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THE TERRESTRIAL VEGETATION OF AN INDIAN OCEAN CORAL ISLAND: WILINGILI, ADDU ATOLL, MALDIVE ISLANDS

I. TRANSECT ANALYSIS OF THE VEGETATION

by R. A. Spicer and D. McC. Newberry

II. A LIMITED QUANTITATIVE ANALYSIS OF THE VEGETATION DISTRIBUTION

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I. TRANSECT ANALYSIS OF THE VEGETATION

by R.A. Spicer[1] and D.McC. Newbery[2]

ABSTRACT

The vegetation of a little-disturbed Indian Ocean coral island, Wilingili, Addu Atoll, is described both subjectively and in terms of three sea to lagoon transects. Exposure and edaphic factors were measured and the possible effects of these on vegetational pattern discussed. It is concluded that because soil maturity and exposure are both dependent on proximity to the strands, investigation of the relative importance of the influence of these variables on vegetational pattern is impossible from transect analysis in this case. However, the three transects spanning different widths of the island probably reveal vegetational differences determined by the salinity of the ground waters.

A list of plants collected in the course of the work is presented which represents practically the complete flora of Wilingili and includes eight confirmed new records for the Maldive Islands.

INTRODUCTION

The problems concerning the low floral diversity of oceanic islands and the factors influencing the distribution of vegetation

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have, to date, received little attention beyond a subjective appraisal. In the work reported here one island, Wilingili, was selected for detailed study in a more quantitative manner. Wilingili is a constituent island of Addu Atoll ($0^{o}38'S., 73^{o}10'E.$) which lies at the southern extremity of the Maldive Island chain.

The J. Stanley Gardiner expedition of 1899-1900 was the first to make extensive plant collections in the Maldive group. Soon afterwards Agassiz (1903) remarked "The vegetation..... of Wilingili .... [is] perhaps, as luxuriant as that of any island in the Maldives." Until 1972 the most recent work in this area was carried out by an expedition led by D.R. Stoddart in 1964. For political reasons work was confined to the heavily populated islands of Gan and Hittadu and it was suggested that the vegetation of a less disturbed island should be studied for comparison (Sigee 1966).

Wilingili with its lack of permanent human population provided a suitable site for such work which was undertaken by the authors during their six week (16 August to 28 September 1972) expeditionary visit to the Atoll.

GEOMORPHOLOGY

The total land area of Addu Atoll (Fig. 1) measures some 11.19 sq. km, with Wilingili, the sixth largest island in the group, occupying 0.79 sq. km. In 1836 Wilingili was charted as two separate islands but by 1900 (Gardiner 1903) it had become one and remains so to this day. Stoddart (1966) classifies the island as a seaward edge type since the seaward beach, lies only 90 m from the reef edge. This beach is mainly composed of rounded coral fragments 20 cm. or more in diameter.

The margins of coral islands usually show the highest relief due to the formulation of unconsolidated ridges of coral debris along seaward and, occasionally, lagoon shores. The material comprising the marginal ridges varies from fine sand through to cobbles and boulders (Fosberg & Carroll 1965). The Wilingili seaward ridge was noted by Agassiz (1903) as being "perhaps the highest we have seen in the Maldives". The vegetation, often consisting entirely of *Pemphis acidula* (Table 1), acts as a wind break with the result that a deposit of wind blown sand forms on the landward side of the seaward ridge. Unlike many Pacific islands the marginal ridge of Wilingili contained no large boulders, presumably because the high energy agents of transport and deposition, e.g. typhoons, are never experienced on Addu Atoll. No lagoon ridge was observed on Wilingili but there was some evidence of erosion along the southern lagoon shore which, like most of this beach is composed of fine coral sand.

Although drainage through unconsolidated coral debris is practically perfect, the porous nature of this material allows retention of often considerable amounts of rain water. The presence of a well (Fig. 2) indicates that a non-saline ground water lens is present, as on many other coral islands, and approaches the surface in numerous shallow hollows within the *Pisonia* forest (Fig. 2). Substantial amounts of fresh water are absent however in the narrower parts of the island and some hollows are at least periodically filled with brackish water.

CLIMATE

It was not possible to make extensive meteorological observations during the period of our stay on Wilingili, but the expedition of 1964 obtained data from the R.A.F. Staging Post on Gan and the following is summarized from Stoddart (1966).

The annual rainfall fluctuates between 300 cm and 188 cm with a mean of 229 cm and exhibits no clear seasonal pattern. The temperature, like the high humidity, is controlled by the surrounding ocean and has a mean of 28°C throughout the year. The diurnal temperature variation of 5.5°C far exceeds the annual range of 1.66°C.

Surface winds show the following pattern:

January	WNW - NNE
February	N - NE
March	W
April	W
May	W
June	SW - SE
July	S - SE
August	S - SE
September	SW
October	SW - W
November	W
December	WSW - NNE

Gales and strong winds are rare but winds up to 36 m/sec have been recorded during squalls.

TRANSECT METHODS

Three transect lines were set up in the positions shown in Fig. 2. Detailed measurement of microclimate was not possible, but an effective estimate of the relative exposure in different parts of the island was found from the loss of material tattered from 25 cm by 40 cm cloth flags (method of Lines & Howell 1963). Two flags were set up at the mid-point and extremities of the three transects and tattering proceeded over 35 days (21 August 1972 to 25 September 1972), after which the area lost was measured for each flag. The mean values for each site are shown in Fig. 3.

In the following studies of the vegetation representative specimens of each species encountered were collected and returned to the British Museum (Natural History) where they are now lodged, and were determined by Mr. E.W. Groves unless otherwise stated. It is considered that the species listed here (Appendix 1) represent the majority of those species to be found on Wilingili at the present time.

Records of the vegetation along each transect were made on a simple presence and absence basis for each metre interval of the transect length.

Soil pits, 30 - 40 cm deep, were dug every 20 m along the middle and southern transects and every 40 metres along the northern transect. pH measurements and soil samples (approx 150 g net weight) were taken at 5, 10 and 20 cm depths supplemented by observations on the appearance of the soils. It was not possible to dry the soils completely in the field, and therefore they were stored wet and dried on return to England. Analysis of the soils was then carried out as described in Newbery and Spicer (this issue).

SUBJECTIVE DESCRIPTION OF THE VEGETATION

The 'soil' of the southern tip of Wilingili was composed of coral blocks 10 - 20 cm in diameter in which *Scaevola taccada, Tournefortia argentea, Guettarda speciosa,* and *Pemphis acidula* survived.

To the north the vegetation increased in height to about two metres with *S. taccada* and *G. speciosa* predominating. Approximately 200 m from the southern tip *Pemphis acidula* was abundant under a canopy of coconut palms which continued northwards but with an increasingly dense understorey of *S. taccada*. Unlike the rest of the island the vegetation here was free of *Passiflora suberosa*. The seaward ridge supported *Pemphis acidula* which commonly grew down to, and often below, high water level.

Approximately 600 m from the southern tip of the island isolated individuals of mature *Pandanus* sp. were encountered along the lagoon shore though nowhere on Wilingili did this plant grow in abundance. Some 400 m south from the southern transect in the centre of the island a depression in the coral was found, covered with a pure stand of *Pemphis acidula*. It may be that this depression is periodically filled with brackish water.

Further north coconut palms formed dense vegetation, rich in such species as *Kalanchöe pinnata* and *Euphorbia* sp.

The area of the southern transect was rich in *Scaevola taccada*, many of the plants being covered in the parasitic leafless *Cassytha filiformis*. Many of the densely covered *S. taccada* had the appearance of being etiolated with long vertical stems crowned with a rosette of small chlorotic leaves. *Thuarea involuta* and *Lepturus repens* formed the ground cover in the clearings.

A number of individuals of *Cordia subcordata* were seen growing above cemented beach rock of a small bay on the Lagoon shore north of the southern transect. Northwards the coconut palms became sparse and stunted and the vegetation was composed mainly of *S. taccada, P. acidula* and *G. speciosa* with isolated plants of *Pandanus* sp., *Morinda citrifolia* and *Hibiscus tiliaceus*, many of which were covered in *Passiflora suberosa*. *Digitaria horizontalis* and *Boerhavia diffusa* occurred along the edges of trampled ground.

The open scrub vegetation reached as far north as the brackish water lake in the centre of the island (Fig. 2). Here the mangroves *Rhizophora mucronata* and *Bruguiera cylindrica* were found in abundance spreading north behind the seaward ridge.

The canopy of the northern part of the island was formed by *Pisonia grandis* and in the extremely high humidity of the forest community *Carica papaya, Morinda citrifolia, Neisosperma oppositifolia, Asplenium nidus* and *Tacca leontopetaloides* were to be found. Almost the entire understorey of the forest area was covered with the creeper *Passiflora suberosa*.

The most extensive coconut groves occurred on the lagoon side of the *Pisonia* forest. These areas are not planted as such but the growth of any germinating coconut appears to be encouraged by clearing the undergrowth around it.

An area of the forested region has been cleared and supports crops of *Zea mays* and castor oil *Ricinus communis*. Wherever the ground has been disturbed the weed *Wedelia biflora* was found in abundance.

The north-western tip of the island appeared to be similar to the southern tip in that the coral blocks comprising the extremely juvenile soil are subject to periodic marine disturbance and consequently only *P. acidula, S. taccada* and *G. speciosa* were found. In places however *Cassytha filiformis* was seen to be growing over bare coral debris and *Scaevola taccada*.

RESULTS

The occurrences of the various species encountered along the transects are given in Fig. 4.

Similarly the results of the soil analysis are presented in Figs. 5, 6 and 7, with pH measurements in Table 1.

Table 1. pH measurements of the soils sampled along the three transects.

Northern Transect — Sample Sites

Depth	A	B	C	D	E	F	G	H
5cm	8.5	7.7	7.9	8.2	8.2	7.7	7.0	7.7
10cm	8.6	8.2	7.8	8.5	8.0	8.1	7.2	8.3
20cm	8.5	8.4	7.9	8.4	8.5	8.3	7.1	8.3

Middle Transect — Sample Sites

Depth	A	B	C	D	E	F
5cm	8.3	7.9	7.8	7.7	7.6	8.4
10cm	8.7	8.5	8.3	7.8	8.2	8.8
20cm	8.7	8.5	8.3	8.5	8.3	9.2

Southern Transect — Sample Sites

Depth	A	B	C	D	E	F
5cm	8.2	8.0	8.1	8.5	8.0	8.5
10cm	8.3	7.8	8.3	8.5	8.0	8.5
20cm	8.3	8.3	8.2	8.7	8.4	8.8

DISCUSSION

The flora of Wilingili, as with many other oceanic islands, is extremely restricted, being almost totally represented by the 72 species presented here. Consequently the expression, by the vegetation of environmental variables is often concealed (Stone 1953).

The primary sources of land material are reef organisms (except for pumice which is common on a number of atolls (Sachet 1955), and which is locally abundant on Wilingili), and it is only with time that the coral debris becomes altered to provide a variety of habitats that may be reflected by vegetational patterns. This differentiation into communities might be expected to reflect proximity to the sea and maturity of soil. Naturally these two factors are strongly linked.

As can be seen from the tatter flag data (Fig. 3) proximity to the sea is also associated with exposure, thus it may be difficult to isolate the effects of single environmental factors on the vegetation, from simple transect analysis.

If percentage organic matter is an indicator of maturity in atoll soils then the soils of the northern transect are the most developed (Fig. 6). Their most striking feature is the high phosphate levels associated with the more mature *Pisonia grandis* forest (Figs. 4 and 6). Such an association is commonly found in Pacific atolls (Fosberg 1953) and is probably the result of guano from roosting sea birds. It is not likely that *P. grandis* is dependent on the phosphate for its growth as has been suggested by Shaw (1952) since it is also found on relatively low phosphate soils e.g. sample site F. The association of *P. grandis*, phosphorus, and a layer of relatively acid raw humus has been discussed by Fosberg (1954, 1957a). He has pointed out that the acidity of raw guano (pH 6.0) is not sufficient to take the calcium phosphate present in guano into solution and it is only when guano falls onto the thin, acid, raw humus layer, characteristic of mature *P. grandis* forests, that the phosphate passes into solution later to be precipitated as a phosphate hardpan when the underlying coral debris is reached. Wiens (1962) concludes that while *P. grandis* does not necessarily require phosphate and acid soils for germination it undoubtedly thrives in such an environment since its relatively shallow root system is often directly exposed to such conditions. However the development of a raw humus layer and acid conditions characteristic of Jemo soils, as described by Fosberg (1954), are not fully developed on Wilingili (Table 1).

