed in the channels serve to lessen erosion.

In addition to Guettarda and Scaevola, several other marginal species are represented. According to their relative importance they include Pandanus tectorius, Messerschmidia argentea, Cordia subcordata, Terminalia samoensis, Clerodendrum inerme, and Barringtonia asiatica.

On some of the smaller islets such as Matuketuke and Matawhei the marginal vegetation is completely absent except for coconut and sporadic Pandanus. This may be a result of salt spray, erosion, cutting or a combination of these factors.

The effects of marginal erosion and salt spray are most striking along the windward sides. Here root systems are often partially or almost completely exposed. Coconut palms are sometimes eroded out and their trunks found strewn on the beach. Clumps of Scaevola are also washed away. Probably the paucity of this species in these areas is correlated with its less extensive more shallow root system compared to that of Guettarda. Of these marginal species Guettarda, Cordia, and Terminalia are most conspicuously affected by salt spray (see section on Climatic Influences).

Some of the natives apparently recognize the protection afforded by this marginal band in the interception of salt spray and islet stability. Others, however, cut or burn the old Guettarda if they no longer produce wood useful in construction.

B. Lagoonward

Although leaning coconut are characteristic along the lagoon shore, the understory is often less continuous, especially where houses or other native structures occur. Pandanus is commonly associated with Scaevola and Guettarda. On the larger islets large trees of Calophyllum inophyllum 12-24 inches in diameter lean out over the lagoon. Their restriction to the lagoon shore is unique. Only two trees were found elsewhere: one seaward severely damaged by salt spray and another in the interior in excellent condition. Although seedlings occur on the beach, most of these trees are planted.

At the ends of the islets sand bars project lagoonward. Some are ephemeral with little or no vegetation while others are covered with scattered clumps of Scaevola and Messerschmidia as pioneers. Within this low shrubby matrix young coconut are planted by the natives. In other areas, where the advance of pioneers keeps pace with the accumulation of sand, a step-like band of Scaevola results. Here rows of Scaevola seedlings on the back shore give way to Scaevola 3-6 feet in height which are backed by a taller band 9-12 feet in height. Guettarda forms a tree layer beyond.

As the islets migrate lagoonward Guettarda and Scaevola persist inland. Large Guettarda occur scattered under the coconut or sometimes on former beach ridges left behind as the islets built lagoonward. Some appear to be quite old and others have been cut many times and resprouted. If these are relicts of the earlier pioneers, the building processes are taking place extremely rapidly. On Ringutoru the rate of migration was estimated from data furnished by the natives regarding the position of former marginal trees. In this area the cove sector of the beach between the sand bars is building at the rate of 1 foot per year. From the vegetational pattern, the adjacent sand bars are probably building even faster.

All along the lagoon beach, drift seedlings are common. On the back shore detailed observations were made on seven islets regarding the frequency and abundance of seedlings. The list which follows includes the most important species arranged according to their relative abundance.

Scaevola sericea
Guettarda speciosa
Pandanus tectorius
Messerschmidia argentea
Barringtonia asiatica
Hibiscus tiliaceus
Morinda citrifolia
Calophyllum inophyllum
Premna obtusifolia
Hernandia sonora

The first six species occurred on over two-thirds of the islets studied. Although saplings of Barringtonia asiatica were present on all islets analyzed only one mature tree was found. Apparently the severe insect and crab damage prevents more trees from attaining maturity. On the beach four new species of drift origin, not presently represented in the flora as mature specimens, were found. These included Mucuna gigantea, Intsia bijuga, Barringtonia racemosa and Kleinhovia hospita.

In addition to the numerous tree seedlings, herbaceous cover is also abundant in some areas along the beach. On several islets Vigna is the dominant pioneer and commonly forms dense tangles over the adjacent marginal species. This species often attains such denseness that trees such as Pandanus must be periodically cleared of it. Other herbs frequently found include Ipomoea pes caprae and Triumfetta procumbens.

On Pumatahati, in contrast to the typical sandy beaches, the lagoon beach is formed of coral rubble. Here Cordia 35 feet high forms a border 50 feet in width. The trees exhibit a poor growth form as a result of cutting and possible disturbance by storms in the past. Herbaceous cover is wanting.

V Inhabited areas

The majority of the 426 natives live on Touhou and Werua. On the former the entire area is inhabited while on the latter only the lagoon and inter-islet shore areas are populated. A few families live on the outlying islets. Throughout the villages coconut or an admixture of breadfruit and coconut predominate. In addition to the regular coconut two recently introduced varieties are represented: the so-called "red coconut" with a distinctive reddish fruit, and a dwarfed type which is productive when 10-12 feet in height. As previously mentioned, the breadfruit canopy on Touhou extends closer to the beach than on any other islet. It occurs on an average of 30-50 feet from the high tide mark but at one point comes to within 12 feet of the water. The occurrence of breadfruit so close to the margins may be correlated with the considerable elevation of the islet above sea level - maximum 12 feet - in contrast to the others. According to the natives this topography has resulted from the accumulation of rubble and sand from former cooking sites. As on other islets, occasional branches of the breadfruit are killed back, especially those facing the prevailing easterlies. One of the largest breadfruit on the atoll is found along the village street on Werua. It is 77 inches in diameter and 115 feet in height.

The undergrowth is characterized by an abundance of Pandanus and recently introduced species. Even on Touhou where the native houses are closely spaced, each family owns sufficient land to support several Pandanus which supply a readily available source of food. Other understory species include Morinda, Pisonia, Premna, and Guettarda. The leaves of Pisonia were formerly mixed with taro in cooking. However, the sparsity of this species (taro) no longer necessitates planting Pisonia and it is therefore not as common in the village areas as previously. Banana and papaya are scattered throughout the villages although productive specimens are rare. Recently introduced ornamentals include Codiaeum variegatum, Plumeria rubra, Zephyranthes rosea, Polyscias scutellaria, Polyscias fruticosa, Crinum sp. and Hibiscus sp. (hybrids). Plumeria is highly valued for its flower which is used in making leis. These ornamentals are especially conspicuous around the cemeteries. The shrub Polyscias scutellaria is commonly used as a border along the streets and to demarcate property lines.

Although the natives weed and clean up fallen leaf debris a few scattered introduced weeds persist among the gray coral rubble. These include Adenostemma lavenia, Eclipta alba, Phyllanthus niruri, Portulaca oleracea and Hemigraphis reptans as well as scattered patches of grasses and sedges. On the bare rubble Premna and Morinda seedlings are especially abundant under Pandanus and other trees which are visited by starlings. However, there is little evidence that these seedlings survive. Around a few of the houses small nurseries of breadfruit, Calophyllum, and recently introduced species are encountered. Seedlings of drift origin such as Calophyllum are protected in these nurseries until moved to the plantations.

VI Associated fauna and related influences

Since the determination of certain groups is incomplete at this writing general common names are used in certain sections. The ecological role contributed by the more important group follows.

A. Annelids (Earthworms)

Earthworms (Pheretima upoluensis, P. bicincta, Dichogaster sp.) though not common, 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 under piles of decaying coconut husks. In one such area 101 specimens were collected in a sample plot $\frac{1}{2}$ by $\frac{1}{2}$ meter and 15 cm. in depth which had been treated with mercuric chloride. They were also found under old logs, fern clumps, and piles of plant debris. Their influence is apparently localized in areas of high organic content.

Dr. G. E. Gates who determined the annelids reports one new species. Its origin is puzzling but "...it must be somewhere in Southeast Asia or the Malaysian islands including New Guinea."

B. Crustaceans (Land, Hermit and Coconut Crabs)

In the plantations, the most abundant forms of animal life are the land crabs (Cardisoma rotundum, Gecarcoidea lalandei) and hermit crabs (Coenobita brevimanus, C. perlatus). Other land crabs of lesser importance include: Metasesarma aubryi, Sesarma rotundatum, Geograpsus crinipes and G. grayi. These crabs play a major role in the incorporation of organic matter into the soil and their numerous burrows aid in soil aeration as well as in increased porosity. They are found on all islets but are most abundant on the larger ones. The land crabs occur either above or below the ground. Above ground they are characteristically found in association with hermit crabs under old piles of coconut husks scattered throughout the plantations. The pandanus prop roots, as well as the buttressing breadfruit bases, also afford excellent cover. In the scattered bedrock areas innumerable holes, resulting from the weathering of the porous limestone, offer a natural habitat. Here coconut crabs (Birgus latro) are also found. In the sandy or loosely consolidated rubble soils, land crabs dig burrows at least 18 inches in depth. Areas were observed in the loose rubble where up to fifteen holes occurred within a 10 by 10 foot area. The banks surrounding the puraka pits are undermined with holes which occur in a layer-like fashion among the breadfruit roots. The amount of constant sloughing of the banks indicates considerable activity. The crabs, except for the smaller hermits, are usually not readily observed during the day save in the more moist and shaded situations.

In a strip transect on Torongahai involving fifteen 52 by 52 foot quadrats the crab population was studied by actual count of those found under coconut husks, old logs and other debris as well as the number of holes (Fig. 30). A total of 316 hermit, 205 land and 5 coconut crabs was found in the 40,560 square foot area. The maximum number recorded for a single quadrat was 72 hermit and 38 land crabs. This quadrat occurred under the largest and oldest coconut where the rubble was extremely compact. In contrast, the largest number of holes occurred in the sandy or loose rubble areas. Although the number of piles of coconut husks per quadrat varied, thus modifying the data, certain trends are evident when the number of burrows and number of crabs are plotted. The maximum number of crabs was observed in the compact rubble where they were utilizing the piles of coconut husks for cover. In contrast, on the adjacent loose rubble banks and in the sandy areas lagoonward burrows were very numerous but actual numbers of crabs observed were generally low. One exception occurs 200 feet in from the lagoon, but here the high population apparently correlates with a greater number of piles of coconut husks. The absence of crabs in certain areas appears to be compensated by an increase in burrows which suggests that the population may be comparable in the different sites but not evident because of the different habitats they utilize in the different areas.

Smaller hermit crabs were numerous, especially near the beach. Recently fallen or discarded Pandanus keys and exposed coconut meat were rapidly covered with hordes of these small crabs. Few coconuts were available for them but occasional opened ones were observed. The larger hermits probably open the nut after which both large and small forms eat the meat. In order to have coconuts for planting the natives either tie mature nuts on branches above the ground or lay them on their roof tops until good sized sprouts are formed. They are apparently unharmed by the crabs after they have germinated to this point. These small crabs were also observed chewing the tips of the twigs of Barringtonia asiatica and petioles of Guettarda were also damaged. Terminal portions of seedlings of breadfruit, Calophyllum and Hibiscus tiliaceus were nipped off, probably by crabs. Although not observed feeding they were found on low Premna sprouts.

Land crab and larger hermit crab activity began at twilight and continued into the night. Nocturnal observations revealed numerous crabs either pulling breadfruit leaves into their burrows or actually feeding on them. Although breadfruit leaves appeared to be the preferred food other materials found in their burrows included coconut husks, twigs, and Pandanus leaves. One whitish intermediate sized species was observed with a dead gecko.

The coconut crab, found either in the cavernous bedrock areas, puraka banks, or large hollow breadfruit trees, is the only land crustacean utilized by the natives for food. Because they are primarily nocturnal, they are hunted at night with lights. The pressure on this delicacy keeps the population at a minimum.

C. Insects and arachnids

Although insects are common there are no major pests. In the plantations orthopterans (primarily grasshoppers), lepidopterans and hemipterans (leafhoppers) are abundant in the Stenotaphrum and Thuarea grass cover. In the more open areas a larger lepidopteran (butterfly) is relatively common. Over the puraka pits dragon flies are characteristically found apparently feeding on smaller insects. Under piles of coconut husks and other debris ants, earwigs, cockroaches, scorpions, spiders, and sowbugs (Crustacea) are numerous. Two species of the Phasmidae, seldom seen by the natives, were collected from the understory vegetation. In the bombed areas, craters and old cisterns accumulate stagnant water which provides excellent breeding sites for the mosquito. These areas could be readily controlled by an application of oil.

Certain trees and shrubs show considerable insect damage. The leaves of Scaevola are frequently attacked by a leaf miner. New shoots and buds of Calophyllum and Barringtonia asiatica are often infested to the point of disrupting the normal growth pattern, especially in the latter. The scalloped foliage of Premna and other species is indicative of leaf feeding or cutting forms. The smaller Pandanus trees are sometimes parasitized by mealy bugs to the point that they are cut and burned.

The flying insects are probably of primary importance in the pollination of most species. However, on Guettarda ants apparently play a similar role in the process of feeding on the sweet nectar.

In the inhabited areas insects were uncommon during the day except where marine specimens were drying or fish were being handled. Around such material dipterans (common flies) were abundant. In the plantations they are sometimes a troublesome pest, especially on the lee sides of the islets. In the evening lepidopterans (small moths) and coleopterans were relatively common around the lights. Ectoparasites were found on birds and rats as well as on the natives.

D. Reptiles (Skinks and Geckos)

Skinks and geckos are the only reptilian forms on the atoll. Of these the skinks are more abundant and occur on all islets. They are seen almost everywhere rapidly scampering over the fallen leaf debris in the plantations. Their abundance is probably correlated with the lack of predators. Although they are primarily insectivorous in habit, earthworms and smaller geckos occasionally become their prey. Geckos, although found on the smaller islets, are most numerous on the larger ones. The larger species is usually found on the coconut trunks or in the axils of the fronds. The small form, although found in the plantations, is most commonly seen in the native houses.

E. Birds

The avifauna comprises permanent residents, migrants, and occasional visitors. Of the former, the Micronesian starling (Aplonis apacus), reef heron (Demigretta sacra sacra), noddy tern (Anous stolidus pileatus), white tern (Gygis alba candida), and white-capped tern (Anous minutus marcusi) nest in the plantations. According to the natives the frigate bird (Fregata sp.) does not nest but merely roosts on Tirakaume islet. A domestic variety of the introduced fowl (Gallus gallus) occasionally escapes from captivity and also seeks refuge in the surrounding plantations. The New Zealand cuckoo (Urodynamis taitensis), a migrant, was observed several times gliding secretively through the breadfruit-coconut canopy. Along the shore, migrants such as the whimbrel (Numenius phaeopus), plover (Pluvialis dominica fulva), and turnstone (Arenaria interpres interpres) are common feeding on the marine life. The black-naped tern (Sterna sumatrana sumatrana) is relatively common and, according to the natives, nests on the elevated reef rock. Two visitors, the brown booby (Sula leucogaster plotus) and crested tern (Thalasseus bergii pelecanoides) were seen only once during the two months.

Those birds found nesting in coconut or Pandanus include starlings, reef herons, noddy and white terns. In contrast, the white-capped terns nest exclusively in the large breadfruit trees. Of these birds only the starlings feed on land. Their main sources of food comprise the fruit of Premna, Morinda, and breadfruit. A preference for the latter has made it necessary to pick the fruit while still immature. In contrast, the main diet of the noddy, white-capped, and white terns is fish. Large flocks are often seen feeding in the lagoon, especially around the coral mesas. The solitary reef heron wades the outer and inter-islet reef areas at low tide feeding on the various marine forms.

The gregarious nesting habit of the white-capped tern may have considerable influence on the breadfruit. The natives report that these birds have actually killed their trees in the past. In one 90 feet in height and 2 feet in diameter eighty nests were estimated, all of which were concentrated in the upper 30 feet of the crown. On one branch 6 inches in diameter and 15 feet in length, twelve nests 1-2 feet apart were recorded. Where the nests are this abundant at least 75% of the branches are white with fecal matter. Below these nests no branches occur. Previously existing branches were probably severely injured or killed as a result of the birds, thus necessitating removal.

The role played by these birds presents a real dilemma. Do they prefer those branches partially defoliated, possibly by salt spray or ground water salinity, or has this condition resulted solely from the activities of the birds? Although these terns are occasionally found nesting in the outer branches of denser more vigorous breadfruit, the concentrated populations are most conspicuous on partly defoliated limbs. Since the branches where the nests are most numerous are similar in appearance to those resulting from saline effects this may be the initial factor, followed by the avian influence. If the birds prefer this type of nesting site their continuous fecal accumulations on the branches may further accentuate the effect. On the ground under the trees a rank odor prevails. Here the fecal whitened leaves of Asplenium, Nephrolepis and Guettarda are turning brown and dying. The high concentrations of fecal matter which accumulate in the soil may also have a detrimental effect upon the breadfruit.

Although the natives report that these birds have killed their trees in the past they were unable to indicate any trees recently killed in this manner. Today they constantly destroy the nests. Possibly this judicious care of their trees accounts for the lack of any recently killed.

On Tirakaume huge flocks of frigate birds roost in the coconut palms. From the fecal deposits there results an extremely unpleasant odor. At present no adverse effects are evident on the vegetation. However, the small size of the islet, the sparse flora and recent clearing make interpretation difficult.

The highly phosphatic soils in the interior of Pumatahati are of especial interest. This area was formerly covered with large Pisonia trees where large flocks of boobies and frigate birds nested. Around 1920 the Pisonia was cut and the area planted to coconut. Today, under the coconut, the soil is quite different from that on the other islets. An acidic dark brown humus layer pH 4.5 gives way to a brownish cemented layer containing 100% apatite. At 18 inches in depth this layer is less consolidated and crumbles easily. The formation of this distinctive soil type is presumably correlated with fecal deposits resulting from birds nesting in Pisonia trees (Fosberg 1954). The theory of origin of this soil profile is that the humus from Pisonia leaf litter is normally acid and the calcium phosphate deposited on this 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. When the solution reaches calcium carbonate beneath the humus, it becomes alkaline and phosphate precipitates out cementing the sands and gravel particles together into hardpan. With further bathing by this solution the calcium carbonate may become partially or wholly replaced by calcium phosphate.

With the exception of the lighter brown consolidated layer, the upper horizons are similar to those described by Fosberg (1954) as the Jemo soil series. Since the cementation and replacement processes probably ceased following the cutting of Pisonia, this lighter color is probably due to weathering. Although the cemented layer was not excavated to a sufficient depth to determine whether unconsolidated material was present, at 18" in depth pockets of very crumbly material were encountered. It would appear that the process described was at least operative in part in the formation of this phosphatic complex. The coconut trees within this area exhibit extremely weird growth forms.

The presence of a larger bird population in the past has already been indicated in the case of Pumatahati islet. Prior to habitation birds were probably much more abundant. The presence of high concentrations of phosphorite in the interior of some islets and on the reef rock remnants is highly suggestive. Its presence in the reef rock suggests that these deposits probably occurred when these areas were vegetated. Since that time erosion has removed the vegetation and left only the projecting phosphatic remnants.

F. Mammals

The mammals represented include the Polynesian rat (Rattus exulans), cats and pigs. As reported by Miller (1953) rats are uncommon on the densely populated islets of Touhou and Werua where the cats are supposedly keeping them under control. In contrast, they are locally abundant in the living areas on some of the outlying islets. On Hare islet several were trapped during the day in a boat house. However, none was seen in the plantations and no damaged coconuts were observed. The pigs are small and inbred but are regarded as a luxury because coconut is their chief food. Since they are not permitted to roam in the plantations they are either tied to a tree or kept in pens made of coconut logs. Where they are tied in the plantations the area is completely uprooted and whenever they escape from captivity young breadfruit or other plantings may be destroyed.

VII Human influences

In interpreting the land ecology human influences are by far the most important. Man's influence is most evident in the origin of the present flora as well as in his manipulation and utilization of the vegetation (Table I).

Of the total flora over one-half of the species have been introduced by man. Several of the earlier introductions such as coconut, breadfruit, Pandanus and puraka now comprise the dominant vegetational aspect. Of lesser abundance, but more importance in numbers of species, are the more recent introductions. These consist primarily of ornamentals which are constantly being brought in from surrounding islands such as Ponape and Nukuoro. On Kapingamarangi, as well as other islands in the Pacific, man has played a very important role in the dispersion of plants as has been recently emphasized by Merrill (1954).

In contrast to the dominants, most of the species which comprise the understory are rarely propagated by man. Though unimportant in furnishing food, they provide a valuable source of wood for construction and other purposes. Therefore, throughout the plantations continuous clearing by cutting is quite selective; the larger better trees being spared. Another clearing technique involves burning the bases of large trees. Gnarled

Guettarda of little value are sometimes removed in this manner, as well as larger Premna, when competing with plantation species. In contrast, the dense herbaceous cover, primarily Wedelia and ferns, is entirely cleared by cutting or actual removal by pulling. However, roots and rhizomes, which again produce a lush growth, frequently remain. This general clearing of the undergrowth may be annual or more often, depending upon islet size and seasonal conditions. As previously mentioned, the sharp lines of demarcation which are evident throughout the understory are a result of differential clearing by the various land owners.

In addition to obtaining food and shelter from the land the natives also export some copra. This business reached its peak during the Japanese period when exports reached 300 tons per year. At that time Pandanus were frequently cut in order to allow more space for coconut. With American occupation exports have decreased considerably, now ranging from only three to thirty tons every two months. During July and August 1954 fifteen tons were exported. This decrease in copra production may be correlated with several factors. First, the population has been constantly increasing and second, there is an abundance of older less productive trees. In addition, the recent demand for their superb handicrafts now affords a new and equally good source of income. For example, the current demand for Pandanus mats has initiated extensive planting of Pandanus in lieu of coconut in certain instances. The most recent demand has been a contract for 100,000 square feet of mats. Therefore, the young Pandanus are being stripped of their leaves as rapidly as they mature. This emphasis on handicrafts is also reflected in the demand for Calophyllum whose wood is highly prized for coconut graters, some of which are sold. These trees are disappearing from the lagoon shore faster than they are being replaced. In general, however, the natives are extremely cognizant of their dependence upon their environment as is evidenced by the excellent care given their plantations. Further evidence is seen in their reluctance to sell a canoe, which means the loss of another large productive breadfruit, which must be used to build a new hull.

