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THE VEGETATION OF ALDABRA ATOLL: PRELIMINARY ANALYSIS AND EXPLANATION OF THE VEGETATION MAP

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[Pullout 1]

CONTENTS

This paper describes the construction of a vegetation map of Aldabra atoll in the Indian Ocean, at a scale of 1:25000, and discusses the island's vegetation in terms of its structure and relationships with other vegetation types.

The map was based on a classification of 487 rélevés, in each of which the numbers of each species of woody plant and the percentage cover of different species of ground layer vegetation were recorded. Classification was done within a hierarchy of criteria, of which the relative abundance of common woody plants was taken to be the most important, followed by the relative abundances of ground layer species, the other woody plant species, and total woody plant and ground layer vegetation cover.

Twenty-six vegetation types were mapped at a 1:25000 scale. The vegetation varied from open ground, with sparse vegetation on bare rock, through a range of scrub forest types, to structured vegetation 10–15 m tall.

Changes in vegetation type were spatially correlated with topographical changes, with shelter from the prevailing southeast trade winds, and with the amount of grazing by giant tortoises.

Patterns of environmental and biotic change resulted in vegetation heterogeneity at scales ranging from decimetres to kilometres. The nature of these mosaic patterns needs further investigation, but they probably have a strong effect on the vegetation and on the giant tortoise population.

Aldabra island has a remarkably species-rich flora for an atoll. This may be due to its being a raised atoll, to its large land area *per se*, to the land area providing scope for the development of an unusually large freshwater lens, and to the shape and structure of the atoll providing a range of wind-shelter characteristics.

The vegetation types are similar to those found on raised reef and other coralline deposits on the East African coast. In earlier times these vegetation types may have been typical of raised reef deposits throughout the world: lack of quantitative recording and especially the extent of human interference on other raised atolls mean that Aldabra's vegetation is now an isolated example of this set of vegetation types. The effects of a large herbivorous reptile help to set the vegetation structure and make Aldabra unique.

Introduction

Aldabra island is of great ecological interest because it is one of the last raised atolls undisturbed by man and because it provides a unique example of a community whose herbivore–plant interactions are dominated by a reptile, the giant tortoise *Geochelone gigantea* Schweigger. It is also of conservation interest, not least because the giant tortoise population is, at *ca.* 150000 individuals (Bourn & Coe 1978), the largest remaining in the world.

As a first step towards an understanding of the vegetation of the island, and to provide a basis

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for the study of tortoise–vegetation interactions, a reliable vegetation map of the whole of Aldabra was required. There has been much previous work on the vegetation (see, for example: Renvoise 1971*a*; Grubb 1971; Hnatiuk *et al.* 1976; Hnatiuk & Merton 1979; Wickens 1979; Newbery & Hill 1981). However, these studies have either been extensive, not based on quantitative data, or intensive, for specific purposes covering only part of the atoll. Neither type of study allowed the construction of a quantitative vegetation map of the whole island.

This paper describes an island-wide survey of Aldabra's vegetation, presents a classification of the sites surveyed and describes the construction of a vegetation map by matching survey results with aerial photographs. The map itself is included as pull-out 1.

Methods

(*a*) *Study sites and recording of the vegetation*

Aldabra has a land area of 156 km², including lagoon fringe mangrove swamps (figure 1). The island has a tropical seasonal climate, with most of the 349–1467 mm (mean 1075 mm; Stoddart & Walsh 1979) of rain falling in the northwest monsoon from December to April. Southeast trade winds blow for the remainder of the year, usually bringing little rain. Variation in the duration and intensity of the seasons produces great differences in rainfall between years (Hnatiuk 1979; Stoddart & Walsh 1979).

Previous studies by Fosberg (1971), Grubb (1971) and Hnatiuk & Merton (1979) suggested that, except in the east of Grande Terre (figure 1), the vegetation of Aldabra was arranged in concentric bands from the seaward side of the atoll land mass to the lagoon side. In eastern Grande Terre, more complex patterns were evident (Grubb 1971), both in the vegetation itself and in the underlying topography. The additional effects of grazing and trampling by the giant tortoise increased the range of potential complexity and meant that a wide range of scales of pattern could be expected.

Any sampling régime had to be both extensive enough to cover the main large-scale axes of variation expected in the vegetation and intensive enough to detect patterns at a wide range of scales. The vegetation was conspicuously two-layered (Fosberg 1971; Hnatiuk & Merton 1979) and hence these strata needed to be sampled separately. Sampling methods were further constrained by the rough terrain and thick scrub cover over most of the island, which made free movement impossible.

The above knowledge suggested a belt transect method of sampling rather than one based on purely random quadrats. A set of 27 squares of side 1 km was chosen at random across the atoll. Where existing paths ran through thick vegetation in these squares, these paths were used for belt transects. Where such paths through thick vegetation were absent, they were cut. In more open vegetation in eastern Grande Terre, two 1 km straight belt transects were surveyed across the 1 km squares, one running north–south and the other east–west.

Figure 1 shows the locations of the different belt transects. All were marked with painted numbers at 50 m intervals. Those in open vegetation were also marked with cairns to aid long-term relocation.

The transects were divided into 50 m lengths for recording vegetation. Three different widths were used for recording woody vegetation; in very open areas the 50 m recording segments were 20 m wide, covering 1000 m², in intermediate areas they were 10 m wide (500 m²) and in very thick vegetation 4 m wide (200 m²). In the last case the cut path itself was ignored and the 2 m on either side of it were used for recording. Check quadrats at right angles to the path showed that edge effect introduced by this method was negligible.

In each segment of the belt transect, the number of individuals of each woody plant species was recorded, as was the mean height of the woody vegetation and the presence/absence of tortoise and/or feral goat browse lines on each bush.

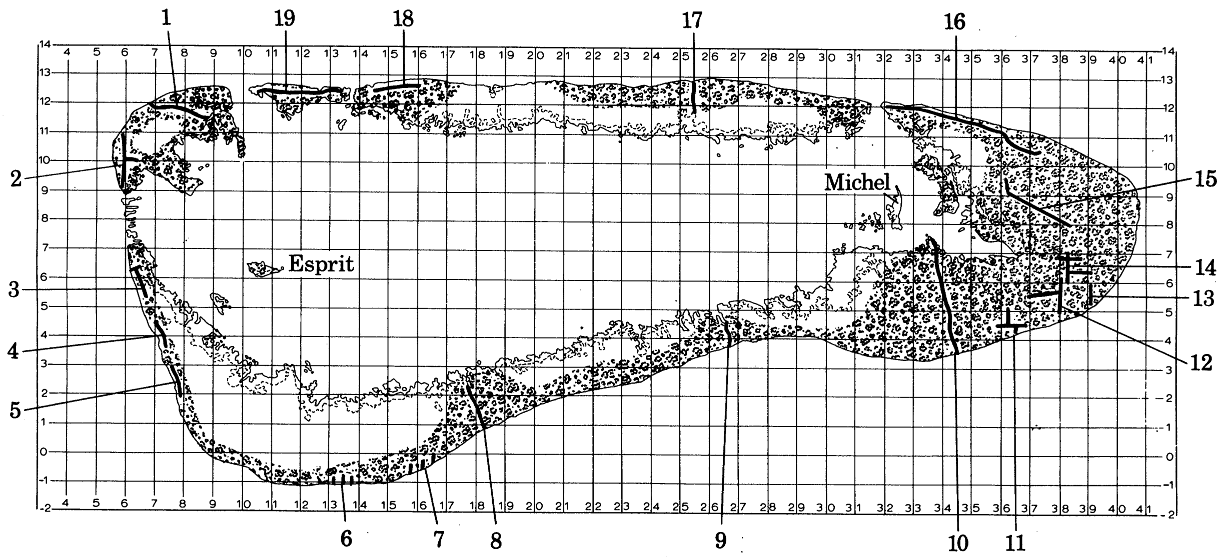

FIGURE 1. Aldabra atoll, showing positions of the study areas. Transects are as follows (some transects cross more than one 1 km square): 1, Picard, Anse Var; 2, Picard, back path and Bassin Cabri; 3, Anse Mais I and lagoon; 4, Anse Mais II; 5, Anse Mais III; 6, Aux Vacoas; 7, Dune d'Messe–Aux Vacoas; 8, Dune d'Messe; 9, Dune Jean-Louis; 10, Takamaka; 11, SW/date palm; 12, Ibis; 13, southern; 14, Coco; 15, airport trace; 16, Point Grande Terre and Anse Cèdres; 17, Malabar; 18, Gionnet; 19, Polymnie. Shaded areas are those considered adequately explored for interpretation of air photographs to be definite. The four large islands are Picard, Polymnie, Malabar and Grande Terre (clockwise from the northwest). Other islands are: Moustique, southeast of 'Esprit'; Île aux Cèdres, northeast of Michel; and 'unnamed', due east of Michel. Grid lines are shown at 1 km intervals. Small numerals refer to positions on the Aldabra grid.