By comparison the middle and southern transects represent more open scrub vegetation. Here the island is only a third of the width of the northern transect, thus a substantial fresh water lens cannot be supported (Stone 1953), with obvious consequences in times of relative drought.

The absence of a non-saline groundwater lens is indicated in the southern transect by the widespread distribution of the salt tolerant bushes *Scaevola taccada* and *Guettarda speciosa*. These plants do however provide cover and locally humid conditions to allow *Passiflora suberosa* to survive.

The coconut palms on the southern half of the island appear to be less vigorous and set further apart than on the northern lagoon shore and it has been noted by Wiens (1962) that the density of coconut palms tends to be less on drier atolls. However Hatheway (1953) has stated that the coconut thrives over an extremely wide range of environmental conditions, consequently it is "utterly worthless as an indicator of environmental differences". Although this is true, particularly with reference to ground water salinity, the fronds appear to suffer from sea spray damage. It is thus a common practice to protect coconut groves from direct spray by leaving a band of essentially natural vegetation on the seaward side of an island, thus the greatest density of coconut palms is found along the lagoon shore of Wilingili.

It may be readily seen from Fig. 5 that the concentration of magnesium is consistently higher on both lagoon and sea strands. Stone (1953) has noted that some reef organisms, e.g. *Lithothamnion*, may contain up to 25% magnesium carbonate. However this is relatively soluble and becomes leached from the older soils, hence its lower concentration in the middle of the island. This hypothesis is also supported by a general increase in magnesium concentration with depth.

Sodium, however, shows a uniform distribution across the Island apart from the mangrove peat. Undoubtedly the contribution of sodium in spray must be considerably higher towards the strands but this is not reflected in the analyses. One is led to conclude, therefore, that any contribution by spray is rapidly leached from the surface soils.

CONCLUSIONS

Coral islands are generally considered to exhibit a strong environmental gradient from windward to leeward and from sea shore to lagoon shore. On Wilingili the former gradient is not evident due to the variable nature of the prevailing wind direction. Exposure however is considerably less in the centre of the island than along the strands and because of the proximity of the seaward ridge to the reef edge, the effect of spray is more marked on the seaward side. The maturity of soils as indicated by percentage organic matter and associated ionic availability, is mainly correlated with distance from the strands, hence it is difficult to isolate exposure effects from edaphic factors. This argument also applies to textural differences in the soils. However there are marked vegetational differences between the northern transect and the two more southerly ones which are probably determined by the salinity of ground waters. Where the island is wide enough to support a fresh ground-water lens the development of a *Pisonia* forest has in turn greatly modified the soil.

Superimposed upon this natural vegetation pattern are the activities of man especially with regard to the managing of coconut groves and ground disturbance. Where this is most marked weeds such as *Wedelia biflora* are able to grow in abundance.

ACKNOWLEDGEMENTS

As members of the 1972 Imperial College Maldive Islands Expedition we should like to record our thanks to the many who supported and financed us, especially the Imperial College Exploration Board, The Royal Geographical Society, The Royal Air Force, the Maldivian Government and the British Museum (Natural History). We would also like to take this opportunity of expressing our gratitude to Mr. E.W. Groves for determining plant specimens and preparing the species list. Sincere thanks go to Dr. A.J. Morton of this department for helpful discussion and Professor A.J. Rutter for use of facilities for soil analysis.

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Appendix 1. Botanical Specimens collected on the Imperial College of Science & Technology (London) Expedition to the Maldive Islands, Indian Ocean, 1972.

Material determined by Mr. E.W. Groves, Dept. of Botany, British Museum (Natural History) London unless otherwise stated. The collection has been deposited in the Herbarium of that Museum.

* indicates new species recorded to the Maldives.

ANGIOSPERMS

DICOTYLEDONS

Portulacaceae

Portulaca tuberosa (Roxb.) Trin.

Guttiferae

Calophyllum inophyllum L.

Malvaceae

Hibiscus tiliaceus L.
Sida humilis Willd.

Tiliaceae

**Triumfetta procumbens* Forst. f.
Corchorus aestuans L.

Surianaceae

Suriana maritima L.

Oleaceae

**Ximenia americana* L. var. *americana* (det. F.R. Fosberg July 1973)

Rhamnaceae

Colubrina asiatica (L.) Brongn.

Leguminosae

Caesalpinia bonduc (L.) Roxb.
Canavalia cathartica Thou.
Cassia occidentalis L.
Vigna marina (Burm.) Merrill

Crassulaceae

Kalanchoe pinnata (Lam.) Pers.

Rhizophoraceae

Bruguiera cylindrica (L.) BI.
Rhizophora mucronata Lam.
**Ceriops tagal* (Perr.) C.B. Robinson (det. F.R. Fosberg July 1973)

Lythraceae

Pemphis acidula Forst.

Turneraceae

Turnera ulmifolia L.

Passifloraceae

Passiflora suberosa L.

Caricaceae

Carica papaya L.

Cucurbitaceae

Cucumis melo L.

Aralisceae

Polyscias guilfoylei (Bull.) Bailey (det. F.R. Fosberg July 1973)

Rubiaceae

Morinda citrifolia var *bracteata* Hook. f.
Guettarda speciosa L.

Compositae

Launaea pinnatifida Cass.
Wedelia biflora (L.) DC.
Tridax procumbens L.
Conyza bonariensis (L.) Crong.
Vernonia cinerea var. *parviflora* (Bl.) DC.

Goodeniaceae

Scaevola taccada (Gaertn.) Roxb.

Apocynaceae

Neisosperma oppositifolia (Lam.) Fosberg & Sachet.
(*Ochrosia oppositifolia* (Lam.) K.Schum).

Boraginaceae

Tournefortia argentea L.f.
Cordia subcordata Lam.

Convolvulaceae

Ipomoea pes-caprae L.
Ipomoea macrantha R. & S.
Jacquemontia paniculata (Burm.f.) Hallier f.

Scrophulariaceae

Bacopa monnieri (L.) Wettst.

Nyctaginaceae

Pisonia grandis R. Br.
Boerhavia diffusa L.

Amaranthaceae

Alternanthera sessilis (L.) R.Br.
Achyranthes aspera L.

Lauraceae

Cassytha filiformis L.

Hernandiaceae

Hernandia peltata Meissn.

Euphorbiaceae

Ricinus communis L.
Euphorbia cyathophora Murray
**Euphorbia indica* Lam.
**Laportea interrupta* (L.) Chew (det. F.R. Fosberg, July 1973)
Agyneia bacciformis (L.) Juss.
Phyllanthus urinaria L.

Moraceae

Ficus benghalensis L.

MONOCOTYLEDONS

Amaryllidaceae

Crinum asiaticum L.

Taccaceae

Tacca leontopetaloides (L.) O.Ktze.

Pandanaceae

Pandanus sp. (juvenile material)

Aroideae

Colocasia esculenta L.

Cyperaceae

Cladium jamaicense Crantz. var *chinense* (Nees) Koyama
Cyperus ligularis L.
Cyperus conglomeratus Rottb. forma *pachyrrhizus* (Nees) Kukenth.
Cyperus dubius Rottb.
**Fimbristylis cymosa* ssp. *spathacea* (Roth) Koyama
Fimbristylis ferruginea (L.) Vahl

Gramineae

Eragrostis tenella (L.) Beauv.
Apluda mutica L.
**Digitaria horizontalis* Willd.
Dactyloctenium aegyptium (L.) Willd.
Thuarea involuta (Forst) R.Br.
Lepturus repens (Forst.f.) R.Br.
**Oplismenus* sp. (possibly *O. compositus*)

PTERIDOPHYTES

Psilotaceae

Psilotum nudum (L.) Beauv.

Aspleniaceae

Asplenium nidus L.

Davalliaceae

Nephrolepis hirsutula (Forst.f.) Presl

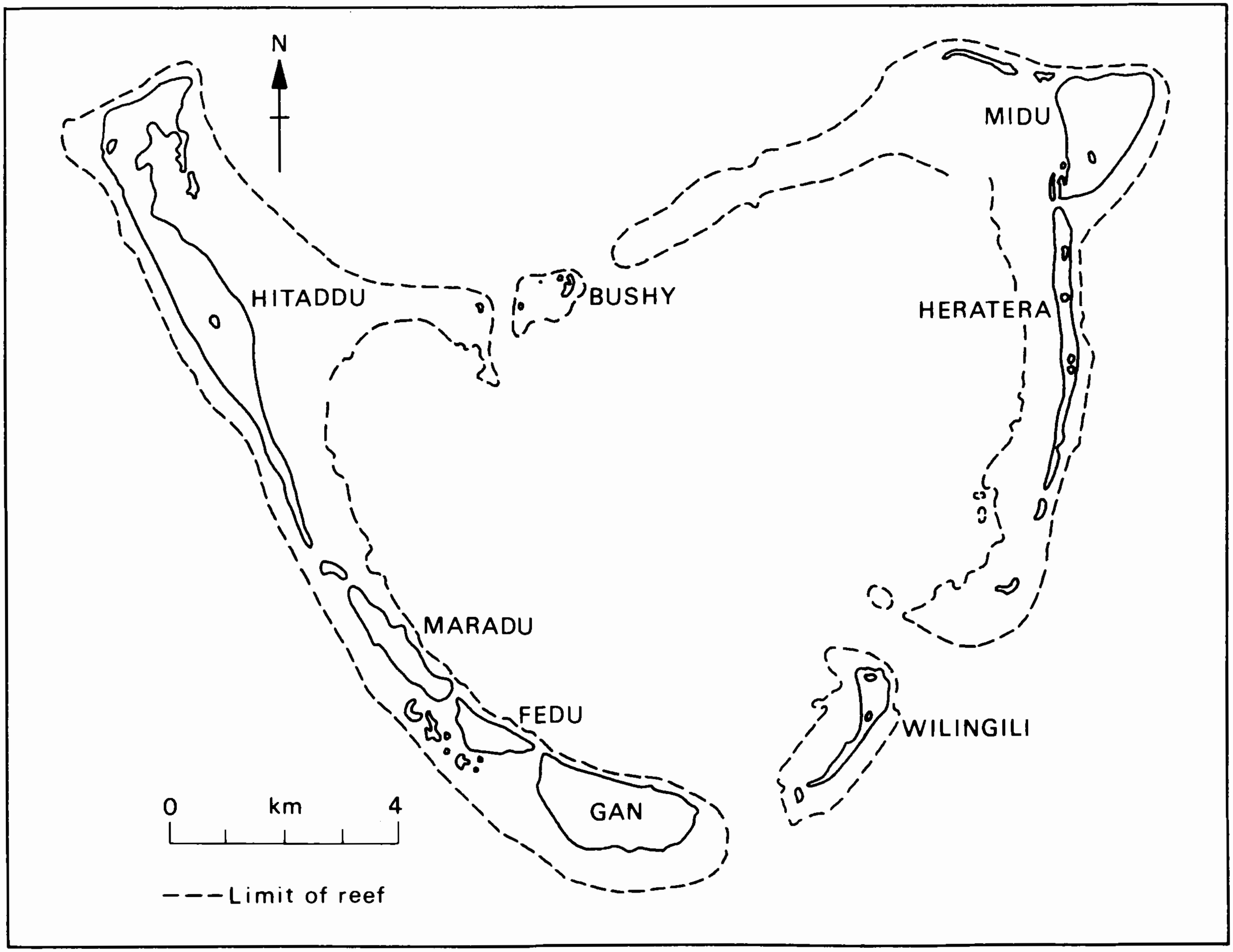

Fig. 1. Addu Atoll, Maldive Islands.