On an atoll comprising 0.42 square mile of land there is a very definite limit to the number of people such a microcosm can adequately support. Any crisis can precipitate a catastrophe. For example, the prolonged drought of 1916-18 brought death to ninety Kapingans. Of course, it was accentuated by the restriction placed upon the taking of coconuts and fish. Following this incident a Kapinga village was established on Ponape to relieve the situation. However, since 1920 the population of 300 on Kapingamarangi has been steadily increasing and reached a peak of 527 in 1947 at which time more people moved to Ponape. It is estimated that 450 is the limit which Kapingamarangi can support. With the present demands of the 426 natives now living on the atoll this figure approximates the limit: 0.64 acre per person.

VIII Climatic influences

Although numerous climatic factors modify the biota, several are of especial importance. Probably the most continuously operative is that of prevailing winds laden with salt spray. Throughout the summer when the

Species	Wood	Leaves	Fruit	Root	Flowers
**Cocos nucifera	*construction	mats, baskets *roofing, brooms, food wrapping, torches, "fishing rope"	1.green:*water, baby food 2.mature:*food, copra, oil 3,sprouted:food, husk: *rope, fuel, "toilet tissue"		sweet drink
**Artocarpus altilis	*canoe construction, canoe bailer, Kamit boxes, crafts: model canoes, bowls	food wrapping, ground oven	*food		
**Pandanus tectorius		*mats, baskets, *roofing	*food	string from prop roots	
**Cyrtosperma chamissonis				*food	
Guettarda speciosa	*construction, implements			shark hook	lei
Morinda citrifolia	*construction				
Premna obtusifolia	*construction, *canoe paddle				
**Calophyllum inophyllum	construction, implements, *crafts				lei
Messerschmidia argentea	implements, crafts				
Cordia subcordata	construction, implements				
**Hibiscus tiliaceus	implements, *canoe pole, bark: lava-lava				
Clerodendrum inerme	fish trap				
Tacca leontopetaloides				food-source of starch	
**Musa spp.		ground oven	food		

TABLE I - Utilization of species.

* major uses.
** species present primarily as a result of planting.

rainfall is frequently at a minimum this salt spray, combined with the drying effect of the wind, has pronounced effects upon the vegetation. Although the atoll is outside the typhoon belt, another but more erratic influence is that of the severe storms which can modify the vegetational pattern for many years thereafter.

While the dominant vegetation is tolerant of saline influences, its degree of tolerance varies. For example, among the marginal species the foliage of Guettarda is more easily damaged than that of Scaevola. Oceanward the leaves of the former show a general browning of the margins while lagoonward this is not at all evident. In contrast, Scaevola is unaffected except for occasional shrubs with dwarfed rosettes of leaves. Along the marginal areas as well as in the interior of some of the smaller islets the lower coconut fronds are often brownish and dying. However, the success of these three species along the marginal areas would suggest that these effects are relatively superficial. In contrast, other marginal species of lesser importance such as Cordia and Terminalia samoensis are more adversely affected, which may account for their minor role. All Terminalia observed were extremely depauperate with only a few leaves at the ends of the branches which exhibited very slow growth. Another species, Cordia, shows considerable wind sheared, or as is probably more correct, spray sheared effects (Fosberg 1953). Here many of the stems were killed back 6-12 inches or more by the end of the survey. This condition may be the result of a combination of salt spray and drought since the rainfall during the survey was extremely low.

Whenever typical interior species such as Premna and Morinda occur in the marginal zone, probably as a result of erosion inland, dead or dying branches are evident and leaves show marked salt spray damage. A similar condition is present where the marginal vegetation is absent and the full force of the salt laden winds directly strikes the unprotected undergrowth in the interior. Where the breadfruit canopy projects above the surrounding coconut, dead or defoliated branches are evident. According to the natives the upper branches frequently lose their leaves following a severe storm. However, new ones usually appear later. Ground water salinity (see section on Ground Water Influences) is apparently another interacting factor which is fundamental in delimiting the breadfruit distribution (Fosberg 1949). Another species very sensitive to salt spray is Calophyllum which is planted exclusively along the lagoon shore. The lone specimen observed oceanward showed both salt spray damage and serious insect infestation.

In order to give some idea of the relative tolerance of the more common species a list follows beginning with the most salt tolerant group.

Cocos nucifera
Pandanus tectorius
Messerschmidia argentea
Saaevola sericea
Guettarda speciosa
        Cordia subcordata
        Clerodendrum inerme
                Terminalia samoensis
                        Premna obtusifolia
                        Morinda citrifolia
                                Calophyllum inophyllum
                                        Artocarpus altilis

As previously mentioned, periodic droughts occur. Although the effects of the 1916-18 drought are not completely known, at least coconut and breadfruit production was greatly reduced at that time. Shorter periods, such as a summer of low precipitation, can also result in decreased production. Even in the puraka pits where the ground water lens is usually at the surface the replacement of taro by puraka is attributed to the greater drought resistance of the latter. These dynamics may also be operative in other areas.

Although the lack of typhoons lends a remarkable stability and uniformity to the plantations compared to that of other atolls, periodic storms or tidal waves result in sporadic damage as revealed by the data available back to 1858. These earlier storms (1858, 1886, 1896) all resulted in numerous windthrows and damaged or dead trees. Around 1920 a thunderstorm resulted in the loss of considerable coconut. A 1937 storm was followed by one in 1947 which was probably the most severe during this generation. At that time salt water inundated the interior on the lagoon sides of Touhou, Werua, Ringutoru and possibly others. On Ringutoru six puraka pits were destroyed by the salt water. An estimated sixty-seven breadfruit and ten coconut were killed or windthrown and many others suffered damage but remained alive. Today some of these large breadfruit, probably killed or weakened by this storm, still stand within the breadfruit-coconut zone. Many of the breadfruit killed were removed and utilized for canoes or general construction following the storm.

IX Physiographic influences

Erosion and deposition are constantly modifying the islets and subsequently the vegetation. Erosion on the oceanside is undermining and removing marginal species such as coconut, Guettarda, and Scaevola. During bad storms the smaller islets are severely eroded. For example, during the storm of 1858 Matukerekere, then about 0.7 acre in size, was completely destroyed. However, rebuilding occurred until by 1947 it supported ten coconut, when another storm destroyed nine of them as well as most of the islet. Immediately upon our arrival the meager vegetation of this 25 by 100 foot islet, comprising one mature coconut and five immature chlorotic palms and numerous drift seedlings, was accurately mapped. A remapping after seven weeks indicated that 25% of the land surface had been washed away including one of the smaller coconuts and numerous drift seedlings. No storms of any consequence occurred during this period indicating the ease with which these smaller islets undergo retrogression. On the sand bars continuously forming lagoonward, new areas are constantly being exposed for the invasion of pioneers such as Scaevola and associated species (see section Marginal Vegetation). Recently this process has been accelerated on some islets by the construction of coral boulder causeways across the channels.

Although no one species appears to be restricted to a particular site, certain species are more abundant and characteristically found in certain areas. For example, on the boulder beach ridge Guettarda is most typical. Since seedlings frequently occur its success here is apparently correlated with its ability to get established in this boulder complex. Although herbaceous cover is usually sparse or absent, Asplenium readily becomes established wherever coconut husks occur on the large boulders. In the interior its restricted occurrence on old coconut stumps, bases of trees and other organic matter would indicate the importance of an organic substrate for its establishment. On the unaltered sandy soils, such as the recently formed sand bars, Scaevola and Messerschmidia are typical pioneers. Herbaceous species commonly found in sandy areas include Lepturus repens, Fimbristylis spathacea, Ipomoea pes caprae and Triumfetta procumbens.

Although mineral analyses of the soils are not yet available, no striking deficiencies were evident such as those reported from Arno Atoll in the Marshall Islands (Hatheway 1953). However, on the recently deposited sands, with little or no organic matter, the smaller coconut are very chlorotic. Along the marginal areas Scaevola leaves are often yellowish-green or covered with yellow spots. In the living areas the leaves of banana are also chlorotic. In these instances the casual factor is probably a nitrogen deficiency. The lack of organic matter also retards the growth of coconut. This is especially evident on the recently filled Herengaua causeway on Hare islet. Here coconut planted circa 1943, prior to the ones in the adjacent bombed areas, are smaller and merely attaining the productive stage. In contrast, those planted since the war on Hare, circa 1946, are taller and producing fruit. A similar situation is evident on the recently deposited sands forming Pepeio.

Mature chlorotic coconut trees of low productivity are rare. On Torongahai these occur on a narrow elevated bank dividing two puraka pits. Here restriction of root development, rather than a mineral deficiency, may be the causal factor.

X Ground water influences

The role of ground water salinity in the restriction of breadfruit to the interior regions has been suggested by several investigators (Fosberg 1949; Cox 1951). From present studies it is apparently controlled by a complex of factors; namely, previously mentioned storms, salt spray, ground water salinity as related to soil permeability, and minor topographic differences in elevation.

During storms, salt water frequently inundates the islets resulting in breadfruit damage. Many trees which were killed as a result of the 1947 storm are still standing.

As previously mentioned, the upper exposed branches of many trees are killed back or defoliated by salt spray. However, the effects of ground water salinity appear quite similar. An incident which occurred during the summer is indicative of this. During a high tide accompanied by strong winds and accentuated by a causeway obstructing the natural flow of water between islets, salt water rose to within 50 feet of a small breadfruit 5 inches in diameter. The leaves turned brown and a month later four branches were dead and some brown leaves still persisted.

Ground water samples were analyzed from dug wells and puraka pits where breadfruit occurred in order to determine, if possible, its distributional pattern in relation to salinity (Table II). Within the breadfruit-coconut plantations, the extremes ranged from 18 ppm. on the lagoonward side of Torongahai to 3,840 ppm. near the ocean on Nunakita. Although the trees are in good condition on both islets, their relative size and abundance differ considerably. On Torongahai they are larger, 3-4 feet in diameter, and more continuous in contrast to Nunakita where they are only 1-1½ feet in diameter and very localized. The latter, near a bomb crater, are apparently post-war plantings. In the pure breadfruit grove on Werua, where some of the largest trees occur, the salinity ranged from 28-46 ppm. In general, the larger and more productive trees are found from the center of larger islets lagoonward where the salinity is less than 350 ppm. This compares favorably with the 300-400 ppm. mentioned by Cox (1951).

The interrelationship of the soils, bedrock, and salinity, as affecting breadfruit distribution, is also of interest. Oceanward, the bedrock and coarse overlying materials more readily permit the movement of salt water in contrast to the fine sandy sediments lagoonward. Therefore, the breadfruit extend closer to the lagoon shore where the water is less saline than oceanward where salinities rise rapidly as one approaches the beach ridge. On Torongahai, where the lowest salinity was recorded, the parent material is dominantly sand and scattered rubble, and bedrock outcrops are absent compared to the other larger islets. The influence of this sandy substrate is also evident on one of the smaller islets, Parakahi (3 acres) where, although no breadfruit are found, the salinity is lower compared to other larger islets with breadfruit which are covered by rubble and underlain in part by bedrock.

On several islets marked fluctuations in the salinity occurred between the two sampling periods. The salinity increased in all six wells on Taringa and Werua as well as the community well on Touhou (Table II). These increases might well be correlated with the low precipitation (4 inches) during seven weeks of the survey. Although breadfruit is not usually considered a phreatophyte (a plant which utilizes water from below the water table) during such dry periods the vadose water (that water held in the soil above the water table) may be inadequate and through capillary rise the underlying salt water may exercise adverse effects (Cox 1951). If this was the case, it was not yet evident at the end of the survey. However, some wilting of the other vegetation occurred, especially in the exposed sites.

On one of the smaller islets, Hukuhenua, 5 acres in size, the salinity fluctuation was very erratic. Here, in contrast to the increases previously recorded, a marked decrease occurred between the sampling periods. The first sample was quite salty (1,740 ppm.) while the second was relatively fresh (480 ppm.). The few breadfruit were in poor condition and one dead tree was evident. In this case the small size of the islet, the erratic salinity fluctuation, and the condition of the breadfruit suggest a relatively shallow fresh water lens. Therefore, changes in the salinity would be easily affected. For example, light rains, or even very high tides could cause considerable fluctuations and storms would result in even greater changes.

ISLET	OCEANWARD high (tide)	low	MIDDLE OF ISLET high (tide)	low	LAGOONWARD high (tide)	low	REMARKS
Taringa							
7/30	2600	2600	776	900	100	106	Dug wells; breadfruit-coconut type occurs from middle of islet lagoonward; breadfruit large and productive.
8/20		3800		1100		340	
Werua							
7/30	2200	1000	28	28	30	28	Dug wells; one of the largest islets; breadfruit-coconut and pure breadfruit types dominate areas sampled; very productive.
8/20		2860		46		54	
Parakahi							
7/30					380	380	Dug wells; small lagoonward islet; parent material dominantly sand; coconut plantation excellent; no breadfruit.
8/20						380	
Hukuniu							
7/30	16,800	17,480					Dug well; oceanward islet; dominantly bedrock; sample taken lagoonward; no noticeable adverse effects on coconut, although extremely xeric and lacking in herbaceous cover; no breadfruit.
8/20	16,840	16,440					
Hare							
8/6			(56)				Puraka pit; breadfruit productive.
8/19			(310)				
Touhou							
6/26			(202)				Community well; upon arrival. Breadfruit very productive.
7/31			(214)				Following rain.
8/8			(284)				----------
8/27			(286)				Upon departure.
Matiro							
8/18			(50)				Puraka pit; breadfruit good condition.
Torongahai							
8/14			18				Puraki pit; breadfruit large, very productive.
Nunakita							
8/25	3,480						Bomb crater; breadfruit 10-12 in. d.b.h.; good condition; no fruit evident.
Takairongo							
8/16				140			Puraka pit; breadfruit vigorous.
Hukuhenua							
8/17				1,740			Puraka pit; breadfruit very poor condition; many dead or defoliated branches; one dead tree.
8/27			(480)				

TABLE II - Salinities (ppm.) of Ground Water Samples. Data ascertained by silver nitrate titration technique. On the wider islets oceanward samples were taken approximately 100 ft. from high tide mark; lagoonward samples 50-100 ft. Tide level data not available for those salinities in parentheses. For comparison, salinity of ocean water 17,760 ppm. near breakers; lagoon water 19,600 ppm.

Since only scattered trees are present on islets less than five acres, this apparently approaches the minimum size where breadfruit culture is feasible on this atoll. Of course, some variability occurs depending upon geological structure. On Hukuhenua the underlying materials are primarily loose rubble and boulders with slight cementation at 3-4 feet in depth. In contrast, on the even smaller sandy islet of Parakahi, less saline conditions were encountered. Therefore, breadfruit would probably grow more successfully on Parakahi than on Hukuhenua even though the islet is smaller. This emphasizes the importance of the substrate as well as islet size in regard to breadfruit distribution.

Another possible factor involved in breadfruit distribution is the minor differences in topography. The slightly higher elevations oceanward where the water table is 5-5½ feet below the surface, may account for the younger breadfruit extending as far oceanward as they do. In these areas, even during dry periods, it is doubtful whether capillary action would occur through the coarse materials to the point of reaching the roots of these smaller trees. Other elevated areas include the puraka banks. An observation made on Hare concerning the role of these banks is pertinent. Here two trees of equal size which occurred practically at equal distance from the lagoon, one on the bank and the other several feet below, were very differently affected by the 1947 storm. The tree on the bank several feet above the average level of the islet shows no adverse effects. In contrast, the adjacent tree, located off the bank at a lower level, was killed. On the somewhat raised islet of Touhou this may account for the presence of large productive breadfruit trees which extend closer to the beach there than on any of the other islets. The presence of these trees on the banks throughout the entire atoll may in part account for their survival during severe storms and other critical periods. Observations over a longer period are needed before definite conclusions can be drawn on the interaction of these various influences as related to breadfruit distribution.

In contrast to breadfruit the distribution of coconut is not noticeably influenced by salinity. Although the trees are largest and most productive on the larger islets where the salinity is low, vigorous and productive trees completely cover the smaller islets, such as Hukuniu, where the ground water salinity is comparable to that of the ocean.

XI Biotic influences

Since the faunistic aspects have been discussed under Associated Fauna this section will consider the floristic and vegetational aspects.

Only one species, the parasite Cassytha filiformis, has any direct adverse effects upon its associates. It is most commonly found on Scaevola and Guettarda. Here it forms such dense tangles around the stems and leaves that portions of the former are frequently killed.

The influence of the marginal vegetation as an interceptor of salt spray, and therefore a protector of the interior areas, has been mentioned. The more mesophytic character of the vegetation on Ringutoru and Torongahai may be correlated with the dense continuous band surrounding these islets in contrast to the other larger ones lacking a comparable border. In addition, this may have also been accentuated by less clearing of the understory which, over a long period, would add to the mesic condition. At least today the understory is extremely dense compared to that on the other islets. However, an equally important factor is their more oval shape, along with their considerable width.

Another protective aspect of the vegetation is evident in a technique occasionally employed by the natives to protect their young breadfruit. This involves leaving a small circular stand of vegetation such as Morinda around smaller trees in order to reduce the direct effects of salt spray.

In a region of extremely immature soils, possibly the most important influence of the vegetation is in soil formation as a result of organic accumulation. Although the depth of organic development averages 6-8 inches in the rubble areas, it is usually much less in the sandy soils which are of more recent origin. However, on two islets extreme organic accumulations were encountered: Tokongo, 18 inches and Rikumanu, 30 inches. If it can be assumed that the degree of accumulation is proportional to the length of time the area has been vegetated without disturbance, it would appear that these two islets have had the least disturbance in the past. When the topographic features are examined this seems likely, especially for Rikumanu. Here the islet is elevated on a bedrock pedestal several feet higher above sea level than any of the others. Therefore, it may not have been subjected to the constant erosional and depositional action operative on the other islets in the past. Although no noticeable topographic difference was evident, on Tokongo the slightly greater accumulation of organic material may merely indicate the chance of somewhat less disturbance than occurred on the surrounding islets. It is interesting to note that this islet has the largest number of species for its size and is dominated by a Premna-Morinda understory similar to that found on the larger more mesic islets. This may also reflect its longer existence.

The rate of organic accumulation was also investigated by studying the depth of the organic layer on the two Hare islet causeways. The older Rawa-Hare causeway, which filled in about 100 years ago is of especial interest. In several samples the maximum accumulation of organic material was approximately 1 inch since about 1865. This would indicate that in sandy soil under a coconut type vegetation the rate of organic accumulation is about 1 inch per century. If this figure is now applied to Rikumanu islet where 30 inches was detected the length of time involved would be about 3,000 years. This dates back to the end of the xerothermic period which occurred from 3,000-6,000 years ago (Flint & Deevey 1951). During the peak of the xerothermic it is presumed that the ocean level was several feet higher than at present. Therefore, the islets may not have been formed until the end of the xerothermic or approximately 3,000 years ago, which correlates with the organic accumulation evidence here presented. Further research is necessary before definite conclusions can be formulated since this represents one isolated example.

PAST VEGETATION AND PRESENT TRENDS

Since the entire land area is now under extensive management a reconstruction of the past vegetation, prior to the arrival of man, is extremely hypothetical. There is little evidence of a continuous aspect comparable to the present coconut and breadfruit except on Pumatahati. Here, as formerly mentioned, a large Pisonia forest dominated until around 1920 when it was cut in order to expand the coconut plantations. Today all that remains is the base of one of these large trees and the understory is dominated by their stump sprouts. The presence of a similar understory occurring locally on other islets would suggest the former importance of Pisonia. From their present role Guettarda and Premna probably comprised the dominant aspect. Even in the recent past these species were more important and occurred as larger trees. Other species such as Hernandia sonora, Ochrosia oppositifolia, Cerbera manghas, Thespesia populnea, and Soulamea amara possibly occurred either as scattered trees or locally as pure stands. The herbaceous flora was very limited. Those represented, such as ferns and grasses, formed a dense ground cover. The marginal vegetation was probably similar to that found today except for its greater density. Along the beaches a few pioneers may have been present. However, the restricted distribution of these species today suggests that they are relatively recent to Kapingamarangi.

Within the last century several changes have occurred. From the natives it was learned that breadfruit and Pandanus were more abundant in the past. Although little evidence was found for the former, the decrease in Pandanus probably resulted from cutting during the Japanese regime in order to make room for more coconut. However, with American occupation Pandanus is again on the increase because of the current demand for mats and other handicrafts. Although man plays the dominant role in regulating the abundance of coconut, breadfruit, and puraka, Pandanus reproduction in the plantations is of considerable importance. The natives claim that such trees produce only useful leaves and that the fruit is of inferior quality. With man's continual clearing there is little indication of successional change in the understory. Only on sandy lobes of the larger islets is a successional trend evident from the early pioneers - Scaevola, Messerschmidia and Guettarda - to a Premna-Morinda type. On the recently formed sand bars, Scaevola and Messerschmidia are the typical pioneers. Even in this early stage, coconut are planted and as the plantations develop Guettarda also becomes a part of the understory. However, eventually a succession similar to that described above occurs. In the over-all plantation complex, areas of breadfruit-coconut type are expanding into the pure coconut plantations while the latter is expanding onto the continuously forming sand bars. A slight increase in puraka areas is evident within the breadfruit-coconut plantations. Although introduced species are now very abundant, especially in the living areas, their role may be of even greater importance as native travel is facilitated.

SUMMARY

1. Kapingamarangi Atoll comprises thirty-three islets representing 0.42 square mile. Due to man's influence, the entire area is dominated by coconut, breadfruit, Pandanus, and puraka (Cyrtosperma chamissonis). Although coconut plantations dominate the smaller islets, on the larger ones a typical zonation is evident. Here coconut plantations form an outer band and give way in the interior to an admixture of breadfruit and coconut, or pure breadfruit, interspersed with puraka pits.