One area, the pinnacle zone of southeast Grande Terre, was not suited to this recording scheme. Here the presence/absence (rarely more than one individual) of each woody plant species growing in each of 796 pot-holes was recorded and the results pooled to give the percentage of pot-holes occupied by each species. These pooled data were regarded as from a single site.

Ground layer vegetation was recorded in the transect segments by the following method. Where ground layer plants other than shrub seedlings were present over wide areas, a 50 m tape was laid along the length of each transect segment. The ground cover along each 10 cm of this line was recorded in sequence. Continuous cover data were thus obtained for lengths of up to 1 km on a 10 cm scale, giving the maximal practicable resolution for pattern analysis.

In areas such as Picard and Malabar islands (figure 1), where ground layer vegetation other than the seedlings of woody plants was present only in patches of a few hundred square metres, such patches were identified and the ground cover recorded as above but on a cross of two 50 m lines at right angles to each other, one line running north–south and the other east–west.

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(b) *Methods of analysis*

(i) *Species richness and diversity in the woody flora of segments of individual belt transects*

The species diversity of each transect segment, in addition to the number of species there, might help in understanding its relationship to other sites. In particular, changes along transects might help to identify and characterize the boundaries between vegetation types.

The calculation of the number of species in segments is straightforward, but there has been recent debate on the validity of 'diversity' measures which attempt to take equitability into account (see, for example: Taylor *et al.* 1978; May 1975). In this study, species richness was taken as the main base for comparing the diversities of sites, but a widely used index of diversity (the Shannon–Wiener index) was also calculated to provide a quick check for any extra information that it might convey.

(ii) *Relations between sites: identifying 'vegetation types'*

The major aim of this analysis was to identify sets of transect segments with similar vegetation that could be recognized on air photographs and thus mapped. Analysis was therefore site-orientated rather than species-orientated (Mueller-Dombois & Ellenberg, 1974).

Methods for assessing similarity between sites and for classifying them are legion (Sneath & Sokal 1973; Goodall 1978) and a brief discussion of the reasons for using the simple methods employed is given below.

Once a site-orientated classification is decided upon, the choice and execution of a method for vegetation analysis depends on three decisions. These are (i) the choice of criteria on which the classification is based (classification method), (ii) the choice of way of expressing one site's relationship to another (similarity or distance measure) and (iii) the choice of algorithm for classifying the sites on the basis of this similarity measure. Since the varying results that different similarity measures give are in part dependent on their design with respect to the originator's judgement of which criteria are important in classification (for review see Whittaker 1978), the choice of similarity measure should largely depend on the choice of classification method.

This can be illustrated by reference to simple extreme examples. Any similarity measure that uses only presence–absence data will regard site 1 with 9999 individuals of species A and one each of species B–Z as identical to site 2 with equal numbers of individuals of species A–Z, but very different to site 3 with 9999 individuals of species A and none of any other species. The relevance of this problem to a particular case on Aldabra is shown later. Likewise, any similarity measure that takes the range of abundance of a species across all sites into account is mixing the criteria of relative abundance of different species and of the total number of individuals in a site. Consider four hypothetical sites 4, 5, 6 and 7 with the following characteristics. Site 4 has 20 individuals of each of species A–E and none of F–J, site 5 has none of A–E and 20 each of F–J, site 6 has the same species composition as site 4 but only one individual of each species and site 7 has the same species as site 5 but only one individual of each. A similarity measure correcting for the range of abundance of different species will give sites 4 and 6 as markedly dissimilar and sites 6 and 7 as very similar.

The similarity measures used in any vegetation analysis should be chosen with a clear idea of which criteria are considered to be most important in classifying the vegetation. In the present study, the criteria used were separated and formed into a hierarchy of importance as given below. Classification then proceeded within each step of the hierarchy.

The chosen hierarchy is analogous to Raunkaier's (1934) but differs from it in taking vegetation structure and environment into account at a later stage. The hierarchy was as follows:

(*A*) the relative abundance of the commonest woody plant species;
(*B*) the relative cover abundance of different ground layer types, excluding bare rock;
(*C*) presence/absence of the less common woody plant species;
(*D*) the extent of woody plant cover;
(*E*) literature search and search of the island on foot (figure 1) as a check for radically different vegetation not covered in the quantitative survey.

The reasons for using the criteria in this order of importance were as follows.

The commonest woody plant species were those considered to be most likely to be potential determinants of the environment in which other species occurred (Hall 1970; Goodall 1976). Rarer species were removed to minimize problems from a high percentage of zeros in the data matrix, which can affect many similarity measures (Clifford & Stephenson 1975).

Ground layer vegetation was considered to be the next most important criterion as it allowed further quantitative information about the vegetation to be used. In fact, some areas of Aldabra are devoid of woody plant cover and thus could only be classified on the basis of ground layer vegetation.

The remaining, rarer, woody plant species were represented by effectively presence/absence data; although the numbers of individuals were counted, few sites had more than one individual of any of these species. However, this data set also gave information on the species compositions at the sites, which were considered more important than absolute cover (Hnatiuk & Merton 1979) on Aldabra.

Finally, criteria (*D*) and (*E*) were used to check for further gross distinctions among the vegetation structure that were not also reflected in the species compositions of sites or that had been missed altogether in the quantitative survey.

The overall procedure was as follows: all suitable sites were classified by using the Spearman rank correlation coefficient as a similarity measure, by first using criterion (*A*), then criterion (*B*). Criteria (*C*)–(*E*) did not require examination of the full data, as most recognizable types had been sorted out by this stage (see Results).

The following detailed procedures were used for criteria (*A*) and (*B*). Since the Spearman rank correlation coefficient is expensive in computer time, the woody plant and ground layer data were first reduced by the method of Janssen (1975). Sites that were correlated with a Spearman r_s of $> +0.8$ were considered as effectively the same and their data were pooled to form initial clusters. This preliminary clustering resulted in a combined data set of 82 preliminary clusters (reduced from 447 sites) for the woody plants and 60 preliminary clusters (reduced from 198) for the ground layer. Sites with only one, or with no, species of either ground layer or woody plants were discarded from the analysis and kept for the final synthesis in the vegetation map.

Cluster analysis was then done in turn on the preliminary clusters, first of woody plant species and then of ground layer sites. Single linkage analysis was used first (Sneath & Sokal 1973). This simple method is prone to producing 'chaining' of sites with some data sets; it is debated whether this is an aesthetic or a theoretical objection (Goodall 1978). This chaining was not a serious problem in the woody plant data; so the single linkage results were accepted for criterion (*A*).

Chaining did occur in the ground layer analysis, and may have been open to a serious theoretical objection. Therefore a second clustering method (average linkage; Sneath & Sokal 1973) was also employed. Classification on the basis of criterion (*B*) was only considered acceptable when both methods agreed.

Criteria (*A*) and (*B*) identified a large number of vegetation units which could be mapped on a scale of 1:25000. Thus the clusters produced by these criteria needed to be examined for qualitative differences both within and between them only by means of criteria (*C*)–(*E*).

(iii) *Relation of 'vegetation types' to features on aerial photographs and making the map*

Vegetation types identified by the methods of the previous section are not necessarily functional associations or real 'communities'; they are answers to questions such as 'What sort of vegetation does one expect to find in this area?' and 'How different is the vegetation here from that over there?'. They can thus form the basis for the type of vegetation map that can be used by researchers needing to choose their study sites or to pose questions about community structure and dynamics.

The map was based on three sets of information: the quantitative data described above, the Department of Overseas Surveys (D.O.S.) aerial photographs of Aldabra taken in 1960, and field observations on the gross appearance of the vegetation and search for plant species present on visits to every possible area on the island (figure 1 gives extent of search).

To construct the large-scale map, detailed maps of the vegetation transects were made at the same scale as the aerial photographs and superimposed on them to seek boundaries between vegetation types that could be identified on both. The subjective ground control described above was used to interpolate these boundaries between transects. The boundaries were then traced from the air photographs.

The reliability of this method in particular cases is discussed under Results.

Results

(*a*) *General note*

The extent of the raw data on which this paper is based made its publication in full impracticable. The full data set is accessible through the authors. It resides on the Oxford University ICL 2980 computer and is intended to be permanently accessible to those who might wish to examine it. Copies will be deposited in the archives of the Royal Society and in the British Library, Lending Division.†

(*b*) *Patterns of species richness and diversity*

As expected from previous studies (Hnatiuk & Merton 1979; Newbery & Hill 1981), species richness and diversity changed systematically in two directions: first across the radii of Aldabra from the seaward side to the lagoon and secondly, particularly in eastern Grande Terre, but also across the whole island, along a direction parallel to that of the southeast trade winds.