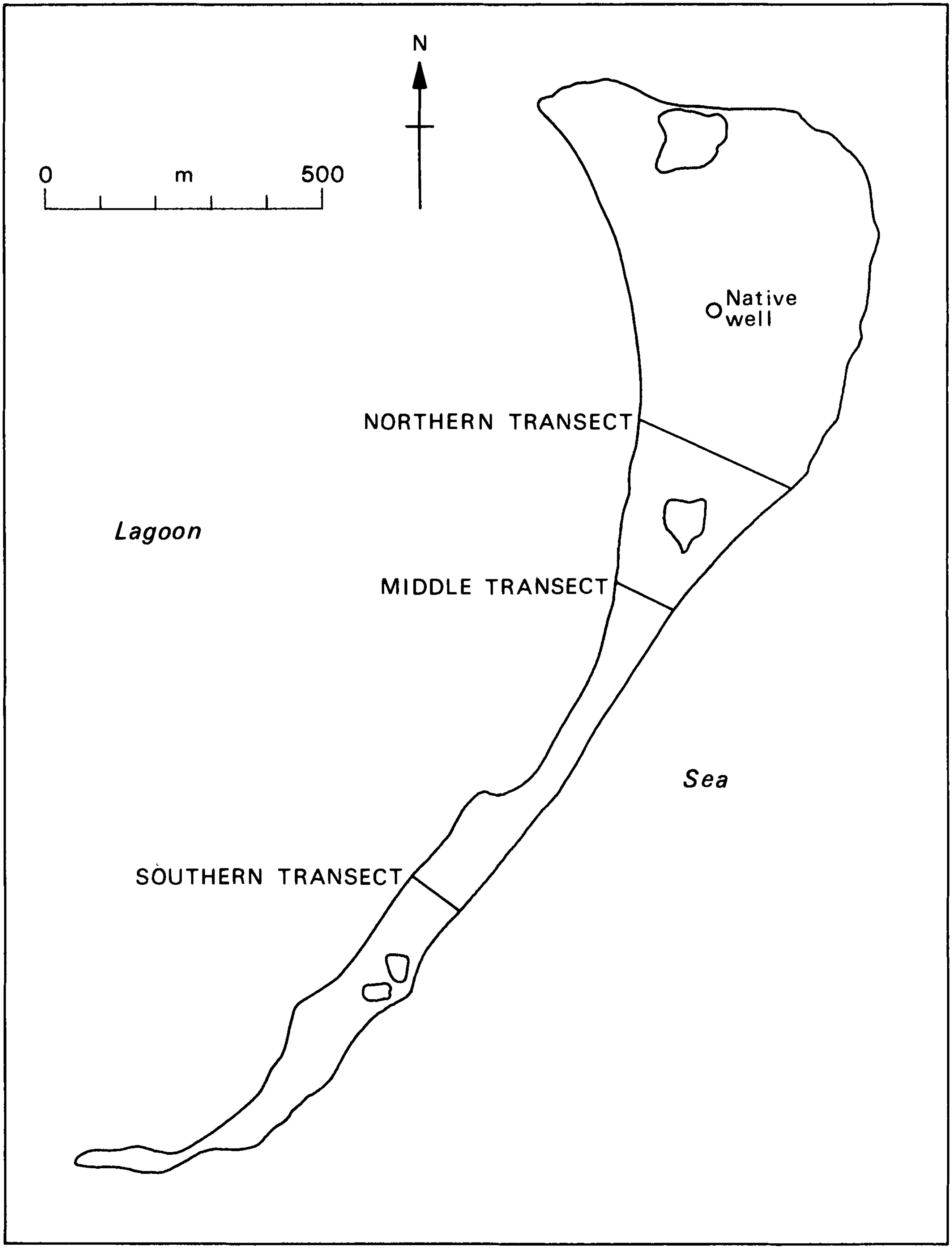

Fig. 2. Wilingili, Addu Atoll, showing the positions of the transects. Tatter flags were positioned in the centre and at the ends of the three transects.

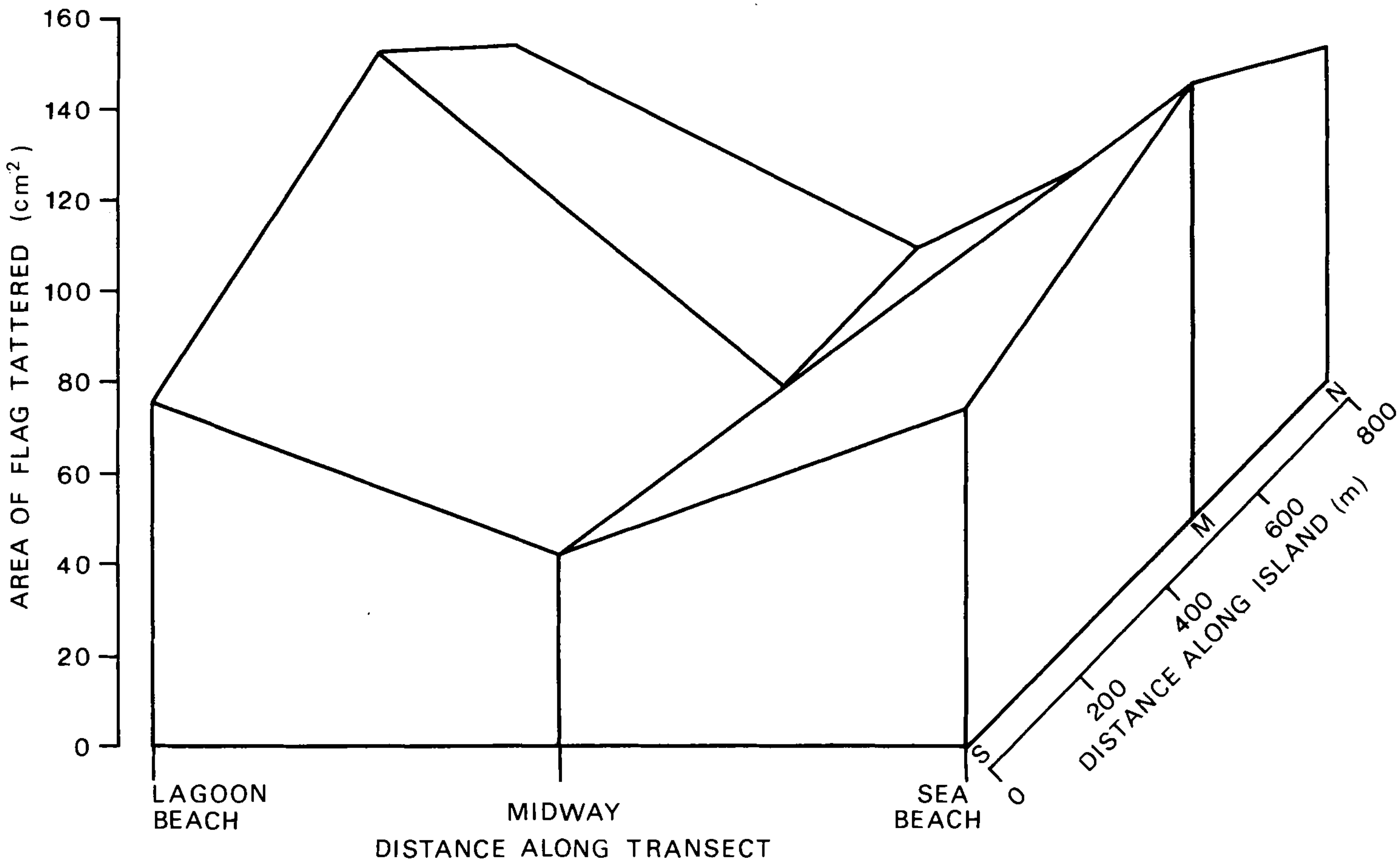

Fig. 3. Three dimensional representation of relative exposure at nine points on the Island as measured by tatter flags.

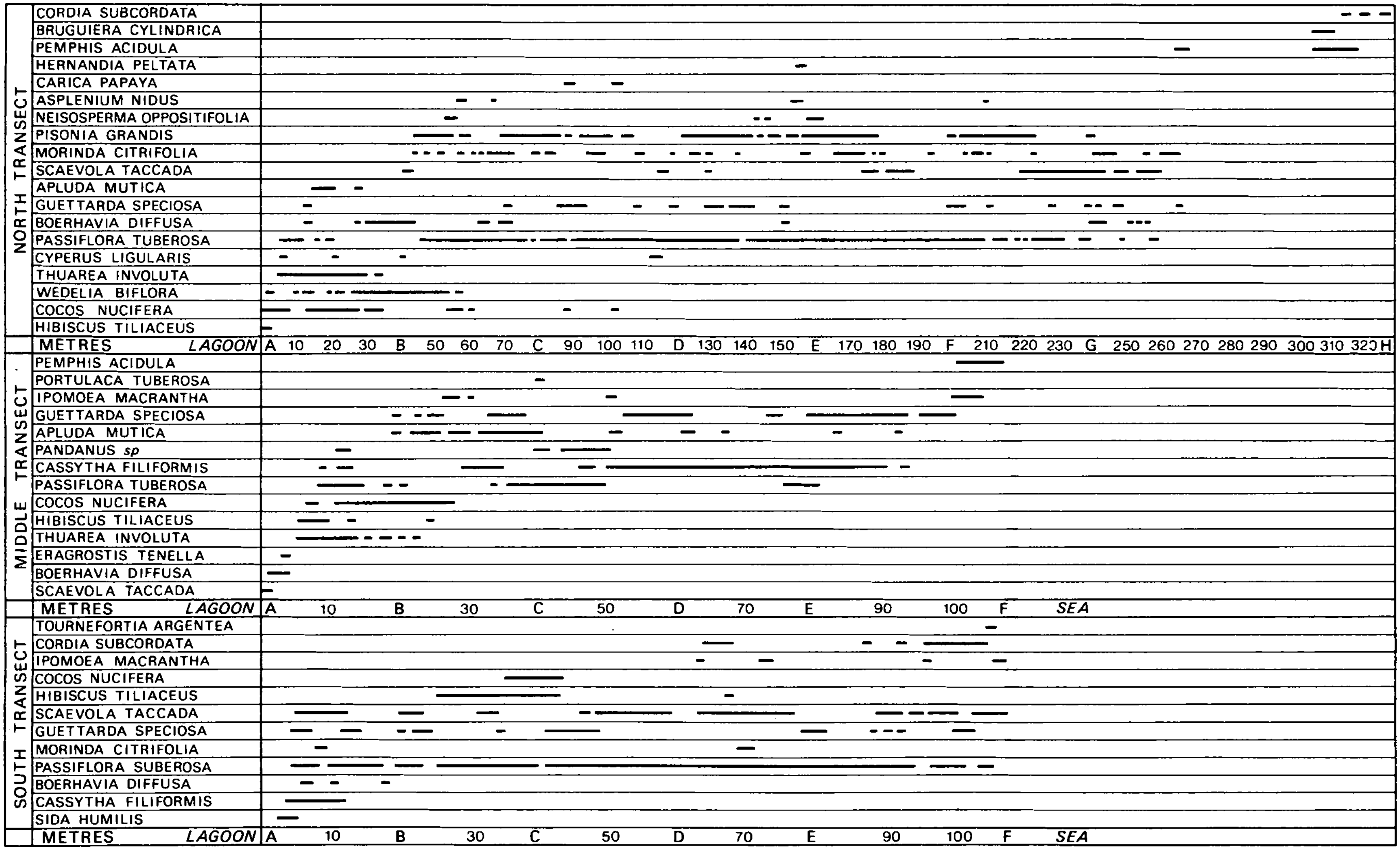

Fig. 4. The distribution of species along the transects. The presence of a species in every 1 metre section of the transect is marked by a horizontal bar.

