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**VEGETATION AND FLORISTICS
OF THE TONGATAPU OUTLIERS**

BY

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Abstract

On the 21 small islands located within the northern bays and reef systems of Tongatapu, Tonga, species of terrestrial flora present were identified, and vegetation units and geomorphological features surveyed on 12 that were previously unmapped. A species/ area plot of the data shows that rock islands are consistently more diverse than sand islands. Size of flora is also a function of frequency of human use of islands, which increases with area, and proximity to the mainland. Floristic composition varies from east to west across the group, with increasing shelter provided by the mainland from prevailing winds.

Introduction

Tongatapu is the largest of a group of islands that form the Kingdom of Tonga in the southwest Pacific (Latitude 21°08'S, Longitude 175°11'W). The island has an area of 245 km², with a maximum dimension of 35 km from east to west. It is composed of raised Quaternary limestone (Taylor & Bloom 1977), with a low undulating topography. The cliffed south coast is fringed by a raised algal ridge (Ladd & Hoffmeister 1927), while the leeward north shore is fringed by mangroves and discontinuous barrier reefs.

In association with this reef system 21 islands of 0.008 to 51.8 ha. (0.02 to 128 acres) occur to the north of Tongatapu (Figure 1). They are of two geomorphological types: "sand cays" are back reef sand deposits consolidated by beachrock (Tufaka, Fafa, Pangaimotu, Manima, Oneata, Malinoa, Monuafe, Onevai, Onevao, Motutapu, Fukave, Nuku, Ata and Tau), whereas "motus" are of raised limestone (Toketoke, Atata, Polo'a, Alakipeau, Velitua Hihifo, Velitua Hahake and Mokotu'u). The larger islands of the former type may have a raised limestone core around which sand and reef breccia have accumulated. Islands are mentioned in east-west order throughout this paper.

The islands result from the late Pleistocene and Holocene sea level history of the area. A narrow terrace at 7 m in the southern cliffs of Tongatapu was formed during the last interglacial (135±18 ka) (Taylor 1978). Since all raised limestone islands of the

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Tongatapu outliers are of 6 to 7 m in height, they would seem to be reef remnants from this highstand. The Holocene sea level record has included a stillstand 2.2 m higher than present, dated between 6500 and 5800 BP (Bourrouilh & Hoang 1976, Taylor & Bloom 1977). This mid-Holocene highstand was of regional extent, and the recent fall of sea level to present levels has been shown to promote sand islet formation (Schofield 1977). The sand cays of the Tongatapu islets are likely composed of dead reef material and scoured sand deposited on reef flats as sea level fell.

The climate of Tongatapu is tropical, with two seasonal divisions. The warmer wet season is from November to April, with warmest mean monthly temperature of 26.1°C in February (Thompson 1986). Two thirds of the 1900 mm mean annual rainfall falls during the wet season, which is also the cyclone season. The cooler dry season is from May to October, with coolest mean monthly temperature of 21.2°C in August, when droughts may occur periodically.

The south-east trades show remarkable constancy of direction, winds blowing from the eastern quadrant for 64.8% of the time (Thompson 1986). Cyclones during the historic period show periodicity of 20 to 30 years (McLean *et al.* 1977, Oliver and Reardon 1982) with moderate to severe cyclones affecting Tongatapu 1874-1883, 1912-1913, 1930, 1964 and 1982. The most severe storm damage in recent years came with cyclone Isaac, tracking south-west through the Tonga group in early 1982 (Thompson 1986, Revell 1982). This affected Tongatapu most severely on the 2nd and 3rd of March, with winds moving from south-easterly, through easterly, then strongest winds from the north-east and north on the 3rd, with gusts up to 92 knots recorded. On Tongatapu, most low-lying northern areas were badly affected by floods from high seas and a heavy swell (Oliver & Reardon 1982, Woodroffe 1983). Variability in damage was a function of aspect, and degree of protection within the central lagoon and behind reefs.

Ocean tides at Nuku'alofa are semi-diurnal with a slight diurnal inequality. The mean tidal range is 1.07 m, and the spring range is 1.22 m (US National Oceanic and Atmospheric Administration 1986).

The terrestrial flora of Tongatapu comprises 340 vascular plants (Arthur Whistler, pers. comm.). The natural vegetation of inland Tongatapu has been cleared for *Cocos* plantations and intensive small-holder agriculture (Thaman 1975), except for a small forest near Fua'amotu airport. Mangrove forests fringe the north shore and the central Fanga 'Uta lagoon, and natural coastal forest fringes the rugged south coast, and occurs on the northern islets. The vegetation of four sand cays nearest to Tongatapu: Pangaimotu, Makaha'a, Manima and Oneata was mapped by Stoddart in 1969 (Stoddart 1975). Following Cyclone Isaac in 1982, Woodroffe mapped these as well as Tufaka, Fafa, Monuafa and Malinoa (Woodroffe 1983).

Tongatapu is the most populated island in the Kingdom of Tonga, with 61 000 in the 1976 census, most living around the capital, Nuku'alofa. The terrestrial ecosystems of all outlier islands have been disturbed as a result of human influence. The intensity of human impact can be categorised on the basis of visitor frequency or size of the resident population.

- 1) Islands with many visitors a day include Atata, Fafa and Pangaimotu, with tourist resort developments; Manima and Oneata, which can be walked to easily at low tide; and Ata, which is a low security prison camp.
- 2) Islands with several visitors a week are those with a resident family, comprising Onevai, Velitoa Hahake and Fukave. Motutapu, periodically used for training by the Tonga Defence Force (TDF) is also included, as is Velitoa Hihifo, which is used as a TDF store, and looked after by the family on Velitoa Hahake.
- 3) Islands with several visitors a month are those used for cultivation, or popular stopping places on fishing or recreational boat trips. These include Polo'a, Alakipeau, Makaha'a and Nuku.
- 4) Islands with infrequent visitors may have low intensity agricultural use, and tend to be smaller and/or further away from Tongatapu. These include Toketoke, Tufaka, Monuafe, Malinoa, Mokotu'u, Onevao and Tau.

Examination of the combined effects of alternative geomorphological types, varied area, isolation and degree of human disturbance on the distribution of members of a relatively large pool of terrestrial plant species forms the basis for this study.

Methods

Islands were visited between May 1987 and January 1988, and on all except the larger island Atata, a total species count was made of vascular plants. Morphological features and vegetation units were mapped for those islands not covered by Woodroffe (1983), and area determined.

It is possible to walk to Pangaimotu (approaching from the east), Manima and Oneata, with sand flats between being quite dry at low tide. Polo'a and Alakipeau can be reached by horse, or a wet walk, along a path through seagrass from Muifonua Point. All other islands must be reached by boat, with a frequent tourist boat service to Atata, Fafa and Pangaimotu.

Morphological features and vegetation units were mapped on Toketoke, Polo'a, Alakipeau, Velitoa Hihifo, Velitoa Hahake, Onevai, Onevao, Motutapu, Fukave, Nuku, Ata and Tau (Figures 2 to 13), these islands not being mapped previously. On smaller islands (Toketoke, Alakipeau, Velitoa Hihifo and Tau), this was by tape-and-compass, with a central line and perpendicular offsets to each coast every 25 m, and by pace-and-compass on larger islands, with systematic transects run inland from the coast. Maps of other islands from 1982 are given by Woodroffe (1983).

Area was determined by laying a transparent grid over these maps, and counting square mm. Island areas given in Table 7 are defined by limit of vegetation, not high tide mark. Future researchers should note that the area figures available from the Ministry of Lands and Surveys are rounded to the nearest acre, and are of variable accuracy.

Physiognomic types identified in mapping were coastal trees, shrubs, herbs, coconut woodland and mangroves, though sections dominated by a particular species are identified separately. Most units were diverse, a function of the relatively large flora of Tongatapu. Species present were noted or collected during surveying, hence larger

islands were less intensively covered than smaller. Suggested error margins for species missed on the total species figures (Table 7) are +1 on small islands and +5 on larger islands .

Species names and physiognomic classifications are largely taken from Yuncker (1959), Smith (1979-81), and Whistler (1983), also a number of experts assisted in identifying species, acknowledged below. Use was also made of Yuncker's herbarium collection, held at the Ministry of Agriculture, Forestry and Fisheries Research Farm at Vaini.

Vegetation units

An inventory of the species of trees, shrubs, herbs, vines, grasses and sedges, and ferns on each island is presented in Tables 1 to 6. Island areas and species totals are given in Table 7. A total of 203 vascular plants were identified, inclusive of weeds and cultivated plants. The vegetation units shown in Figures 2 to 13 are described below.

COASTAL TREES

The composition of coastal tree units varied from west to east across the island group, with shelter provided by Tongatapu from the prevailing south-east trades increasing westwards. Maria Bay is sheltered behind the reef to the east of Polo'a and Atata (Figure 1), causing western shorelines of Polo'a, Alakipeau and the southern spit of Atata to be dominated by Vitex, in association with Thespesia, Cerbera and Hibiscus.

Coastal thickets dominated by Hibiscus occurred on islands central to the group, on Pangaimotu, Makaha'a, Manima and Oneata, as shown in Woodroffe's (1983) maps. Beach thickets were in association with Thespesia, Hernandia and Cordia. On the raised limestone islands of Toketoke, Northern Atata, and parts of Alakipeau and Velitoo Hihifo, particularly dense Hibiscus stands occur.

In more exposed, windward locations, Acacia, Pandanus, Tournefortia (= Messerschmidia), Pisonia and Phaleria, Terminalia and Leucaena become dominant. The maps of Toketoke, Polo'a and Alakipeau show Pandanus stands on the edges of east facing overhanging rock, and Table 1 in listing islands from west to east clearly shows increased occurrence of these species towards the east. Casuarina also showed greater frequency towards the east, but only on rocky outcrops. Tournefortia and Pandanus frequently occurred opportunistically within shrub and herb units, as shown in Plate 1.

Certain islands were unusually dominated by one species in particular, showing that competitors were absent or poorly established. Examples were Leucaena on Tufaka and Monuafe, Neisosperma on Fafa, Syzygium richii on Motutapu and Pisonia on Fukave and Nuku. Motutapu featured an unusually diverse and well established coastal forest, presumably due to conservation by TDF ownership.

COASTAL SHRUBS

Frequent components of the coastal shrub unit were Scaevola, Colubrina, Wollastonia (= Wedelia) and Jasminum didymum on all islands, also Clerodendrum more commonly on western islands, and Suriana more commonly on eastern islands. Wollastonia was most frequent on the edges of raised limestone cliffs, and Scaevola opportunistic of sand areas recently colonised by vines and herbs, such as the south point of Malinoa.