† Copies of the material deposited may be purchased from the British Library, Lending Division, Boston Spa, Wetherby, West Yorkshire LS23 7BQ, U.K. (reference SUP 10040).

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Figures 2–4 exemplify these patterns. These figures show that equitability (as measured by the Shannon–Wiener information index) added little information on trends in diversity to that provided by species richness per transect segment, and so only the latter measure is used from now on.

In the coast–lagoon transects (figures 2, 3), species richness was low at the seaward coast, peaked sharply inland, and then fell off to a minimum at the lagoon. This lagoonward fall was brought about by the disappearance of more and more of the 'mixed scrub' (Fosberg 1971) flora and its replacement by species such as *Pemphis acidula* and the associated *Vernonia grandis* and *Scutia myrtina*.

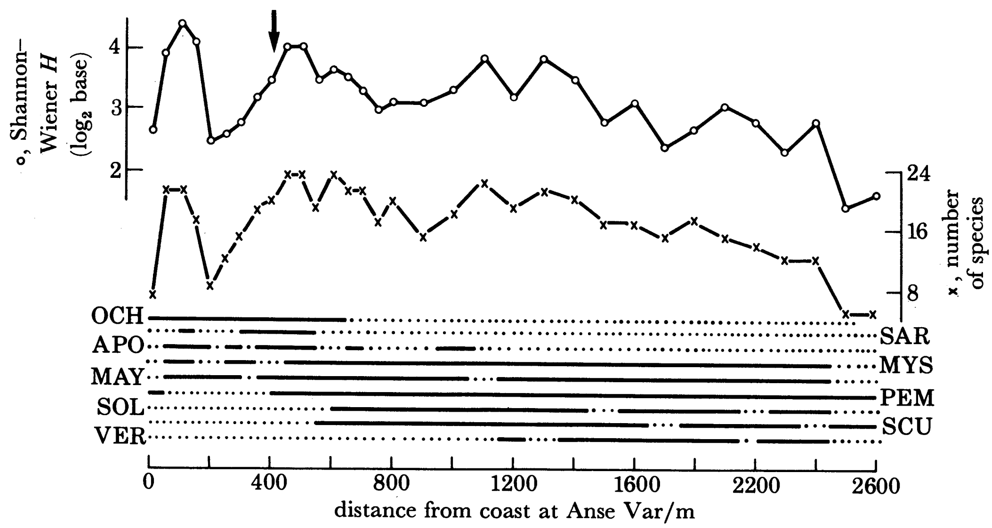

FIGURE 2. Variations in species diversity along the Anse Var transect on Île Picard as shown by species numbers per 200 m² transect segment and by Shannon–Wiener H (transect 1 on figure 1). Presence of selected species is shown by solid lines, to illustrate changes in species composition. *Key to species shown:* OCH, *Ochna ciliata*; SAR, *Sarcostemma viminale*; APO, *Apodytes dimidiata*; MYS, *Mystroxylon aethiopicum*; MAY, *Maytenus senegalensis*; PEM, *Pemphis acidula*; SOL, *Solanum indicum*; SCU, *Scutia myrtina*; and VER, *Vernonia grandis*. The arrow indicates first occurrence of *P. acidula*.

In the set of belt transects made in eastern Grande Terre, exemplified by figure 4, species richness was low at the southeast end and increased towards the north and west (lagoonward) side. This trend in scrub (not containing *P. acidula*) was not just a phenomenon of the coast–lagoon, but could be identified continuing across the island from southeast to northwest (following figure 4 through the richness peaks in figures 2 and 3). The highest number of species on transect segments was on belt transect 2 (figure 1) on Île Picard, where most segments contained 22–25 species. This richness peak was generated by indigenous, not introduced, species. Although introduced species were more widespread on Île Picard than elsewhere, relatively few individuals of only three species (*Ricinus communis*, *Lantana camara* and *Passiflora suberosa*) were recorded on the Picard transects. Of these, *P. suberosa*, a climber, was the commonest.

These patterns of species richness also give an insight into the limits of a classification exercise. For practical purposes, boundaries between vegetation types must be delineated in order to draw a vegetation map. If such boundaries were real and sharp, we might expect this to be reflected by sharp changes in species richness and/or composition, especially in the change

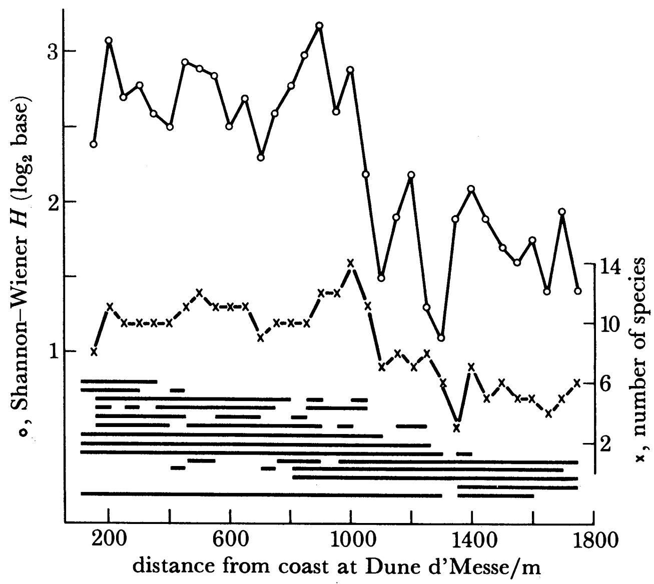

FIGURE 3. Changes in species diversity along the Dune d'Messe transect (transect 8 in figure 1) as shown by species numbers of woody plants and by Shannon–Wiener *H*. Presence of selected species in transect segments is shown by solid lines beneath the diversity graphs. Species run in order from top to bottom as follows: *Guettarda speciosa, Colubrina asiatica, Flacourtia ramontchii, Euphorbia pyrifolia, Tarenna trichantha, Ochna ciliata, Mystroxylon aethiopicum, Polysphaeria multiflora, Sideroxylon inerme, Acalypha claoxyloides, Pemphis acidula, Vernonia grandis* and *Maytenus senegalensis.*

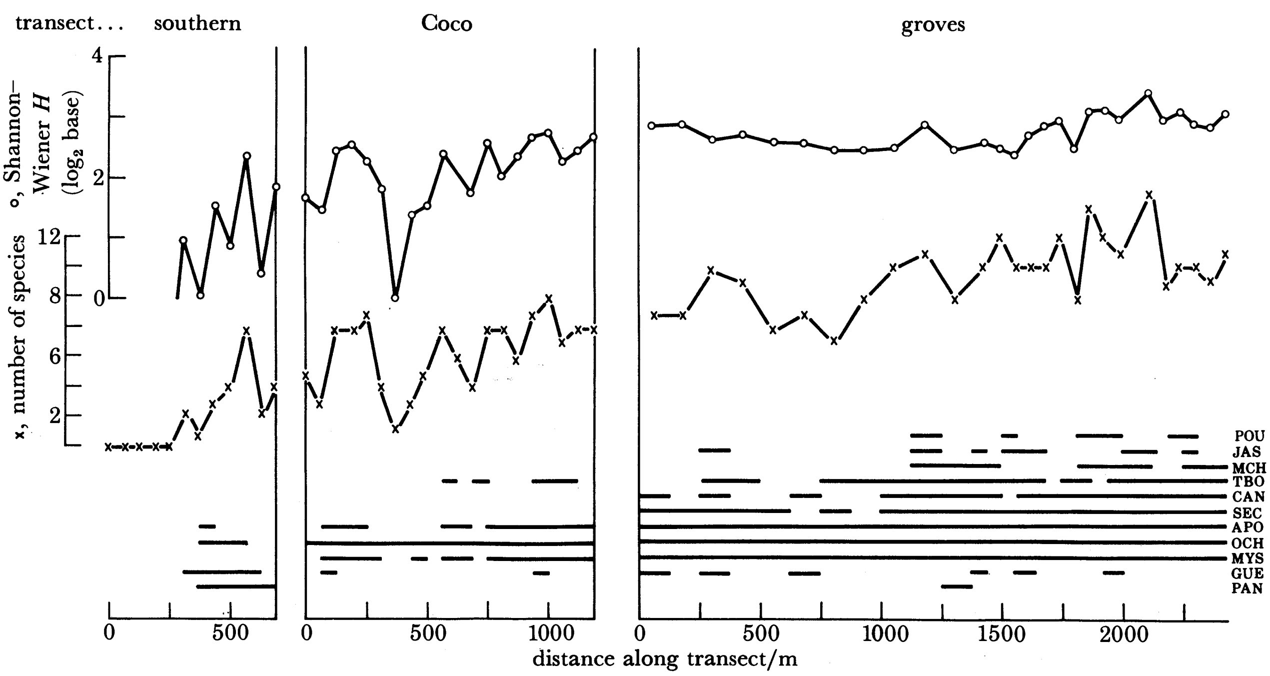

FIGURE 4. Changes in species richness, Shannon–Wiener *H*, and presence of particular woody plant species along transects in southeast Grande Terre. Transect names as in figure 1. The first transect starts on the seaward coast going inland, the second (Coco) starts on the southern east–west end of the transect, moves along it until it meets the north–south arm and proceeds to the northern end. The third and last follows the 'airport trace' transect from southeast to northwest. *Key to woody plant species:* POU, *Operculicarya gummifera*; JAS, *Jasminium elegans*; MCH, *Macphersonia hildebrandtii*; TBO, *Terminalia boivinii*; CAN, *Canthium bibracteum*; SEC, *Secamone fryeri*; APO, *Apodytes dimidiata*; OCH, *Ochna ciliata*; MYS, *Mystroxylon aethiopicum*; GUE, *Guettarda speciosa*; and PAN, *Pandanus tectorius.*