2. The strand vegetation, of dominantly indigenous species, is restricted primarily to the undergrowth and marginal areas. On the smaller islets the understory is predominantly Guettarda speciosa, while on the larger ones Morinda citrifolia and Premna obtusifolia are most conspicuous in the plantations. On all islets Pandanus is relatively common as scattered trees or as extensive plantings on the puraka banks. Herbaceous cover increases on the larger islets. Here Asplenium nidus, Nephrolepis hirsutula, and two grasses, Stenotaphrum micranthum and Thuarea involuta are most typical. This entire pattern is continuously being modified by man's clearing operations.

3. The marginal vegetation comprises a conspicuous border of Guettarda and Scaevola. Although the former is common throughout, Scaevola is most important in the less severely eroded sectors. On the recently formed sand bars, Scaevola is the characteristic pioneer.

4. The inhabited areas are also dominated by breadfruit and coconut. However, the undergrowth is predominantly Pandanus with an abundance of recent introductions.

5. Of the vascular flora, comprising ninety-eight species, thirty-eight are estimated as indigenous, fifty-eight introduced, and four as drift seedlings not yet established as mature specimens.* On the nineteen islets 3.5 acres or less in size, the number of species found is relatively uniform in contrast to the larger ones where a general increase in number of species occurs with islet size.

6. Man's influence is most evident in the origin of the present flora as well as in his manipulation and utilization of the vegetation. Some copra is exported. In addition, the native handicrafts, among the finest in the Pacific, are increasing in importance.

7. Of the associated fauna, insects, land and hermit crabs, skinks, geckos, and birds are most common. Land crabs play a vital role in the incorporation of organic matter into the soil. The more important land nesting birds include starlings, noddy and white-capped terns. Due to their gregarious nesting habit, the latter are reported to have killed breadfruit in the past. Although no such killed trees are evident today, the natives' judicious removal of the nests may account for the lack of them.

*Since two species are considered to have more than one means of entry, the various categories, when totaled, slightly exceed the actual flora.

8. Among the climatic influences, the salt laden winds, accentuated by extremely dry periods, modify the vegetation considerably. Those species most tolerant of salt spray include coconut, Scaevola, Messerschmidia, Pandanus, and Guettarda. In contrast, those most sensitive are breadfruit and Calophyllum. Although severe storms occur the lack of typhoons lends remarkable stability and uniformity to the plantations.

9. No restriction of species to a particular soil type was evident. However, Guettarda is most abundant in the bouldery areas while Scaevola, Lepturus repens, Ipomoea pes caprae, and Triumfetta procumbens are typical on the sandy soils. Although no striking mineral deficiencies are evident, chlorotic coconut and banana occur wherever the soils are lacking in organic development. Evidence of the Jemo soil series, presumably correlated with birds nesting in Pisonia trees, is found on Pumatahati.

10. The complex of factors apparently operative in breadfruit distribution includes salt spray, ground water salinity, and minor differences in topography. Breadfruit attains its maximum development lagoonward on the larger islets where the salinity is usually less than 350 ppm. Oceanward the salinity is higher in the bedrock areas overlain with coarse rubble and boulders. In contrast, it is lowest in the sandy-rubble soils lagoonward. This accounts in part for the present distributional pattern. Although variation occurs, depending upon the substrate, the minimum size islet where breadfruit culture is apparently feasible is about 5 acres.

11. Although the marginal vegetation is of considerable importance in the interception of salt spray, a more important influence of the vegetation is in soil formation. Extreme organic accumulations on several islets may indicate less disturbance in the past. When the rate of accumulation, approximately 1 inch per century, is applied to these areas the time involved would be 3,000 years. The presumed origin of the islets at this time correlates with the organic accumulation.

12. The past vegetational pattern is extremely hypothetical. Although there is little evidence of an aspect comparable to the coconut and breadfruit plantations, Guettarda, Premna and other larger indigenous trees, such as Pisonia, probably comprised the dominant vegetation. Although there were fewer herbaceous species those present possibly formed a more continuous cover. Marginal areas were probably similar except for an increase in density.

13. Today in the over-all plantation complex, areas of the breadfruit-coconut type are expanding into the pure coconut plantations while the latter is expanding onto the continuously forming sand bars. A slight increase in puraka is evident within the breadfruit-coconut type. Although recent introductions are especially common in the living areas, they will probably continue to increase as native travel is further facilitated.

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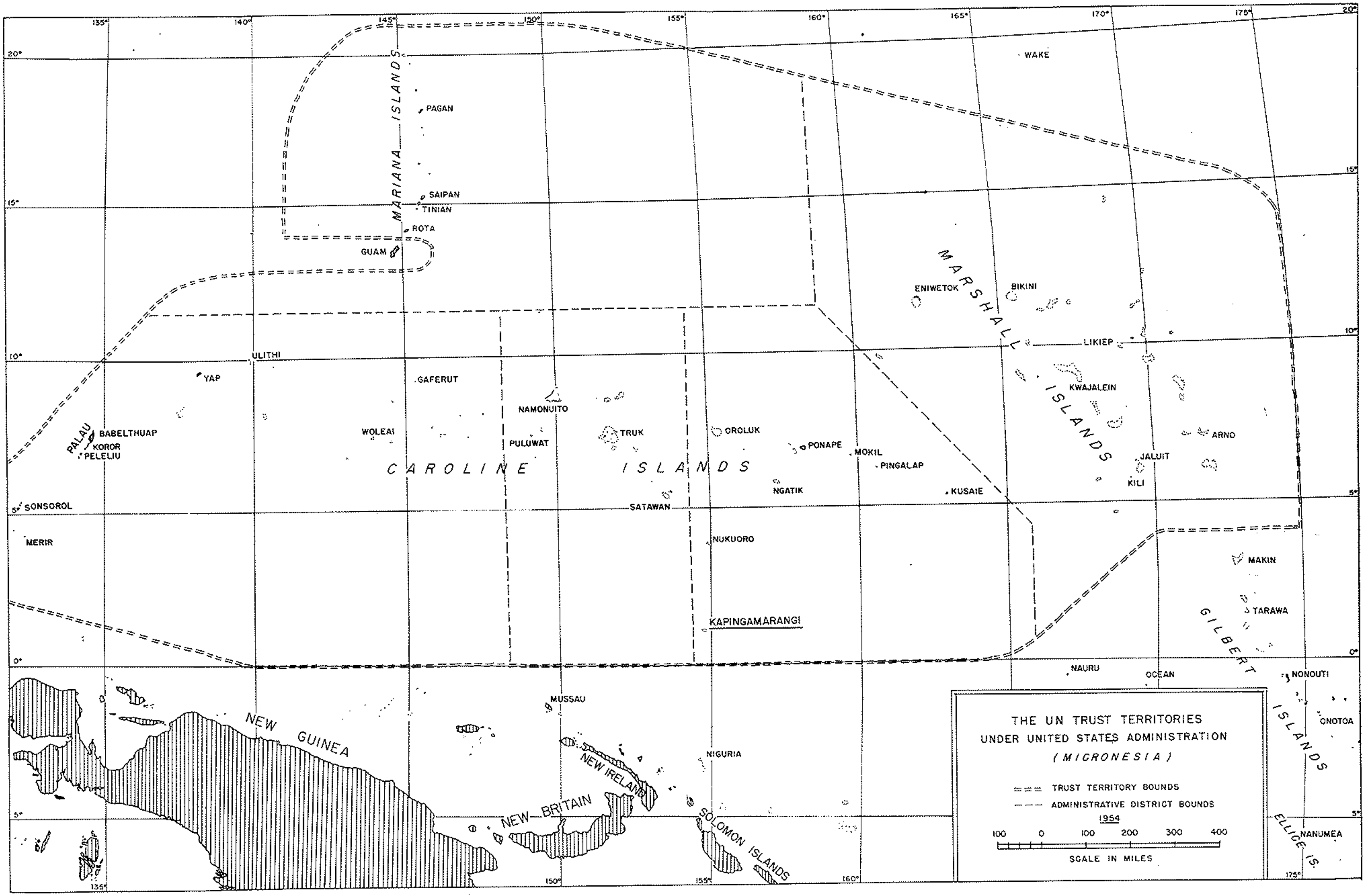

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UNDER UNITED STATES ADMINISTRATION
(MICRONESIA)
TRUST TERRITORY BOUNDS
ADMINISTRATIVE DISTRICT BOUNDS
1954
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SCALE IN MILES
MARIANA ISLANDS
PAGAN
SAIPAN
TINIAN
ROTA
GUAM
WAKE
MARSHALL ISLANDS
ENIWETOK
BIKINI
LIKIEP
KWAJALEIN
ARNO
JALUIT
KILI
ULITHI
YAP
GAFERUT
NAMONUITO
WOLEAI
PULUWAT
TRUK
OROLUK
PONAPE
MOKIL
PINGALAP
NGATIK
KUSAIE
SATAWAN
CAROLINE ISLANDS
PALAU
BABELTHUAP
KOROR
PELELIU
SONSOROL
MERIR
NUKUORO
KAPINGAMARANGI
MAKIN
TARAWA
GILBERT ISLANDS
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OCEAN
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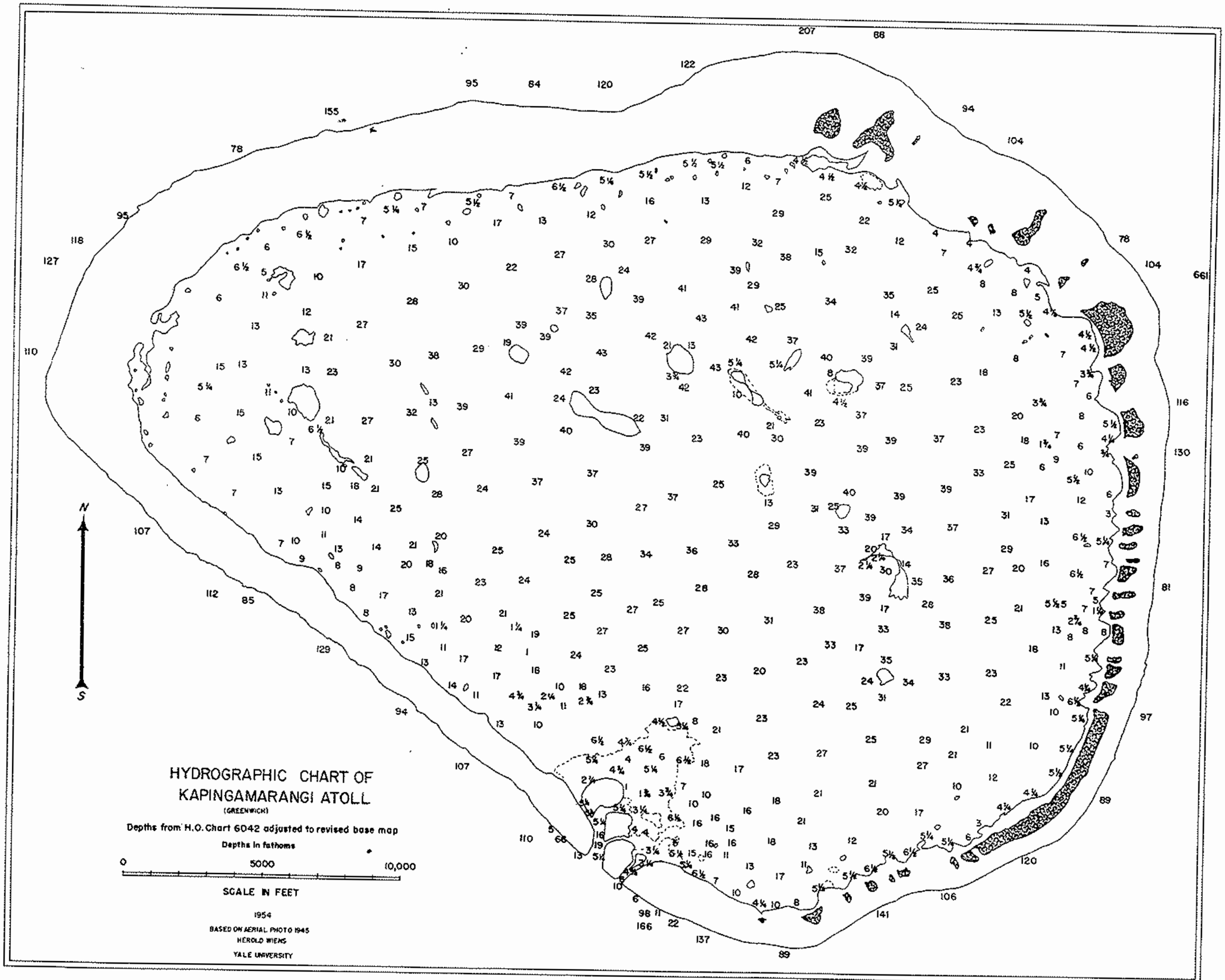
FIGURE 1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KAPINGAMARANGI ATOLL
(GREENWICH)
Depths from H.O. Chart 6042 adjusted to revised base map
Depths in fathoms
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5000
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SCALE IN FEET
1954
BASED ON AERIAL PHOTO 1945
HEROLD WIENS
YALE UNIVERSITY
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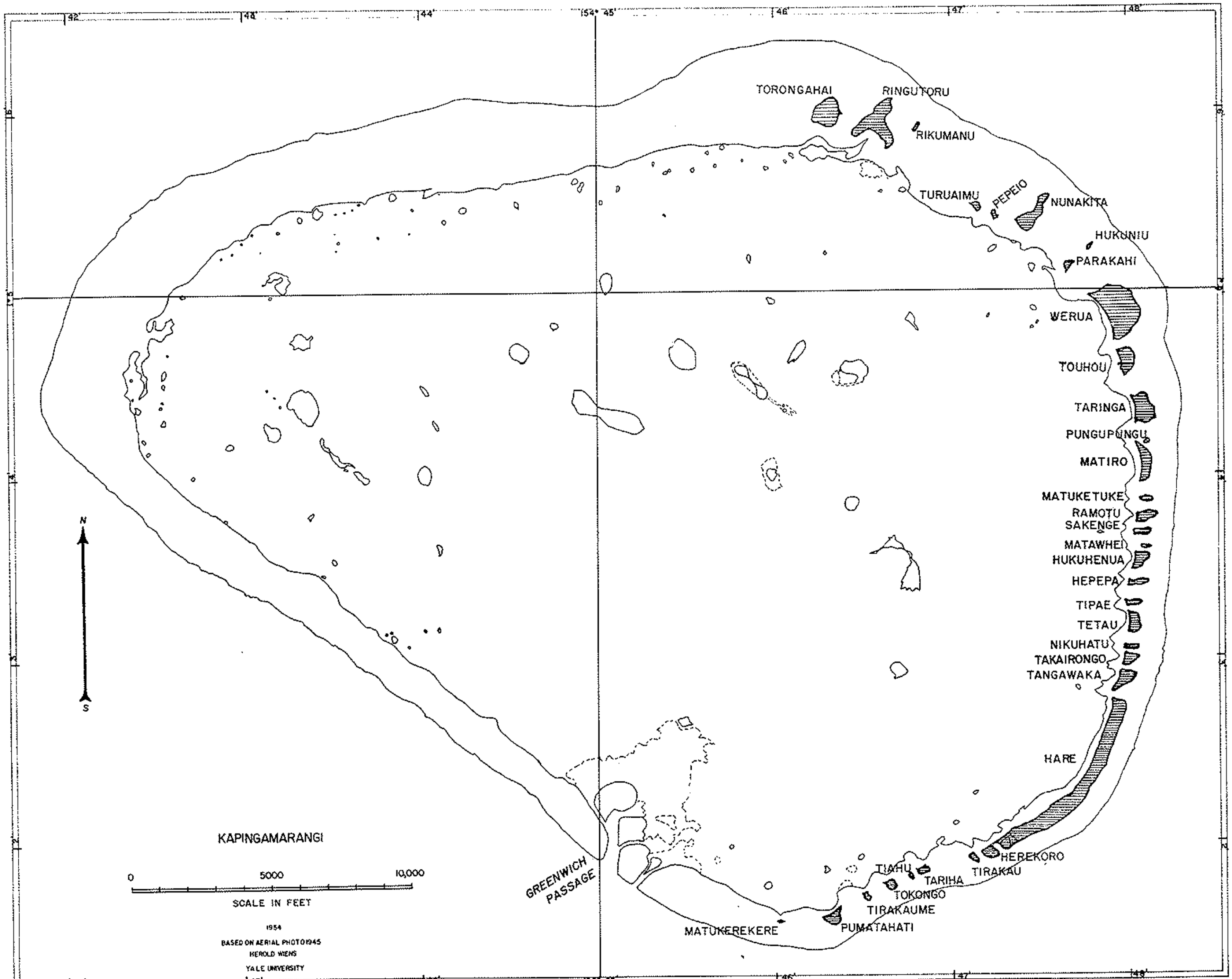
FIGURE 2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RINGUTORU
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TURUAIMU
PEPEIO
NUNAKITA
HUKUNIU
PARAKAHI
WERUA
TOUHOU
TARINGA
PUNGUPUNGU
MATIRO
MATUKETUKE
RAMOTU
SAKENGE
MATAWHEI
HUKUHENUA
HEPEPA
TIPAE
TETAU
NIKUHATU
TAKAIRONGO
TANGAWAKA
HARE
HEREKORO
TIRAKAU
TIAHU
TARIHA
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FIGURE 3

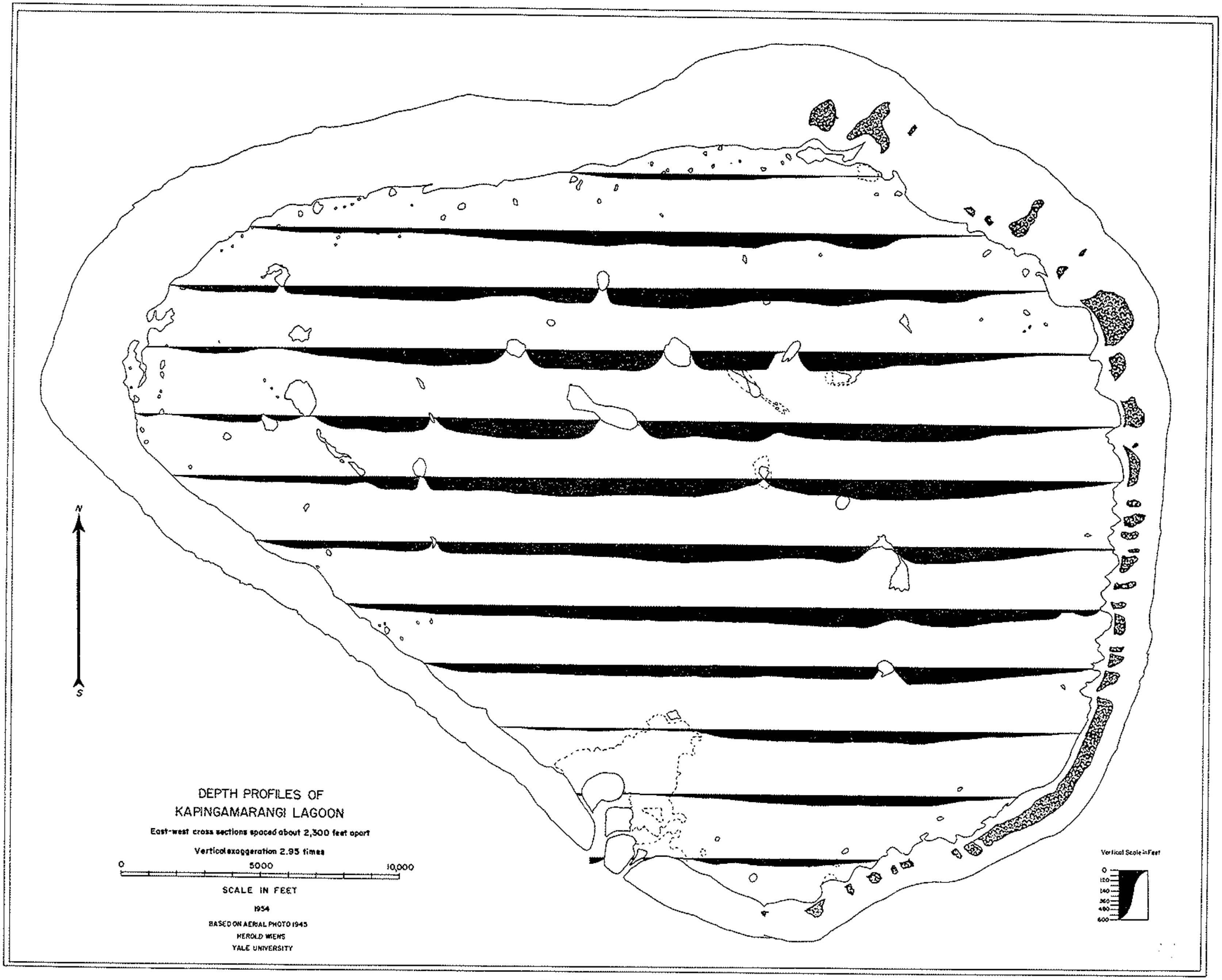

N
S
DEPTH PROFILES OF
KAPINGAMARANGI LAGOON
East-west cross sections spaced about 2,300 feet apart
Vertical exaggeration 2.95 times
0
5000
10,000
SCALE IN FEET
1954
BASED ON AERIAL PHOTO 1945
HEROLD WIENS
YALE UNIVERSITY
Vertical Scale in Feet
0
120
240
360
480
600