HERBS

Most of the 52 herbs listed in Table 3 are weed species inadvertently introduced by man. Hence the islands identified as most frequently visited have floras significantly increased by these weeds (Pangaimotu, Manima, Oneata and Ata), while those uncommonly visited have very few or none (Toketoke, Tufaka, Malinoa, Mokotu'u and Tau).

The weeds Rivina, Stachytarpheta and Lantana are most successfully established, commonly on untended cultivated areas under Cocos. Rivina forms extensive stands across central areas of Fukave, Stachytarpheta being absent, as shown in Plate 2.

Bidens, Emilia, Euphorbia hirta, and Malvastrum are also common. These weeds are most successful in open areas under Cocos, forming a lawn-like cover around buildings, such as around the resorts on Fafa and Pangaimotu, also the west of Velitua Hihifo and Motutapu, and the east of Fukave and Ata.

Goats on Motutapu and pigs on Makaha'a disrupt the herb layer by rooting and grazing, causing fewer herbs to be present on these islands.

Of the native coastal herbs, Sesuvium is most common, occupying large expanses within the mangrove area of the centre of Onevai, also colonising offshore rocks and upper portions of beachrock on other islands.

On the more extensive beaches of Malinoa and Tau in particular, areas of loose beach sand are colonised by the vines Canavalia, Vigna and Ipomoea pes-caprae, and the grass Thuarea, as shown in Plate 3. Euphorbia atoto is also a successful coloniser of loose sand, seeming to be a native element of the flora.

MANGROVES

The largest mangrove area on the Tongatapu outliers is the central area of sand flats on Onevai, now open to tidal influence from the south, though the chart by Aldrich (1888) shows this area to open to the west. Patch stands of Rhizophora stylosa are most extensive, though Bruguiera gymnorrhiza and Rhizophora mangle (= R. samoensis) also occur. Slightly higher intertidal sands are covered by Sesuvium.

Rhizophora occurs on sheltered shorelines of other islands, but merely as isolated individuals, offshore of the northwest point of Pangaimotu, as photographed by Stoddart (1975), and on beachrock to the west of Polo'a and Alakipeau. R. stylosa is more common than R. mangle in these locations, showing the preference of the latter for more brackish waters (Chapman 1970).

Excoecaria is a mangrove species, but occurs on most islands as individual trees in beach habitats.

COCOS WOODLAND

On most islands, Cocos woodland occurred inland, and many examples of planting were seen. The east of Tau was cleared and planted with Cocos in 1985, and Woodroffe (1983) described young Cocos palms to 7 m on Monuafe, which were absent in 1987. Planted lines are particularly apparent on Fafa and Pangaimotu. Headless stumps from the 1982 cyclone still remained on Toketoke and Tufaka. On Onevao and Makaha'a, Cocos occurs to the edge as these islands are badly eroding, with loose soil cliffs to 2 m in height on all sides.

Cocos occurs in emergent association with coastal trees such as Calophyllum, Neisosperma, Barringtonia, Cerbera, and Hibiscus. Planted species such as Carica, Morinda and Artocarpus are also common, as well as the weed-like Psidium. More disturbed units under Cocos are sub-classified on the maps as "Cocos over herbs and low weeds", including both the lawn-like cover described above and recently cleared areas on Tau; "Cocos over shrubs and scrub" is a less tended version of this, and where the palms rise above a ground cover of tall Panicum maximum, "Cocos over grass" is used.

GRASS

Areas of open grass occurred only on raised limestone islands, of tall clumps of Panicum (up to two meters high) interdispersed by occasional weeds, vines and shrubs. Large areas occurred on Toketoke and Velitua Hihifo, and could be resultant from neglect after clearance of Hibiscus thicket.

The shooting range on Motutapu is also mapped as grass, but this is a closely mown open lawn.

Fauna

Three islands had large bird populations: the reef heron (Egretta s. sacra) on Toketoke, and the common noddy (Anous stolidus) on Fukave and Nuku. The latter were in association with the large Pisonia stands. Identification was from Watling (1982).

The flora of Mokotu'u is an interesting reflection on transportation of seeds by birds. This is a limestone outcrop to the NW of Onevai, 10 m in diameter and about 6 m high, undercut on all sides. Drift seeds could not reach it, and though I heard

accounts of people climbing onto it, this would be extremely rare. Hence the species present must result from seed dispersal by birds.

Discussion of floristics

A log area/ number of vascular species plot for the Tongatapu outliers is given in Figure 14, showing that there is an approximately linear relationship as described by Preston (1962) and MacArthur and Wilson (1967). The scatter of data around this trend can be explained by several factors.

Sand cays and motus are distinguished on the graph, clearly showing that at all island sizes, raised limestone islands are more diverse than sand cays. Two factors seem to be of importance, degree of storm disturbance, and habitat heterogeneity. Woodroffe (1983) noted that raised reefal limestone coasts underwent little morphological change during Cyclone Isaac, while greatest changes were observed on sand islands. Hence, referring to MacArthur & Wilson's (1963) equilibrium model, where species number is a result of balanced immigration and extinction rates, the extinction rate resulting from storms will be higher on a sand cay than a motu of the same area. Protection is given by the irregular and immobile rock surface, that also provides a diversity of microhabitats between hollows and outcrops, as well as a surface area that exceeds the spatial area of the island. By comparison, sand cays are uniform in microclimate and micromorphology. This refinement of the MacArthur & Wilson (1967) species/ area model of island biogeography on the basis of habitat diversity was made by Sauer (1969) and Buckley (1982), the latter finding similar variance in diversity of flora on sand and limestone islands in the Lowendal archipelago, Western Australia.

Floristics of the islands is also shown to be influenced by the degree of human disturbance, on four recognisable scales as described. Chaloupka & Domm (1986) found on 10 cays of the Southern Great Barrier Reef that percentage of alien plant species recorded on a cay is positively related to the frequency of human visitor traffic to that cay, independent of cay size. On the Tongatapu outliers, it would seem that resources on islands larger than 8 ha. cause them to be inhabited regardless of location, while all islands under 4 ha. are uninhabited, with the exception of Velitua Hahake. In Figure 14, the sand cays show greatest vertical scatter of data within these area thresholds, some being frequently visited and therefore having larger floras with weeds and cultigens, while others are of a similar area and yet relatively undisturbed.

Within this marginal range of 4 to 8 ha., degree of human influence and consequent species number is a function of distance from Tongatapu. Oneata is permanently inhabited, Motutapu intermittently inhabited, and Nuku deserted to leave decaying buildings. As stated earlier, habitation of Velitua Hahake is an unusual case, resulting in lack of normal vegetation units and a disturbed appearance. In this context, MacArthur & Wilson's (1967) proposition that isolation results in a low species number on islands would be true. In the more traditional application, the more distant islands of the group, Malinoa and Tau, occur below the best fit line in Figure 14, but are not significantly more depauperate in flora relative to other sand cays with a similar level of human visitation further south.

Data from other island groups also show greatest range in number of species on islands of 4 to 8 ha., from the Belize sand cays (Stoddart & Fosberg 1982: 531) and Kapingamarangi Atoll (Niering 1963: 137), suggesting that within this range there is variable human influence. This could be due to distance from population centres as shown for Tongatapu, or some other factor of convenience for human use, such as persisting dense thicket, or swampy areas.

Variation in floristic composition of the Tongatapu outliers that is related to island position has been described, all islands east of Motutapu being exposed to prevailing winds, while those to the west are in the lee of Tongatapu. This causes greater frequency of certain plants to the west or east according to their ecological preferences, and on a smaller scale, similar patterns are visible in comparison of west and east coasts of each island.

The Tongatapu outliers data do not show a constant number of species on all islands of less than 1.4 ha. as identified by Wiens (1962) and Whitehead and Jones (1969). Rather, species number of these smaller islands is quite varied, owing to differences in substrate type and frequency of human visitation. However, the flora of small sand islands such as Tufaka and Monuafe did seem to be less well established than larger islands, with many species comprising the counts being just one individual germinated on the upper beach.

Conclusion

Relative to other locations where species/ area studies have been carried out, the Tongatapu outliers have a large local flora owing to the size of Tongatapu, causing an overall greater species density on all islands. This provides a useful data set for comment on the factors controlling floristics of the group. Raised limestone islands are shown to be more diverse than sand cays, reflecting habitat diversity and substrate stability. Floristic composition varies from east to west across the group, from windward to leeward conditions. A threshold of 4 to 8 ha. of uncertainty between no and certain anthropochory is identified, within which degree of human use and consequent floristic changes are a function of convenient use of the marginal island, with distance from the mainland being the most important controlling factor here. These factors cause variation within a basic trend for number of species to be related to island area.