from mixed scrub to that containing *P. acidula* (Fosberg 1971). This was not so in most cases; sharp changes occurred in the first 50–100 m from the seaward coast (figures 2, 3) or even further inland (figure 4), but the *Pemphis* transition could be very gradual (see, for example, figure 2). When this transition was sharper (figure 3), it was as likely to be due to differences in the patterns of topographical change as to floristically determined boundaries. This emphasizes that the use of classification in this case provides a practical guide to the vegetation rather than elucidates the mechanisms that determine community structure.

(c) *Results of classification*

(i) *Step* A: *characterization on the basis of relative abundance of the* 24 *commonest woody species*

Before examining the results of classification, it is helpful to identify some of the particular features of the data set and to assess their likely effect on the exercise. Figure 5 illustrates the abundance distributions of three species to show the range of distribution types encountered. The examples shown are typical of the distribution types of the 73 other species encountered in the belt transects.

The distribution of abundance of *Apodytes dimidiata* in different sites was virtually a straight line when plotted on probability paper, but that of *Acalypha claoxyloides* was distinctly kinked, showing a bimodal distribution. The distribution of *Clerodendrum glabrum* was not only bimodal, but formed linear segments only when plotted on a logarithmic transformation.

Such variation in distribution types conveys useful biological information, but also presents problems for the analysis. There is a dilemma whether to transform and standardize the data for ease of analysis, thereby losing valuable information, or to introduce weightings in a particular manner (Whittaker 1978). In this analysis for large-scale map construction, all we can say is that bimodalities in the distributions of many of the woody species at least indicate that there are separate real vegetation types among the data.

This was not always the case. Figure 6 shows similarity changes along the Anse Var transect on Île Picard. Spearman r_s for two segments with each of the others are shown. If sharp boundaries existed, we would expect sharp changes in the similarity of a particular site with its neighbours; it would either be very similar to them or very dissimilar. This was not the case where expected, namely at the point where *P. acidula* is first found in the mixed scrub vegetation. This reinforces the doubt about this traditional boundary first raised by the species richness changes discussed above.

Figure 7 shows that a relatively small number of discrete groups were formed from 393 out of 447 original sites. The largest 'chaining' problem occurred with the large (158 segments) group of 'mixed scrub–mixed *Pemphis*' sites. The most likely cause of this is the absence of real discontinuities as mentioned above, or that the vegetation was organized at a scale different from the segment size (see Discussion).

High numbers of zero values for species are often a problem in classifications, especially those based on rank correlations (Mueller-Dombois & Ellenberg 1974; Whittaker 1978). Difficulties that remained at this step in classification could usually be ascribed to this cause. The 'unclassifiable' sites were of two sorts; those near freshwater/brackish pools where *Thespesia populneoides* and *Lumnitzera racemosa* were often the only woody plant species and those on the seaward coast. The former sites could easily be accounted for. The latter proved to have the following characteristics. Few species occurred in any one site, but the commonest species were usually drawn from a set which was rarely found away from the seaward coast (see also step C and Results

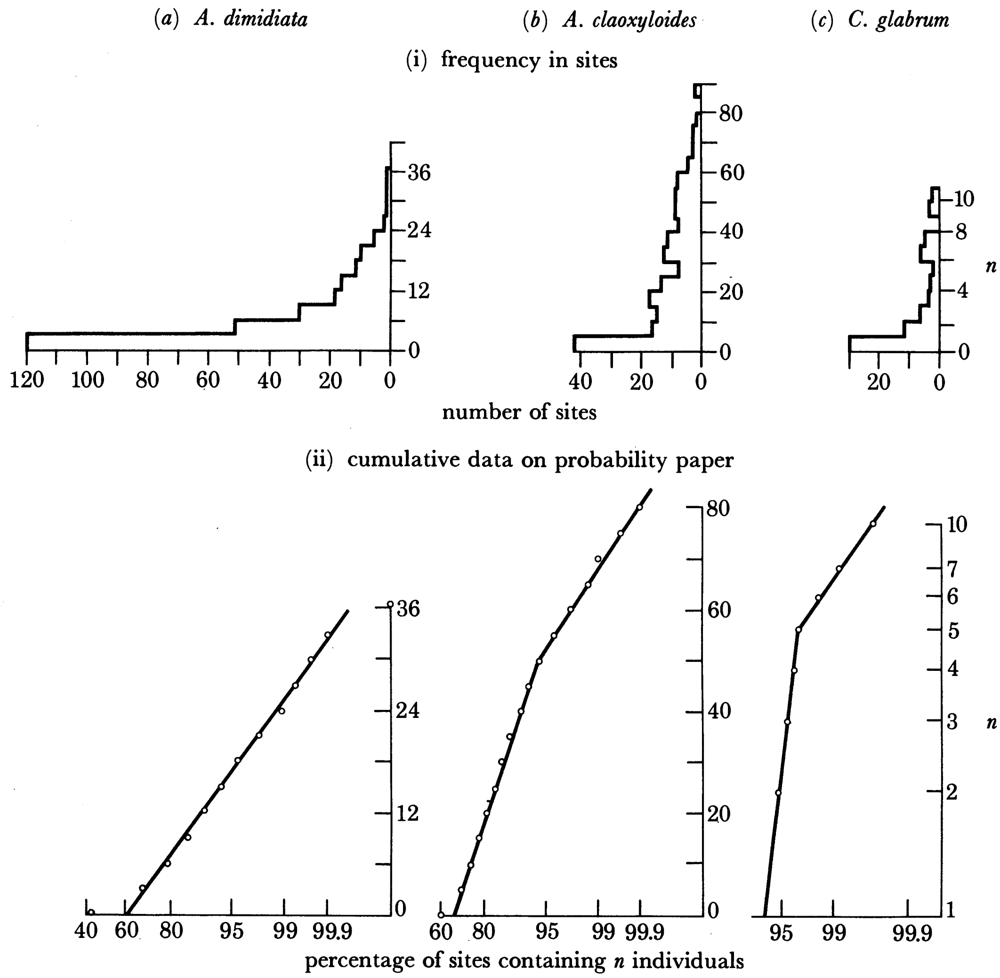

Figure 5. Abundance distributions of some woody plant species on Aldabra, to show the range of frequency distributions encountered. Three pairs of figures are shown. In each case the lower figure of the pair shows the cumulative percentage of sites containing *n* individuals plotted against *n* on (*a*, *b*) linear (*Apodytes dimidiata* and *Acalypha claoxyloides*) or (*c*) logarithmic probability paper (*Clerodendrum glabrum*). The upper figure of a pair shows the distribution of sites with different numbers of a particular species (zeros are omitted). In these, the horizontal axis shows the number of sites containing *n* individuals and the vertical axis shows the number of individuals.

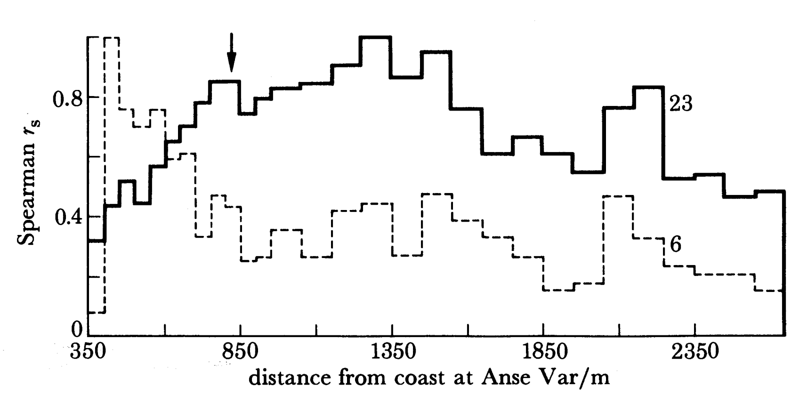

Figure 6. Changes in relative abundance of 24 common woody plant species along the Anse Var transect (figure 1), as illustrated by intercorrelation between the sites' species compositions. The Spearman r_s for two sites with each other site is shown. The solid line shows r_s of site **23** (1250–1300 m from the sea coast) with each other site and the dashed line shows r_s of site 6 (400–450 m from the sea coast) with each other site. The arrow marks the first appearance of *Pemphis acidula* in the sea–lagoon sequence.