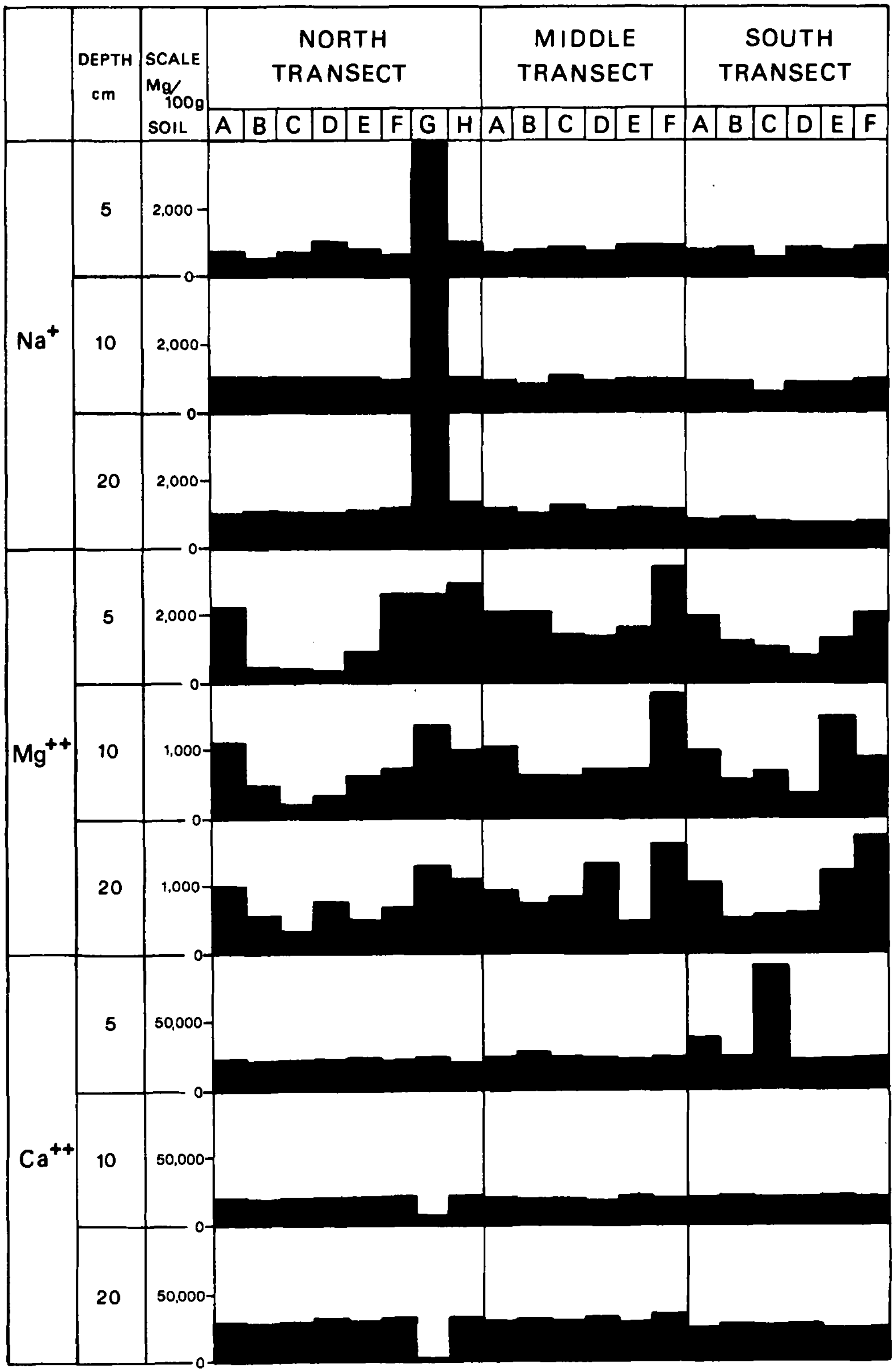

Fig. 5. The distribution of the elements Sodium, Magnesium and Calcium in the soil samples from three transects spanning the width of Wilingili. The values represent the total amounts of the elements present.

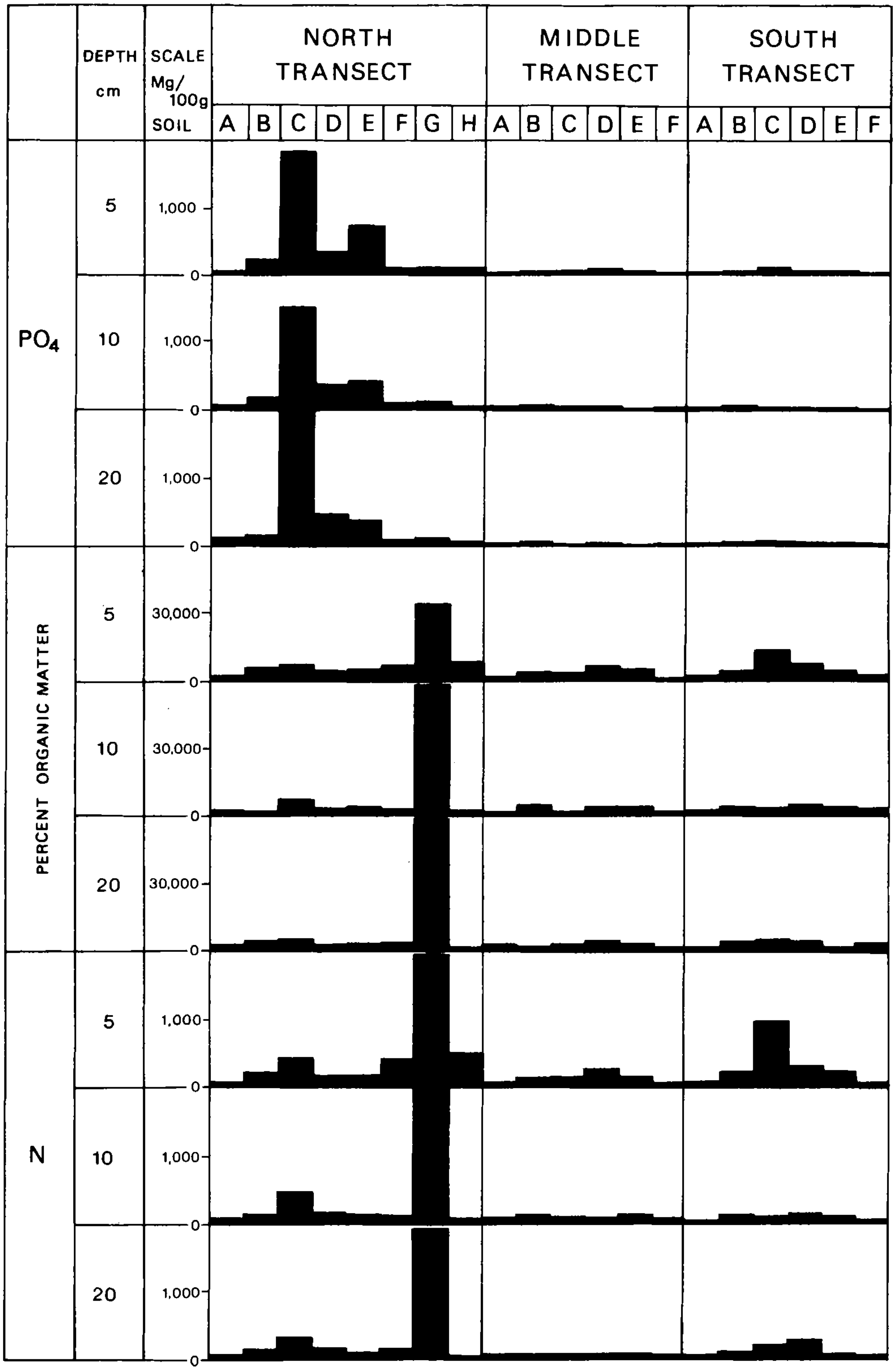

Fig. 6. Total Phosphate and Nitrogen levels, together with percentage organic matter in the soils from three transects.

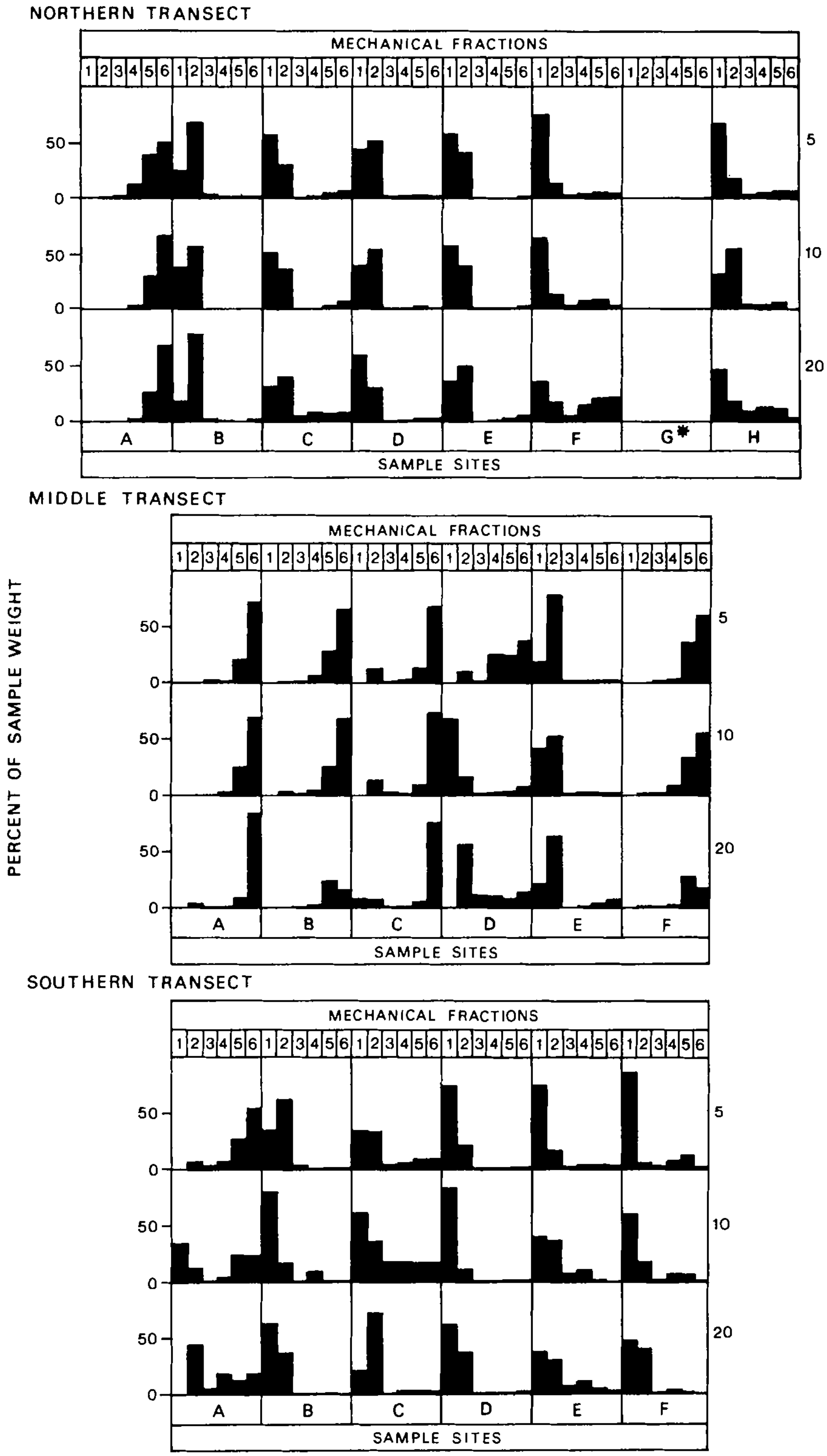

Fig. 7. Mechanical fractions of the transect soils. The asterisks denote those samples composed entirely of organic Mangrove peat.

THE TERRESTRIAL VEGETATION OF AN INDIAN OCEAN CORAL ISLAND: WILINGILI, ADDU ATOLL, MALDIVE ISLANDS

II. A LIMITED QUANTITATIVE ANALYSIS OF THE VEGETATION DISTRIBUTION

by D.McC. Newbery[1] and R.A. Spicer[2]

ABSTRACT

The distribution of the vegetation of Wilingili was assessed by measurement of 45 species and 51 soil variables at each of twenty chosen sites. Principal components analysis (PCA) was used to identify the main gradients of the vegetation, the component scores being correlated with the floristic and environmental variables to detect associations between these variables.