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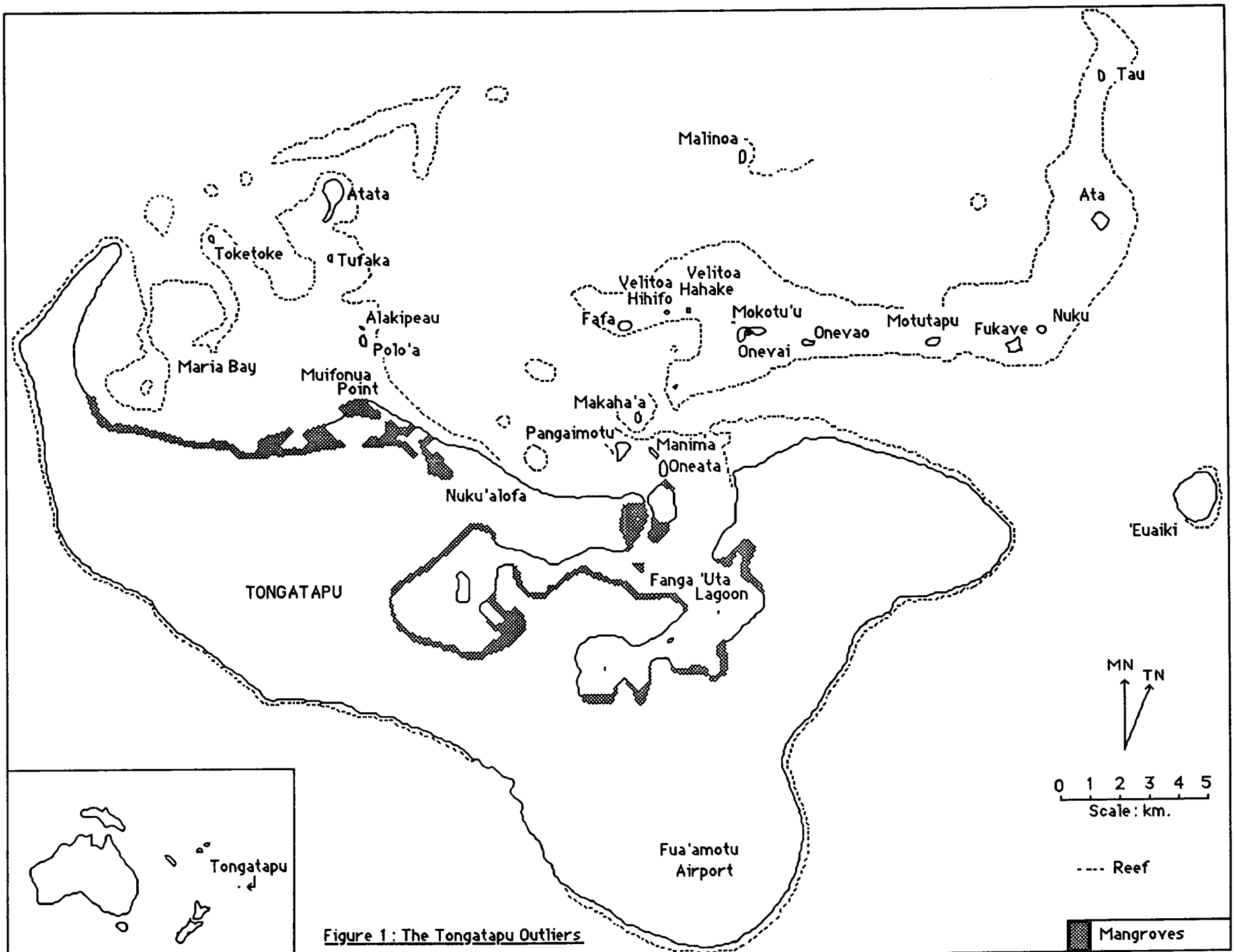



























Figure 1: The Tongatapu Outliers

Key to Figures 2 to 13

	Herbs and low weeds		Pandanus
	Shrubs and scrub		Casuarina
	Coastal trees		Pisonia
	Hibiscus thicket		Excoecaria
	Cocos woodland		Calophyllum
	Cocos over grass		Cerbera
	Cocos over shrubs and scrub		Pittosporum
	Cocos over herbs and low weeds		Tournefortia
	Grass		Hernandia
	Mangrove		
	Beachrock		
	Sand		
	Raised limestone cliff		
	Building		
	Fence		
	Path		