FIGURE 4

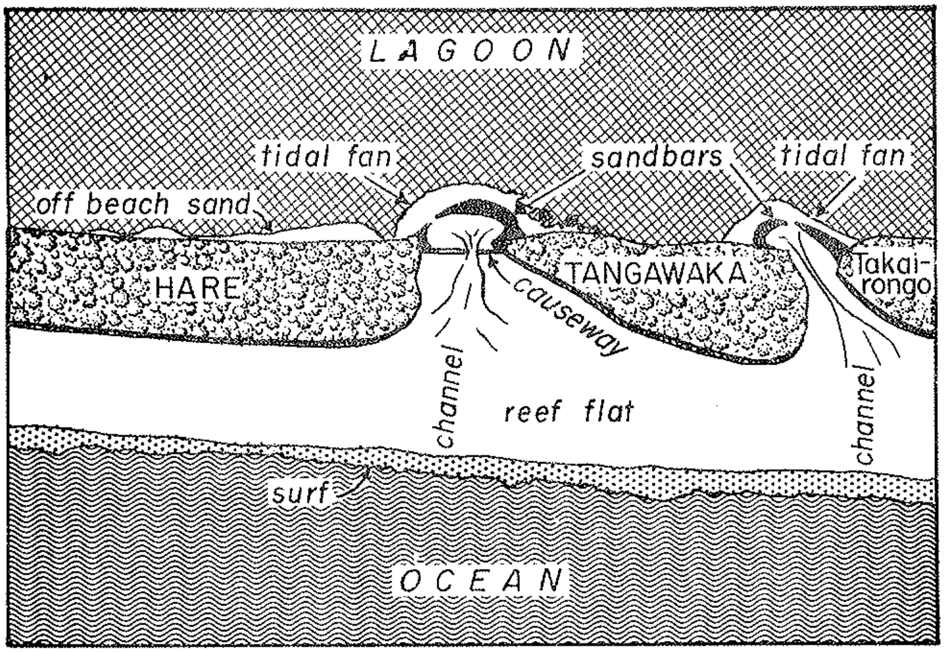


Figure 5

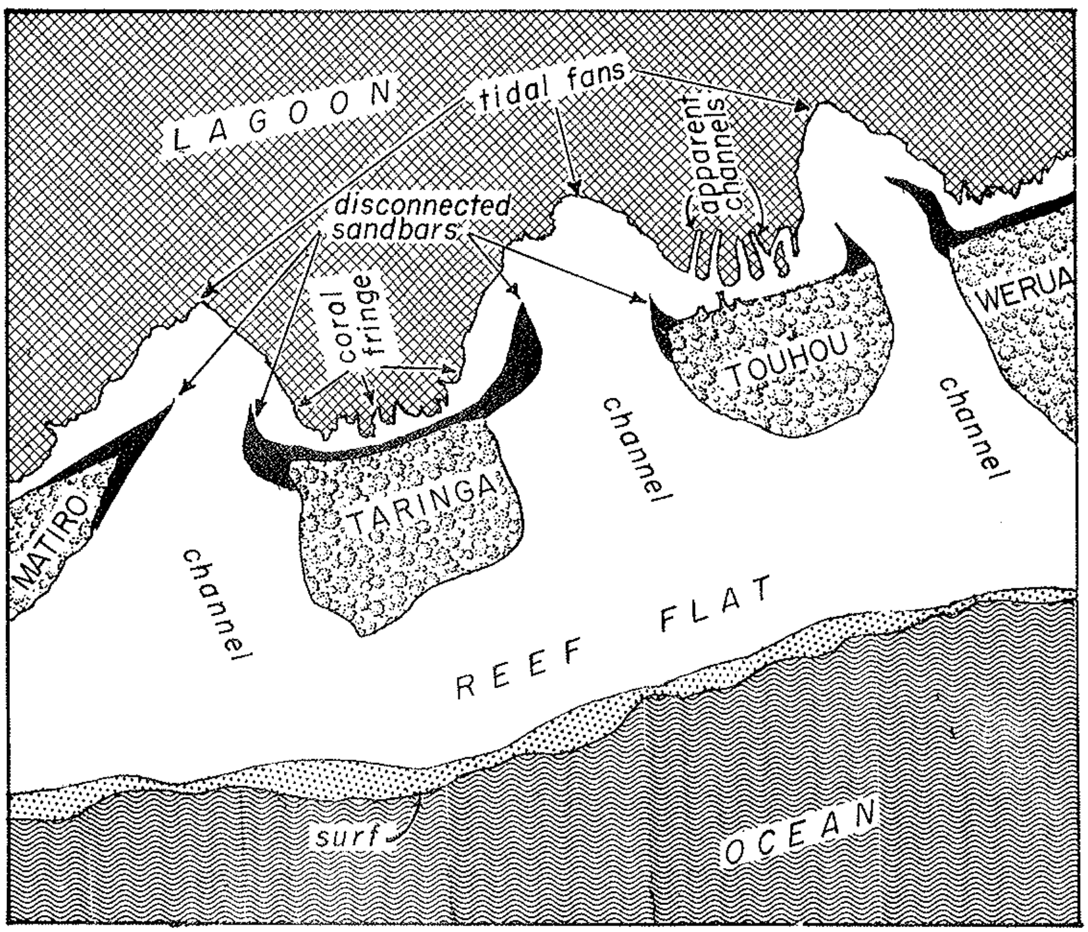
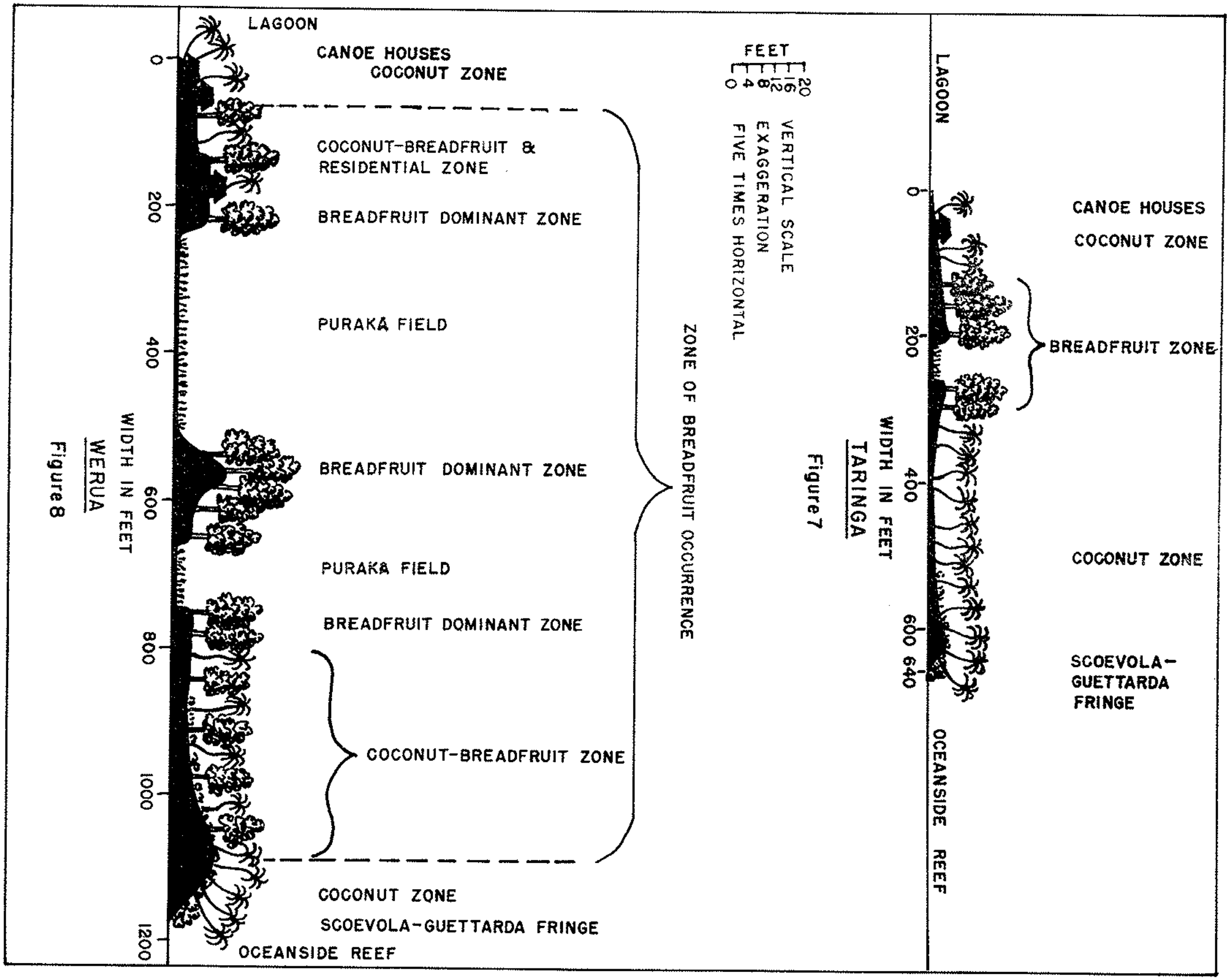


Figure 6

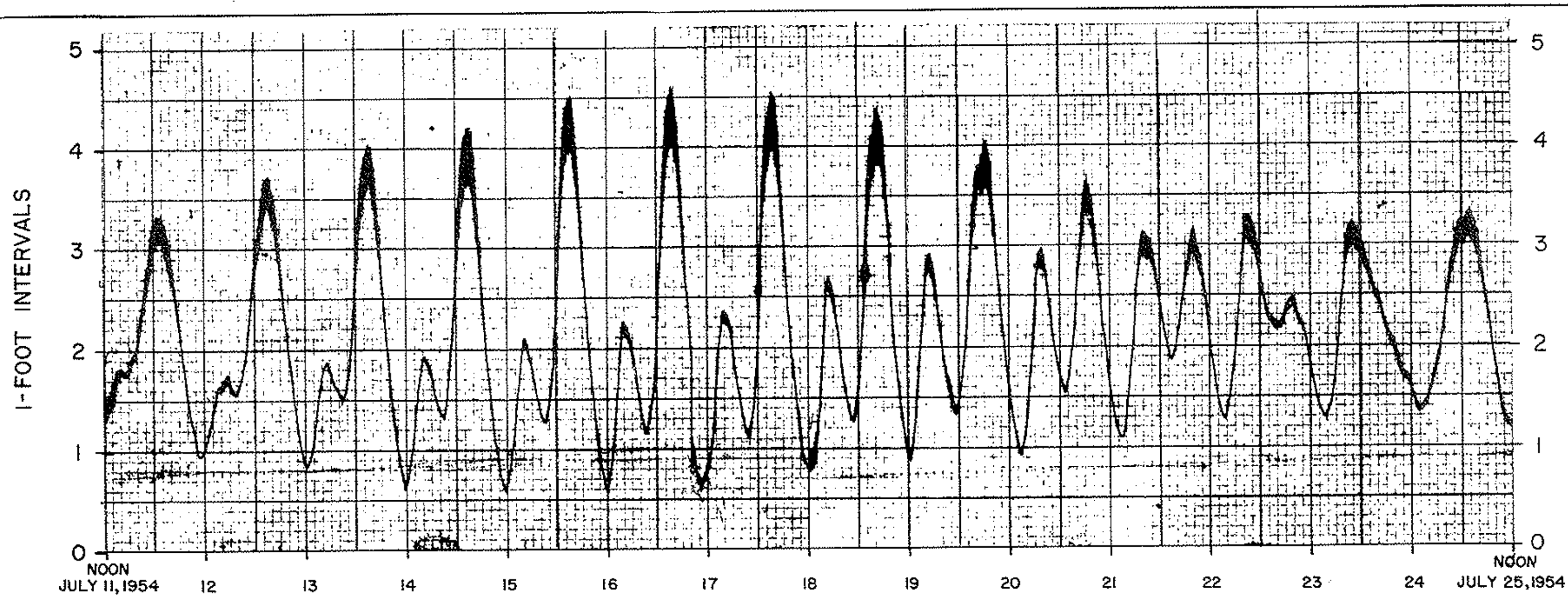


TARINGA

Figure 7

WERUA

Figure 8



Tidal fluctuations at the lagoon dock at Touhou Islet,
Kapingamarangi
Noon July 11 to Noon July 25, 1954