Two gradients were identified. Firstly, a mid-island lagoon to sea shore gradient of decreasing sandiness and increasing sodium along which a change from coconut communities, through bush to strand vegetation was seen. The second, a north to south gradient represented changes from bush to forest accompanied by increasing iron, phosphorus and nitrogen with decreasing sandiness, magnesium and carbonate.

A simple model relating the main types of vegetation, the position of the gradients and an approximate realisation to the successional development of the island is discussed.

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INTRODUCTION

The general features of the vegetation on Wilingili have been described in the previous paper, in which an identifiable lagoon-to sea-shore gradient was studied. Here, we adopt an alternative approach by sampling the vegetation over all the island with a view to the recognition of the main floristic and environmental gradients illustrated by the use of ordination techniques.

The data collected are not extensive and so the application of numerical multivariate techniques and their interpretation will be limited. This paper, we hope, will serve as an introduction to the, as yet, little studied topic of the ecology of terrestrial coral island vegetation.

METHODS

Vegetation and soil measurements of stand sites

Twenty subjectively chosen sites, hereafter referred to as stand sites, were studied in detail with the primary aim being to record the major vegetation types present on the island, and secondly to investigate the possible occurrence of a longitudinal gradient from the southern tip to the northern head of the island (Fig. 1). Furthermore four stand sites (numbers 2, 3, 4 and 5; Fig. 1) were included to show the stages in the common phenomenon of coconut grove regeneration after disturbance, which was super-imposed on the more natural vegetation of the island. This disturbance was chiefly the result of bush clearing and of trampling. On field observation all stand sites, with the possible exception of site 11, could be considered as members of a continuum, rather than distinct groups of differing vegetation.

At each site a 10 m by 10 m area square was pegged out with string and within it more strings laid to subdivide the area into 100 1 m by 1 m quadrats. Thirty five of these quadrats were randomly selected, and in each, the presence or absence of each species was noted, so that on summation for each stand site a local frequency estimate for each species was attained, as a score out of thirty-five. These data, referred to as the floristic variables matrix, appear in Table 1. Fig. 1 shows the relative position of each site on the island.

A soil pit was dug in the central area of each stand site, in a similar manner to transect soil pits (described in the previous paper). Soil pH was recorded *in situ* at each of the three depths, 5, 10 and 20 cm depth (Table 2, col.1). Soil samples of approximately 150 grammes wet weight were also taken at each of these depths in each stand site.

Chemical analysis of soils

On return to England the soil samples were air dried in the laboratory. It had been necessary to store the soils wet in the field.

Because of the somewhat unusual nature of the 'soil' a mechanical fraction scale had to be specially devised. The six fractions, MF/1/X...MF/6/x where x is the depth collected, correspond to the following particle sizes: 1, >20 mm; 2, 20-3.35 mm; 3, 3.35-2.0 mm; 4, 2.0-1.0 mm; 5, 1.0-0.5 mm; 6, <0.5 mm. Each sample was sieved and the mechanical fractions recorded as percentages of the total air dry weight. It will be noted that for site 11, each fraction, because of the peaty nature, was given an equal value of 16.7%.

After the six weeks storage of the soils, wet, and in an anaerobic state, total elemental analysis seemed an appropriate measure of the nutrient status of the soil rather than an analysis for the exchangeable fraction. This former measure of soil nutrients has been successfully employed in previous studies of vegetation whose scale was comparable to that of Wilingili (e.g. Austin, Ashton and Greig-Smith, 1972).

The soil sample was subdivided and a portion (approx. 20 g.) milled in a Glen Creston Sample Mixer Mill (M280) using tungsten carbide balls.

Two digests were prepared: (a) nitric and perchloric acids (4:1 mixture), with two replicates of each sample, and (b) sulphuric acid and hydrogen peroxide. These were made up to 10 per cent acid solution for analysis.

Iron, copper, calcium and magnesium were determined by atomic absorption spectroscopy using digests (a). These digests were also analysed for potassium and sodium by flame emission spectroscopy.

The organic matter content of the soils was determined by loss on ignition at 375^{o}C (Ball 1964) with subsequent subtraction for air dried soil moisture. Samples of pure calcium carbonate heated to this temperature lost no weight, indicating that organic matter losses were not confounded by any losses in carbonate from the samples. This method was preferable to a wet oxidation procedure, which in agreement with Orphanos (1973) was found to be unsuitable for such carbonate rich soils. Carbonate itself was assessed gravimetrically by the method of Bauer, Beckett and Bie (1973).

Phosphate (in the nitric: perchloric acid digests) was estimated by the molybdenum blue and total nitrogen (in the sulphuric acid: peroxide digests), by the alkaline-phenol reaction on a Technicon Auto Analyzer. The results of the analyses are summarised in Table 2 as the means of each variable over the three depths sampled. Variables for each of the three depths constitute the environmental variables matrix (51 variables).

NUMERICAL ANALYSIS

The raw data matrices to be considered in the ensuing analysis are:

(i) Matrix X, the floristic variables matrix, Table 1 (45 spp.), and,
(ii) Matrix Y, the environmental variables matrix (51 variables) a condensed form of which appears as Table 2.

Principal components analysis (PCA) was employed in a numerical analysis of the data, to elucidate those floristic and environmental variables most important in the distribution of, or rather changes in, the vegetation of the island. The method of analysis was Q-type and used the weighted similarity coefficient of Orloci (1966). Classification techniques have not been employed in the work reported here. Computer programmes were written in Fortran lV by Dr. A.J. Morton and one of us (D.McC. N.).

Stand Ordinations

Standardisation for stands (to zero mean and unit variance for each stand) was supplied to matrix X, resulting in matrix A_1. PCA of A_1 provided a stand ordination based on floristic variables (Fig. 2). Matrix B, the result of standardisation of Matrix Y (to zero mean and unit variance for each environmental variable) was also subjected to PCA giving a second stand ordination, this being based on environmental variables (Fig. 3).

Floristic and environmental variables ordinations

Matrix X was then standardised for species (each to zero mean and unit variance) giving matrix A_2 the transpose of which, A_2^T, was subjected to PCA with the production of a species ordination (Fig. 4).

Transposition of matrix B, to B^T and subsequent PCA of B^T produced an ordination of environmental variables (Fig. 5).

Table 3 shows the percentage variance removed by each of the first three components in the four ordinations.

Correlation analysis

To investigate which floristic and environmental variables were associated in the distribution of the vegetation, a correlation procedure was adopted (Flenley 1968, Burden and Randerson 1972).

Considering the principal components removed in the stand ordinations of matrix A_1, each vector of component scores (*sensu* Gittins 1969):

$$C_v \quad (1, 2...20), x = 1, 2, 3$$

was correlated with each vector of floristic variables (i.e. species)

$$F_y \quad (1, 2...20), y = 1, 2...45$$

and each vector of environmental variables,

$$E_z = (1, 2...20), z = 1, 2...51$$

The following different correlations were performed for each pair of vectors:

C.v. (i) Fy, (ii) Ez, and (iii) $\log_e$ (Ez) with the Pearson product moment correlation coefficient, and,
C.v. (iv) Ez applying the Spearman Rank correlation coefficient (Siegel 1961)

Methods (iii) and (iv) were included to cover the possibility of non-linear relationships suggested by the work of Austin and Noy-Meir (1971).

As a criterion, with which to summarise the results usefully and concisely, those correlation coefficients with statistical significance of $P<0.05$ were selected. Table 4 presents such a summary of a correlation analysis, based on the component scores of the PCA of matrix A_1.

DISCUSSION

Methodology

In the preliminary analysis of the data matrices X and Y, a number of principal component analyses (PCAs) were performed on different arrangements of the data. Far be it from the purpose of this paper to present a full discussion of the comparison of the different methods. This has been adequately done by a number of authors, more recently by Whittaker (1973). However, for this particular and somewhat unusual set of data, the reasons for the final adoption of standardisations, used in the above section, will be outlined briefly.

The stand ordination, from a PCA based on unstandardised floristic variables (not illustrated), resulted in the formation of a group of species poor sites (stand sites 6-12 inclusive, Table 1). This was not advantageous to interpretation especially as those sites contained important species which featured in other sites. The effect of standardisation for stands was to spread out these species poor sites across the ordination (Fig. 2), to give truer realization to the position of site 11, and to enable the possible detection of gradient along the length of the island.

Treatment of matrix Y, the environmental variables, to produce a stand ordination, was achieved most efficiently by standardisation for the variables. Straight ordination and an ordination based on logarithmic transformation of matrix Y proved unsatisfactory.

For the species ordination, standardisation for each species was essential, as in its absence, or with only standardisation for stands, all rare species were clumped at the ordinations origin with failure to dissect out the main vegetation types. Ordination of the environmental variables was again best performed with standardisation for each species.

Correlation analysis were applied to the component scores of most of the alternative PCAs mentioned immediately above. Only that analysis, using the component scores from PCA of matrix A_1, provided an intelligible interpretation of the data and the results of which were further supported by those environmental variable ordinations finally adopted. It was felt that this correlation procedure was relevant only to the component scores of the PCA matrix A_1 as matrix X was based on a complete set of floristic data. On the other hand, matrix Y obviously lacks many variables of the environment, since those actually measured had inevitably been selected by circumstance and intuition based on some postulate of their importance. A correlation analysis procedure based on the component scores of the PCA of matrix B did, in fact, lead to very spurious conclusions which neither matched the other correlation analysis in Table 4, nor complemented the groupings of variables inferred by the ordinations. This latter-mentioned correlation analysis procedure is not illustrated and will not be referred to further

<u>Interrelations of floristic and environmental variables</u>

Stand ordinations, from the PCA of matrix A_1 (Fig. 2), and from the PCA of matrix B (Fig. 3) do not suggest any grouping of sites, though sites which are geographically close (Fig. 1) tend to lie near one another on the ordinations and sites 11 and 19 are separated from the rest, for example sites 15, 17 and 19 and sites 2, 3 and 4 in Fig. 2. In general terms axis I (Fig. 3) and axis III (Fig. 3) tend to separate out the sites, with the northerly ones at one end and the southerly ones at the other end. The stand ordination of the environmental variables also illustrates the difference of sites 11 and 19 from the other sites.

More immediate information is to be gained from an examination of the variables ordinations. From the scatter of points on the species ordination (Fig. 4) it is evident that some species are highly associated as groups A, B and C. These groups have not been delimited by a quantitative method such as classification, as this was considered unnecessary for such a small body of data, but seek only to help visual interpretation. Groups A, B and C contain the following species, consistent in three dimensions:

A: *Cyperus ligularis, Psilotum nudum, Oplismenus imbecilis, Fimbristylis cymosa, Cladium jamaicense* and *Euphorbia indica*.

B: *Kalanchoe pinnata, Nephrolepis hirsutula, Colocasia esculenta, Neisosperma oppositifolia, Laportea interrupta* and *Ficus benghalensis*.

C: *Portulaca tuberosa, Sida humilis, Launaea pinnatifida, Lepturus repens* and an unknown species (No. 34, Table 1).

Examination of the third axis Fig. 4b, c reveals four more groups separated from the central mass of points in Fig. 4a. These groups D to F include:

D: *Ipomoea macrantha, Vernonia cinerea* and *Eragrostis tenella*

E: *Guettarda speciosa, Pemphis acidula, Rhizophora mucronata* and *Tournefortia argentea*.

F: *Carica papaya, Polyscias guilfoylei, Achyranthes aspera* and unknown species (no. 39, Table 1).

G: *Passiflora suberosa, Morinda citrifolia, Asplenium nidus* and *Hernandia peltata*.

Group A includes essentially those species which recolonise disturbed coconut groves in the north of the island (sites 2-5) whilst B contains those species of the wetter central forest close to the encampment (such as site 18). The two main species of disturbed areas are *Thuarea involuta* (no. 3) in the heavily trampled parts of the island and *Wedelia biflora* (no. 19),a weed-like species inhabiting disturbed cleared ground. (Fig. 5b, c). Group C on the other hand includes those species recognised from the scrub sites (sites 13 and 14) together with *Cassytha filiformis* (No. 7).