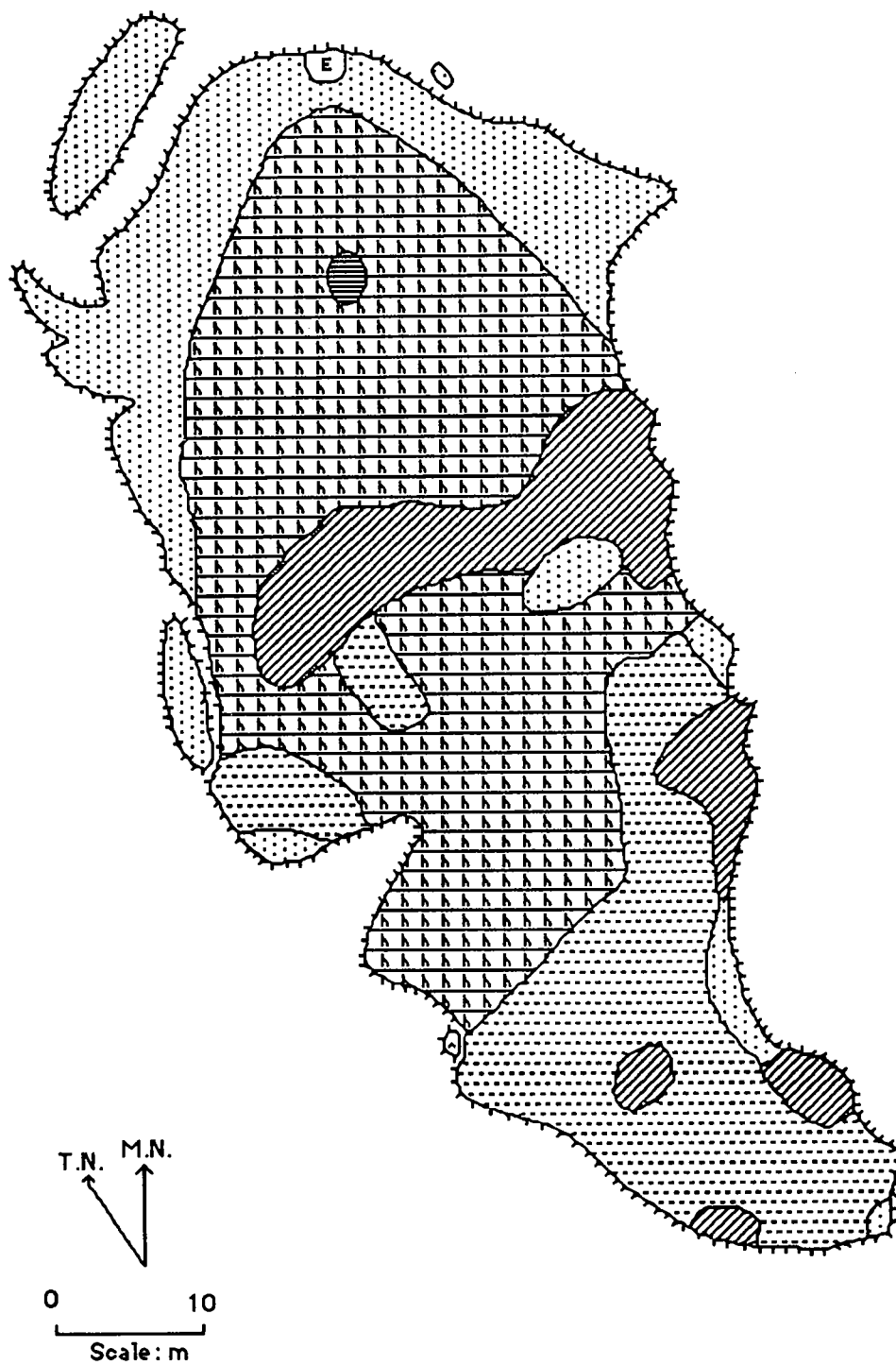


Figure 2: Toketoke

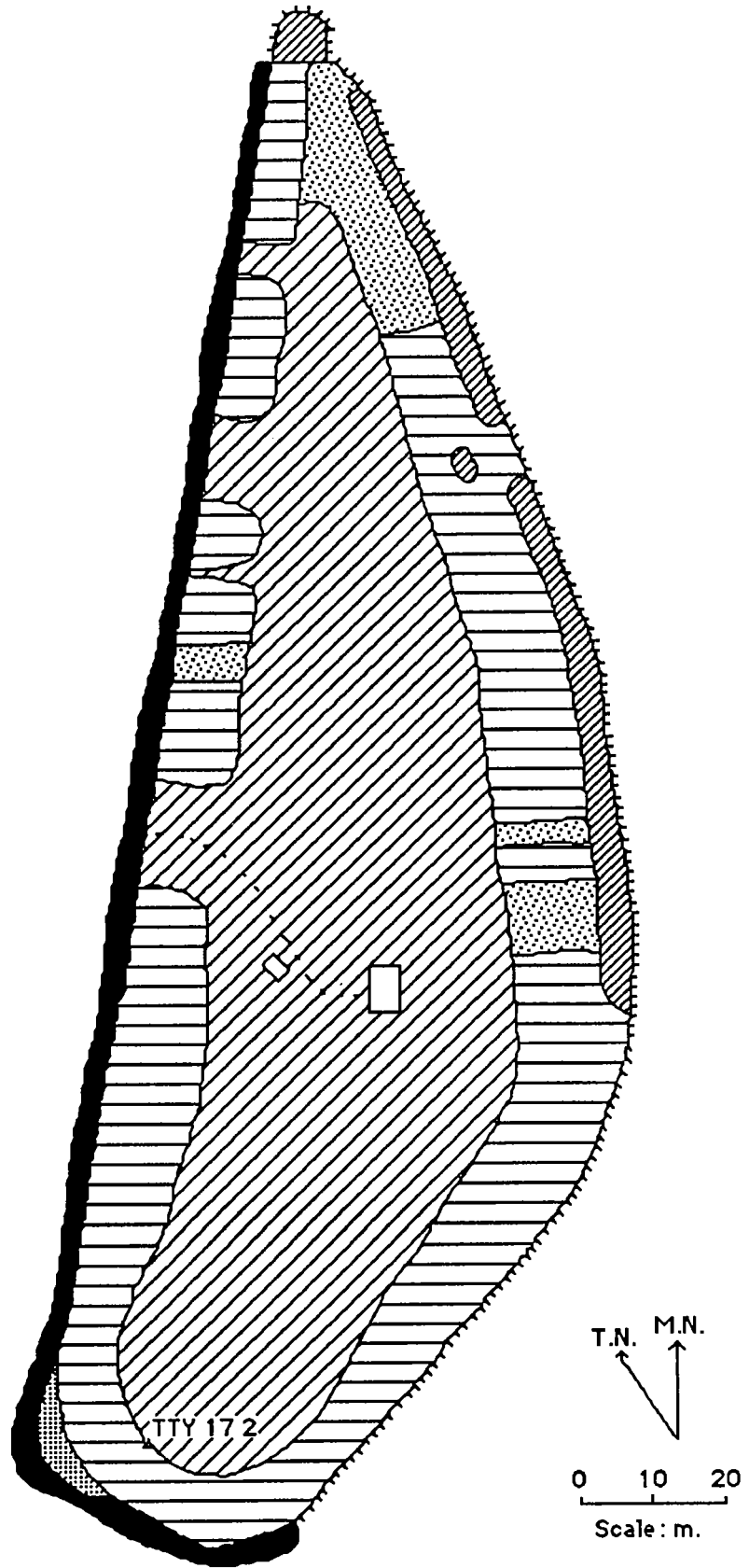


Figure 3: Polo'a

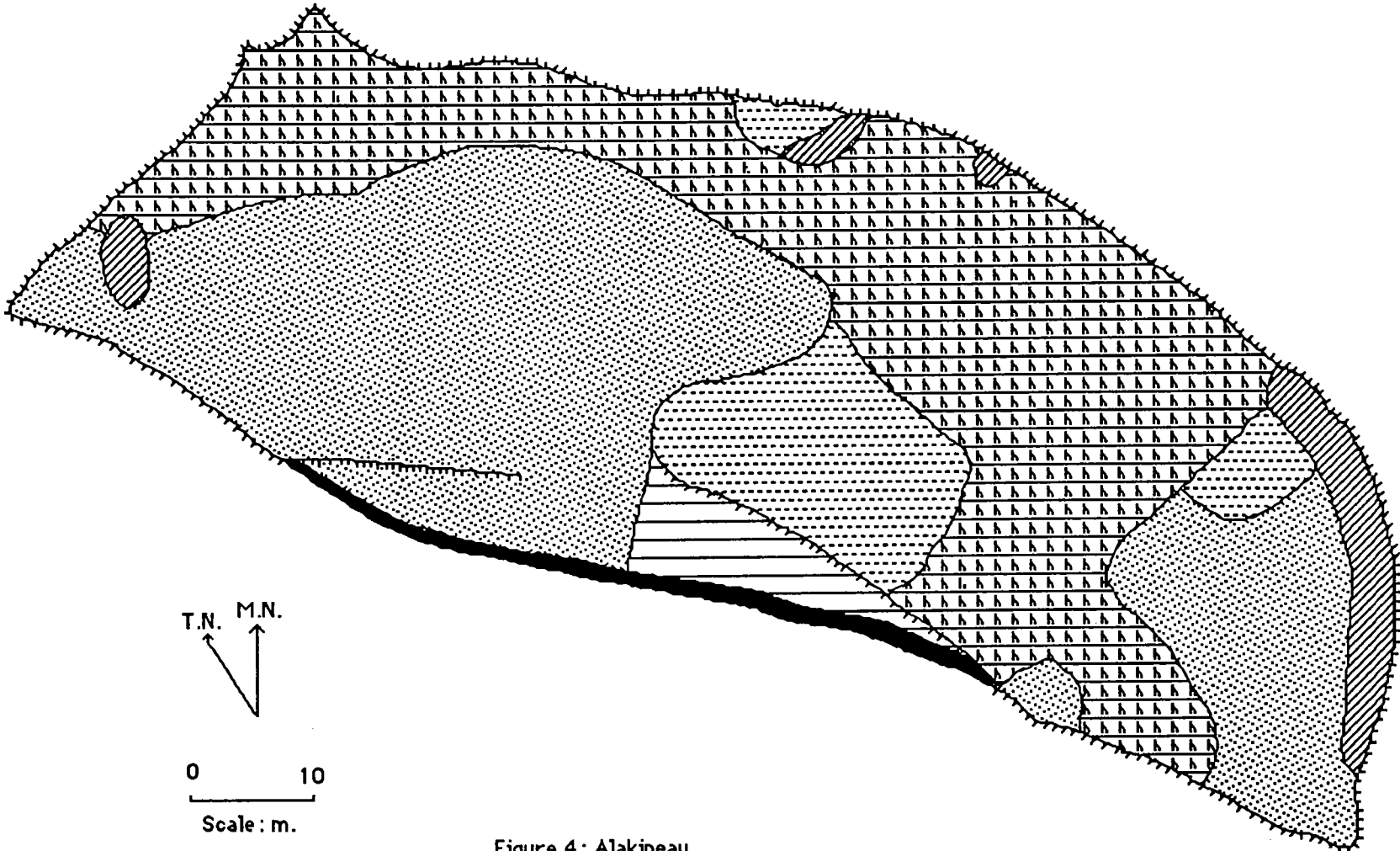


Figure 4: Alakipeau

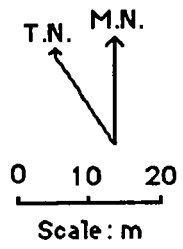
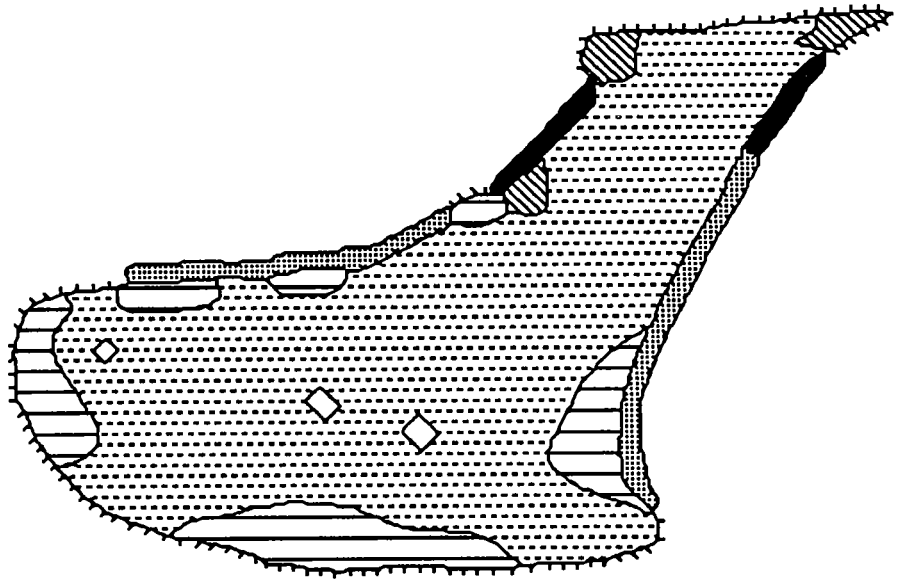