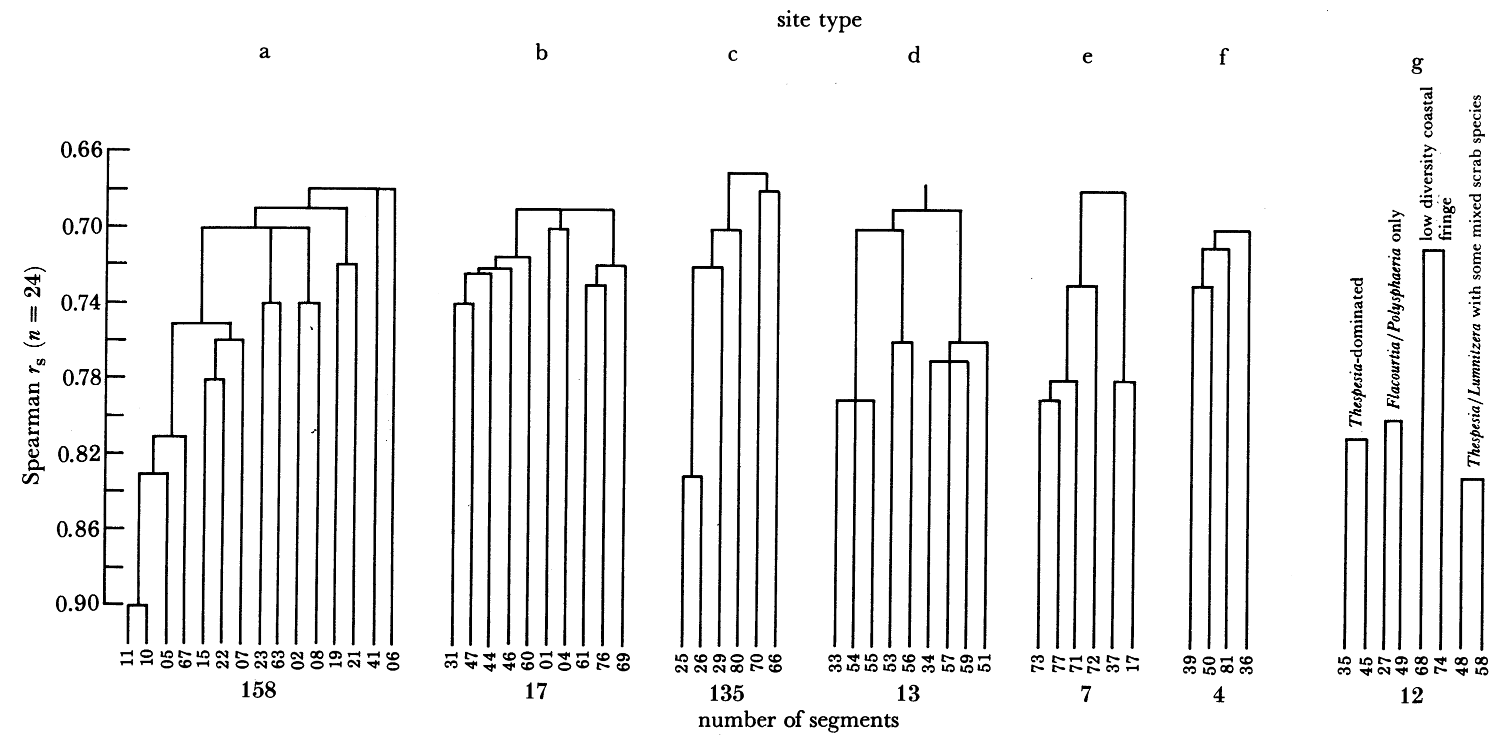

FIGURE 7. The relations between easily classifiable sets of transect segments as shown by single-linkage cluster analysis on the basis of relative abundance of the 24 commonest woody plant species in the whole data set. Similarities represented by Spearman r_s of < 0.67 are not shown; all values greater than this are. On this basis, only 346 individual segments were easily classifiable beyond the initial clustering. The remaining sites were as follows: (i) 47 sites from Île Picard mixed scrub not containing *Pemphis acidula*, in one initial cluster; (ii) six sites in the thickly wooded coastal mixed scrub on the Takamaka transect; (iii) two initial clusters containing nine sites, from the Dune Jean-Louis transect; (iv) two sites from 'Ibis' transect with thick woodland dominated by *P. acidula*; (v) five sites at the mangrove–mixed scrub transition in south-east Grande Terre; (vi) the site from 'pinnacles'; (vii) 16 sites, alone or in small initial clusters, from the coastal fringe; (viii) 15 lone sites with very low numbers of individuals and species of woody plants. *Key to site types on the figure:* a, mixed scrubs usually containing *Pemphis acidula*, of relatively high species richness, in the northwest of Aldabra; b, very low diversity sites dominated by *P. acidula* (1, 4, 61, 76, 69) or *Thespesia/Lumnitzera* (the others); c, southeast Grande Terre mixed scrub sites; d, coastal mixed scrubs from southeast Grande Terre; e, coastal fringe, low diversity mixed scrubs; f, other coastal fringe; g, odd pairs of low diversity sites. Total: 447 sites containing woody plants.

(*d*)). This problem was dealt with at the end of step A by separation of the neatly clustered groups within the mixed scrub–mixed *Pemphis* cluster, erecting a single group for 'pool vegetation' and remaindering the coastal sites until later steps in the analysis.

(ii) *Step* B. *Classification on the basis of relative abundance of ground cover types*

Ground cover was initially recorded in terms of the species present where this was practicable. This was not always so. The species present in 'tortoise turf' and '*Cyperus* other spp.' (table 1) did not all flower and could not be determined reliably on vegetative characters. Robust grass species and all dicotyledonous herbs were so rare that they were pooled as 'long grasses' and 'herbs'. These vegetation cover types (table 1) were used in subsequent analysis with litter and bare soil. All were expressed as percentage cover in a 50 m transect segment.

Table 1. Characterization of ground cover types and non-vegetation ground cover referred to in this study

name	description
tortoise turf	after Grubb (1971)
long grasses	grasses species taller than 10 cm
mosaic rock	rock containing holes less than 10 cm across in which plants were growing, usually tortoise turf species
Sporobolus	the grass *Sporobolus virginicus*
Sclerodactylon	the grass *Sclerodactylon macrostachyum*
Cyperus	the sedge *Cyperus niveus*
Fimbristylis 1	the sedge *Fimbristylis cymosa*
Fimbristylis 2	the sedge *F. ferruginea*
'*Mariscus*'	the sedge *Cyperus ligularis*
Cyperus spp.	other sedges of the genus *Cyperus*, usually *C. bigibbosus*
seedling	woody plant seedling
shrub	prostrate shrubs
herb	dicotyledonous herbs
alga	—
fern	*Acrostichum aureum*
root	—
bare soil	—
sand	—
litter	fallen or detached dead plant material
platin	rock with very low (usually less than 10 cm) relief over a wide area
loose slab rock	detached flakes and paving-stone rocks, lying on other rock or bare soil
rock	rock with greater relief than 'platin' but still less than 50 cm, roughly analogous with the 'pave' of other authors (Stoddart *et al.* 1971)
pool	—
pinnacle	heavily fretted and pot-holed rock with relief overall greater than 50 cm
mud	—
other rock	any rock not falling into the above categories

Rock types (table 1) were recorded with other ground cover, but were not used in the cluster analysis as step B required a criterion of 'vegetation' rather than of 'habitat'.

It was suspected that Aldabra's ground layer vegetation was organized at a range of pattern scales, often differing from the 50 m segment size and not recognizable on air photographs. The unclear patterns arising from the clustering shown in figure 8 added weight to these suspicions. Two decisions were made: first to continue using the 50 m scale for the vegetation map, with the step B cluster analysis, since smaller scales could not be identified from air photographs, and secondly to use the continuous data to identify the real scales on which mosaics were organized.