The forest sites are the four groups D to F plus other species. The arrangement of these groups presents a successional picture from the shrubs and small trees in D, (related to the species of group C) to the mature hardwood forest sites of group G. Group G species are found in such sites as 15, 17 and 19 amongst the main species, *Pisonia grandis* and *Passiflora suberosa*. Group E, again, are intermediary forest sites but drier, typified by site 15 and associated with the pawpaw, *Carica papaya*. Lastly, group F, may be identified by mid-island scrub, including the most common bush on the island, *Guettarda speciosa*, and the mangrove, *Rhizophora mucronata*.

The remaining species, so far not discussed, are probably, in terms of biomass the most important, having associations with two or more species groups between which they lie. *Cocos nucifera* (no. 5), the coconut, for instance, in Fig. 5b, lies between groups A, B, C, D, and E as it shares a distribution among all those sites whose species constitute these five groups, (with the exception of the mangrove). The strand plants, *Scaevola taccada* and *Suriana maritima* (nos. 1 and 41) lie close to the other members of group E, especially *Pemphis acidula* (no. 13), which shares a strand and inland scrub habit, and *Apluda mutica* (no. 10). *Pandanus* sp. (no. 8) and *Hibiscus tiliaceus* (no. 4) cannot easily be placed with any group in particular owing to a somewhat general habit.

The environmental variables ordination, Fig. 5, of which only the first two axes are illustrated, characterises by observation four main groups P, Q, R, and S with the remaining seven variables loosely comprising a group referred to as T.

The five groups consist of the following variables:

P: MF/5 (5, 10, 20), MF/6 (5, 10, 20), Mg (5, 10, 20).
Q: pH (5, 10, 20), Ca (5, 10, 20), CO_3 (5, 10, 20).
R: MF/1 (5, 10, 20), MF/2 (5, 10, 20), MF/4 (5), Fe (10, 20), Cu (10), Phos (5, 10, 20).
S: MF/3 (5), Na (5, 10, 20), K (5, 10, 20), N (5, 10, 20), C (5, 10, 20)
T: MF/3 (10, 20), MF/4 (10, 20), Fe (5), Cu (5, 20).
(Note that the figures in parenthesis denote depth in cm at which the measurement of the variable was made).

The following points of interest may be made:

(i) that the third principal component essentially separates out group R into mechanical fraction sizes 1 and 2 at one end and phosphorus and iron at the other, hence solving the apparently anomalous group R associations.

(ii) Group Q associations are obvious, that is rise in pH with calcium carbonate content, whilst group P illustrates the high magnesium content of fine-grained soils.

(iii) The cationic (monovalent) status is well associated with the organic matter constituents carbon and nitrogen, which together operate as a functional colloidal structure in the matrix of coral blocks which is resistant to leaching of potassium.

Having identified the main groups of variables present, attention may now be returned to the stand ordinations and more particularly to their component scores used in the correlation analysis mentioned above.

Considering the component scores of the stand ordination based on the PCA of matrix A_1, component 1 (Table 4) associates an increase in *Scaevola taccada* and *Pemphis acidula* and a decrease in *Cocos nucifera, Portulaca suberosa* and species of group A with increasing percentage of large particles and sodium. On axis 2, *Pemphis acidula* increase and *Scaevola taccada, Cassytha filiformis* and *Guettarda speciosa* decrease is associated with increase in percentage intermediate particle size. Component 3 associates, increase in *Pisonia grandis* and species of group G and decrease in *Apluda mutica* and *Cassytha filiformis*, with increase in the percentage of large particles, iron, phosphate and nitrogen and decrease in the percentage of small particles, magnesium and carbonate.

With a view to the interpretation of Table 4 the following points are relevant. Firstly, that correlations of environmental variables tend to complement each other. For example where percentage of large particles increases, that of small particles decreases, and those variables that are highly associated in Fig. 5 tend to correlate the scores of the same component together, (Component 3, Table 4). Secondly, species that occur together in the species ordination, such as those of groups A and G, correlate with the scores of the same component; and thirdly, measurement of a variable at three depths acts as a crude form of replication and where two or three of the depth-replicates correlate with an axis simultaneously, the case for an association with that component is strengthened.

As yet meteorological data have not featured in the interpretation of the distribution of vegetation. Spicer & Newbery (1978) have indicated that the exposure at the centre of the island is approximately half that at the shores. With no estimate of exposure at each of the stand sites, a crude measure of shelter (the inverse of exposure) can be taken as the shortest distance from each site to the sea. These distances were correlated with the components of the stand ordination based on matrix A_1. The correlation of shelter with component 1($-r$, $P < 0.01$) agrees with the other variables associated with this component. That is, a short distance inland, i.e. from the beaches, the exposure is high and the sodium deposition great (mainly in the form of sea spray) and it is here that the strand plants *Scaevola taccada* and *Pemphis acidula* survive.

The vegetation system

Successional evaluation of vegetation is normally not possible in many ecosystems without records stretching over a long time period yet in those systems in which the changing geography leads to the quick, continuous formation of new land from the sea an approximate realisation of the processes of colonisation and succession may be found at any one time. The island of Wilingili is a prime example illustrating the successional stages as a longitudinal gradient from the bare coral at the southern tip of the island (Fig. 1) to the mature forest of the northern central region. Indeed, many factors of disturbance are to be found superimposed upon this general picture of the vegetation, such as the encouragement of coconut groves on the lagoon side of the island. On the seaward side the introduction of brackish water systems, in the form of swamps and ponds, influences the system in other ways. Despite these, and other smaller complications a general trend in the development of soils and vegetation can be traced up the central 'spine' of Wilingili, especially, in its southern half. Furthermore, implications of lagoon sea gradients must be borne in mind

(Spicer & Newbery 1978) though these tend to operate in a more pronounced fashion nearer the shores.

For the purposes of the present discussion it is desirable to consider five, rather theoretical, vegetation types. (i) sparse coral strand vegetation, (ii) bush-small tree vegetation, (iii) coconut communities, (iv) forest, and (v) swamp. Amplification of these types to the real situation can be realised by reference to the species ordination (Fig. 4 and above text) of major species and species groups A to G.

The environmental variables may also be summarised into: (i) soil particle size variables (which to some degree also represent drainage properties of the soils), and (ii) organic matter variables, subsidiary to, and related, to which are pH and cationic status.

Returning to the vegetation model, Fig. 6, a number of gradients may be supposed to exist. The correlation analysis procedure, Table 4, has selected and demonstrated the two most prominent in the data.

These are:

Gradient 1: The change in vegetation from strand plants *Pemphis acidula* and *Scaevola taccada* to coconut communities, mainly of *Cocos nucifera* and *Portulaca suberosa* is accompanied by a decrease in percentage of large particles (and increases in small particles) and decrease in sodium. This gradient essentially operates mid island from the 'rocky' sea-ward beach to the sandy lagoon side of the island (Fig. 1 and 6), and is represented by component 1 (Fig. 2 and Table 4) of the stand ordination of floristic parameters. Component 2 (Fig. 2 and Table 4) is partly coincident with component 1 indicating a slight gradient from strand to bush vegetation but probably operating further south down the island beyond the limit of coconuts.

Gradient 2: This represents the change in vegetation from bush-small tree vegetation to *Pisonia grandis* dominated forest in the north, and is accompanied by a decrease in sandiness (small particles) and magnesium carbonate with an increase in larger particles, iron, phosphorus and nitrogen. It is necessary to include within this rather major and composite gradient those changes from bushy recolonising sites. Because of decreasing sandiness it seems that this gradient will operate to the lagoon side of the island and touching these disturbed sites as indicated in Fig. 6. The gradient is significantly supported by correlation of variables with component 3 of the stand ordination (Fig. 2 and Table 4).

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Table 1. Local Frequency estimates of each species at each of the stand sites.

		STAND SITE NUMBER																			
	SPECIES	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	*Scaevola taccada*	30		1		29	7	31	20	29	10				8		31			5	3
2	*Boerhavia diffusa*	5				2					8				4		6		3		
3	*Thuarea involuta*										21				32			6	27		
4	*Hibiscus tiliaceus*	1			6																28
5	*Cocos nucifera*	10	10	34	26	13			3	1				14	7	16	15		17		17
6	*Passiflora suberosa*	9		11	2	5								22		35	13	24		32	14
7	*Cassytha filiformis*	20	20			25					12			34	35						
8	*Pandanus* sp.	18			2									1							
9	*Guettarda speciosa*	8		3	1	20	1	2	18	14	19			1	15	30	20			6	2
10	*Apluda mutica*	26	35	34	27	9					1										
11	*Ipomoea macrantha*	13		3							7				13	3					
12	*Portulaca suberosa*	2												2							
13	*Pemphis acidula*						18	31	8		18	10	35								
14	*Sida humilis*			6										30	5						
15	*Morinda citrifolia*									10						5	10	28		12	
16	*Neisosperma oppositifolia*														3	2			11		
17	*Asplenium nidus*				2				1							3		24			
18	*Tournefortia argentea*							7													
19	*Wedelia biflora*		34	6		16									14				24	20	7
20	*Cyperus ligularis*			3	16	2													2		1
21	*Pisonia grandis*															19		35	1	12	
22	*Carica papaya*															5					
23	*Rhizophora mucronata*									35											
24	*Psilotum nudum*			6	6																
25	*Oplismenus imbecilis*			8	29															1	25

Table 1. (continued)

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
26	*Kalanchoe pinnata*																		30		
27	*Nephrolepis hirsutula*																		7		
28	*Colocasia esculenta*																		15		
29	*Digitaria horizontalis*			2	18									18	19						
30	*Fimbristylis cymosa*				21																
31	*Cladium jamaicense*				4																
32	*Launaea pinnatifida*													17							
33	*Tacca leontopetaloides*																				17
34	*													3							
35	*Polyscias guilfoylei*																			24	
36	*Euphorbia indica*			3	3																
37	*Vernonia cinerea*														3						
38	*Laportea interrupta*																		4		
39	*																	7		27	
40	*Eragrostis tenella*			2											6						
41	*Suriana maritima*								7												
42	*Lepturus repens*								12					18							
43	*Achyranthes aspera*															1					
44	*Hernandia peltata*																	2			
45	*Ficus benghalensis*																		12		

*. Indicates insufficient plant material collected for identification.

Table 2. Environmental measurements for each of the 20 stand sites.

Each value in the table represents the mean of 3 measurements (i.e. at the 3 depths 5, 10 and 20 cm).

	pH	MECHANICAL FRACTION %						TOTAL CONC. CATIONS mg/100g SOIL						TOTAL ANION CONC. mg/100g Soil			%
SITE		1	2	3	4	5	6	Fe	Na 10^2	Mg 10^3	K	Ca 10^4	Cu	P 10^2	CO_3 10^3	N 10^2	Org. Mat.
1	8.23	0.0	1.2	2.8	11.3	52.2	33.3	14.9	7.41	1.01	35.0	2.93	0.89	0.32	42.2	1.03	2.81
2	8.60	0.0	5.1	2.5	4.4	39.9	49.2	11.6	8.09	1.06	36.1	2.68	1.05	0.19	47.1	0.66	3.39
3	8.17	0.0	4.6	2.2	6.8	37.1	48.9	6.7	8.22	1.33	36.0	3.24	0.99	0.14	44.8	0.54	2.91
4	8.10	0.0	12.9	14.2	34.4	28.3	8.6	7.8	7.64	1.03	38.9	2.84	1.34	0.21	46.4	1.17	4.37
5	8.20	0.0	1.3	1.3	5.7	43.6	47.9	10.6	8.14	1.05	37.2	2.82	1.09	0.22	46.6	1.00	4.60
6	8.13	42.8	26.4	4.8	7.9	11.2	7.0	6.8	8.23	1.36	33.6	2.80	0.79	0.16	44.7	0.31	2.78
7	7.97	38.0	31.9	4.1	18.2	7.5	0.2	7.9	9.41	1.26	36.1	3.24	0.79	0.17	47.2	0.31	3.40
8	8.17	13.4	40.8	8.4	12.3	16.1	8.6	10.4	8.07	2.08	35.4	3.19	0.80	0.27	45.4	0.58	4.45
9	8.50	65.2	31.6	1.7	0.8	0.4	0.2	6.1	9.32	0.85	34.2	3.10	1.08	0.29	45.4	0.84	3.94
10	8.20	21.1	60.5	4.1	3.4	6.3	4.3	7.2	9.76	0.58	34.9	2.98	1.38	0.18	42.5	1.00	4.06
11	6.80	16.7	16.7	16.7	16.7	16.7	16.7	9.6	32.34	1.26	206.7	0.22	1.25	0.88	1.2	14.46	52.72
12	8.03	36.2	15.5	7.2	23.6	12.8	5.8	8.9	10.04	1.17	40.6	3.11	0.86	0.31	43.8	0.93	4.27
13	8.37	24.6	22.4	3.9	4.2	10.6	33.8	5.8	7.30	1.31	34.8	2.70	0.97	0.27	44.5	1.00	4.43
14	8.50	12.3	2.4	0.1	1.7	38.4	43.7	8.4	7.94	0.76	36.0	2.73	1.25	0.29	43.8	1.01	4.15
15	7.77	59.8	28.0	2.7	1.9	2.8	4.5	13.7	8.83	0.17	37.7	2.72	1.17	13.30	37.0	2.13	5.15
16	8.40	23.4	15.0	1.4	1.3	2.9	55.3	6.4	8.07	1.10	36.2	2.69	0.65	0.36	42.3	1.14	4.89
17	8.33	37.4	54.7	0.9	1.3	2.0	1.6	8.7	8.40	0.39	35.6	2.65	0.91	6.31	38.1	1.93	4.73
18	8.00	9.9	56.9	11.6	11.8	5.9	2.7	12.0	7.43	0.74	36.4	2.71	1.15	2.88	39.4	3.19	8.41
19	7.93	34.3	12.1	3.6	18.3	17.1	12.8	22.9	4.68	0.32	36.8	2.27	1.38	27.36	23.7	7.34	18.90
20	8.30	0.0	5.0	0.9	14.2	40.5	39.6	10.2	7.14	0.35	35.6	2.91	0.95	1.54	39.2	1.64	3.75