Figure 5: Velitua Hihifo

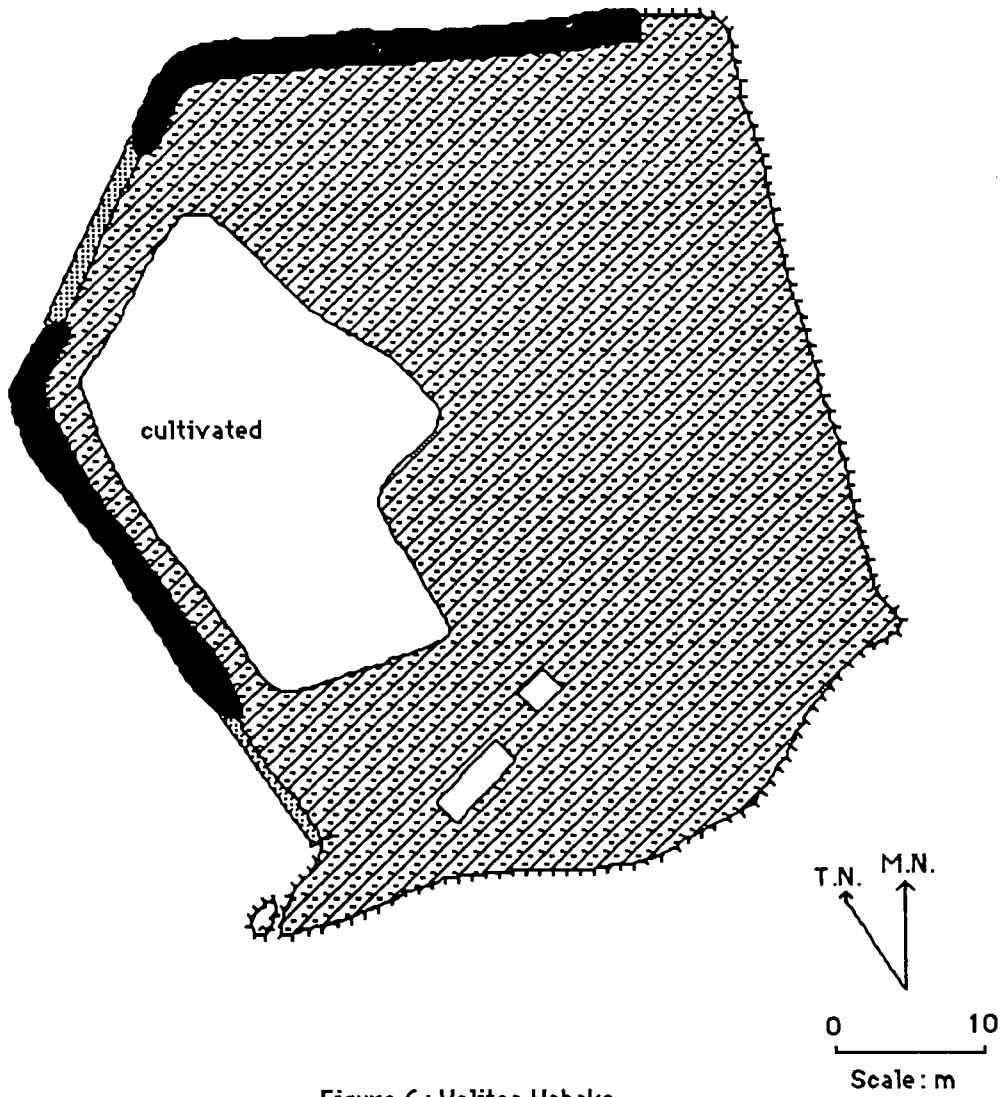


Figure 6 : Velitooa Hahake

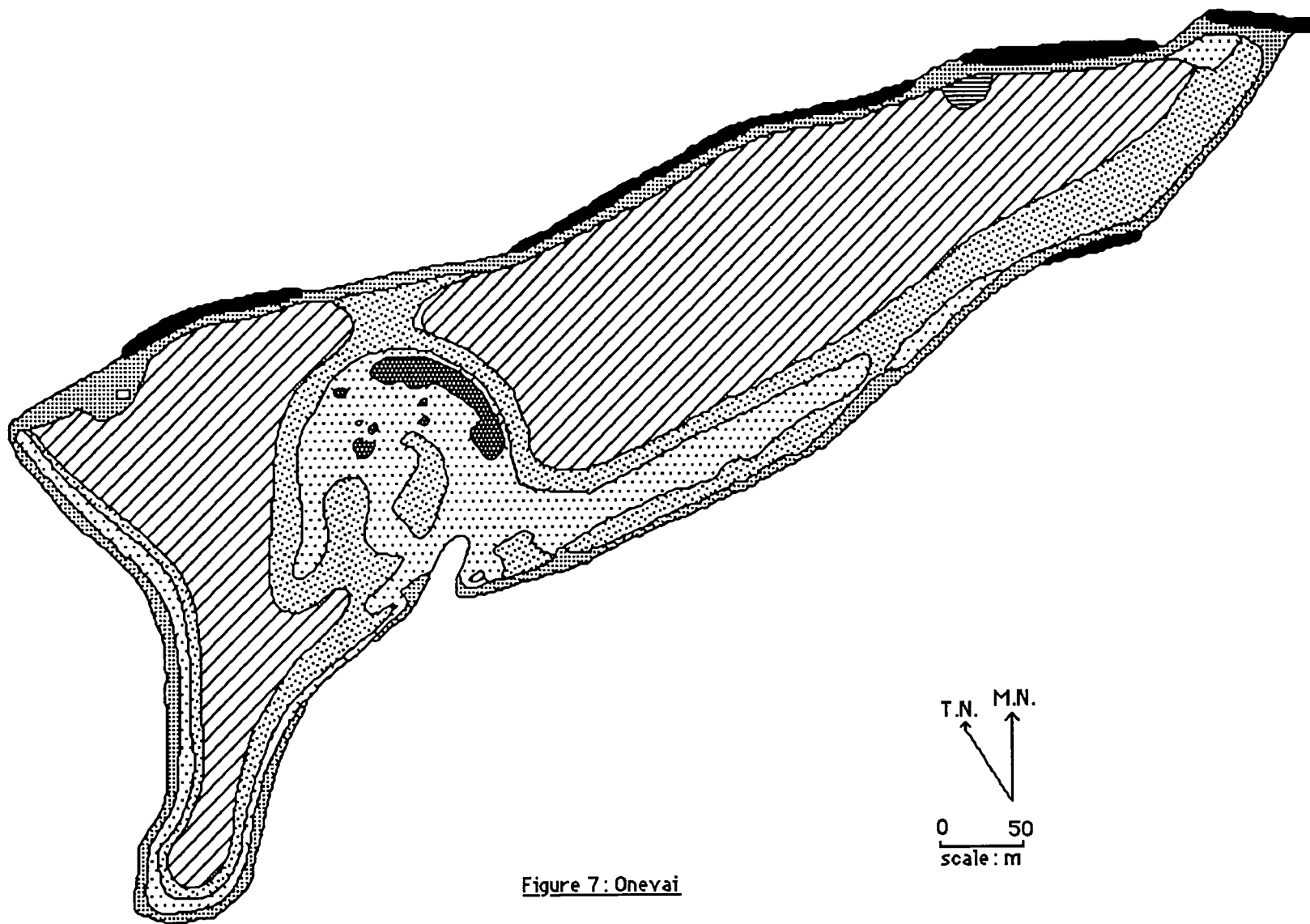


Figure 7: Onevai

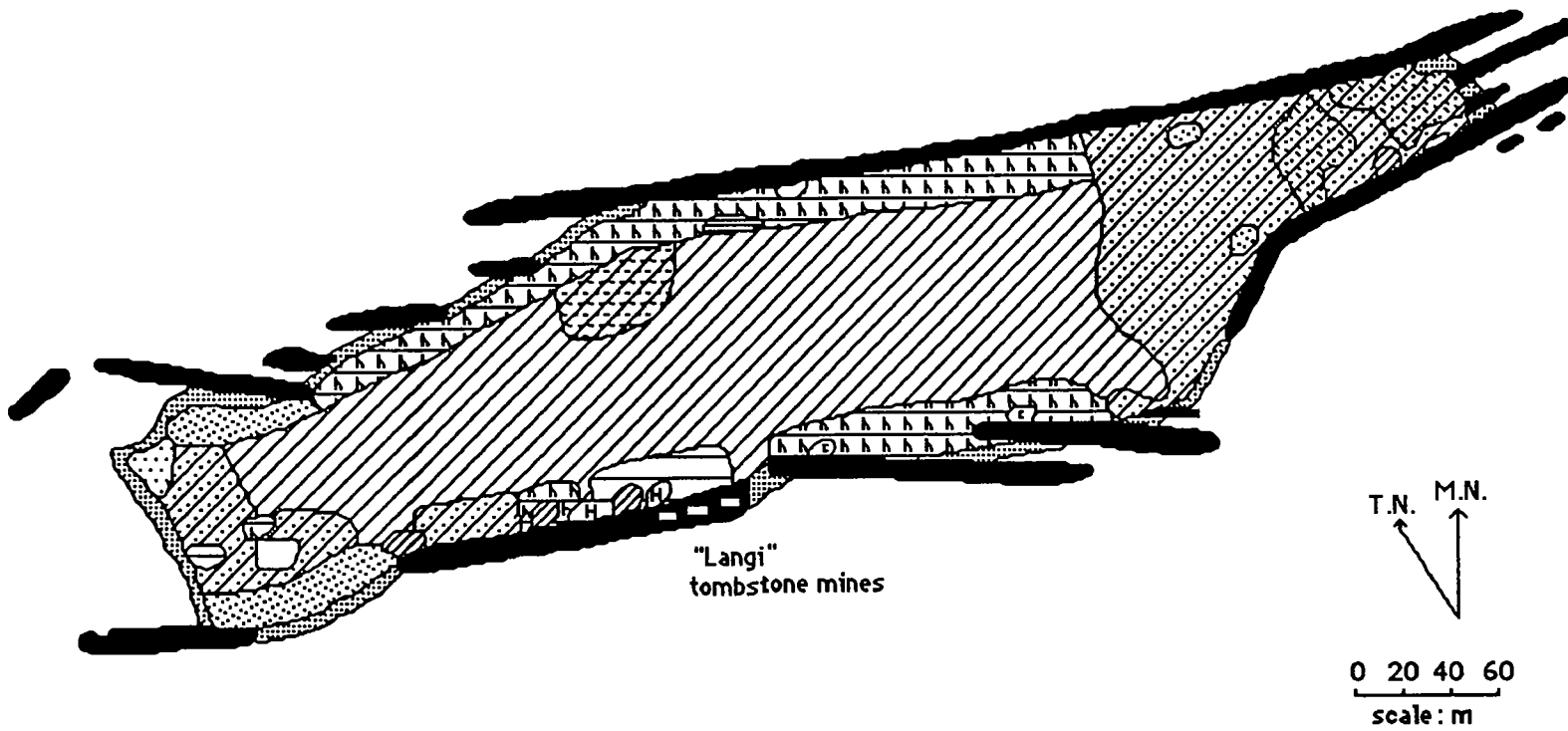


Figure 8 : Oneyao

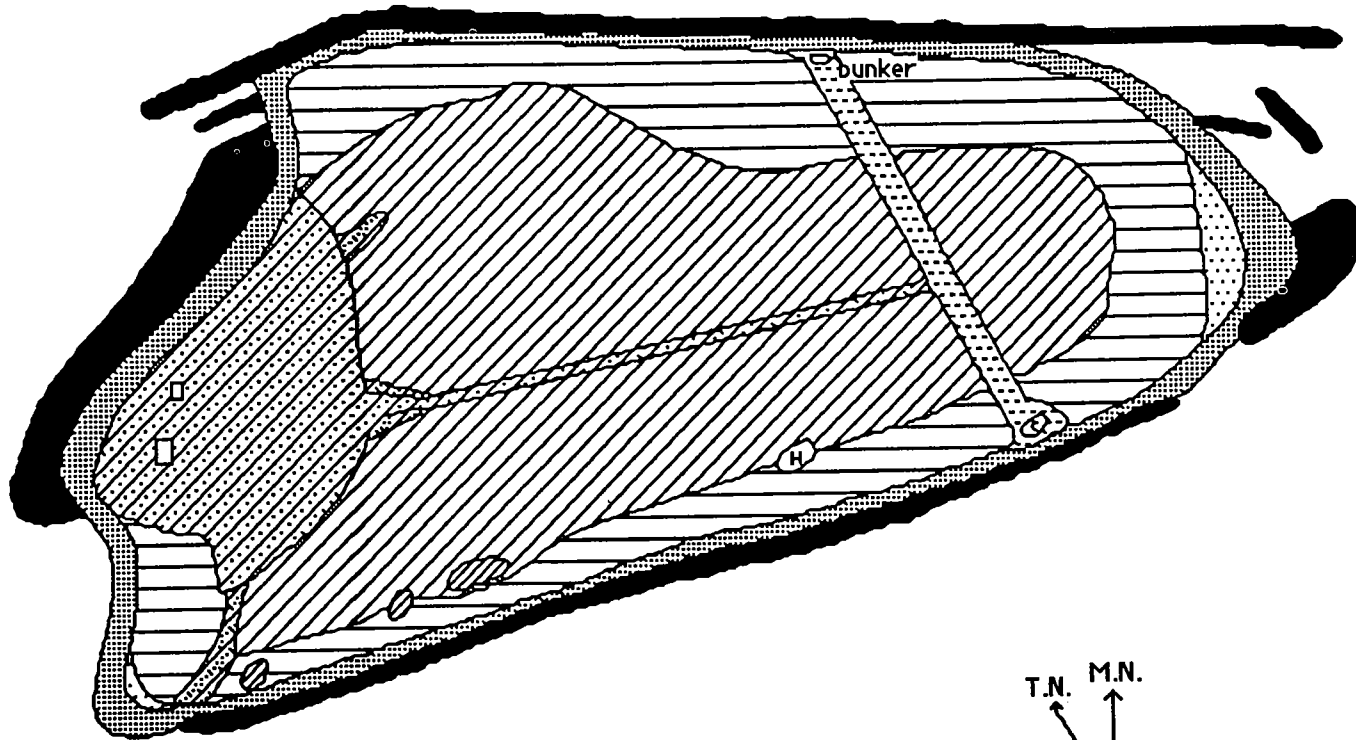
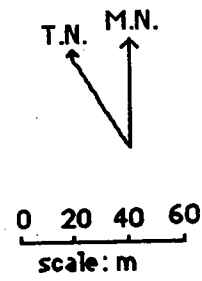