FIGURE 9

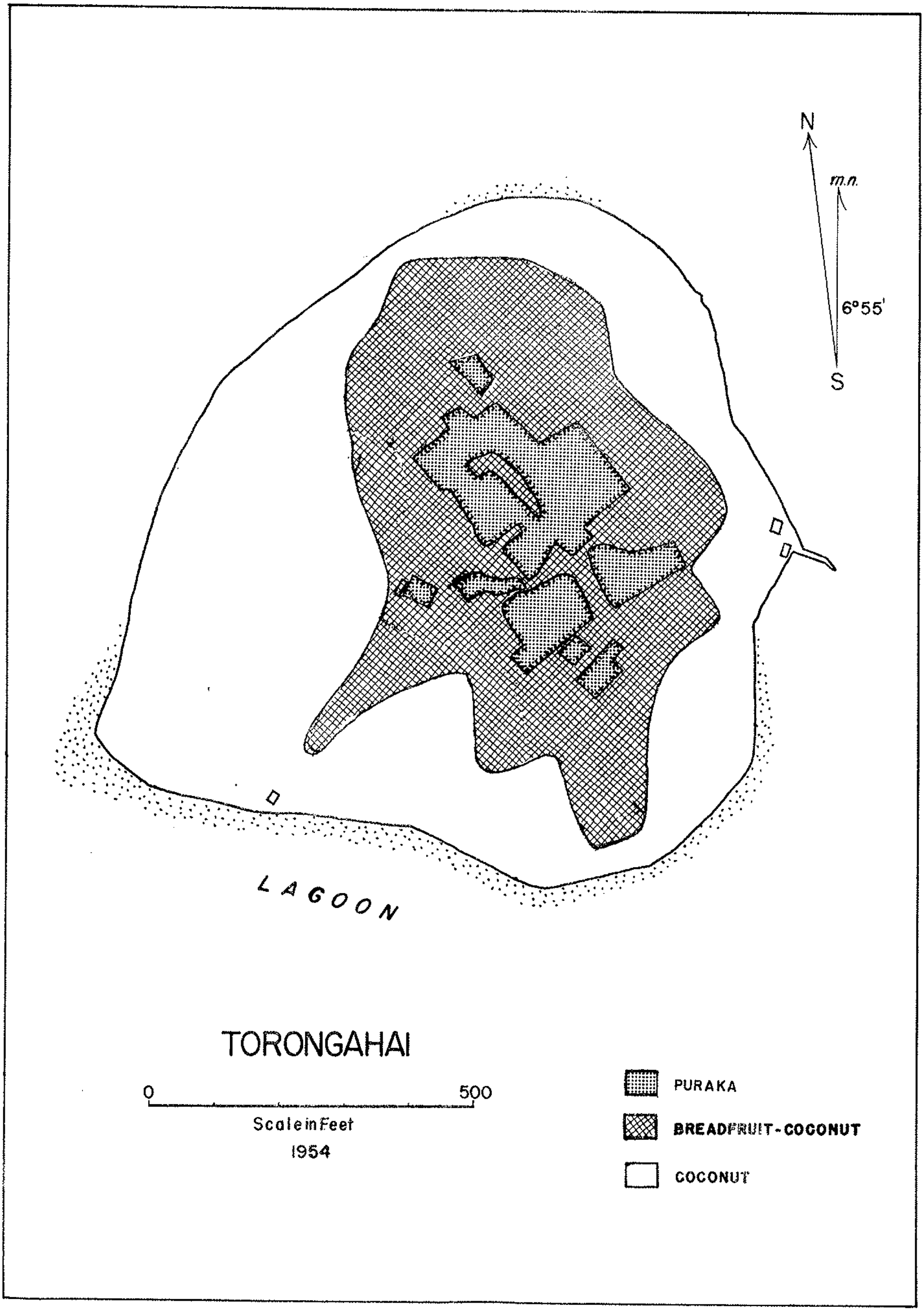

N
m.n.
6°55'
S
LAGOON
TORONGAHAI
0
500
Scale in Feet
1954
PURAKA
BREADFRUIT-COCONUT
COCONUT

Figure 10

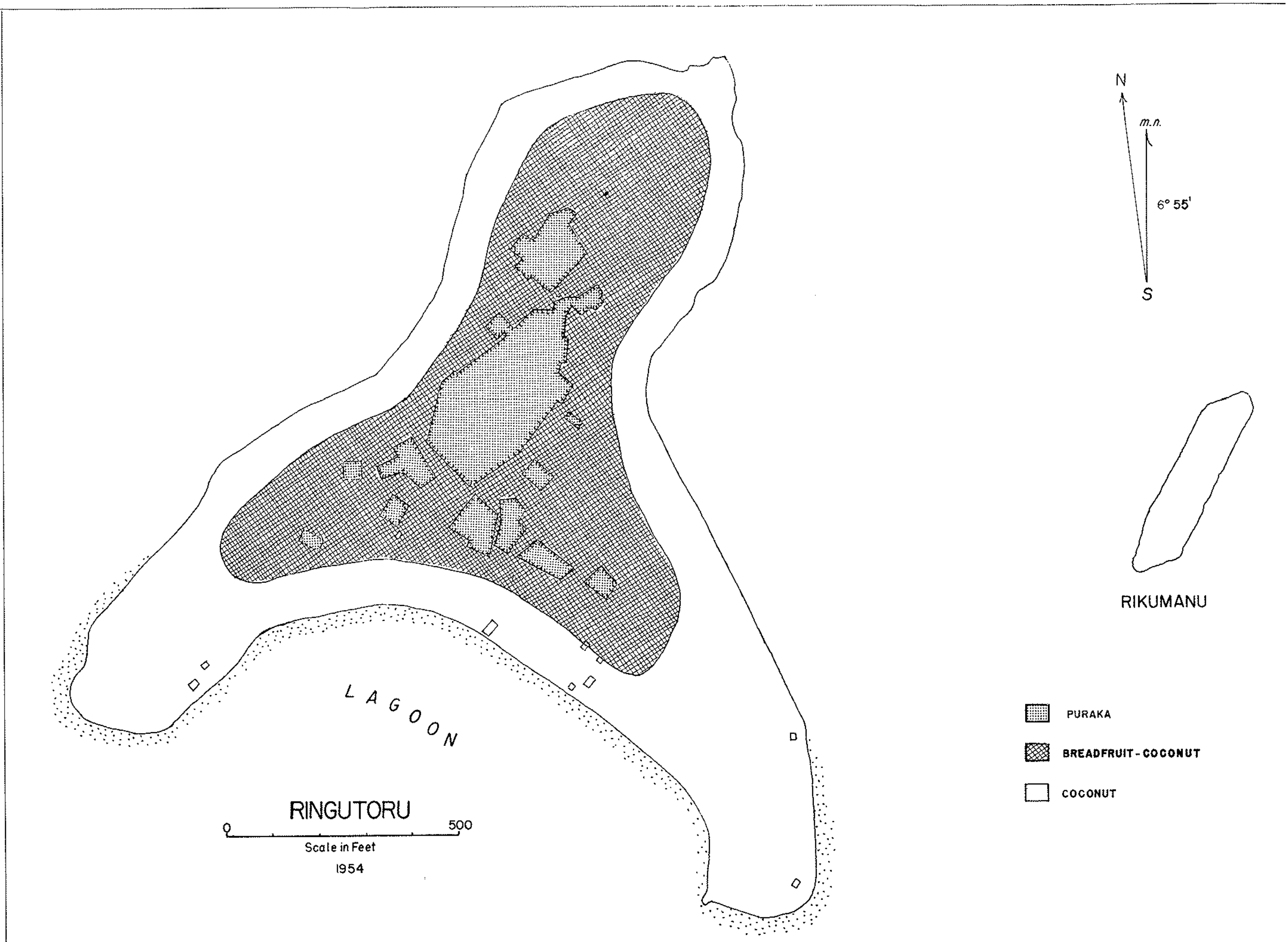

N
m.n.
6° 55'
S
RIKUMANU
PURAKA
BREADFRUIT-COCONUT
COCONUT
LAGOON
RINGUTORU
0
500
Scale in Feet
1954

Figure II

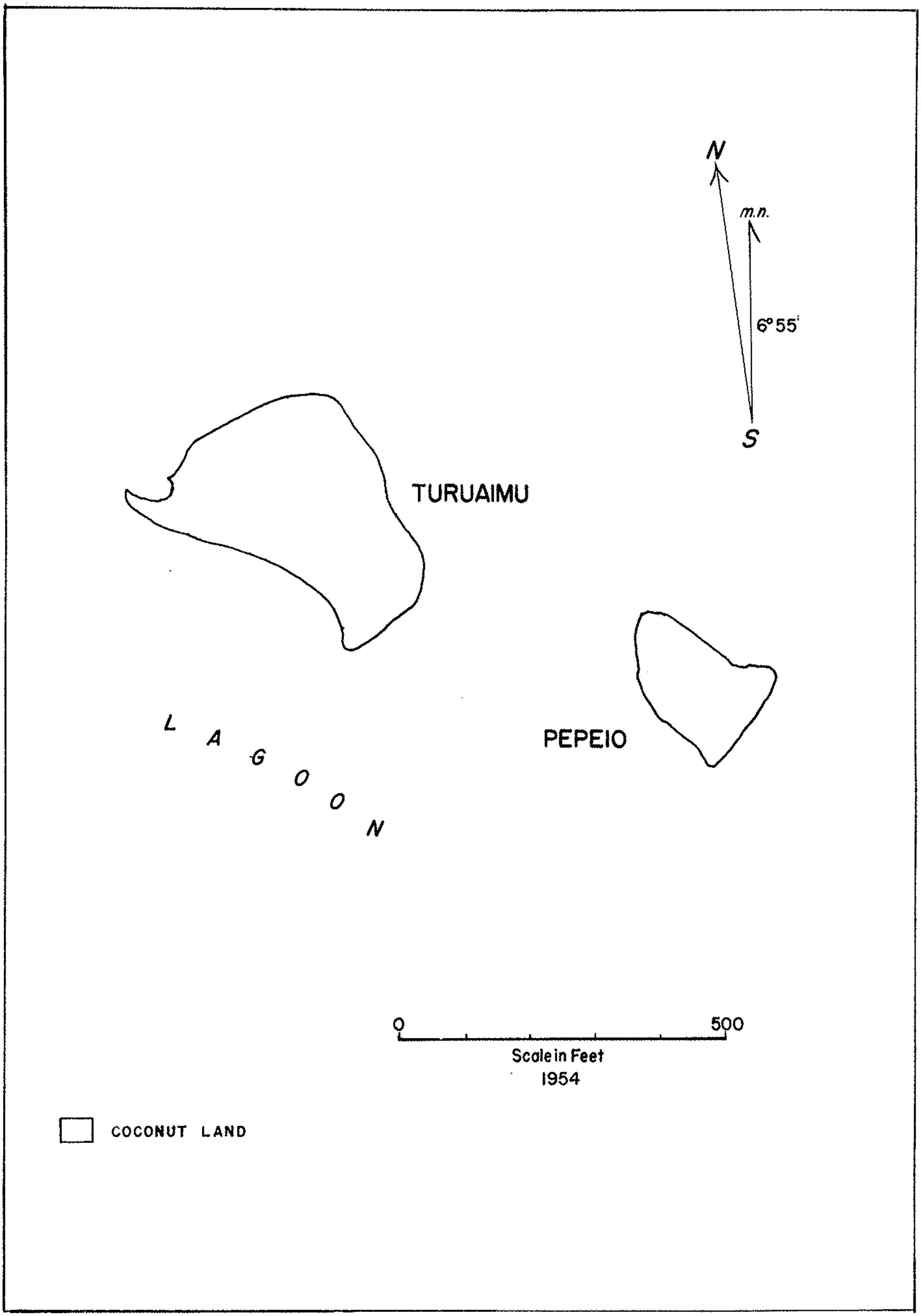

N
m.n.
6° 55'
S
TURUAIMU
PEPEIO
LAGOON
0
500
Scale in Feet
1954
COCONUT LAND

Figure 12

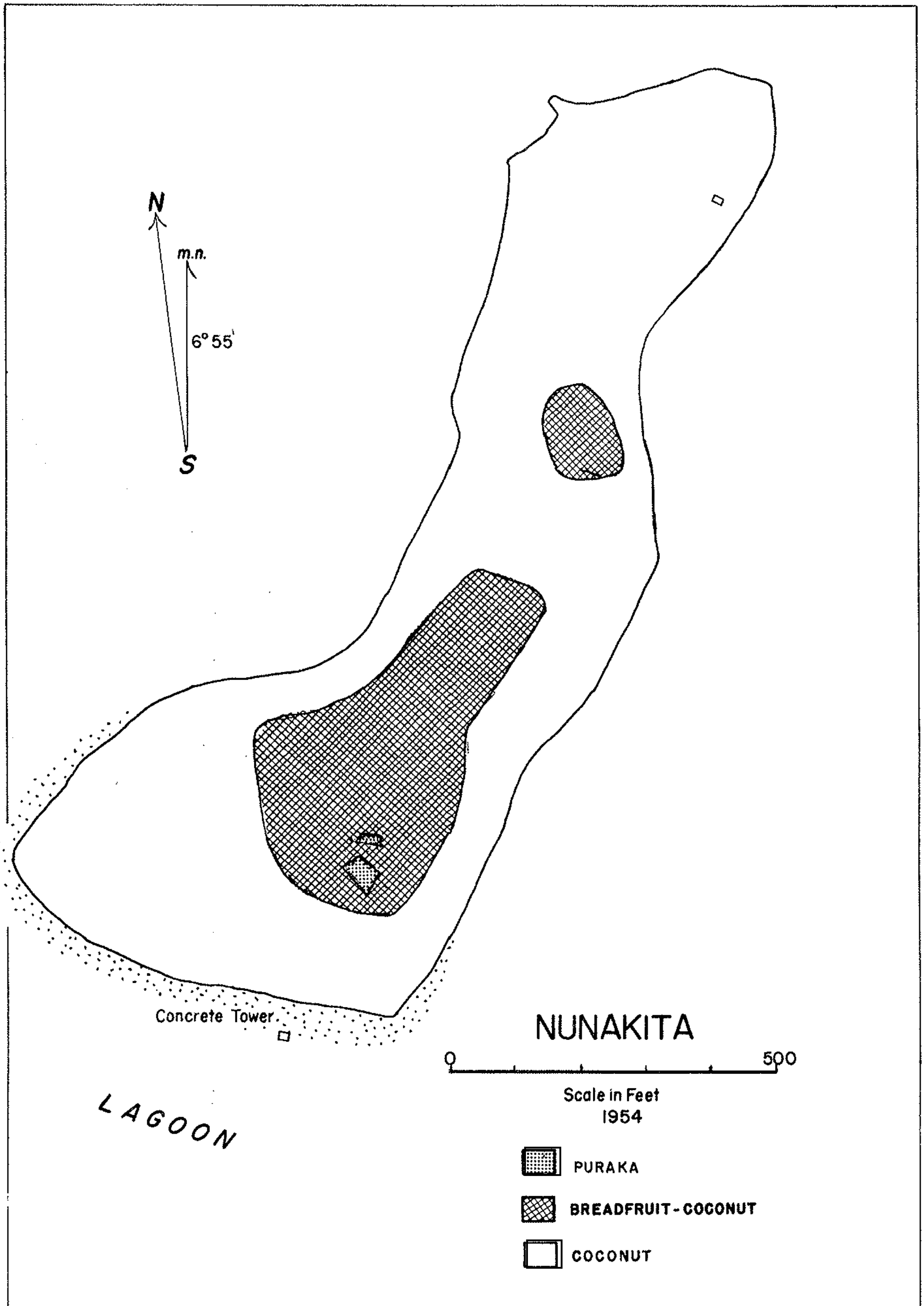

N
m.n.
6° 55'
S
Concrete Tower
NUNAKITA
0
500
Scale in Feet
1954
LAGOON
PURAKA
BREADFRUIT - COCONUT
COCONUT

Figure 13

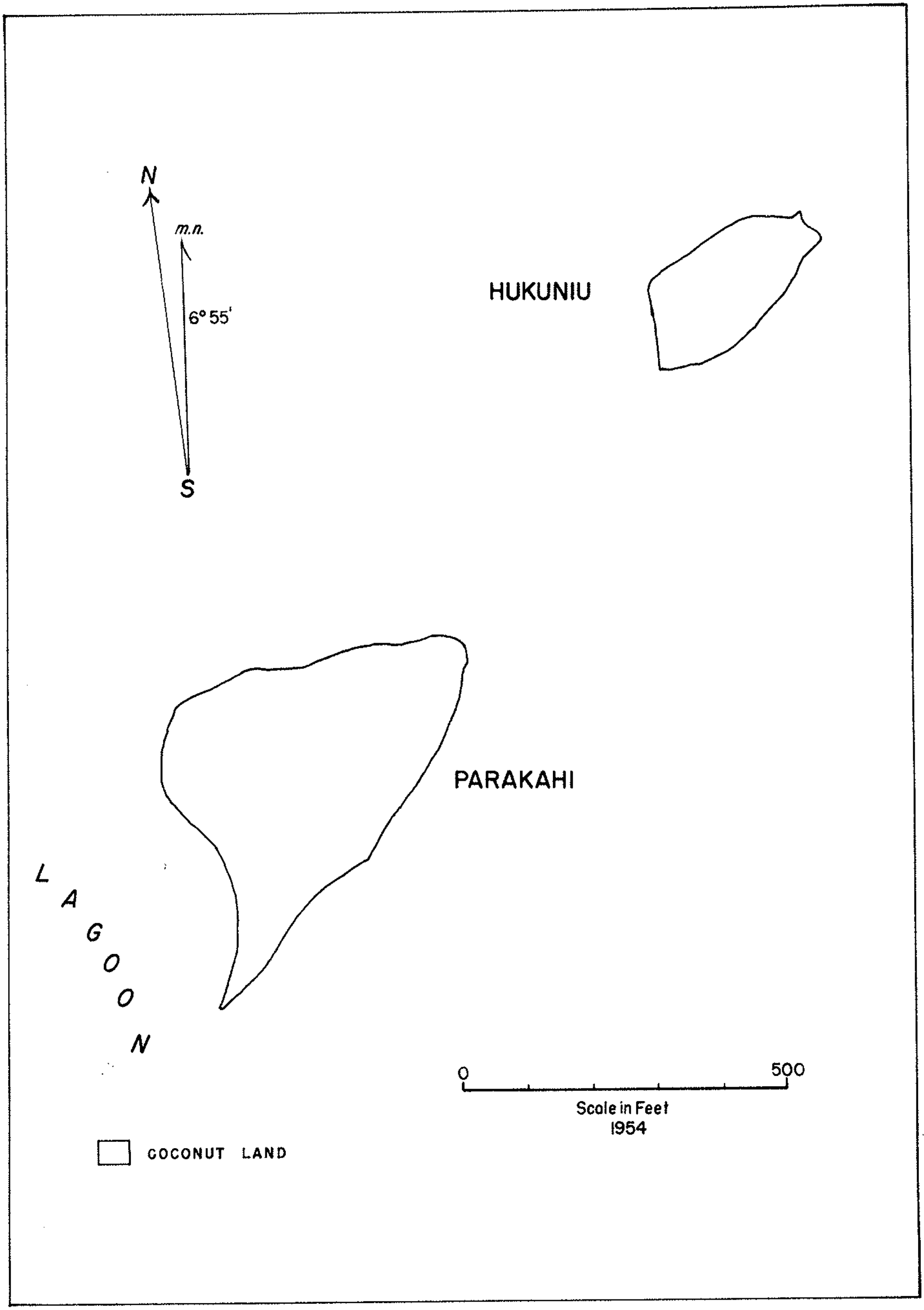

N
m.n.
6° 55'
S
HUKUNIU
PARAKAHI
LAGOON
0
500
Scale in Feet
1954
COCONUT LAND

Figure 14

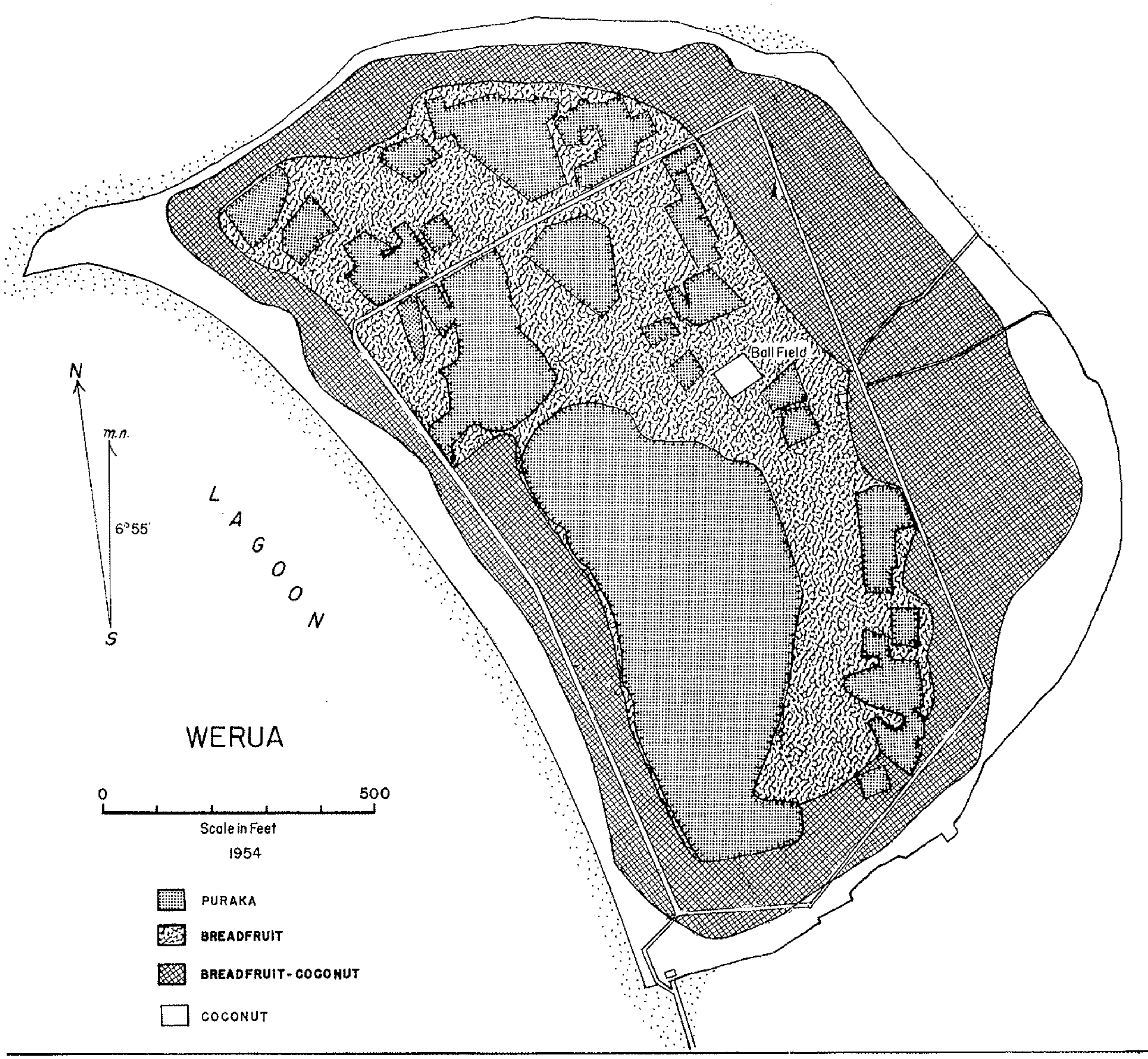

Ball Field
N
m.n.
6°55'
S
LAGOON
WERUA
0
500
Scale in Feet
1954
PURAKA
BREADFRUIT
BREADFRUIT-COCONUT
COCONUT

Figure 15

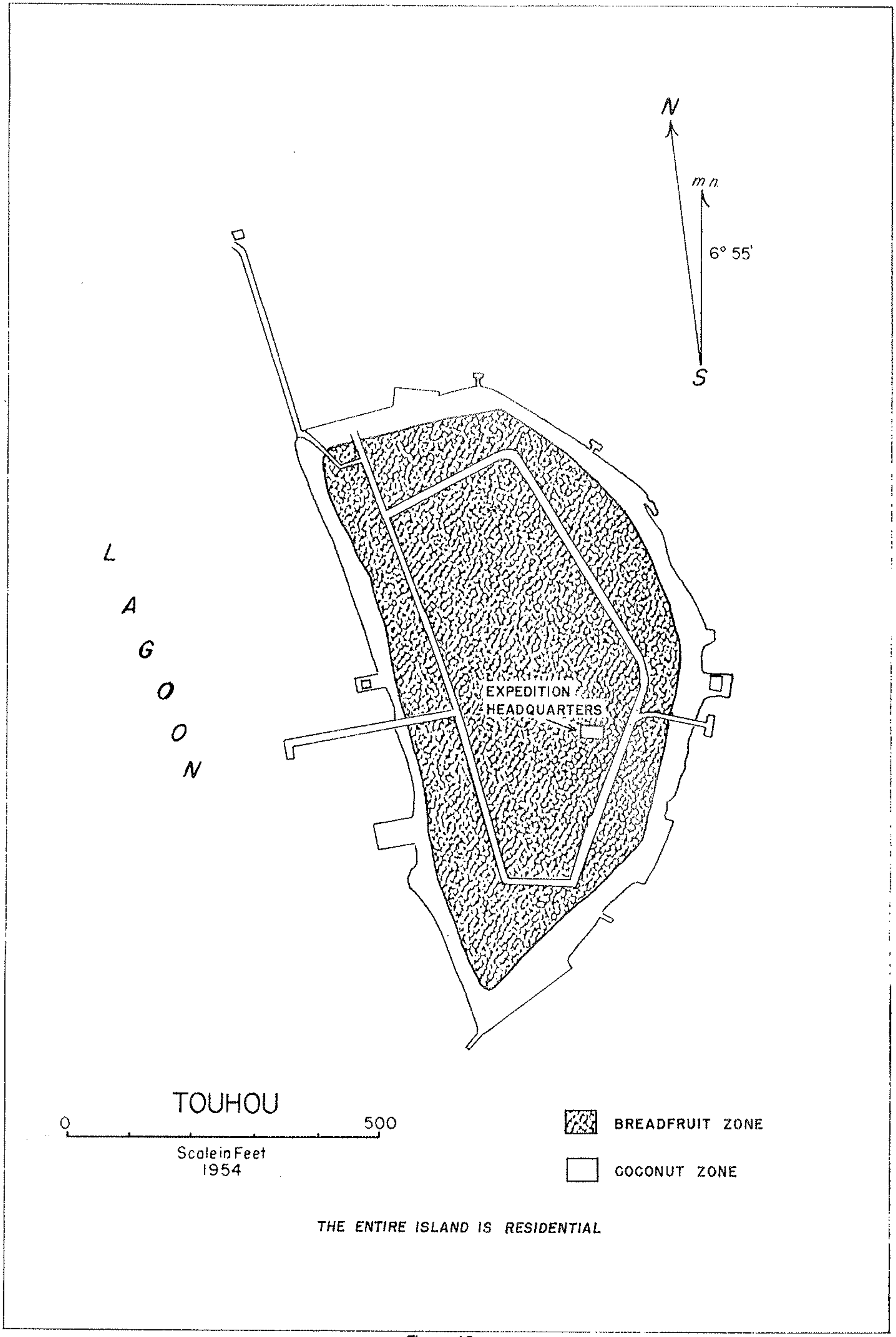
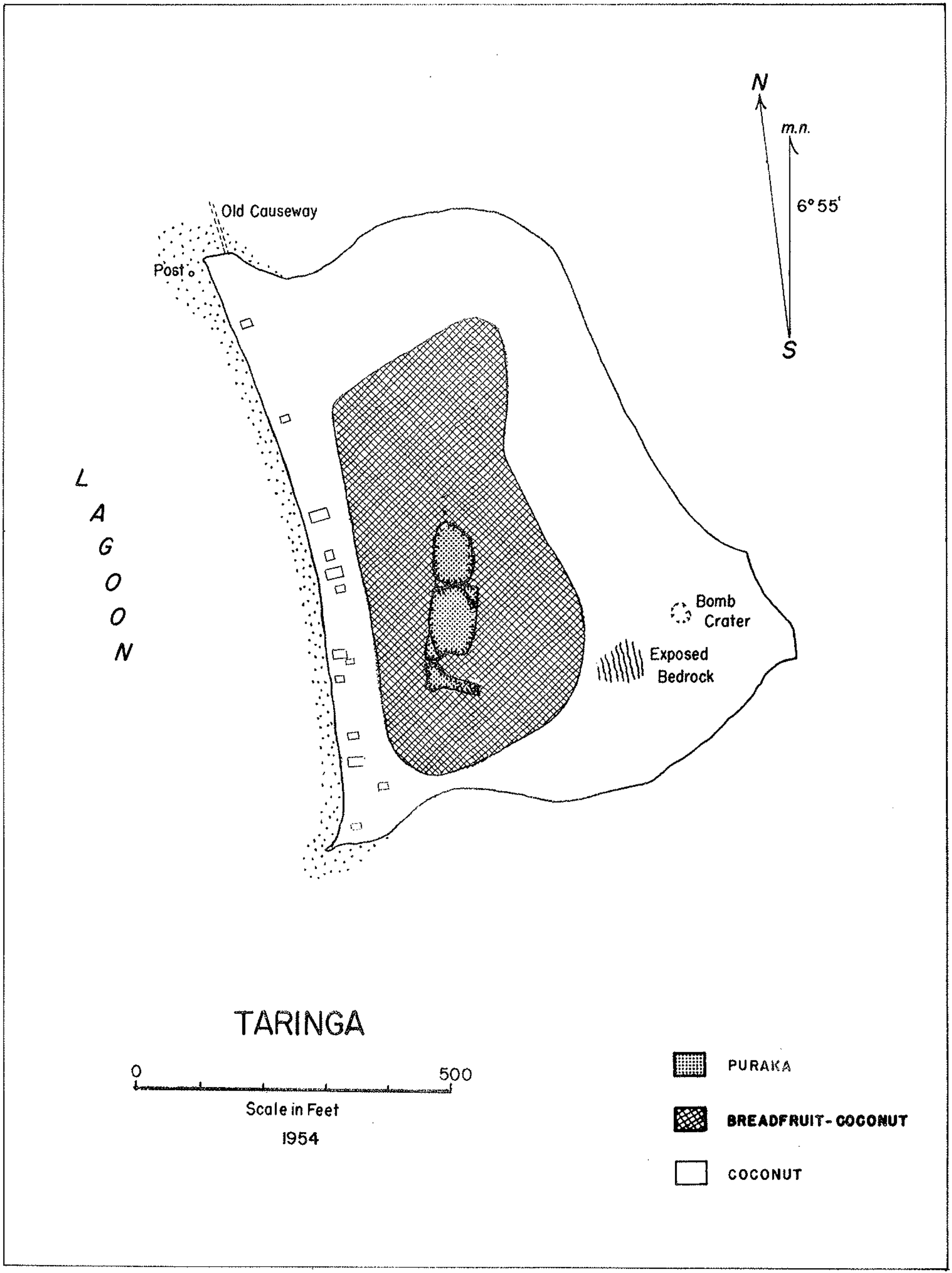
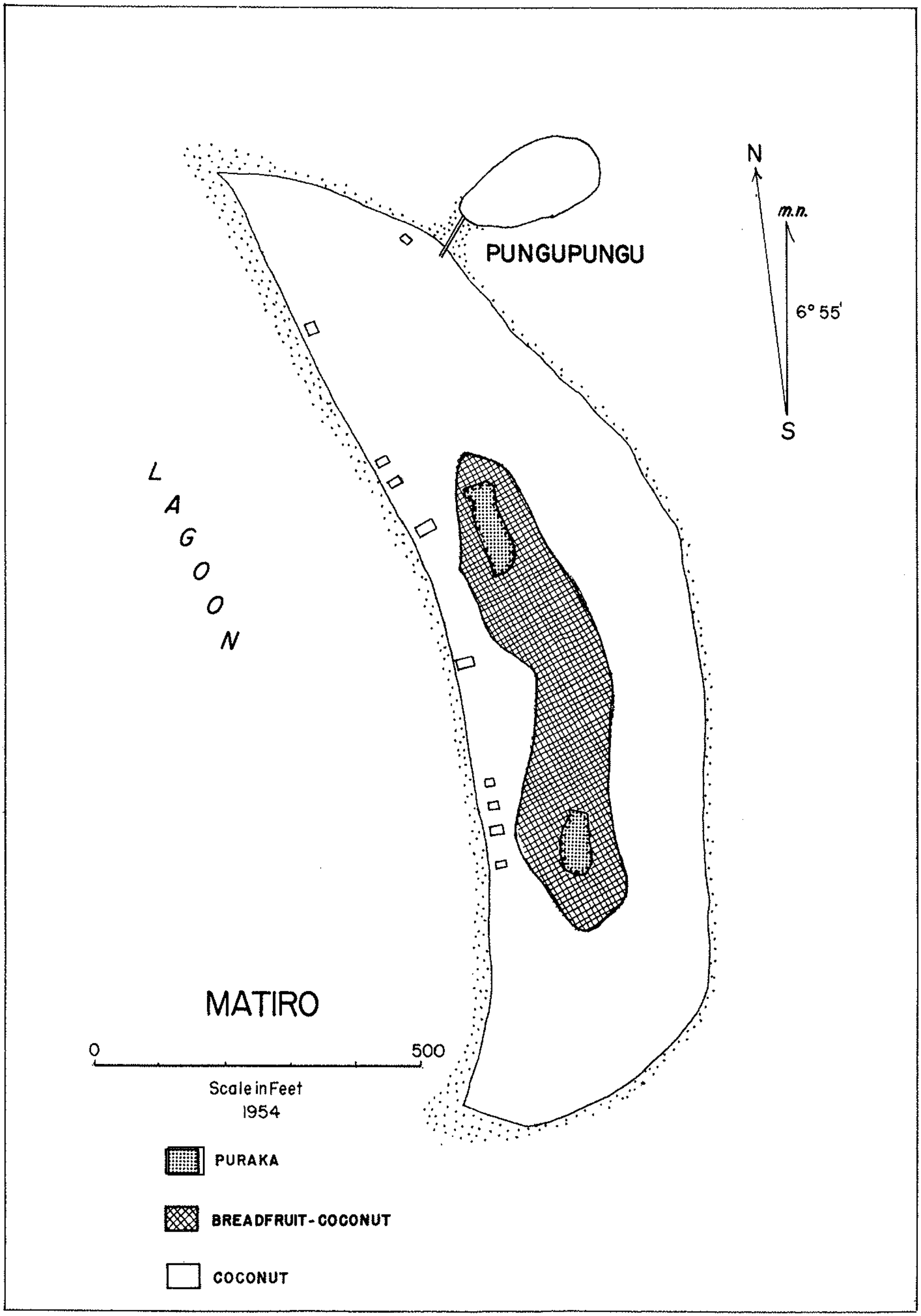