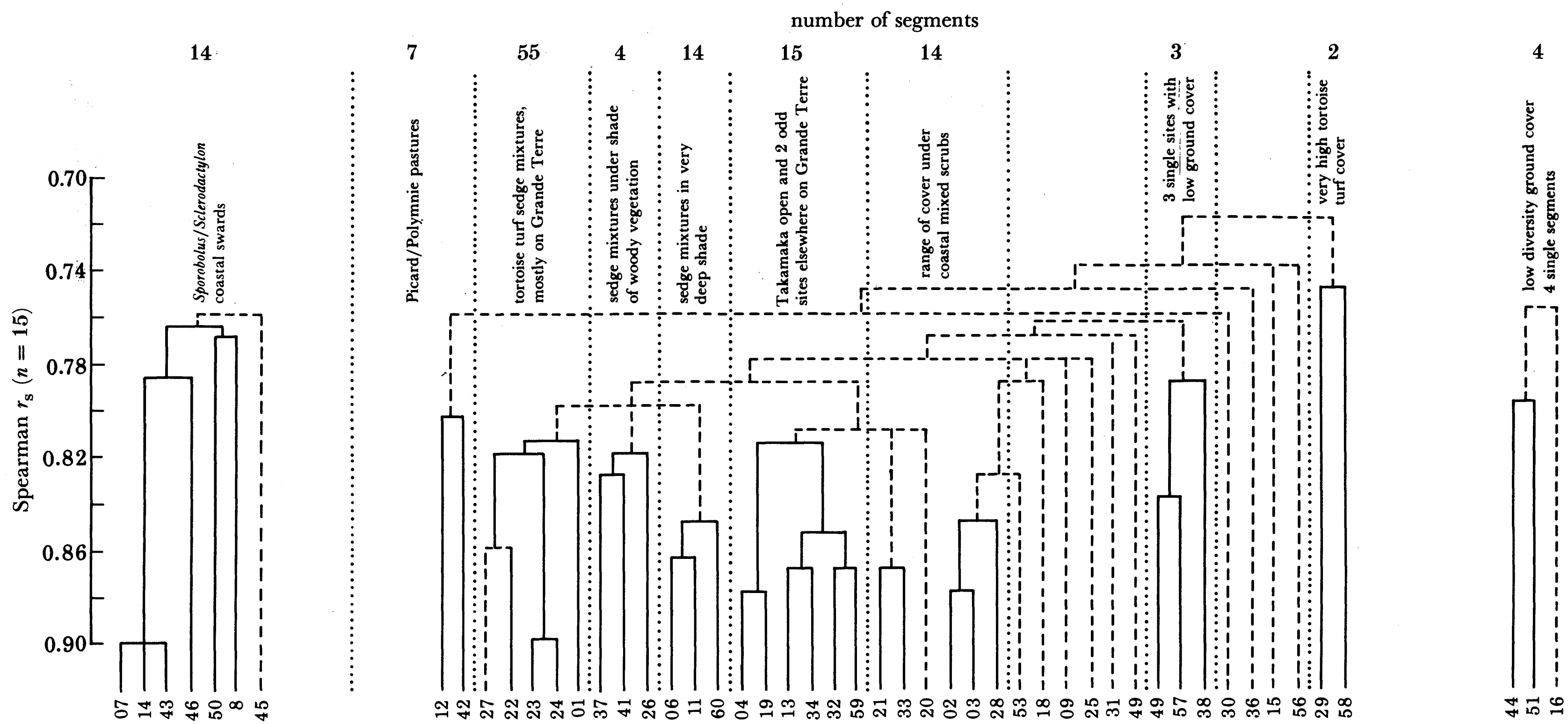

FIGURE 8. The relation between easily identifiable groups of transect segments as shown by cluster analysis on the basis of relative abundance of ground cover types. Similarities represented by a Spearman $r_s < 0.7$ are not shown. All values greater than this are shown. The index numbers of initial clusters do not correspond to those in figure 7. The dashed lines show a dendrogram based on single linkage cluster analysis. The continuous lines indicate where this dendrogram agreed qualitatively with an average-linkage clustering of the sites. Classification was only considered to be certain when both methods agreed on which sites were closest to each other. Using these rules, only 132 sites were classifiable. The remainder comprised: (i) a group of 12 sites with *Fimbristylis ferruginea* and litter as the dominant ground cover, under shrub cover of *Thespesia populneoides* and *L. racemosa*; (ii) 41 lone sites, sometimes in small initial clusters, with variable cover of a wide range of sedge species, sometimes near the edge of freshwater pools with *F. ferruginea*; sites with large amounts of the fern *Acrostichum aureum* all fell in this second group. Total: 185 transect segments containing ground cover, excluding sites with only litter and woody plant seedlings under thick scrub/woodland.

Figure 9 shows the size distribution of the patches of individual species on some of the transects; this suggested that traditional methods of pattern analysis were inappropriate here as individual patch sizes could have a range of means and distribution types around those means. Since further pattern analysis is more appropriate to the scale on which tortoises operate than to that of the air photographs, it will be dealt with in another paper. Figure 9 serves to illustrate the range and complexity of scales on which the ground layer vegetation is organized on Aldabra.

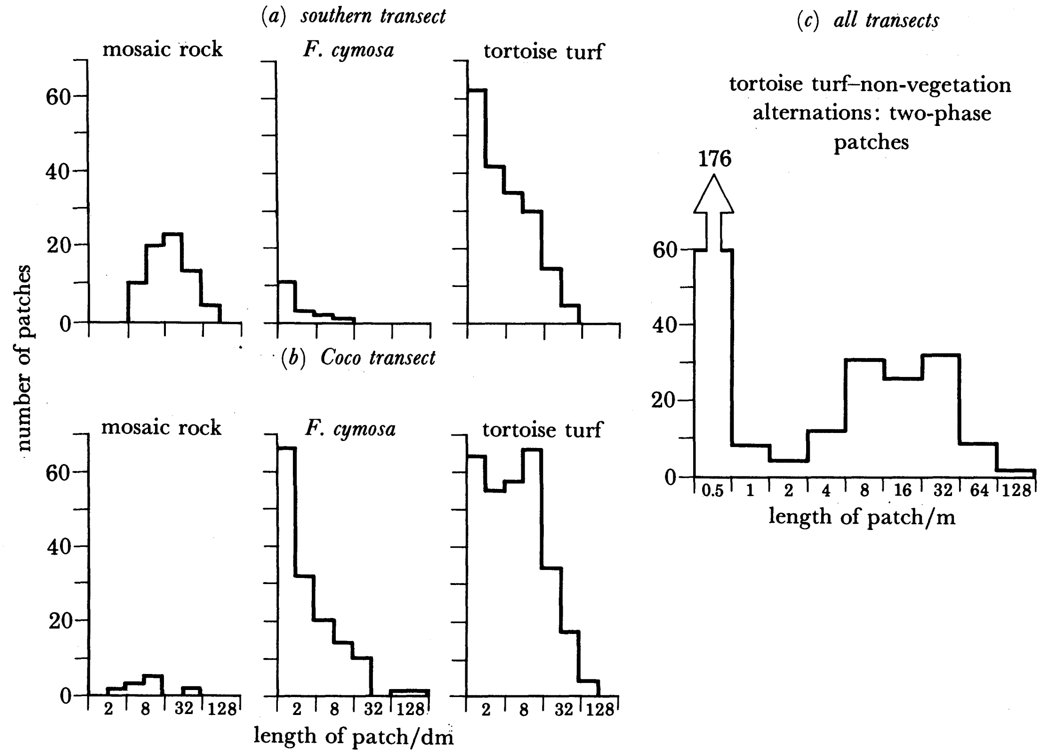

FIGURE 9. Patch sizes of ground cover on southeast Grande Terre. Patch lengths are plotted as less than or equal to the geometric limits shown on the abscissae; ordinates show the numbers of patches in each length class. (*a*, *b*) The frequency distributions of single-cover-type patches on particular transects. Transect names follow figure 1. (*c*) The size distribution of the two-cover-type patch defined as tortoise turf alternating with bare cork, litter or bareground, with no other vegetation in the sequence.

The single- and average-linkage cluster analyses shown in figure 8 agreed only at high similarity values. Despite this, useful information emerges to add to the step A analysis. Step B differentiated those sites lacking shrub cover into groups such as the *Sporobolus virginicus–Sclerodactylon macrostachyum* coastal swards and 'Takamaka open'. This step also identified several groups within the 'southeast Grande Terre mixed scrub', which, despite considerable variation in its appearance (Fosberg 1971; Grubb 1971), had similar composition of common woody plant species throughout. It also identified the Picard and Polymnie pastures as being essentially similar in ground layer vegetation, despite having a different composition of woody plant species, and despite the giant tortoise being absent from Île Polymnie but present on Île Picard (Bourn 1976). Some 'tortoise turf' was present on Île Polymnie, despite the absence of tortoise grazing from that island for at least 90 years (Stoddart & Peake 1979). Evidently this assemblage of dwarf species can find the right growing conditions without, or persist long after, tortoise grazing.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

The ground cover analysis confirmed the peculiarity of the 'fern-pocket *Pemphis*' of southeast Grande Terre, within which there were few sample sites.

(iii) *Step* C. *The presence/absence of rarer woody species*

Most mappable vegetation types had already been separated in steps A and B. Examining the rarer shrub species shed light on two areas where there was still confusion; the coastal fringe woodlands and some of the 'southeast Grande Terre mixed scrub' types. On examining the coastal fringe data, two sets of species were found to be peculiar to these areas. One set usually grew on raised beach sand and the other set grew in rocky areas. The coastal fringe sites were placed into these two groups. In any one site, very few species were found, making them difficult to classify on the basis of step A, but these transect segments always contained woody species drawn from one of the two sets just mentioned.