Figure 9: Motutapu



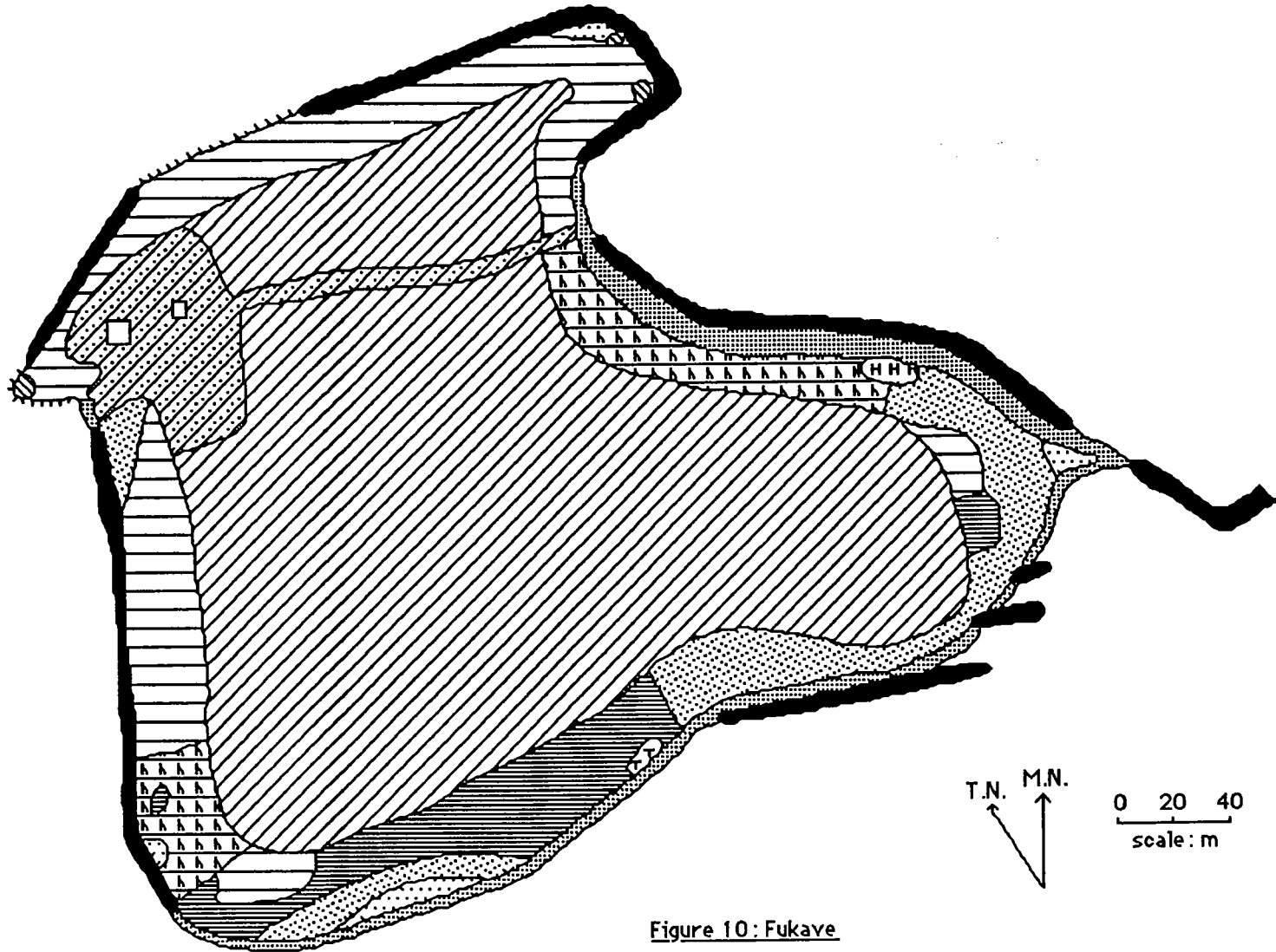


Figure 10: Fukave

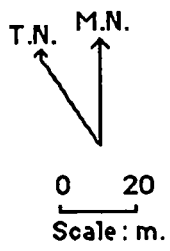
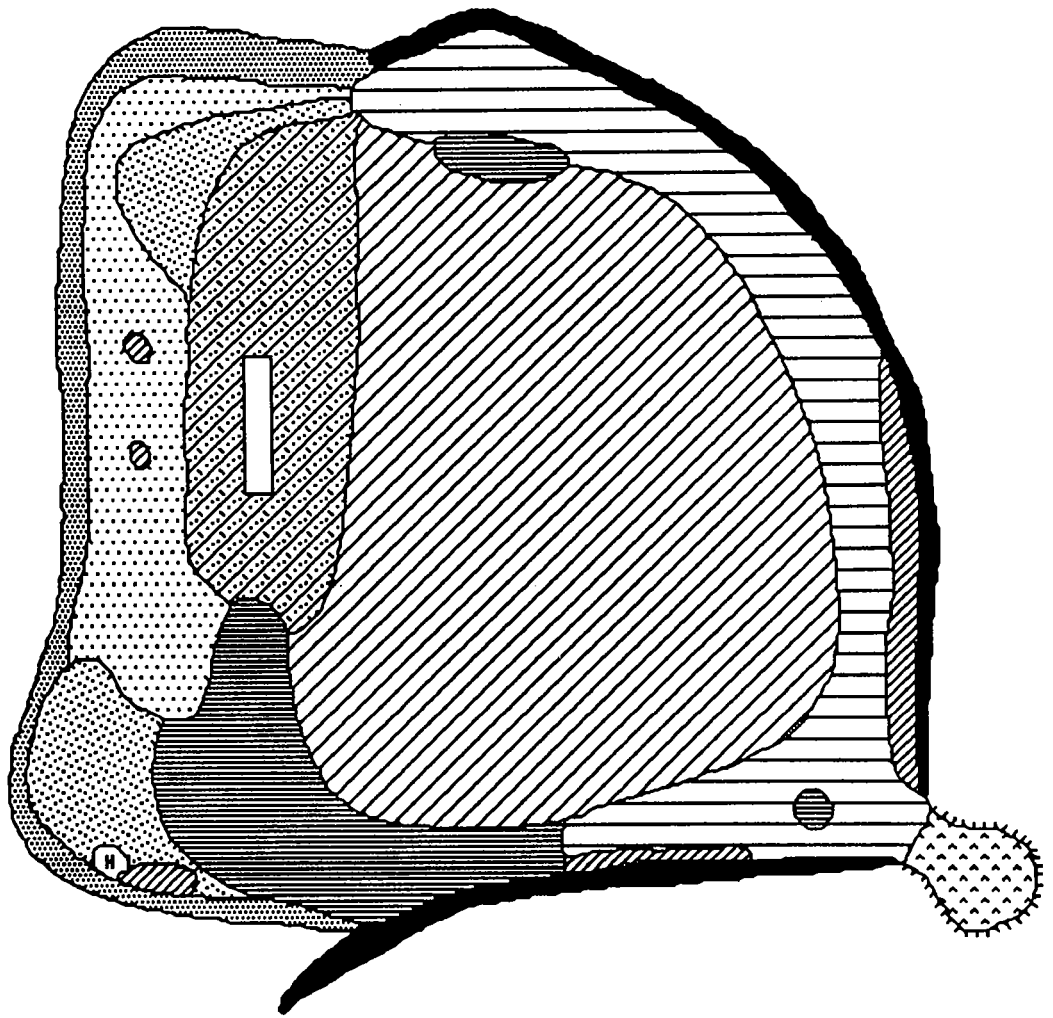
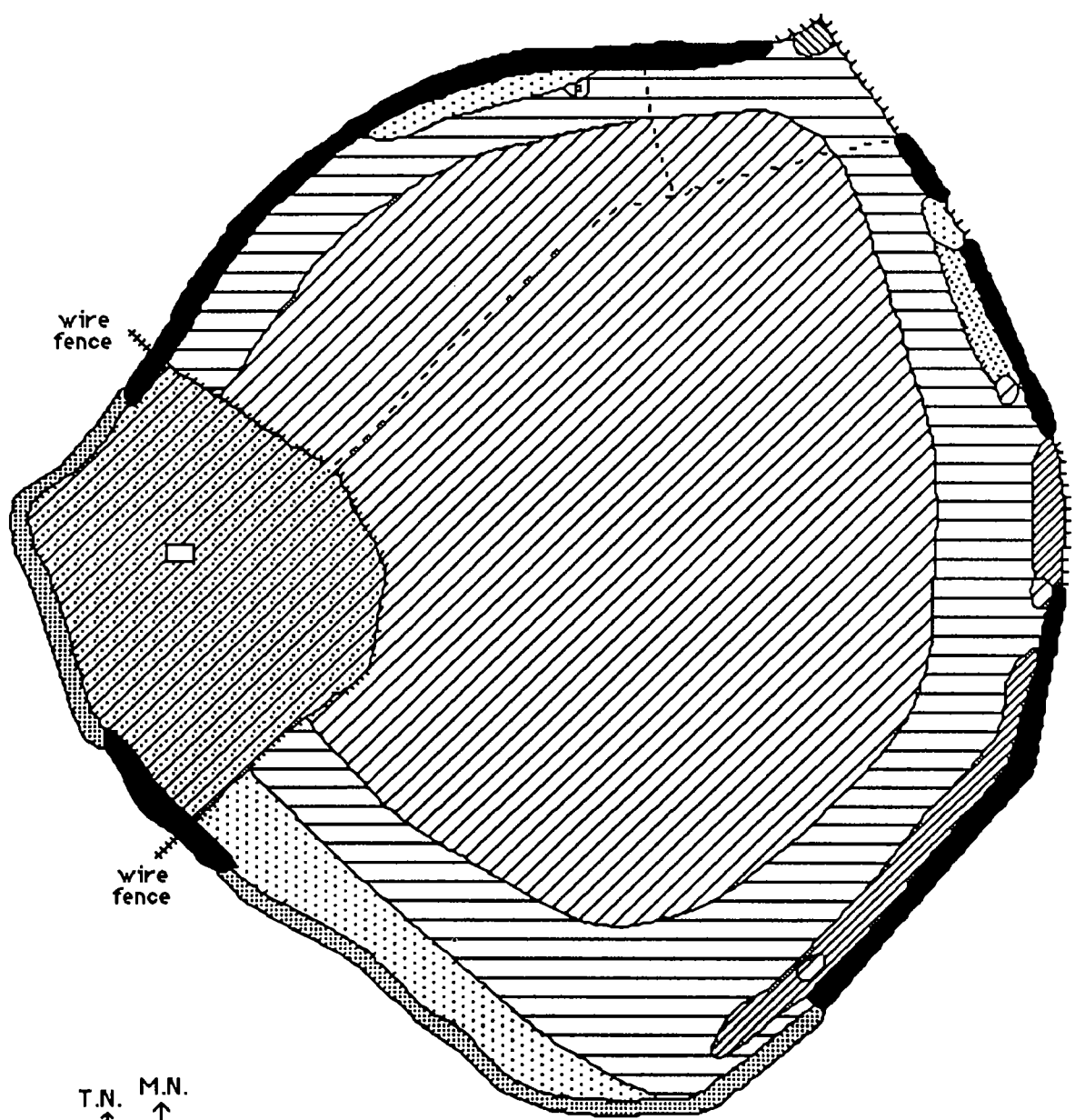