Table 3. Percentage variation removed by principal components for the four ordinations.

PCA	Matrix	Component			Total
		1	2	3	
Stands	A_1	21.3	15.4	13.7	50.4
Stands	B	38.6	18.2	14.2	71.0
Floristic variables	A_2'	16.3	14.5	12.5	43.3
Environmental variables	B'	37.7	18.7	14.5	70.9

Table 4. Floristic (F) and environmental (E) variables correlation with the first three principal component of PCA matrix A_1, using parametric tests unless otherwise indicated.

		-r		+r	
COMPONENT 1	F	C. nucifera	***	S. taccada	*
		P. suberosa	*	P. acidula	***
		A. mutica	*		
		W. biflora	*		
		P. nudum	*		
		O. imbecilis	*		
		E. indica	*		
	E	MF/5/5	**	MF/1/5	***
		MF/6/5	* (pt**)	MF/2/5	NS(np *)
		Cu/5	**	MF/1/10	*
				Na/5	NS(np *)
				Na/10	NS(np *)
				Na/20	NS(np *)
				Mg/20	*
				N/5	NS(pt *)
COMPONENT 2	F	S. taccada	**	P. acidula	*
		C. filiformis	*		
		G. speciosa	**		
	E	MF/6/5	*	MF/3/5	*
		pH/10	*	MF/4/5	NS(pt*, np*)
		pH/20	**	MF/3/10	*
				MF/4/10	*
				MF/3/20	*
				MF/4/20	*
				Na/10	ns(pt*)
				K/10	NS(np*)
COMPONENT 3	F	C. filiformis	*	P. suberosa	***
		A. mutica	*	M. citrifolia	***
				P. grandis	***
				A. iridus	**
				M. peltata	*
	E	MF/5/5	* (np**)	MF/1/5	NS(np*)
		MF/5/10	* (np**)	MF/1/10	*
		MF/6/10	*	MF/2/10	NS(np*)
		MF/3/20	**	MF/1/20	***
		Mg/5	NS(pt**)	MF/2/20	Ns(pt*, np*)
		Mg/10	NS(pt**)	Fe/10	*
		Mg/20	NS(pt**)	Fe/20	*
		Carb/5	*	Phos/5	***
		Carb/10	NS(np*)	Phos/10	***
		Carb/20	Ns(np*)	Phos/20	***
				N/5	NS(np*)
				N/10	NS(np*)

+r, positive correlation; -r, negative correlation; NS, not significant; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; np, non-parametric test applied; pt, parametric (logarithmic) transformation of variables used.

It should be noted that the following notation has been adopted: where (1) the correlation coefficient by method (ii, see text) failed to reach significance, whilst that from methods (iii) and/or (iv) did, or (2), that significance was reached in all three cases with that of (iii) and/or (iv) being greater, these facts are quoted as such with the probability levels for methods (iii) and/or (iv) in parenthesis.

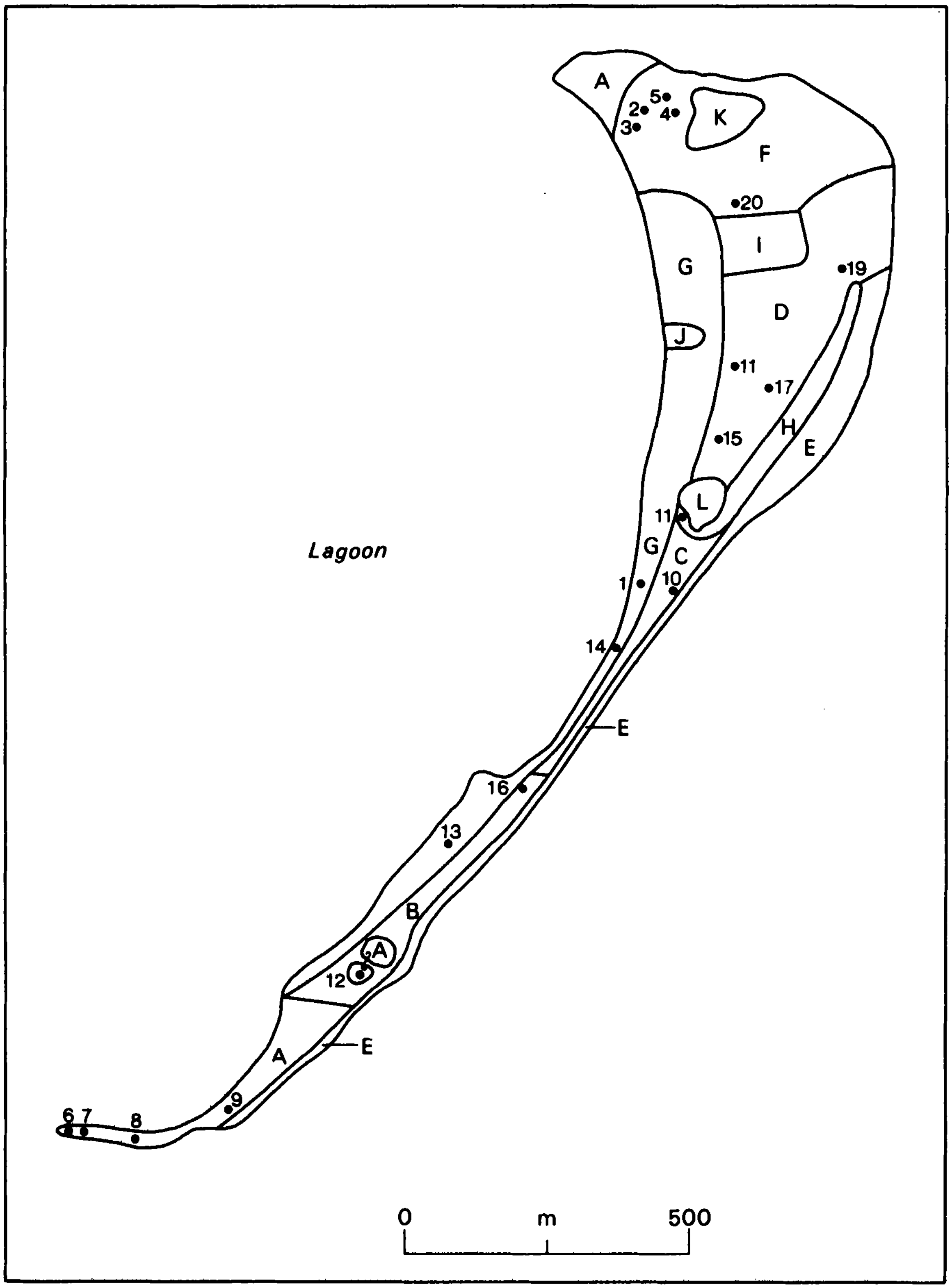

Fig. 1. Map of Wilingili indicating the positions of the stand sites with respect to island geography and general vegetation types. A, Sparse vegetation, *Pemphis acidula* and *Scaevola taccada*; B, Bush vegetation; C, small trees and shrubs; D, central *Pisonia grandis* hardwood forest; E, Strand *Pemphis acidula*; F, Northern *Pandanus*-coconut forest; G, *Cocos nucifera* groves; H, mangrove swamp; I, 'semi-cultivated' area; J, native huts; K, sea-water pond; L, brackish water pond; M, dried out ponds.

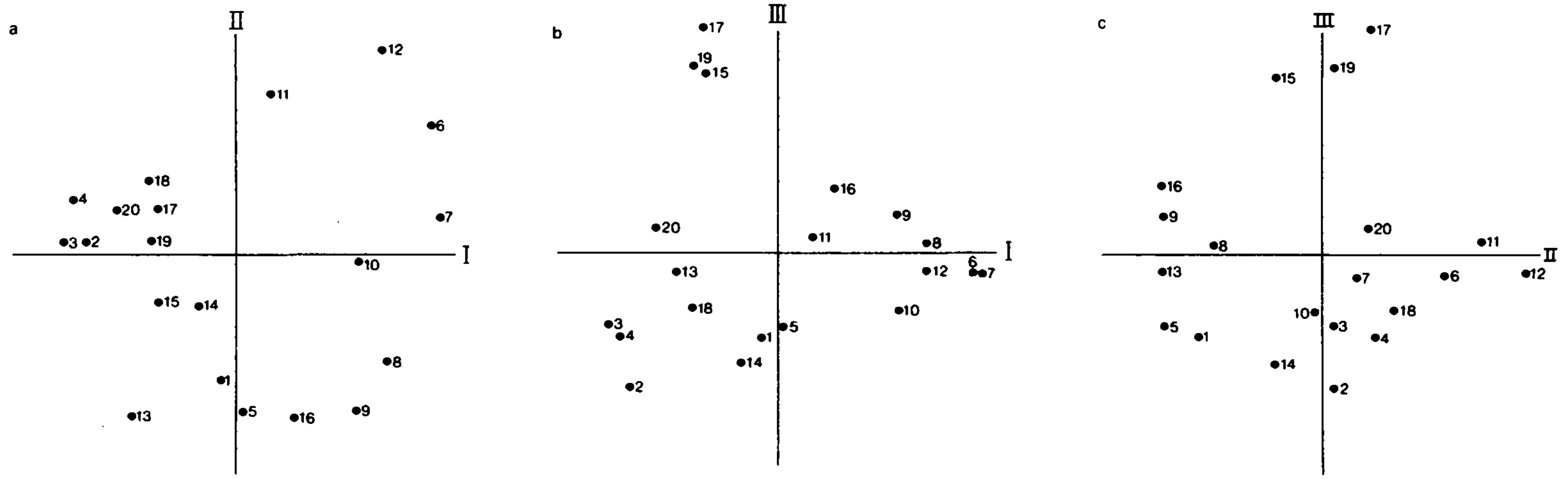

Fig. 2. Stand ordination plots from PCA on the floristic variables matrix A. (a) axes I and II; (b) axes I and III; (c) axes II and III. Numbered points refer to individual stand sites.