Eleven woody species, rare or very rare over the whole island, were only found in the 'groves' and '*Cyperus* park-woodland'. Species otherwise restricted to the northwest of the atoll also reappeared in the 'groves'. These species are listed below.

(iv) *Step* D. *Cover extent and habitat criteria*

This step confirmed the findings of the previous three and added one more vegetation type. Large areas of 'fern-pocket *Pemphis*' had very little woody plant cover, whereas others formed near closed-canopy bush.

(v) *Step* E. *Subjective ground control and use of the literature*

All the further types here are included in Fosberg's (1971) classification or Macnae's (1971) work on the mangrove vegetation of Aldabra. It was impractical to map the mangrove grades listed by Macnae as they could not be identified from air photographs. Thus mangrove vegetation was split into only two types: '*Avicennia marina* and mudflats' and 'mixed mangrove woodlands'. Other mappable types omitted from the quantitative survey were tidal pools, gardens, and one patch of single-species *Scaevola taccada* at the eastern end of Île Malabar. All these types covered very small areas.

Low diversity *Pemphis* scrub, separated on earlier criteria, occurred in two distinct situations. One was at the lagoon end of the atoll radii, in a band of varying width, and the other was a hedge, often only one bush thick, growing around sea coasts relatively sheltered from the southeast trade winds.

(*d*) *Synthesis of the classification steps and characterization of the vegetation types*

Figure 10 summarizes the results of the above classification steps and lists the resulting vegetation types. Tables 2 and 3 show the compositions of woody and ground layer vegetation respectively, in all vegetation types covered in the quantitative survey except '*Casuarina–Cocos* groves'. Many of the vegetation types had no ground layer cover save litter and the seedlings of woody plants; their ground cover is not listed in table 3.

A brief description of each vegetation type is given below.

(i) *Eastern Grande Terre mixed scrubs*

The four subtypes designated below differed considerably in their ground layer vegetation, in which rare woody plants occurred, and in the amount of woody plant cover. Their woody

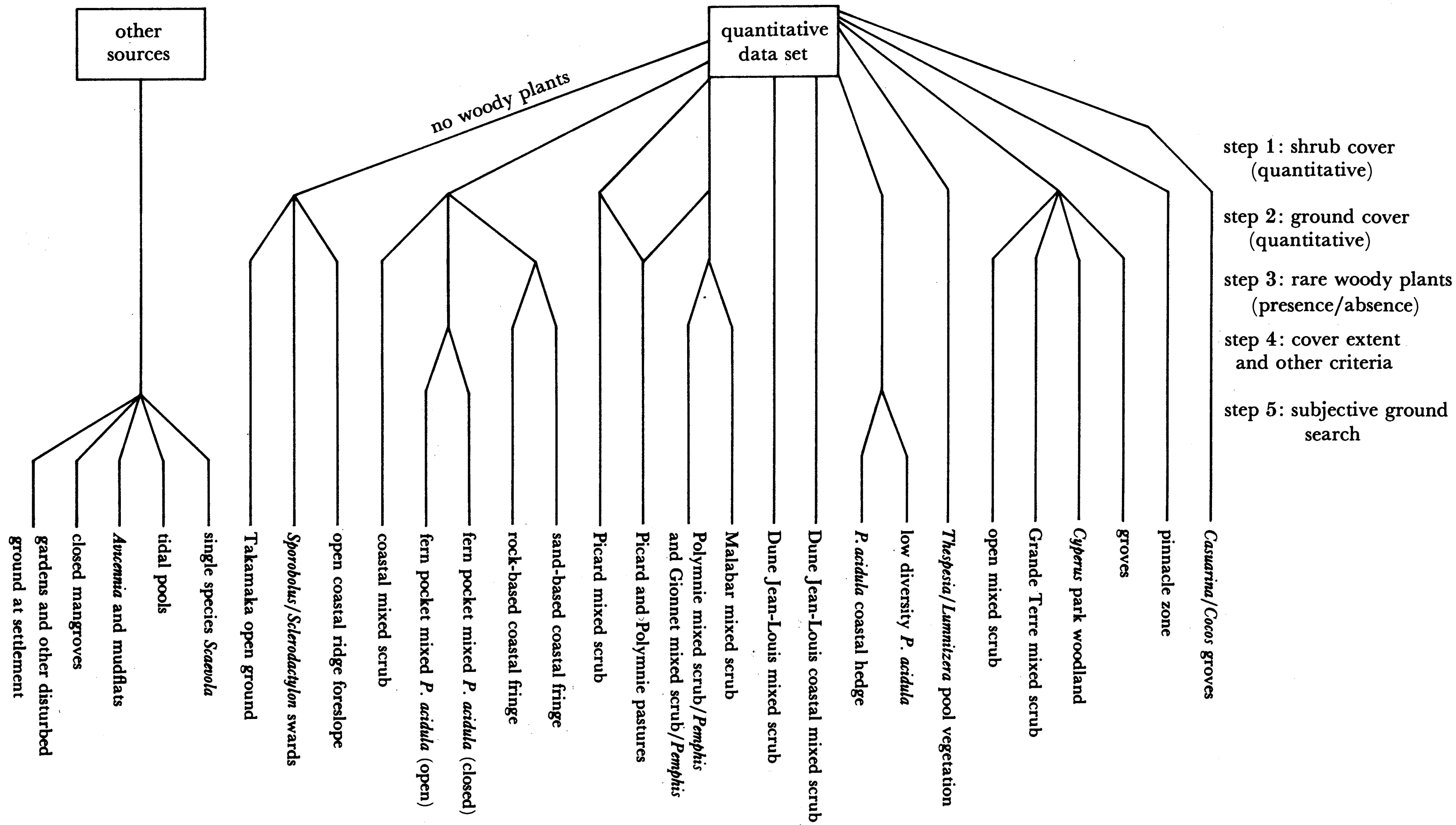

FIGURE 10. Use of the classification exercise to identify mappable vegetation units. Each step in the classification represents one of the criteria outlined in the text, in decreasing order of importance from the top of the dendrogram to the bottom. Thus 'groves' is closer to '*Cyperus* park-woodland' than to the 'pinnacle zone', but the 'pinnacle zone' is equally distinct at this level from 'groves' as it is from '*Casuarina–Cocos* groves'. Tidal pools are not vegetated, so they are not strictly a vegetation type: they are included because they are mappable separately from the freshwater/brackish pools. 'Other sources' include previously published work and the subjective ground search.

TABLE 2. WOODY PLANT COMPOSITION OF THE VEGETATION TYPES MAPPED

(Except in column 6 (percentage of individuals) all entries are numbers of individuals per 200 m^2 or per 1000 m^2 (column 11 only).)