N
mn
6° 55'
S
L A G O O N
EXPEDITION
HEADQUARTERS
TOUHOU
0
500
Scale in Feet
1954
BREADFRUIT ZONE
COCONUT ZONE
THE ENTIRE ISLAND IS RESIDENTIAL

Figure 16



N
m.n.
6° 55'
S
Old Causeway
Post
L A G O O N
Bomb Crater
Exposed Bedrock
TARINGA
0
500
Scale in Feet
1954
PURAKA
BREADFRUIT-COCONUT
COCONUT

Figure 17



PUNGUPUNGU
N
m.n.
6° 55'
S
LAGOON
MATIRO
0
500
Scale in Feet
1954
PURAKA
BREADFRUIT-COCONUT
COCONUT

Figure 18

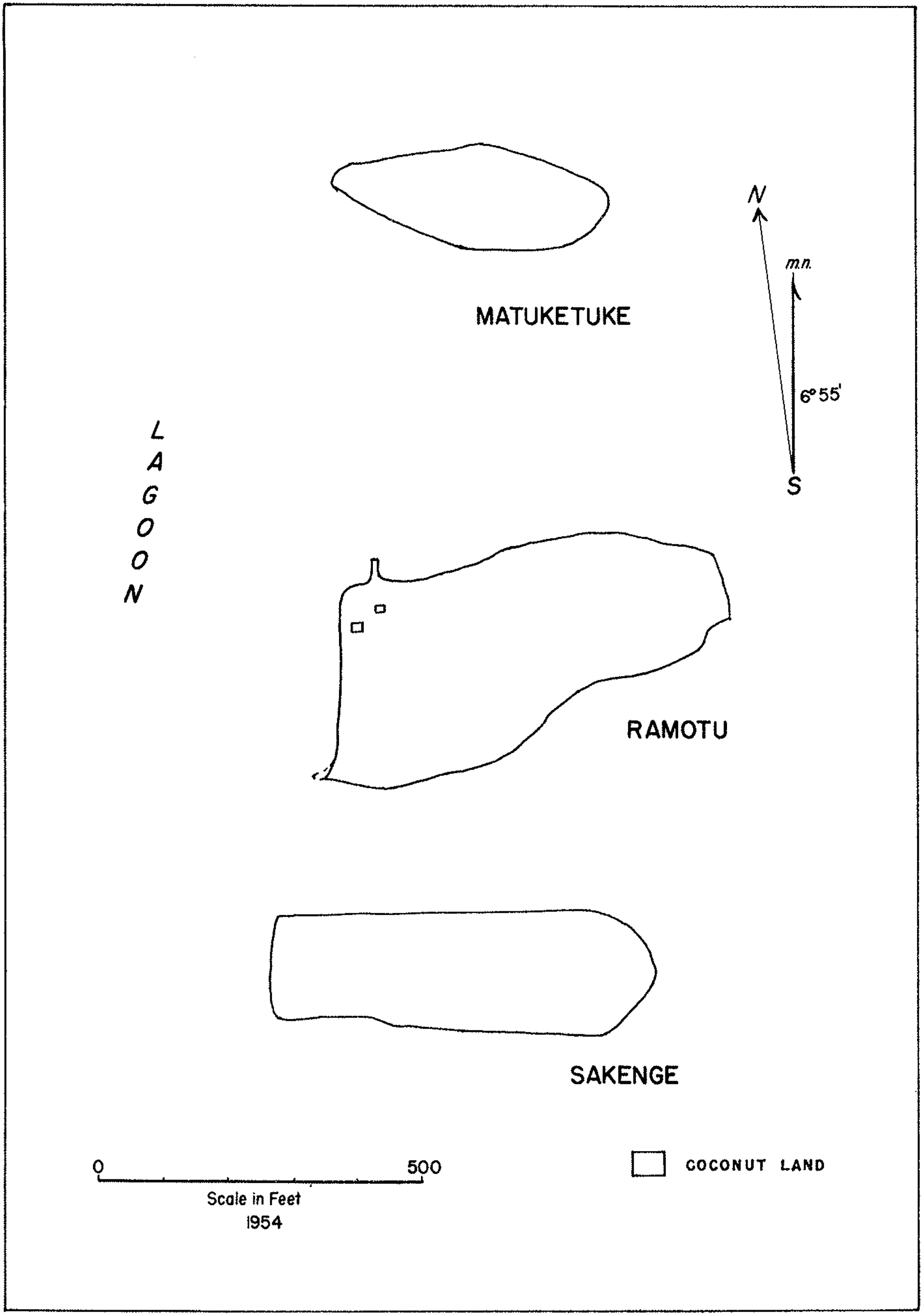

MATUKETUKE
N
m.n.
6° 55'
S
L
A
G
O
O
N
RAMOTU
SAKENGE
0
500
Scale in Feet
1954
COCONUT LAND

Figure 19

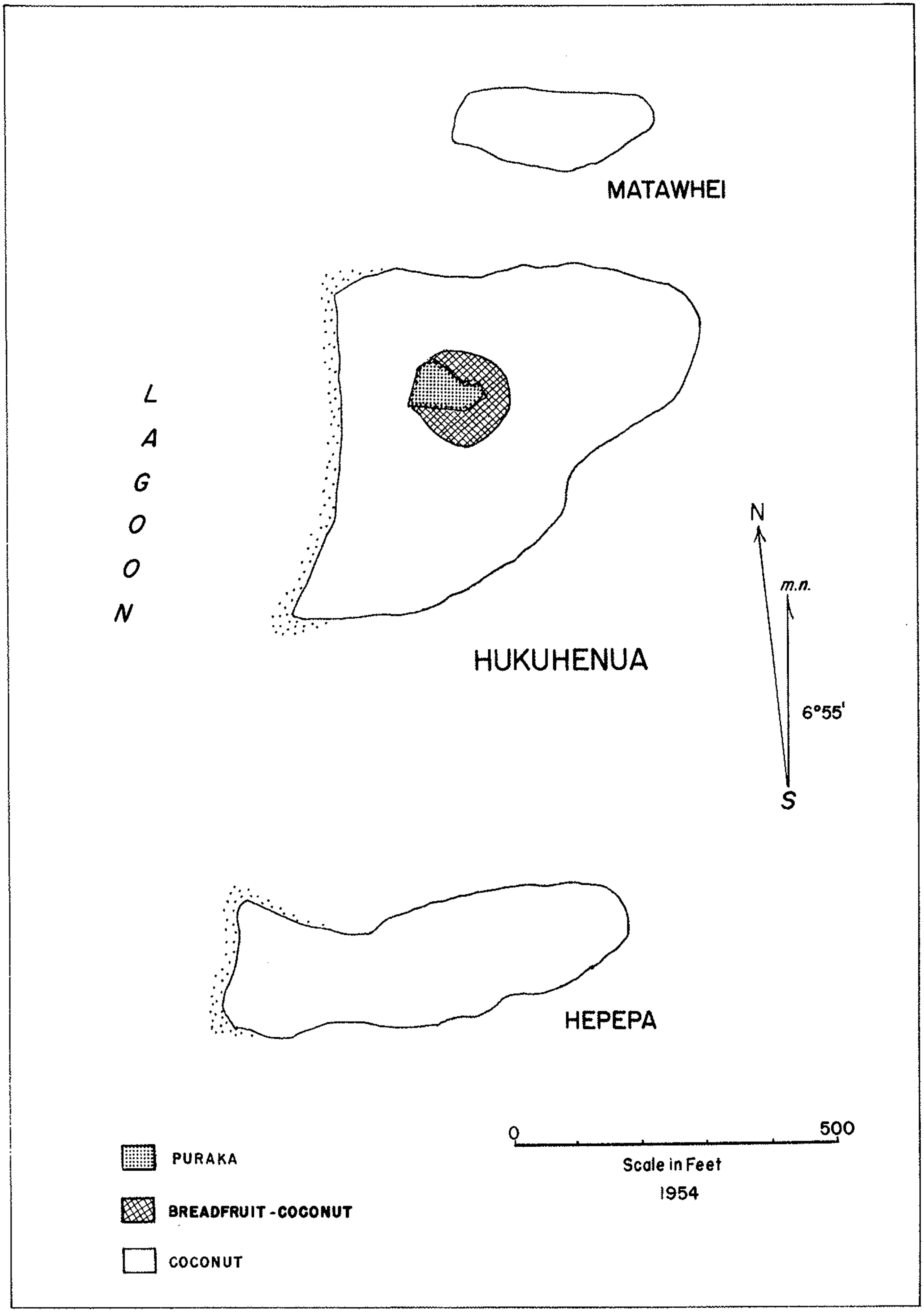

MATAWHEI
LAGOON
HUKUHENUA
N
m.n.
6°55'
S
HEPEPA
0
500
Scale in Feet
1954
PURAKA
BREADFRUIT - COCONUT
COCONUT

Figure 20

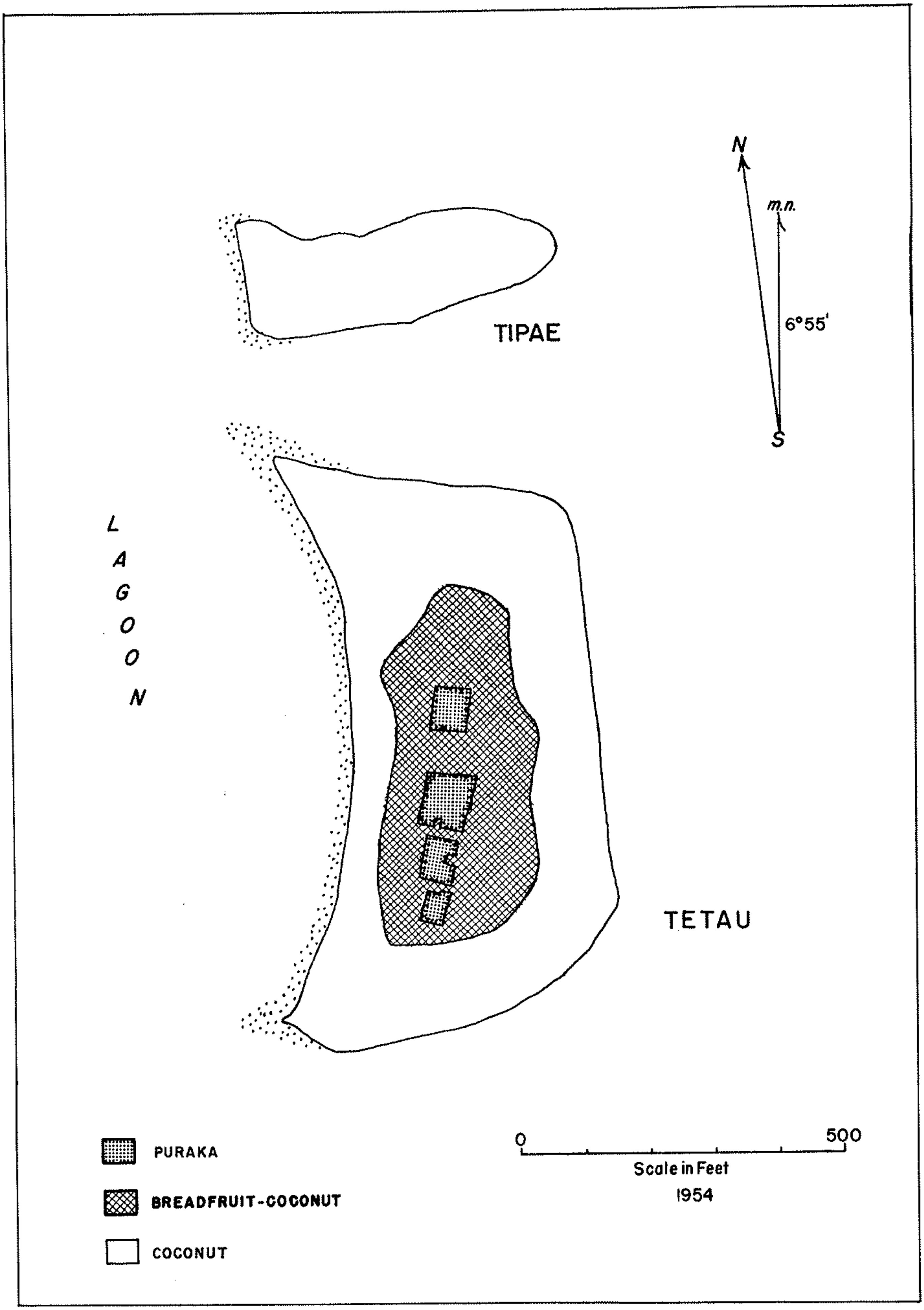

N
m.n.
6°55'
S
TIPAE
L A G O O N
TETAU
PURAKA
BREADFRUIT-COCONUT
COCONUT
0
500
Scale in Feet
1954

Figure 21

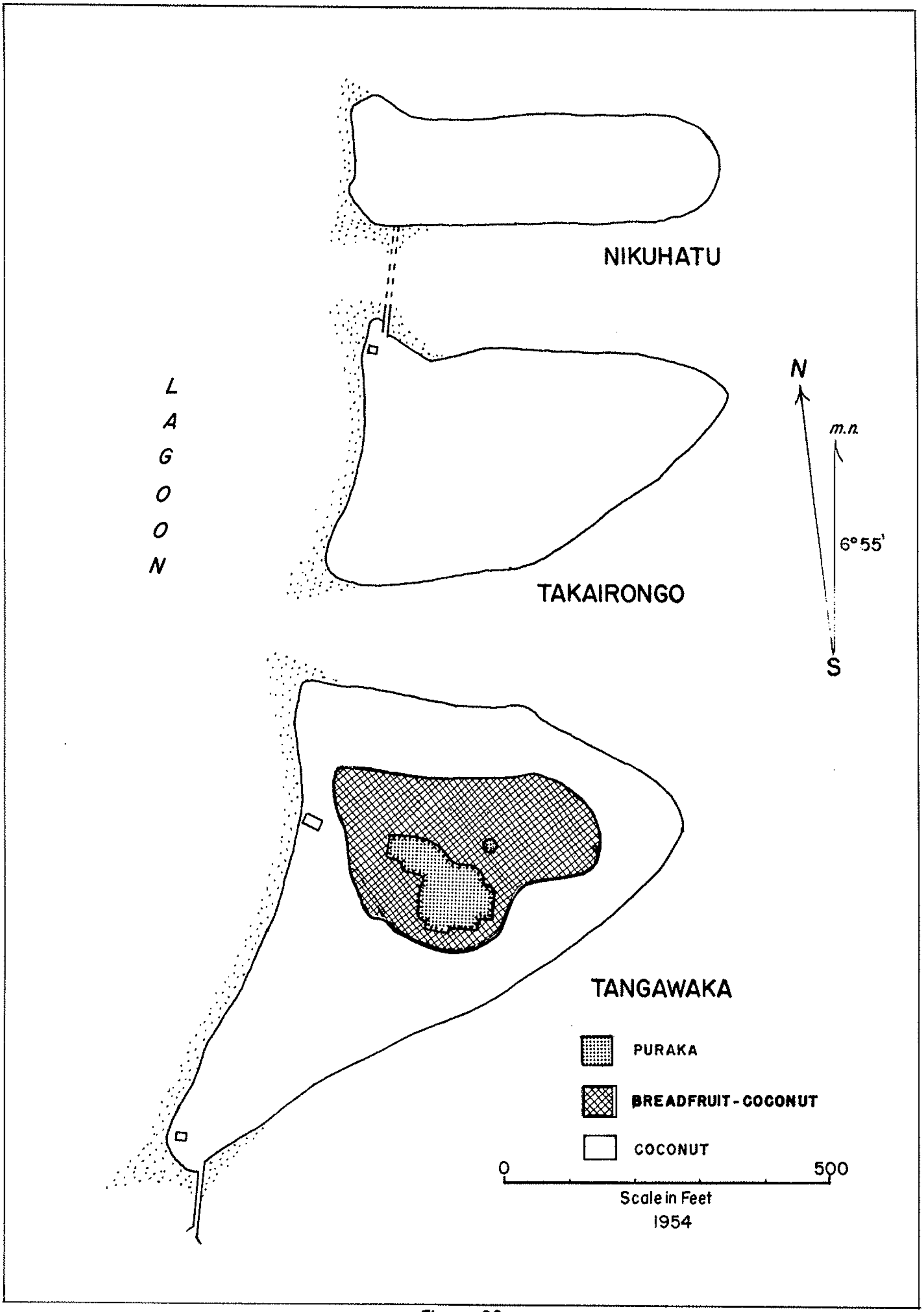

NIKUHATU
L
A
G
O
O
N
TAKAIRONGO
N
m.n.
6°55'
S
TANGAWAKA
PURAKA
BREADFRUIT - COCONUT
COCONUT
0
500
Scale in Feet
1954

Figure 22

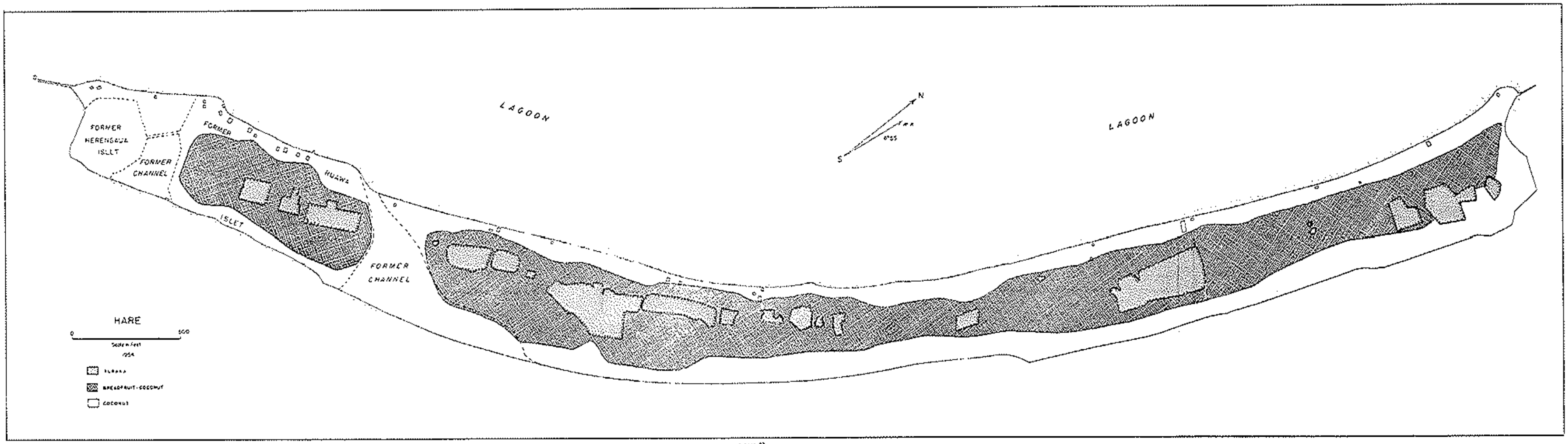

LAGOON
LAGOON
N
S
FORMER
ISLET
FORMER
CHANNEL
FORMER
ISLET
FORMER
CHANNEL
HARE
0
500
Scale in Feet
BREADFRUIT-COCONUT
COCONUT