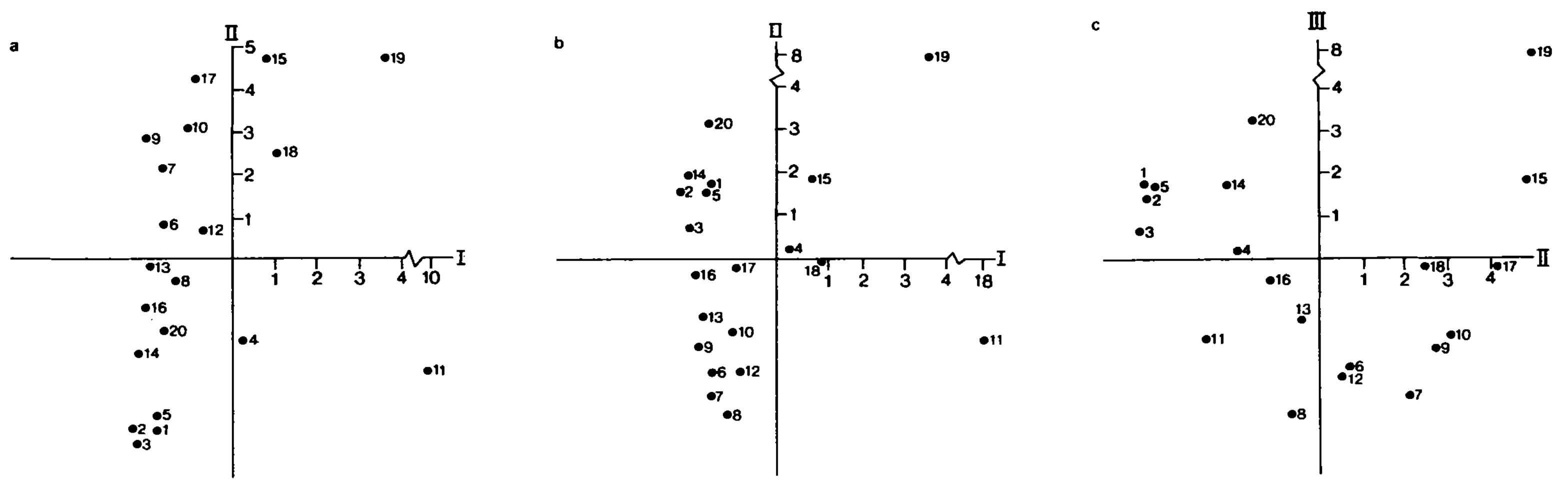

Fig. 3. Stand ordination plots from PCA on the environmental variables matrix B. (a) axes I and II; (b) axes I and III; (c) axes II and III. Numbered points refer to individual stand sites. The scale depicted in (a) also applies to (b) and (c).

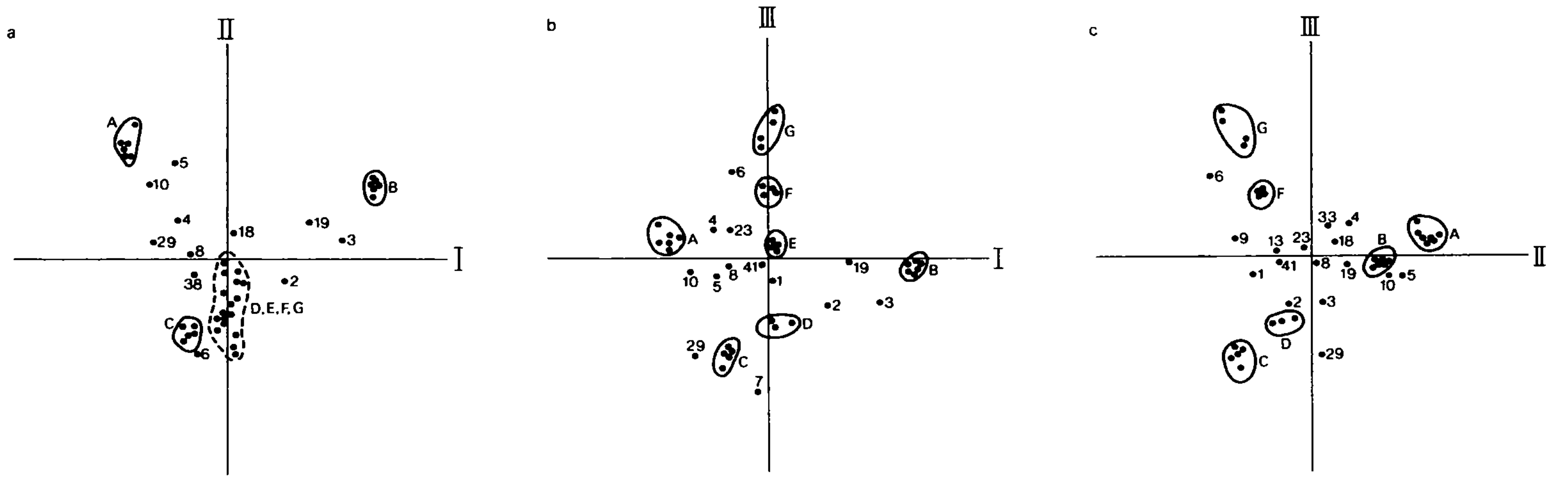

Fig. 4. Floristic variables ordination plots from PCA of matrix $A_2^{\bar{\prime}}$.
(a) axes I and II; (b) axes I and III; (c) axes II and III.
For content of species groups A to G see text, other numbered points refer to individual species recorded in the left hand side of Table 1.

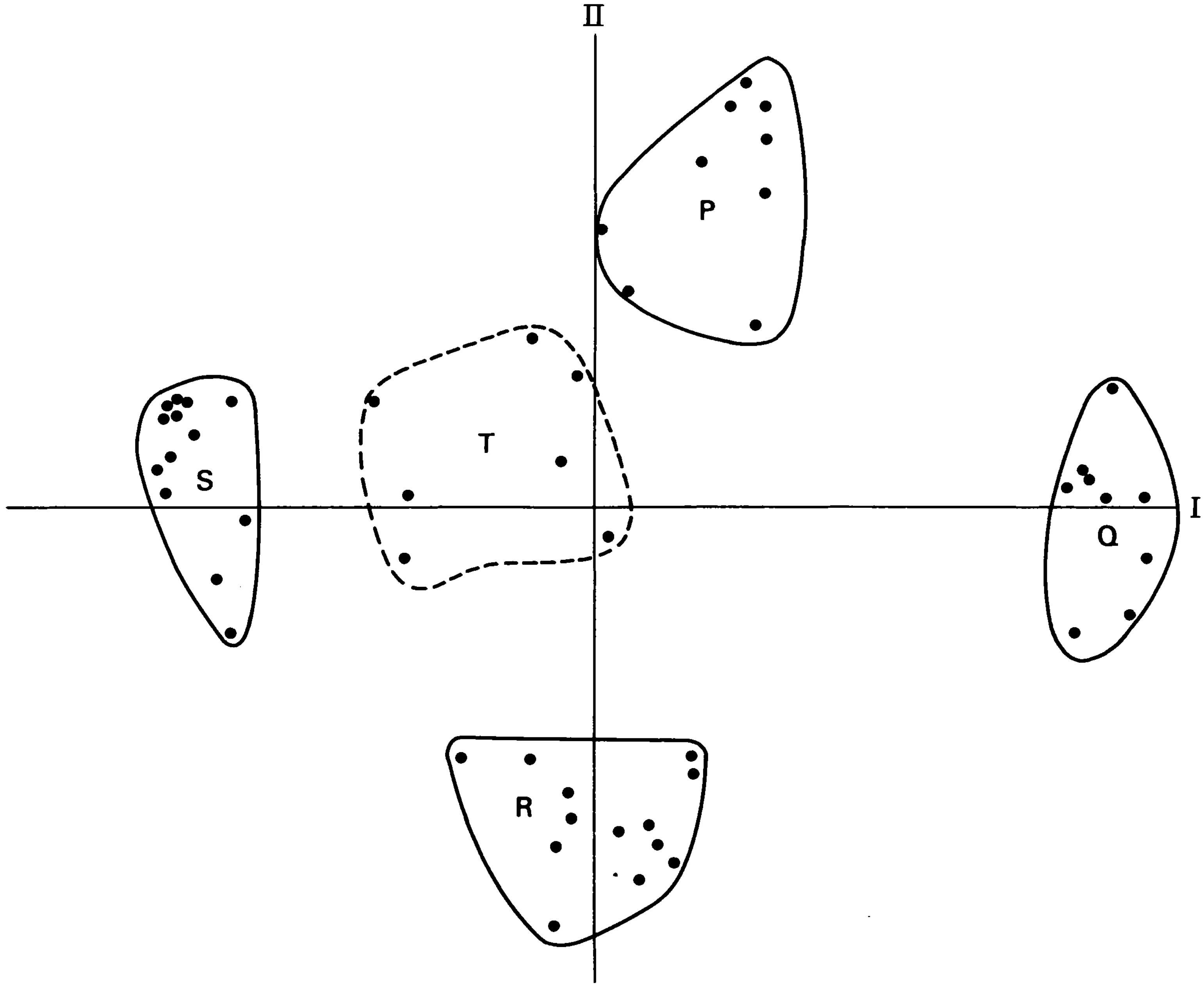

Fig. 5. Environmental variables ordination from PCA of matrix B^T.
For explanation of groupings of the variables see text.

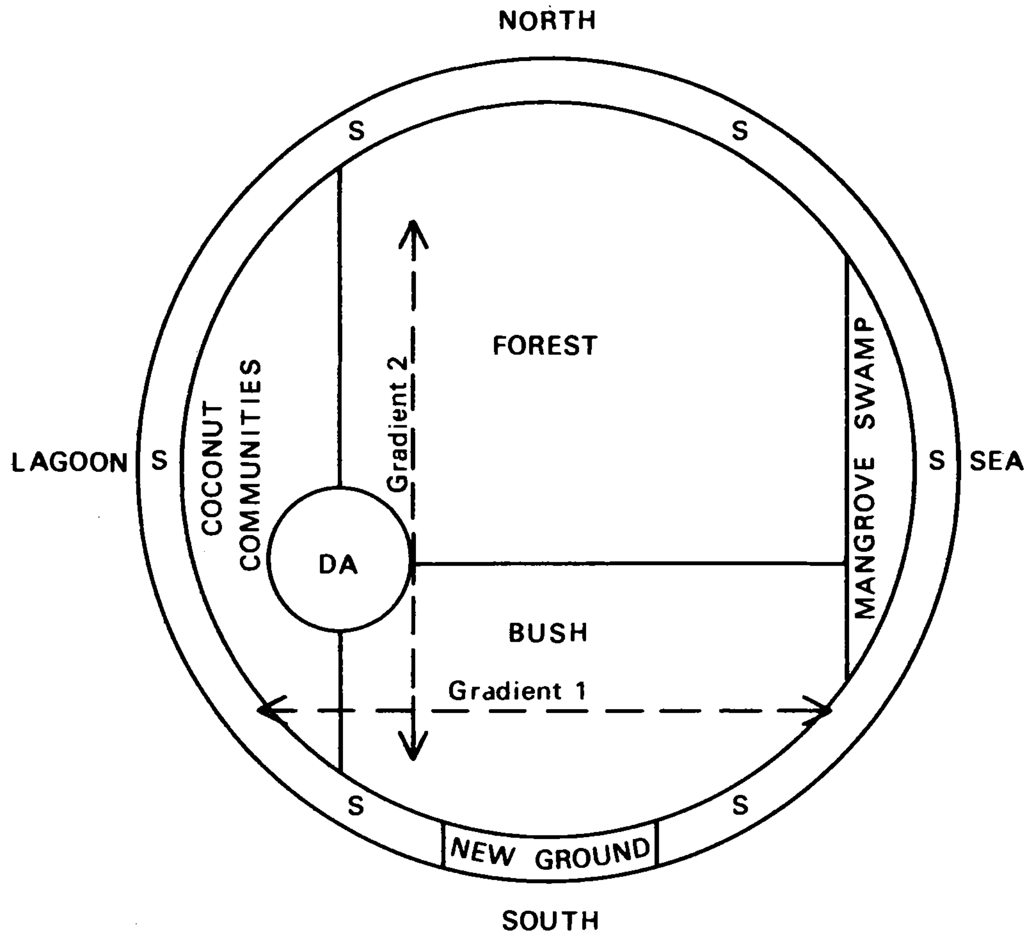

Fig. 6. Simple model of the vegetation illustrating the positions at which the main gradients operate. S, strand vegetation; DA, disturbed areas.