Figure 11 : Nuku



T.N. M.N.
0 20 40
scale : m

Figure 12: Ata

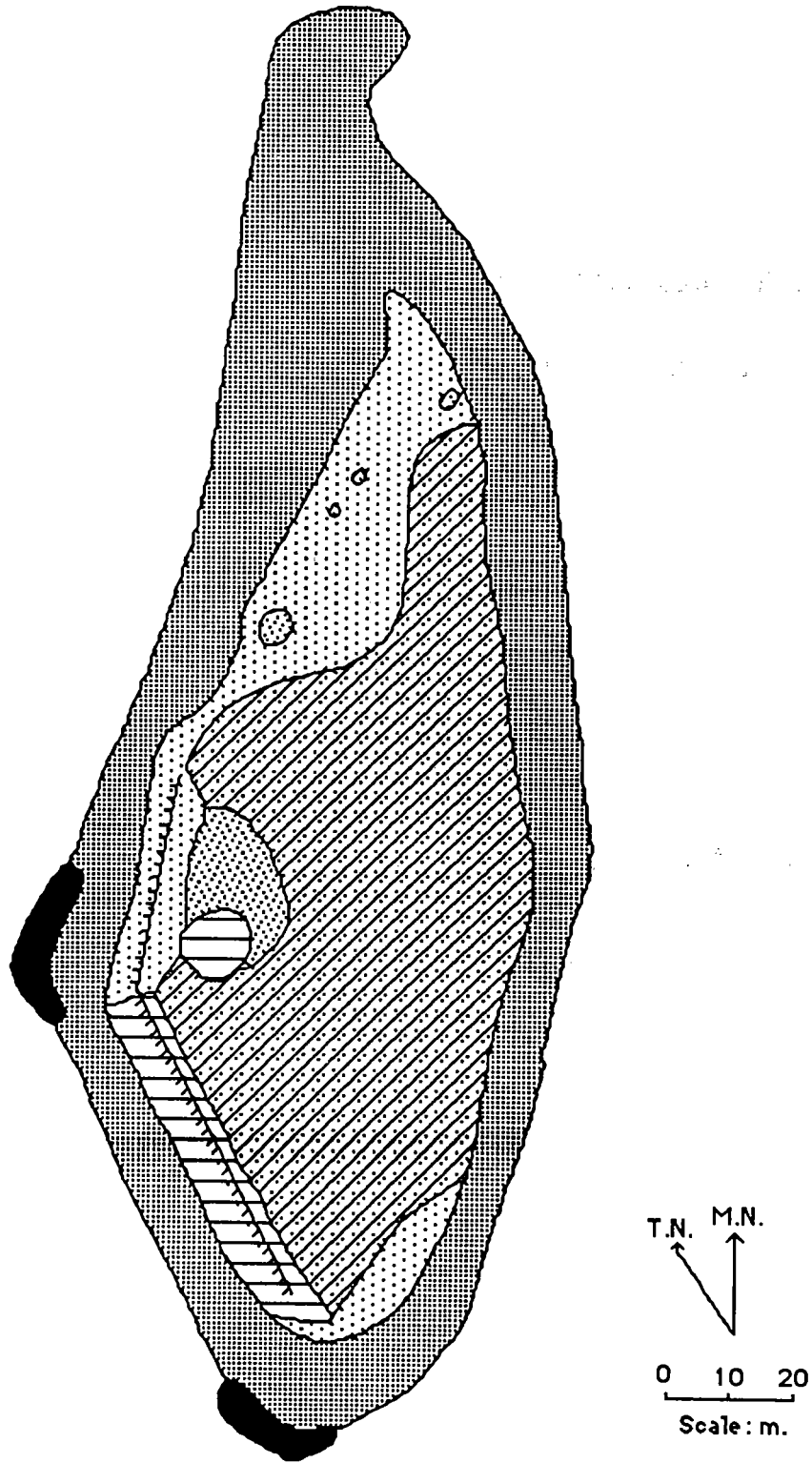


Figure 13: Tau

Figure 14. Number of species/ area plot for the Tongatapu outliers

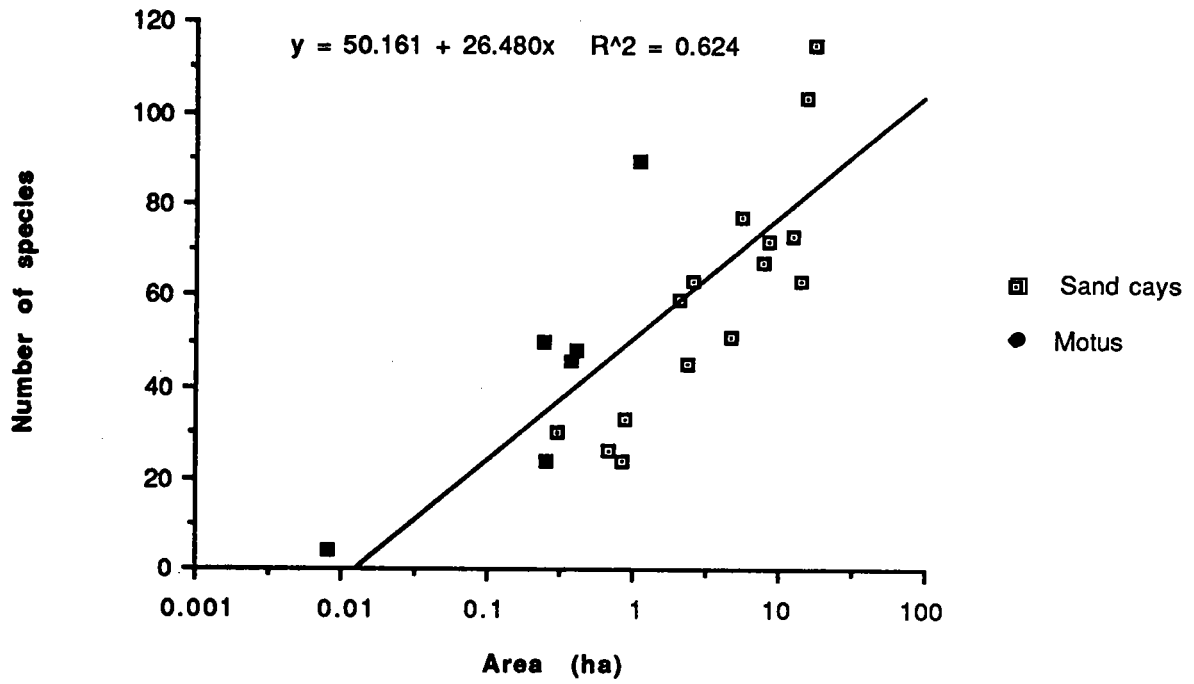


Table 1A. Distribution of tree species on the Tongatapu outliers

	Toketoke	Tufaka	Polo'a	Alakipeau	Fafa	Makaha'a	Pangaimotu	Manima	Oneata	Malinoa	Monuafa	Velitoo	Hihifo	Velitoo	Hahake	Mokotu'u	Onevai	Onevao	Motutapu	Fukave	Nuku	Ata	Tau
<i>Acacia simplex</i>		X			X	X	X	X	X	X	X					X	X	X	X	X	X	X	X
<i>Aleurites moluccana</i>			X					X											X				
<i>Alphitonia zizyphoides</i>					X			X															
<i>Annona reticulata</i>			X																				
<i>Artocarpus altilis</i>						X	X		X									X	X			X	
<i>Barringtonia asiatica</i>			X	X		X			X			X						X			X		
<i>Bruguiera gymnorrhiza</i>																	X						
<i>Bischofia javanica</i>							X																
<i>Calophyllum inophyllum</i>					X	X	X	X	X	X	X					X	X	X	X			X	X
<i>Carica papaya</i>	X	X	X	X	X	X	X	X				X	X	X	X	X	X	X	X	X	X	X	X
<i>Casuarina equisetifolia</i>			X	X	X	X		X				X	X	X	X				X		X		
<i>Canthium barbatum</i>																							
<i>Cerbera odollam</i>			X	X	X	X	X	X	X	X	X	X	X	X	X			X	X			X	
<i>Citrus maxima</i>	X		X		X	X						X	X				X					X	
<i>Cocos nucifera</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Cordia subcordata</i>			X		X	X	X	X	X	X						X							
<i>Cycas rumphii</i>						X							X							X		X	
<i>Diospyros elliptica</i>			X	X		X	X	X									X	X	X			X	
<i>Dysoxylum forsteri</i>			X	X															X				
<i>Elattostachys falcata</i>						X											X						
<i>Erythrina fusca</i>						X												X	X				
<i>Eucalyptus sp.</i>							X																
<i>Euphorbia tirucalli</i>							X										X						
<i>Excoecaria agallocha</i>			X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Ficus obliqua</i>																							
<i>Ficus scabra</i>							X																
<i>Ficus tinctoria</i>			X															X	X			X	
<i>Garcinia pseudoguttifera</i>			X																				
<i>Geniostoma vitiense</i>																	X	X					
<i>Glochidion concolor</i>			X			X	X												X				
<i>Grewia crenata</i>	X				X	X	X	X									X	X				X	X
<i>Guettarda speciosa</i>					X	X	X	X	X								X	X	X	X			
<i>Heritiera littoralis</i>			X	X		X																	
<i>Hernandia nymphaeifolia</i>					X	X	X	X	X	X							X	X		X	X	X	X
<i>Hibiscus tiliaceus</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Inocarpus fagifera</i>								X															X
<i>Jatropha curcas</i>			X																	X		X	
<i>Leucaena insularum</i>					X	X	X	X			X						X	X	X	X	X	X	X
<i>Leucaena leucocephala</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X				X