Figure 23

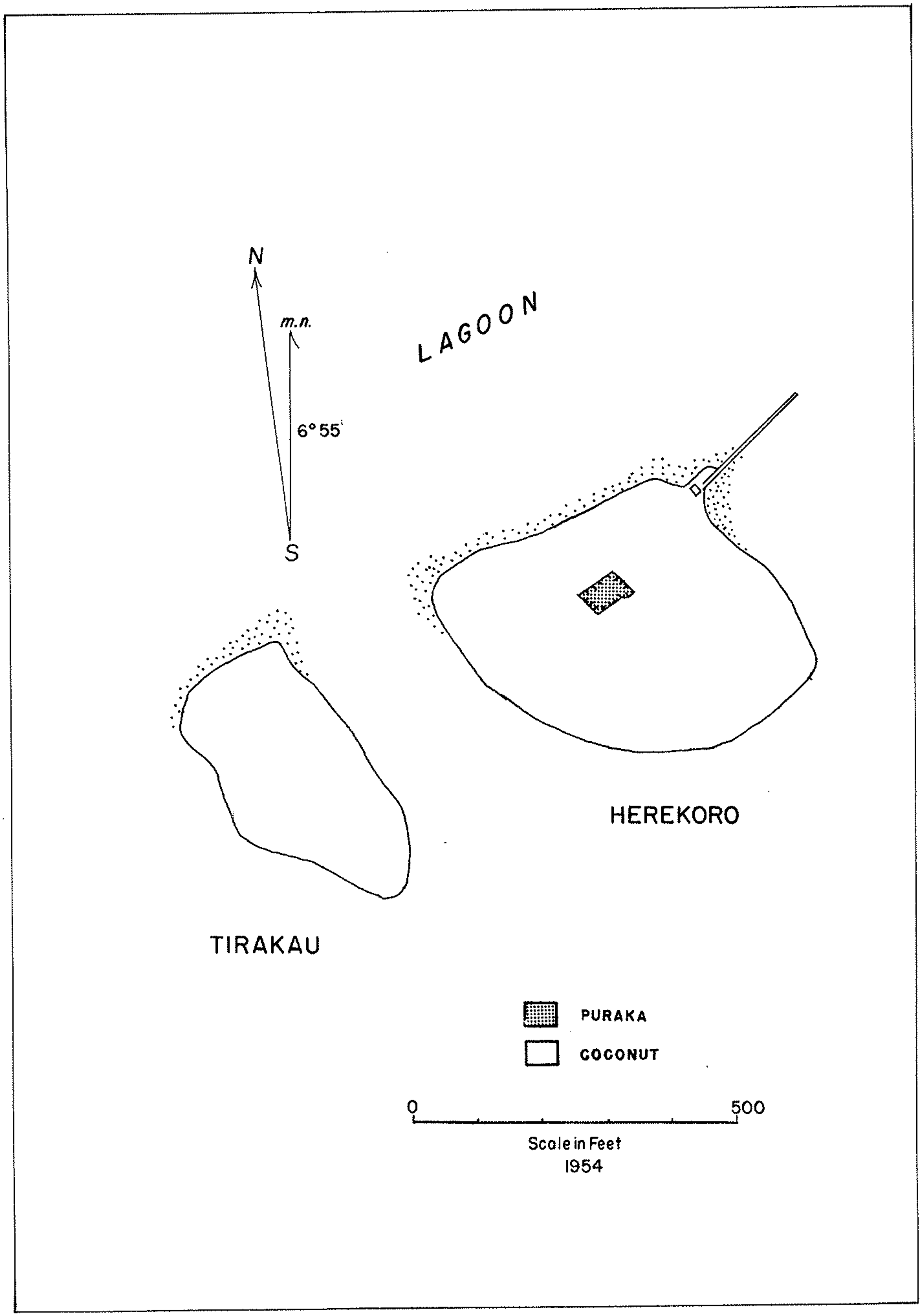

N
m.n.
6° 55'
S
LAGOON
HEREKORO
TIRAKAU
PURAKA
COCONUT
0
500
Scale in Feet
1954

Figure 24

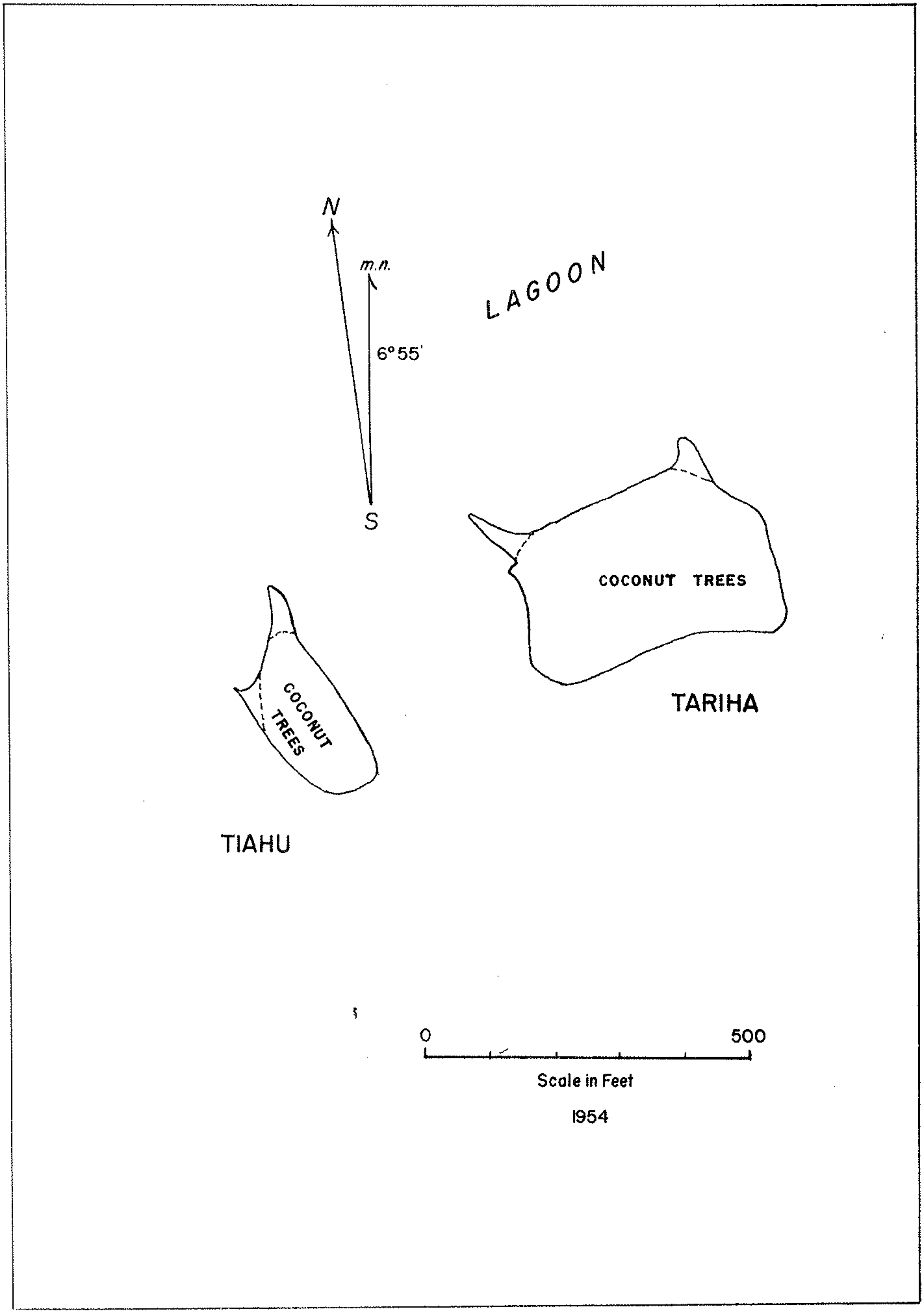

N
m.n.
6°55'
S
LAGOON
COCONUT TREES
TARIHA
COCONUT TREES
TIAHU
0
500
Scale in Feet
1954

Figure 25

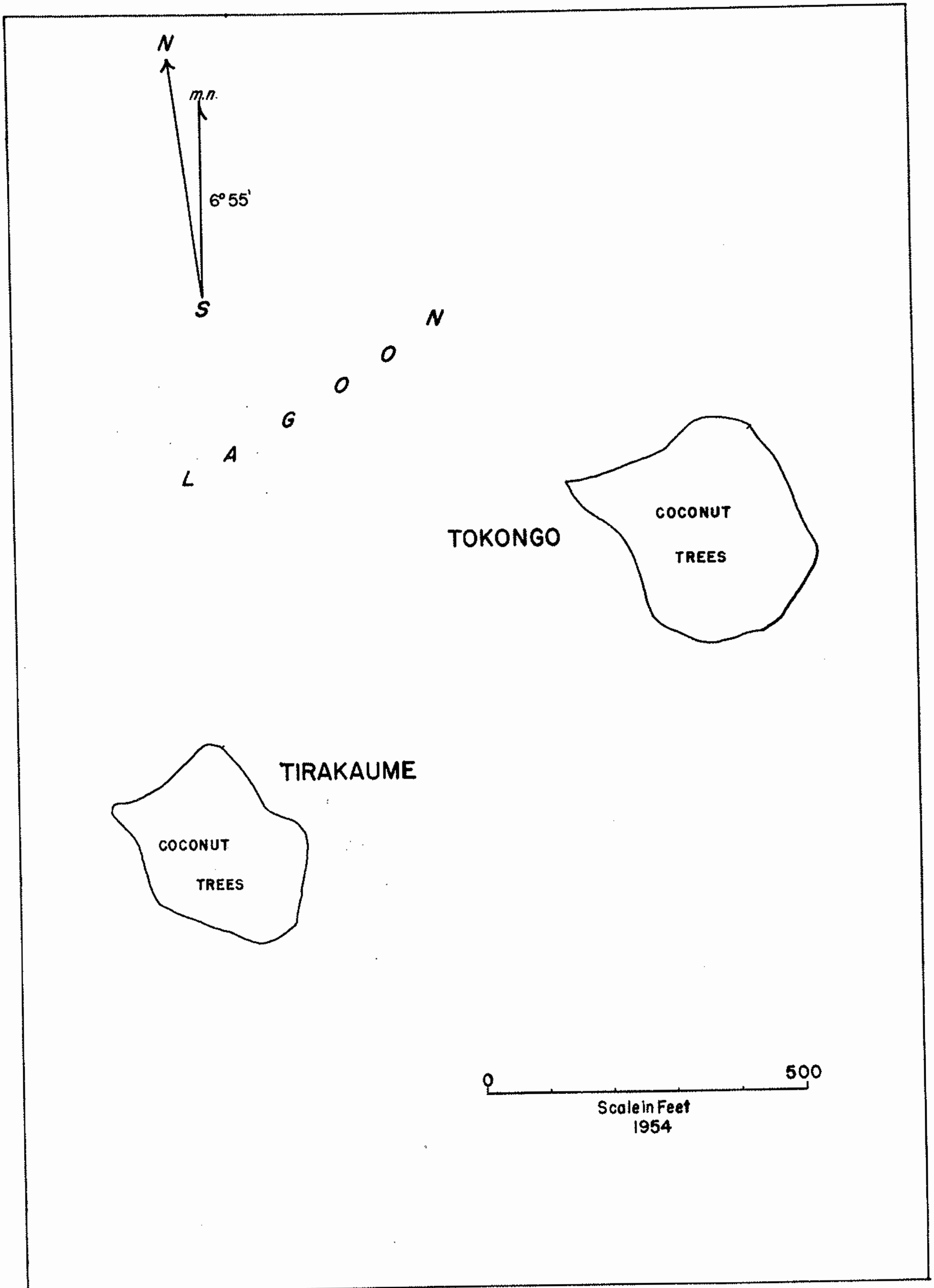

N
m.n.
6° 55'
S
L A G O O N
TOKONGO
COCONUT
TREES
TIRAKAUME
COCONUT
TREES
0
500
Scale in Feet
1954

Figure 26

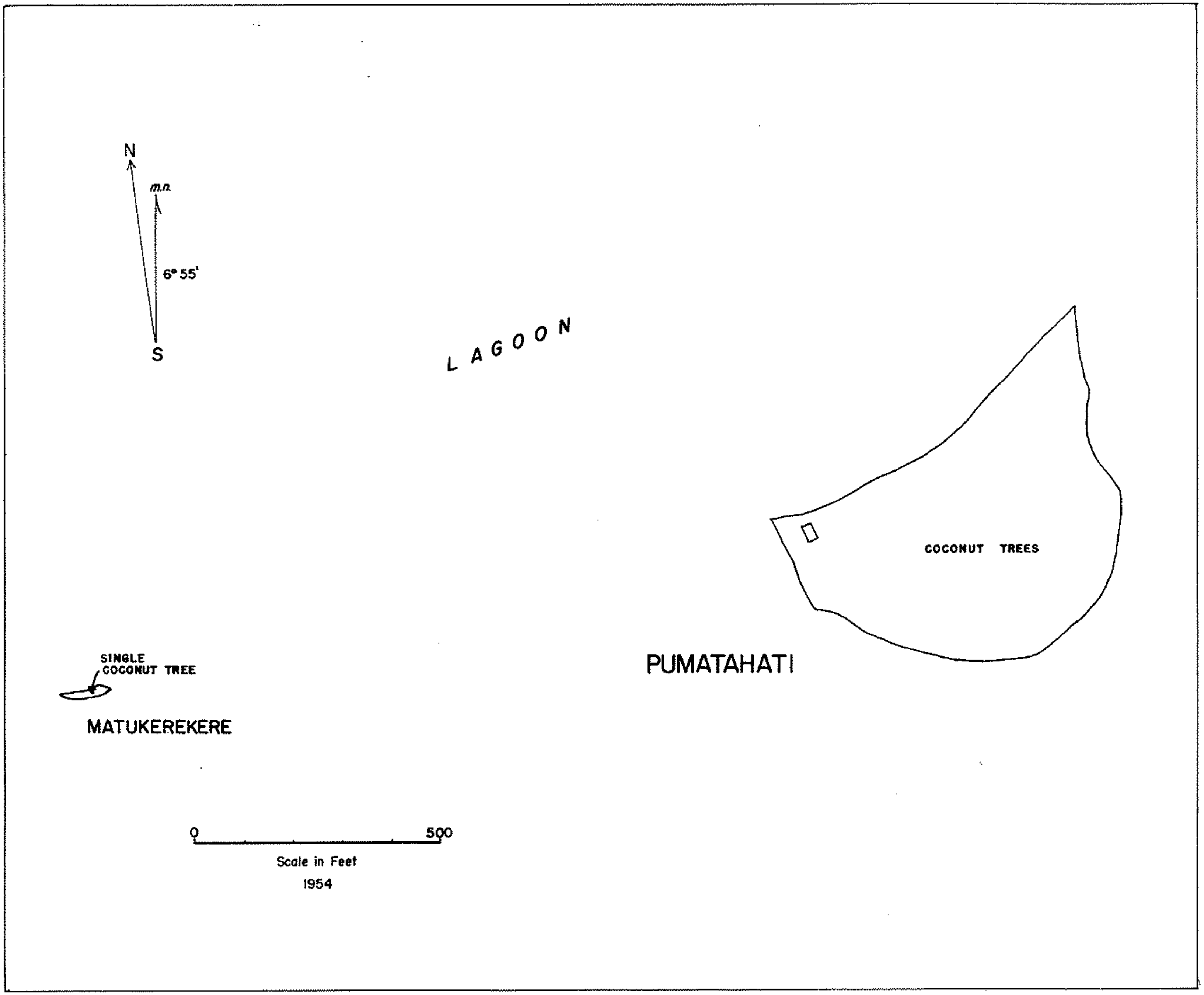

N
m.n.
6° 55'
S
LAGOON
COCONUT TREES
PUMATAHATI
SINGLE
COCONUT TREE
MATUKEREKERE
0
500
Scale in Feet
1954

Figure 27

Fig. 28 Species list of trees and shrubs. Species arranged according to frequency of occurrence on atoll. Islets arranged according to size from smallest to largest. Relative importance of each species indicated by letter: A-abundant; F-frequent; O-occasional; R-rare. Probable origin of each species also indicated by letters: I-indigenous; AI-aboriginal introduction; RI-recent introduction; D-drift seedlings not yet established as mature specimens. Pandanus tectorius has two sources of origin. Although Pipturus argenteus occurs as a tree on other atolls, here it contributed only to the shrub layer. Scaevola frutescens should be called S. sericea. The former name really applies to Atlantic species.

ISLETS

TREES	Matuker.	Pungu.	Tiahu	Mata.	Pepeio	Riku.	Hukun.	Matuket.	Tirakume	Tipae	Toko.	Tirakau	Turu.	Tariha	Niku.	Hepepa	Sake.	Para.	Ramotu	Here.	Taka.	Hukuh.	Puma.	Tang.	Tetau	Touhou	Matiro	Taringa	Nuna.	Toro.	Ring.	Werua	Hare	% freq.	Origin
Cocos nucifera	O	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	F	A	A	A	A	A	A	A	100	AI
Guettarda speciosa		A	F	O	O	O	F	F	O	F	O	O	A	O	A	A	A	A	F	F	F	F	O	F	F	R	F	F	F	F	F	F	F	97	I
Morinda citrifolia		O	O	O	O	O	O	O	O	O	A	O	O	O	O	O	O	O	F	A	F	F	O	A	A	O	A	A	A	A	A	A	A	97	AI
Premna obtusifolia		R	O	O	O	O	O	O	O	O	O	O	O	O	O	F	O	O	A	A	A	A	A	A	A	O	A	A	A	A	A	A	A	97	I
Pandanus tectorius	R	O		F	O	O	O	F	O	O	O	O	O	O	O	O	O	O	F	F	R	F	O	O	O	A	A	F	F	F	F	A	F	97	I-AI
Barringtonia asiatica	R		R		R			R	R	R	R		R	R				R			R	R		R	R		R	R	R	R	R	R	R	63	I
Calophyllum inophyllum	R				R		R											R	R	R	R	R		R		R	O	O	R	O	O	O	O	51	AI
Hibiscus tiliaceus	R					R				R							R	R		R	R	O		R	O		O	F	O		O	O	O	48	AI
Cordia subcordata				R		R							R	R	R			R	R	R		R	F			R			O	F	O		R	45	I
Artocarpus altilis											R									R	R	O		F	F	F	F	F	F	A	A	A	A	42	AI
Messerschmidia argentea				O							O		O					R		R			O		R		R	R	O	O	O		O	39	I
Terminalia samoensis			O				R			R				R	R						R		O					R		R				27	I
Hernandia sonora											R							R				R					R	R		R		R	R	24	I
Cerbera manghas																						R					R	R		R	R			15	RI
Pisonia grandis																							O			O				O	O		O	15	I
Terminalia catappa							R																R				R					R	O	15	AI
Carica papaya																										O					O	R	R	12	RI
Thespesia populnea																											R		R			R	R	12	I
Intsia bijuga																		R					R					R			R			12	D
Erythrina variegata																													R			R	R	9	RI
Pandanus dubius																							R									R		6	AI
Plumeria rubra																										O						O		6	RI
Ochrosia oppositifolia																											O		R					6	I
Adenanthera pavonina																										R								3	RI
Barringtonia racemosa																													R					3	D
Kleinhovia hospita																															R			3	D
Pemphis acidula																												R						3	RI
Pongamia pinnata																															R			3	I
Soulamea amara																													O					3	I
SHRUBS																																			
Scaevola frutescens		F	F	R	F	A	F	O	R	F	F	O	F	F	F	F	F	F	F	O	F	F	F	F	F	O	F	F	F	F	F	F	F	97	I
Allophylus timorensis			R	R		R			R	R	R			R	R						O	R	O		R									36	I
Clerodendrum inerme									F	R							R				R			R	R	R		R		O	O	O		33	I
Pipturus argenteus											R											R	O	R			R			R	R	R	O	27	I
Hibiscus sp.																										O	R			O		O	R	15	RI
Polyscias fruticosa																								R				O				O	O	12	RI
Caesalpinia bonduc																								R							R		R	9	I
Polyscias scutellaria																										F						F		6	RI
Sophora tomentosa																											R				R			6	I
Capsicum frutescens																										R						R		6	RI
Codiaeum variegatum																												O				O		6	RI
Vitex negundo																										R						R		6	RI
Cassia alata																						R						R						6	RI
Tabernaemontana divaricata																																R		3	RI

FIG. 28

Fig 29 Species list of herbs. See Fig. 28 for explanation.