Table 1B. Distribution of tree species on the Tongatapu outliers

	Toketoke	Tufaka	Polo'a	Alakipeau	Fafa	Makaha'a	Pangaimotu	Manima	Oneata	Malinoa	Monuafe	Velitoo	Hihifo	Velitoo	Hahake	Mokotu'u	Onevai	Onevao	Motutapu	Fukave	Nuku	Ata	Tau
<i>Lumnitzera littorea</i>								X															
<i>Mangifera indica</i>			X				X							X				X				X	
<i>Morinda citrifolia</i>			X	X	X	X	X	X	X	X			X	X			X	X	X	X	X	X	X
<i>Musa x paradisiaca</i>						X	X	X															X
<i>Neisosperma oppositifolia</i>			X		X	X	X	X	X								X		X	X	X	X	
<i>Pandanus tectorius</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Persea americana</i>																							X
<i>Phaleria disperma</i>						X	X	X	X				X	X				X	X	X	X	X	X
<i>Pipturus argenteus v. lanosus</i>							X																
<i>Pisonia grandis</i>	X		X			X				X				X	X	X	X	X	X	X	X	X	X
<i>Pittosporum arborescens</i>							X	X	X	X							X		X				X
<i>Planchonella costata</i>														X					X	X	X	X	
<i>Plumeria acuminata</i>							X						X										
<i>Plumeria rubra</i>																		X	X				X
<i>Pometia pinnata</i>			X						X														X
<i>Premna serratifolia</i>			X	X			X										X		X	X			X
<i>Psidium guajava</i>			X	X	X	X	X	X	X				X	X				X	X				X
<i>Rhizophora mangle</i>			X			X	X											X					
<i>Rhizophora stylosa</i>			X			X												X					
<i>Rhus taitensis</i>							X	X	X									X	X				
<i>Santalum yasi</i>							X	X															
<i>Spondias dulcis</i>																							X
<i>Syzygium clusiifolium</i>						X	X	X	X														X
<i>Syzygium richii</i>							X												X		X		
<i>Tamarindus indica</i>																							X
<i>Tarenna sambucina</i>							X	X															
<i>Terminalia littoralis</i>			X	X		X												X	X	X	X	X	X
<i>Thespesia populnea</i>			X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Tournefortia argentea</i>			X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Vavaea amicorum</i>																			X				X
<i>Vitex trifolia</i>			X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X				
<i>Ximenia americana</i>										X	X							X	X	X			X
<i>Xylocarpus moluccensis</i>			X			X														X	X		
<i>Xylosma simulans</i>			X	X																			
unidentified						1								1		1							

Table 2. Distribution of shrub species on the Tongatapu outliers

	Toketoke	Tufaka	Polo'a	Alakiyeau	Fafa	Makahafa	Pangaimotu	Manima	Oneata	Malinoa	Monuafe	Velitoo Hihifo	Velitoo Hahake	Mokotu'u	Onevai	Onevao	Motutapu	Fukave	Nuku	Ata	Tau	
<i>Acronychia niueana</i>					X																	
<i>Aglaia saltatorum</i>							X						X									
<i>Alyxia stellata</i>																					X	
<i>Ananas comosus</i>			X																			
<i>Bambusa vulgaris</i>							X											X				
<i>Bougainvillea glabra</i>							X											X				
<i>Caesalpinia bonduc</i>					X	X	X	X							X					X		
<i>Cestrum diurnum</i>							X															
<i>Clerodendrum inerme</i>		X	X	X	X	X	X	X	X	X	X	X	X		X		X	X	X	X	X	X
<i>Codiaeum variegatum</i>							X															
<i>Colubrina asiatica</i>	X	X	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X	X	X	X
<i>Cordyline fruticosa</i>	X	X	X			X	X	X	X						X	X		X	X	X		
<i>Crinum asiaticum</i>			X	X	X	X	X	X				X			X	X		X	X	X		
<i>Derris trifolia</i>			X	X	X	X	X	X														
<i>Desmodium umbellatum</i>	X																					
<i>Furcraea foetida</i>		X	X			X									X							
<i>Gardenia taitensis</i>								X									X					
<i>Hibiscus manihot</i>								X														
<i>Hibiscus rosa-sinensis</i>					X	X	X	X	X			X										
<i>Indigofera suffruticosa</i>			X	X	X	X	X	X				X	X			X		X		X		
<i>Ipomoea batatas</i>																						X
<i>Jasminum didymum</i>	X	X	X	X	X	X	X	X	X						X	X	X	X	X	X		
<i>Jasminum simplicifolium</i>			X	X	X	X	X	X	X						X		X		X			
<i>Lantana camara</i>		X	X	X	X	X	X	X	X			X	X	X			X	X	X	X	X	X
<i>Macropiper puberulum</i>						X	X										X	X		X		
<i>Malvaviscus arboreus</i>																		X		X		
<i>Manihot esculenta</i>			X			X	X	X				X			X		X		X	X		
<i>Melia azedarach</i>	X																					
<i>Micromelum minutum</i>																	X	X	X	X	X	
<i>Pemphis acidula</i>	X	X	X												X			X	X	X		
<i>Ricinus communis</i>													X									
<i>Rosa sp.</i>					X																	
<i>Saccharum sp.</i>																						X
<i>Scaevola sericea</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Sophora tomentosa</i>					X	X												X				
<i>Suriana maritima</i>		X	X		X				X						X		X	X	X	X	X	X
<i>Triumfetta rhomboidea</i>		X																				
<i>Wollastonia biflora</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Waltheria americana</i>				X																		
unidentified						1	1	1				1			1	1						

Table 5. Distribution of grass and sedge species on the Tongatapu outliers

	Toketoke	Tufaka	Polo'a	Alakipeau	Fafa	Makahala	Pangaimotu	Manima	Oneata	Malinoa	Monuafe	Velitoo	Hihifo	Velitoo	Hahake	Mokotu'u	Onevai	Onevao	Motutapu	Fukave	Nuku	Ata	Tau
<i>Brachiara mutica</i>																X							
<i>Cenchrus echinatus</i>			X	X	X							X	X							X	X	X	
<i>Cyperus rotundus</i>		X						X												X			
<i>Digitaria horizontalis</i>		X																				X	
<i>Digitaria setigera</i>						X															X	X	
<i>Eleusine indica</i>			X			X							X								X	X	
<i>Eragrostis amabilis</i>																	X						
<i>Fimbristylis cymosa</i>				X		X	X		X											X			
<i>Ischaemum mirinum</i>		X	X			X	X		X			X	X			X	X	X					
<i>Kyllinga brevifolia</i>		X											X										X
<i>Lepturus repens</i>		X			X	X	X		X	X		X	X										X
<i>Mariscus javanicus</i>		X	X	X								X	X				X						X
<i>Panicum maximum</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X			X					X
<i>Paspalum conjugatum</i>		X				X															X	X	
<i>Sporobolus virginicus</i>	X	X	X	X	X	X			X		X					X	X	X	X	X	X	X	X
<i>Thuarea involuta</i>	X	X	X	X	X	X	X	X	X	X						X	X			X	X	X	X
unidentified																							

Table 6. Distribution of fern species on the Tongatapu outliers

	Toketoke	Tufaka	Polo'a	Alakipeau	Fafa	Makaha'a	Pangaimotu	Manima	Oneata	Malinoa	Monuafe	Velitoo	Hihifo	Velitoo	Hahake	Mokotu'u	Onevai	Onevao	Motutapu	Fukave	Nuku	Ata	Tau
Asplenium nidus					X	X	X	X															
Polypodium scolopendria	X	X	X	X	X	X	X	X	X	X		X	X		X				X			X	

Table 7. Numbers of species of vascular plants on the Tongatapu outliers

ISLAND	Area (ha.)	No. species	Trees	Shrubs	Herbs	Vines	Grasses /sedges	Ferns
Toketoke	0.26	24	8	7	4	3	1	1
Tufaka	0.67	26	6	9	2	4	5	0
Polo'a	1.11	89	32	15	23	10	8	1
Alakipeau	0.37	46	17	9	9	5	5	1
Fafa	8.56	72	26	14	14	10	5	2
Makaha'a	2.54	63	25	11	12	8	5	1
Pangaimotu	17.14	115	47	21	25	12	8	2
Manima	2.1	59	24	9	13	6	6	1
Oneata	5.55	77	35	14	15	6	5	2
Malinoa	0.88	33	17	6	1	3	5	1
Monuafe	0.3	30	11	6	4	6	3	0
Velitoa Hihifo	0.41	48	14	8	13	6	4	1
Velitoa Hahake	0.24	50	16	9	15	5	6	1
Mokotu'u	0.008	4	2	0	2	0	0	0
Onevai	14.34	63	31	10	8	9	4	1
Onevao	2.3	45	26	9	18	5	6	1
Motutapu	7.81	67	36	11	12	5	3	0
Fukave	12.52	73	27	16	13	10	6	1
Nuku	4.61	51	20	12	10	3	6	0
Ata	15.41	103	40	18	24	9	10	1
Tau	0.85	24	9	4	3	6	2	0

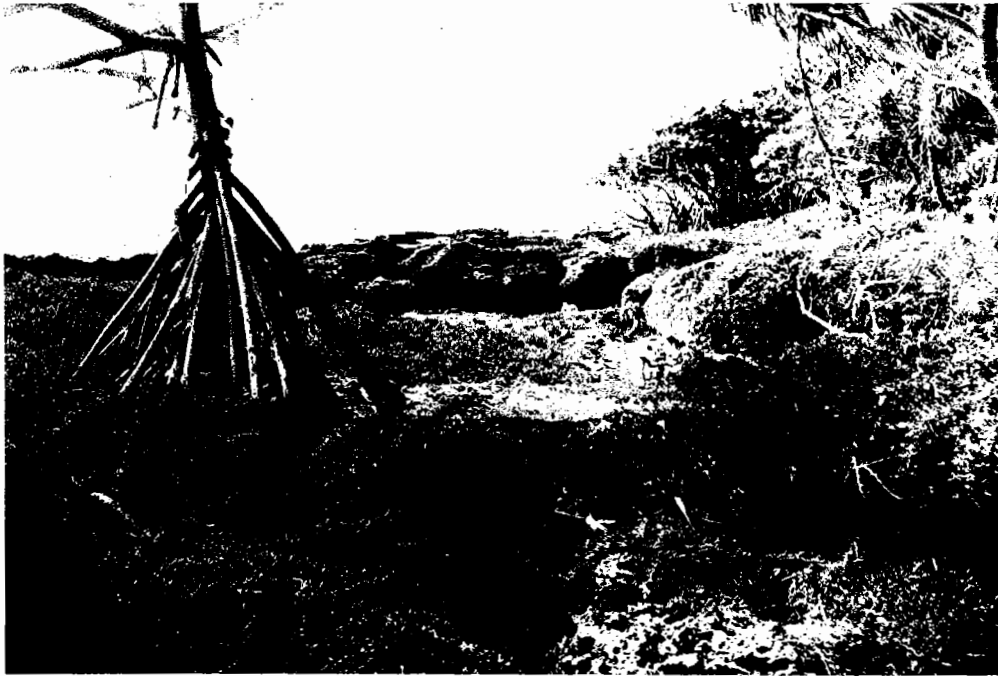


Plate 1: *Pandanus* outposts, east shore of Ata.



Plate 2: *Rivina* under *Cocos* woodland, Fukave.



Plate 3: *Canavalia* and *Thuarea* colonising loose sand, west shore of Ata.