ISLETS

HERBS	Matuker.	Pungu.	Tiahu	Mata.	Pepeio	Riku	Hukun.	Matuket.	Tirakume	Tipae	Toko.	Tirakau	Turu.	Tariha	Niku.	Hepepa	Sake.	Para.	Ramotu	Here.	Taka.	Hukuh.	Puma	Tang.	Tetau	Touhou	Matiro	Taringa	Nuna.	Toro.	Ring.	Werua	Hare	% freq.	Origin
Asplenium nidus						R		R	R		O	R		R						F	F	O	F	F	F		F		F	A	A	F	O	54	I
Tacca leontopetaloides		R		R													R		R	F	O	F		F		R	F	F			O		O	39	AI
Lepturus repens													R		R					O				O	O	O	O	O	F	O	O		O	36	I
Stenotaphrum micranthum															R					F	O			F	F		F	F	F	F	F	F	F	36	I
Thuarea involuta																				F	O			F	F		F	F	F	F	F	F	F	33	I
Cyrtosperma chamissonis																					R	F		F	F		F	F	R	A	A	A	A	33	AI
Crinum sp.							R	R										R				O				F	R	R		O		R	R	30	AI-RI
Fimbristylis spathacea																								O		R	O	O		O		O	O	21	I
Musa nana																						R		R			O	O		O	O	O		21	RI
Vigna marina																		R				O		F	O		O					O	A	21	I
Cassytha filiformis					O	R							A					O											O	O				18	I
Triumfetta procumbens													A						R								R		O	R	O			18	I
Fleurya ruderalis																										R					O	O	O	12	I
Hemigraphis reptans																										R	O		R			O		12	RI
Ipomoea pes-caprae																						R		O								R	O	12	I
Ipomoea littoralis																								R	R							R	O	12	I
Hedychium coronarium																											R	R				O		9	RI
Canavalia microcarpa																														R	R		R	9	I
Eleusine indica																										R						O	R	9	RI
Nephrolepis hirsutula																														A	A	F		9	I
Polypodium scolopendria																														R	R		R	9	I
Wedelia biflora																														O		O	A	9	I
Zephyranthes rosea																										O		O				O		9	RI
Digitaria microbachne																										R						O		6	AI
Eragrostis amabilis																										R						R		6	RI
Euphorbia chamissonis																										R							R	6	I
Fimbristylis miliacea																																O	O	6	RI
Ipomoea tuba																													R			O		6	I
Jussiaea suffruticosa																																A	A	6	AI
Mucuna gigantea																																R	R	6	D
Musa sapientum																										O					F			6	RI
Pteris tripartita																																R	R	6	I
Vernonia cinerea																												O				O		6	RI
Achyranthes aspera																															R			3	RI
Adenostemma lavenia																																R		3	RI
Alocasia macrorrhiza																										R								3	AI
Alternanthera sessilis																																O		3	RI
Angelonia angustifolia																																O		3	RI
Asclepias curassavica																										R								3	RI
Blechum brownei																																O		3	RI
Colocasia esculenta																																R		3	AI
Cucurbita sp.																																	R	3	RI
Cymbopogon nardus																																R		3	RI
Cyperus brevifolius																																R		3	RI
Eclipta alba																										R								3	RI
Gomphrena globosa																										R								3	RI
Lindernia antipoda																																O		3	RI
Ocimum sanctum																										O								3	AI
Panicum ambiguum																												O						3	RI
Paspalum vaginatum																																R		3	RI
Phyllanthus niruri																										R								3	RI
Portulaca oleracea																										R								3	RI
Psilotum nudum																																R		3	I
Saccharum officinarum																										R								3	RI
Dioscorea sp.																						R												3	RI

FIG. 29

Fig. 30 Diagrammatic representation of the vegetation, soils, and crab population on Torongahai. Reconstructed on the basis of strip transect 52 ft. in width from the southwest lagoon back shore to the northeast beach ridge oceanward (see Fig. 10). Most luxuriant development of the vegetation occurs oceanward in the highly organic rubble soil. On the puraka banks, pandanus and grass cover are most conspicuous. In the diagram, banana is shown as associate with the puraka. _Guettarda_ and _Scaevola_ are the typical marginal species. The soils show a gradual decrease in organic development lagoonward. In the line graph the right scale (0-20) refers to number of crab burrows and left scale (0-100) to actual number of crabs found in the 52 by 52 ft. quadrats along the transect. Scale at lower right (0-100 ft.) is applicable to horizontal axis only.

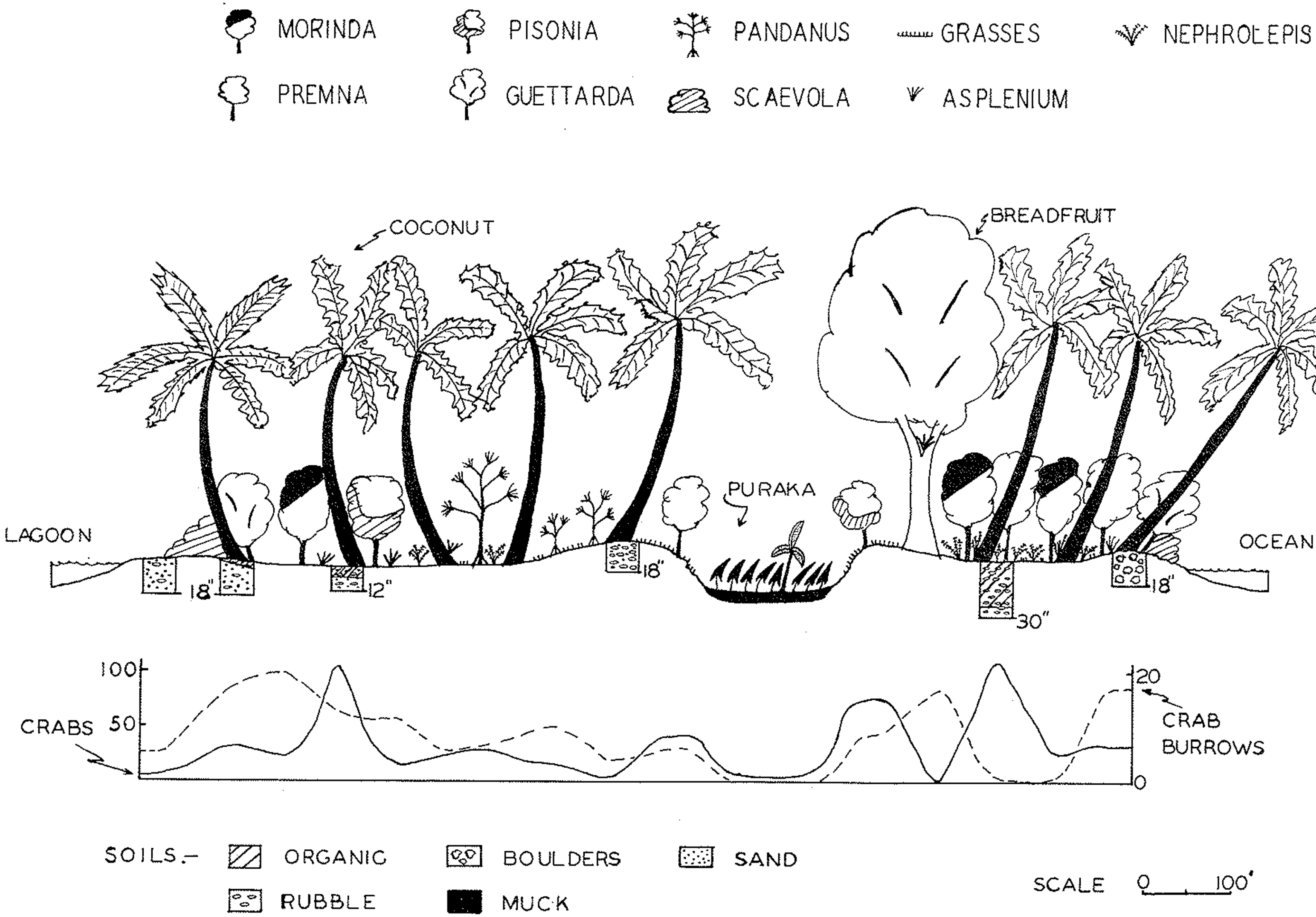

MORINDA
PISONIA
PANDANUS
GRASSES
NEPHROLEPIS
PREMNA
GUETTARDA
SCAEVOLA
ASPLENIUM
COCONUT
BREADFRUIT
PURAKA
LAGOON
OCEAN
18"
12"
18"
30"
18"
100
50
CRABS
20
0
CRAB BURROWS
SOILS.–
ORGANIC
BOULDERS
SAND
RUBBLE
MUCK
SCALE 0 100'

FIG.30

Fig. 31 Bar graph showing number of species found on each islet 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 most densely inhabited islets, Touhou and Werua, recent introductions are most common. Numbers adjacent the islets refer to islet size in acres. See Fig. 28 for further explanation.

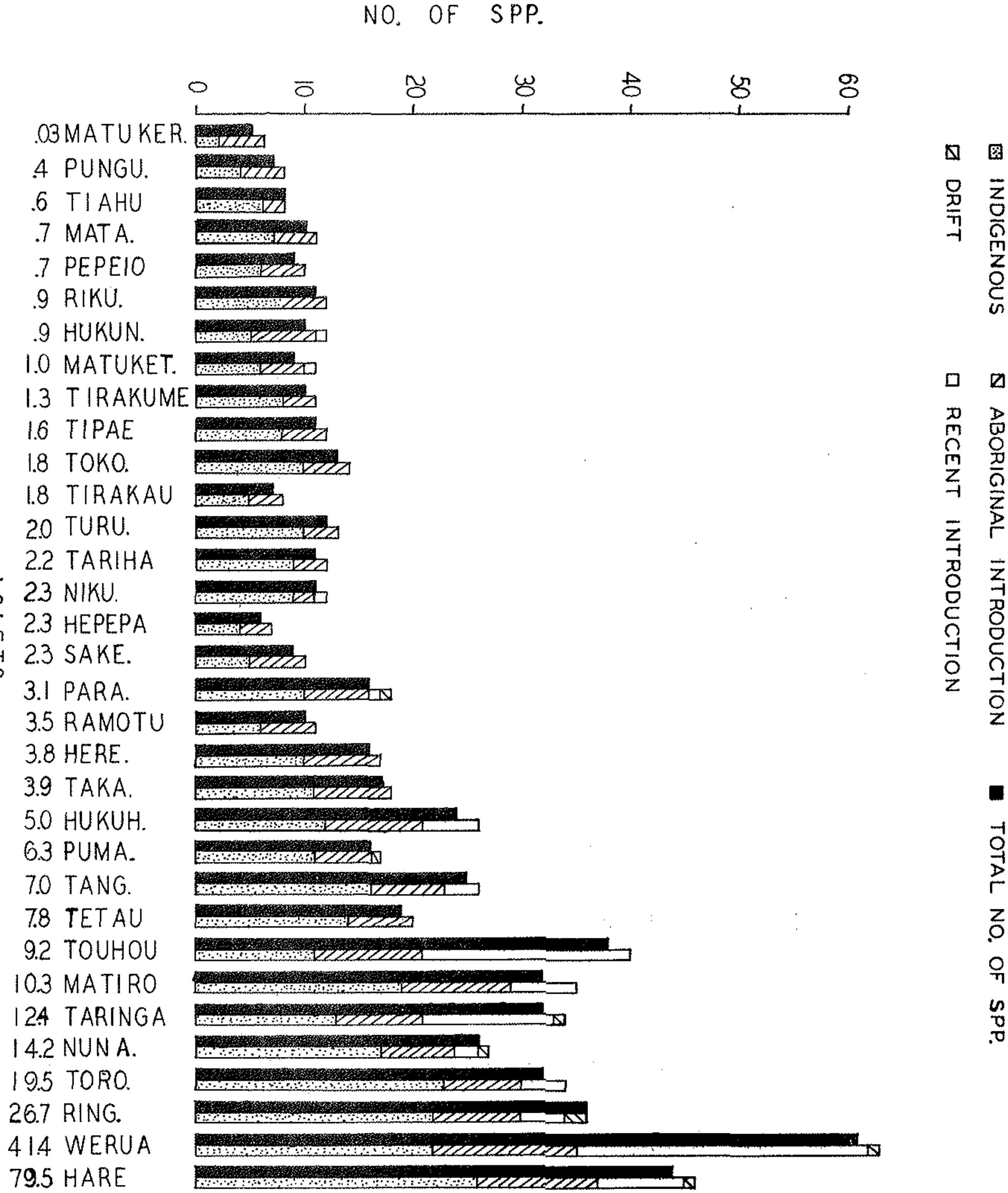

NO. OF SPP.
0
10
20
30
40
50
60
INDIGENOUS
DRIFT
ABORIGINAL INTRODUCTION
RECENT INTRODUCTION
TOTAL NO. OF SPP.
ISLETS
.03 MATUKER.
.4 PUNGU.
.6 TIAHU
.7 MATA.
.7 PEPEIO
.9 RIKU.
.9 HUKUN.
1.0 MATUKET.
1.3 TIRAKUME
1.6 TIPAE
1.8 TOKO.
1.8 TIRAKAU
2.0 TURU.
2.2 TARIHA
2.3 NIKU.
2.3 HEPEPA
2.3 SAKE.
3.1 PARA.
3.5 RAMOTU
3.8 HERE.
3.9 TAKA.
5.0 HUKUH.
6.3 PUMA.
7.0 TANG.
7.8 TETAU
9.2 TOUHOU
10.3 MATIRO
12.4 TARINGA
14.2 NUNA.
19.5 TORO.
26.7 RING.
41.4 WERUA
79.5 HARE
FIG.31

Fig. 32 Line graph showing number of species plotted against islet size. Although the islets vary from .03 of an acre to 79.5 acres the smallest islet was deleted since plotting was facilitated and no change in the relationship occurred.(See Fig. 31). Note the two linear relationships. On those islets 3.5 acres or less there is little variation in number of species per islet. However, on those larger there is a continuous increase in number of species with increase in islet size.

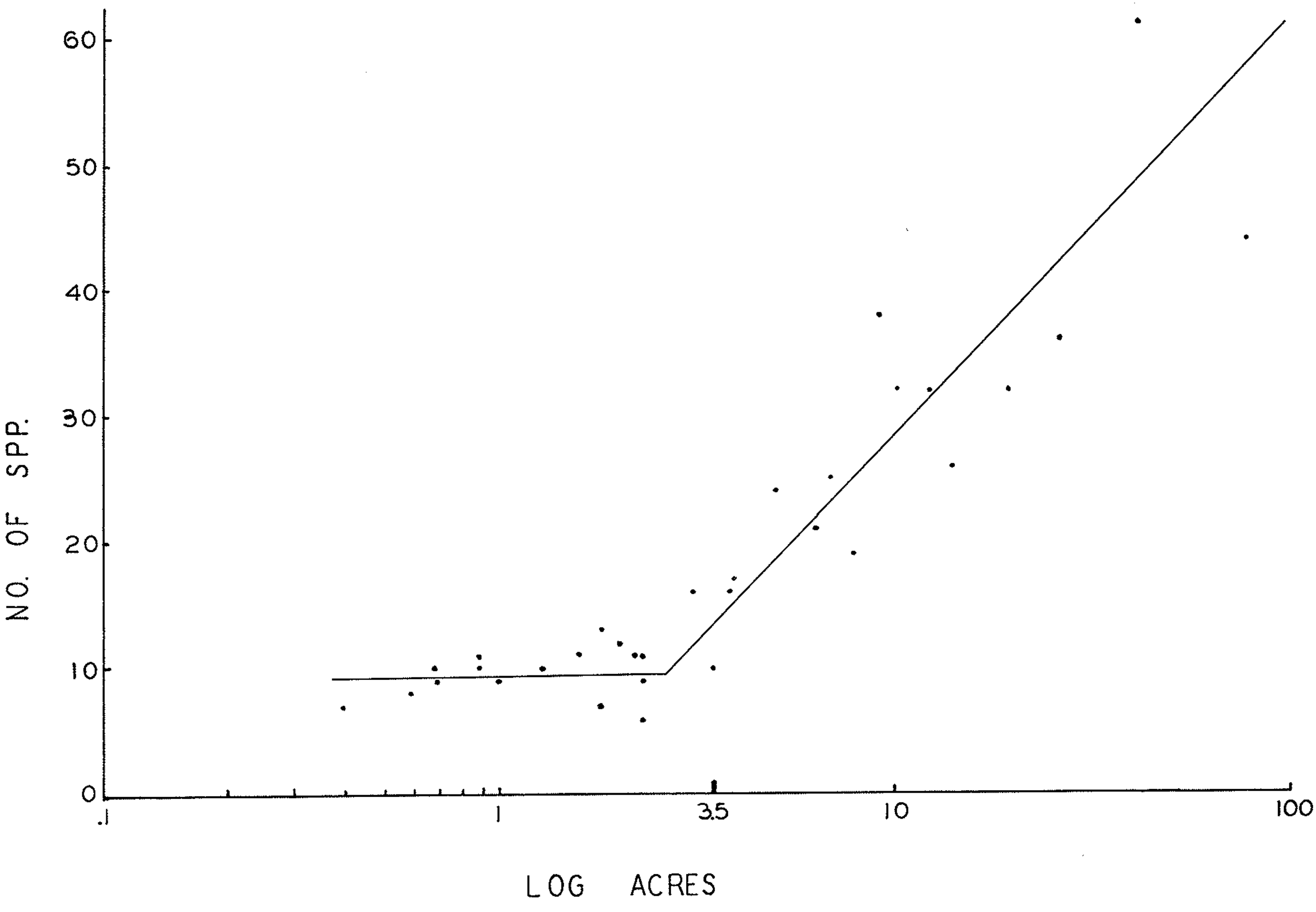


FIG. 32

Fig. 33 Diagrammatic representation of the marginal vegetation on beach ridges and lagoon shore, including sand bars, of the smaller islets. Guettarda speciosa and Scaevola sericea dominate. However, the latter is usually less abundant on the windward side. Its occurrence oceanward is apparently correlated with the protection of elevated off shore reef rock. Lagoonward Scaevola is a conspicuous pioneer on the sand bars.

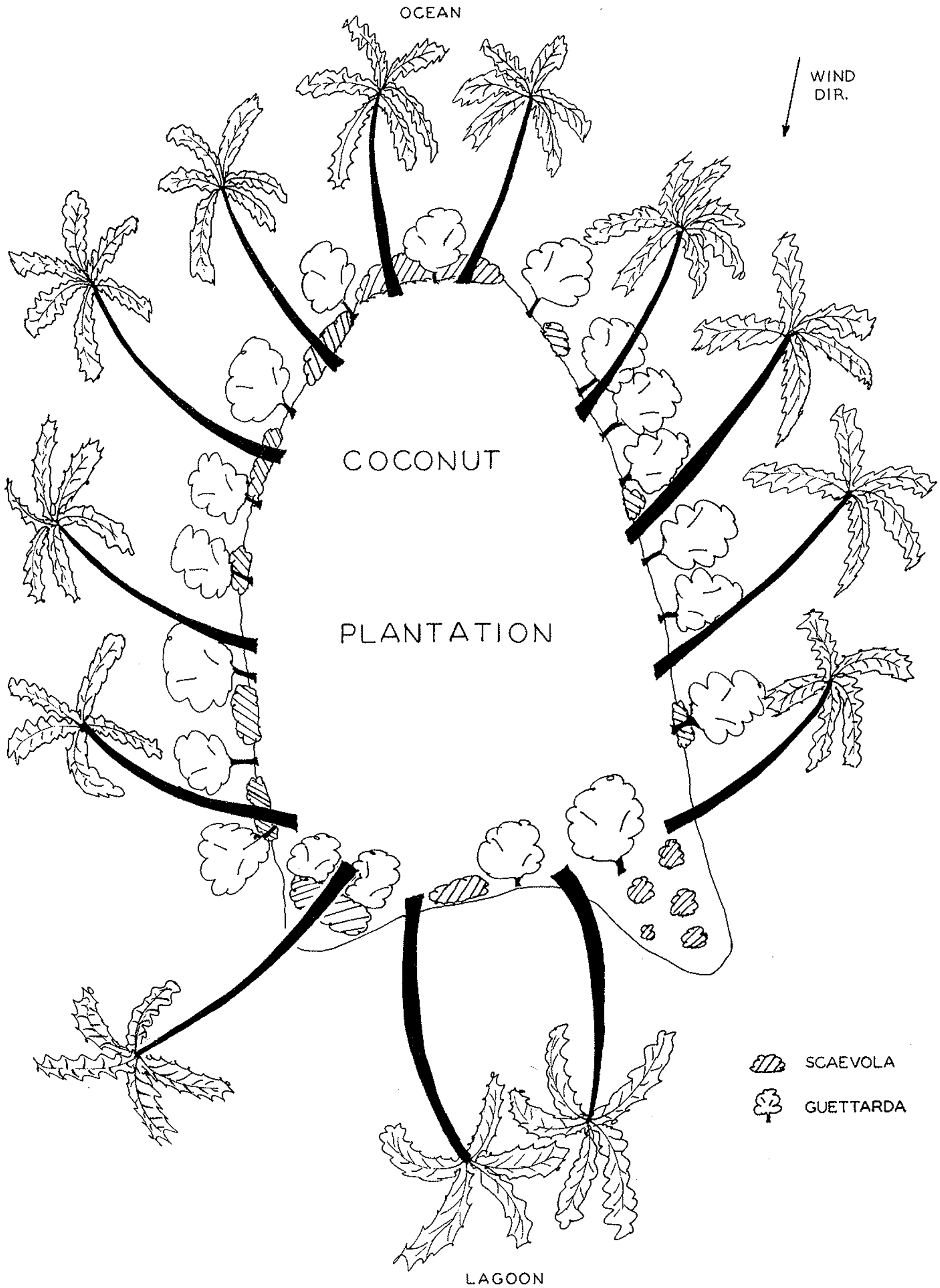

OCEAN
WIND DIR.
COCONUT
PLANTATION
SCAEVOLA
GUETTARDA
LAGOON

FIG. 33