type no.	†...	1	2	3	4	5	6 (%)	7	8	9	10	11	12	13	14	15	16	17
A. dimidiata		—	0.28	0.03	0.07	11.2	—	—	—	1.18	10.7	1.78	2.8	2.36	1.2	0.17	0.16	—
A. percatorius		—	—	—	—	—	—	—	—	0.02	0.02	—	—	—	1.0	1.06	0.01	—
A. angulatum		—	—	—	—	—	—	—	—	—	—	—	—	—	1.2	0.02	0.01	—
A. claoxyloides		—	0.16	—	—	0.33	36.9	—	—	0.02	0.01	—	—	10.8	8.2	28.04	28.9	—
A. aldabricus		0.03	—	—	0.07	—	—	—	—	0.47	0.22	0.81	—	—	0.6	3.83	5.84	—
A. umbellatus		0.01	—	—	—	—	—	—	—	—	—	—	—	—	—	0.26	0.77	—
A. tetracantha		—	0.36	—	—	—	2.11	—	—	0.01	—	—	—	—	2.2	3.0	0.12	—
C. bonduc		—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—
C. alternans		—	—	—	—	—	—	—	—	—	—	0.02	—	—	—	—	—	—
C. bibracteum		—	0.26	—	—	—	—	—	—	0.80	2.15	—	—	4.27	0.6	1.09	0.62	—
C. cartaliginea		—	—	—	—	—	16.2	—	—	0.06	—	—	—	0.55	—	0.26	0.02	—
C. equisetifolia		—	0.32	—	—	—	—	—	—	0.29	—	—	—	—	—	0.85	0.08	—
C. glabrum		—	0.06	—	0.3	—	—	0.25	—	0.09	0.07	0.58	—	—	0.4	2.89	0.44	—
C. nucifera		—	0.20	—	—	—	—	—	—	0.08	—	—	—	—	—	—	0.03	—
C. asiatica		—	2.60	—	—	—	—	32.7	—	0.58	—	—	31.2	—	—	0.06	—	—
C. subcordata		—	0.46	—	—	—	—	—	0.4	0.02	—	—	—	—	—	0.02	—	—
D. polysperma		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.15	—
D. microcephala		—	—	—	—	—	—	—	—	0.02	—	—	0.2	—	—	11.02	0.98	—
D. bemarivensis		—	—	—	—	0.17	0.06	—	—	—	0.05	—	—	—	—	—	—	—
D. reflexa		—	0.10	—	—	—	0.06	—	—	—	—	—	—	—	33.4	1.17	3.97	—
E. acranthum		0.14	0.64	—	—	—	—	—	—	0.34	0.65	0.06	0.4	—	0.6	0.87	0.54	—
E. pyrifolia		—	1.02	0.03	—	—	6.99	25.7	0.2	0.98	0.4	—	38.2	1.45	9.4	8.39	3.74	—
F. avi-avi		—	—	0.17	—	—	2.49	—	—	0.13	0.1	0.01	—	0.36	—	0.02	0.18	—
F. nautarum		—	—	0.08	—	—	8.91	—	—	0.04	0.21	0.01	—	0.09	0.2	0.04	0.04	—
F. reflexa		0.07	0.96	0.06	—	—	3.07	—	—	0.11	0.17	0.04	0.2	0.36	0.4	0.34	0.26	0.2
F. ramontchii		0.09	0.32	0.03	—	0.17	0.29	—	—	0.34	2.02	0.82	—	0.16	—	0.4	0.09	0.8
G. scandens		—	—	—	—	—	—	—	—	—	—	—	—	—	—	8.11	0.14	—
G. speciosa		—	0.94	0.69	0.4	3.33	0.19	0.25	—	0.60	0.28	0.06	1.2	—	—	—	—	—
I. macrantha		—	0.10	—	—	—	—	—	—	—	—	—	—	—	2.0	—	0.16	—
I. pes-caprae		—	2.31	—	—	—	—	—	—	—	—	—	—	—	—	0.06	0.13	—
J. elegans		—	0.32	—	—	—	—	—	—	0.41	0.5	—	—	—	0.8	2.91	0.77	—
L. camara		—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.19	—	—
L. aldabrense		—	0.42	—	—	—	—	—	—	1.54	0.96	0.03	0.4	0.45	9.6	6.36	1.22	—
L. myrtina		—	—	—	—	—	—	—	—	—	0.02	—	—	—	—	—	—	—
L. racemosa		1.51	—	0.25	—	—	—	—	—	—	—	—	—	—	—	—	—	1.28
M. triphylla		—	—	—	—	—	2.39	—	—	0.02	0.04	—	—	—	—	0.02	—	—
M. leroyi		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.05	—

M. senegalensis	0.19	5.92	0.01	—	15.2	0.38	—	1.4	5.09	7.5	1.51	16.0	8.55	3.8	0.7	7.63	0.4
M. hildebrandtii	—	—	—	—	—	—	—	—	0.02	0.35	—	—	—	—	—	—	—
M. oleifera	—	0.13	—	—	—	—	—	—	0.02	0.03	—	—	—	—	—	—	—
M. aethiopicum	0.92	2.06	—	—	0.33	0.1	—	—	3.94	6.52	2.41	3.4	2.0	4.0	2.68	7.29	0.04
O. ciliata	0.13	0.34	—	0.4	1.0	—	—	—	2.82	12.9	5.0	0.6	3.54	0.2	7.53	0.85	0.24
P. tectorius	—	0.53	0.86	2.6	—	1.34	4.5	—	0.04	0.5	0.02	—	—	12.4	0.02	0.32	—
P. suberosa	—	0.06	—	—	—	—	—	—	0.02	—	—	—	—	3.2	1.34	0.32	—
P. acidula	—	4.75	—	—	—	0.67	0.5	15.0	14.0	0.09	0.05	4.8	—	37.8	—	21.7	2.94
P. casticum	—	0.06	—	0.3	—	0.1	—	—	0.18	0.06	0.03	—	0.09	—	—	—	0.18
P. (P.) canomala	—	—	—	—	—	—	—	—	—	0.11	0.04	—	0.18	0.4	—	0.15	—
P. cernuum	—	—	—	—	—	0.67	—	—	—	—	—	—	0.27	3.8	0.15	0.77	—
P. multiflora	0.28	1.79	—	—	25.7	0.38	11.5	—	7.79	16.4	2.68	7.0	35.3	5.0	10.11	5.24	0.46
O. (P.) gummifera	—	—	—	—	—	—	—	—	0.18	0.11	—	—	—	—	—	—	—
P. obtusifolia	—	—	—	—	—	0.19	—	—	—	0.01	—	—	—	—	0.02	0.04	0.14
R. communis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.09	—	—
S. viminale	—	0.06	—	—	—	—	—	—	—	0.1	—	—	—	—	2.98	0.16	—
S. taccada	—	1.79	0.1	—	2.0	4.41	—	—	3.36	0.08	—	1.2	—	0.6	0.02	—	—
S. myrtina	—	—	0.15	—	—	—	—	—	0.02	0.09	0.02	0.2	—	0.4	0.02	1.07	—
S. fryeri	0.07	0.58	—	—	0.17	—	—	—	0.03	1.82	0.22	—	—	—	4.51	0.26	0.18
S. inerme	—	—	—	—	2.67	—	—	—	0.16	0.13	0.07	—	1.55	4.6	0.32	4.26	0.86
S. indicum	—	0.22	0.23	0.3	—	0.48	—	—	0.11	0.08	0.16	0.4	—	3.0	0.26	0.97	—
S. tomentosa	—	—	—	—	—	—	—	—	0.09	—	—	—	—	—	—	—	—
S. maritima	—	0.69	—	—	—	0.1	—	—	0.24	—	—	—	—	3.0	—	—	0.18
T. vedcourtiana	—	—	—	—	—	—	—	—	0.04	0.03	—	—	0.18	0.2	0.3	0.22	—
T. supra-axillaris	—	0.21	—	—	—	—	—	—	0.34	—	—	—	0.73	3.4	10.0	5.60	—
T. tricantha	—	0.02	—	—	1.83	1.05	0.5	—	0.75	1.21	0.04	2.8	2.73	—	0.62	1.71	—
T. boivinii	0.01	0.23	—	0.01	—	—	—	—	0.15	1.36	0.31	—	0.36	3.2	2.45	1.65	—
T. catappa	—	—	—	—	—	—	—	—	0.02	—	—	—	—	—	—	—	—
T. populneoides	4.55	—	—	—	—	—	—	—	—	0.01	0.83	—	—	—	—	—	2.34
T. argentea	—	1.46	—	—	—	—	0.25	—	0.42	0.01	—	—	—	—	—	—	—
T. africana	—	—	—	—	—	—	0.25	—	—	0.03	—	—	—	0.4	0.09	0.04	—
T. sonderana	—	—	—	—	—	—	—	—	0.02	0.37	0.01	—	1.18	0.8	1.26	0.96	—
V. grandis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.04	2.19	—
others†	—	—	—	—	—	5.17	0.25	—	—	0.02	—	—	—	0.2	0.06	0.08	—

† Sites: 1, '*Thespesia/Lumnitzera*'; 2, 'wooded coastal fringe' on sand; 3, 'coastal mixed scrub [open]'; 4, 'coastal mixed scrub [wooded]' at Cinq Cases; 5, 'coastal mixed scrub [wooded]' at Takamaka; 6, 'pinnacles'; 7, 'Dune Jean-Louis coastal mixed scrub'; 8, '*Pemphis* coastal hedge'; 9, 'coastal fringe mixed scrub'; 10, SE Grande Terre mixed scrub [standard]' including 'groves' and '*Cyperus* park-woodland'); 11, 'SE Grande Terre open mixed scrub'; 12, 'Dune Jean-Louis mixed scrub'; 13, 'Malabar mixed scrub'; 14, 'Gionnet mixed scrub'; 15, 'Picard mixed scrub'; 16, 'closed *Pemphis* scrub'; 17, 'fern-pocket *Pemphis* [closed]'.

‡ 'Others' include in quantitatively recorded sites: *Acampe rigida*, *Angraecum eburneum*, *Cassipourea thomasseti*, *Cassytha filiformis*, *Grewia aldabrensis*, *Ehretia cymosa*, *Pandaca mauritiana* and *Pandanus aldabrensis*.

TABLE 3. CHARACTERIZATION OF VEGETATION TYPES ON GROUND COVER

(Numbers express the percentage of ground in a (row) vegetation type covered by a (column) cover type.)

vegetation type	tortoise turf	*F. cymosa*	*C. niveus*	*F. ferruginea*	dicot. herbs	long grasses	*C. ligularis*	other spp. *Cyperus*	*S. virginicus*	*S. macrostahyum*	*A. aureum*	mosaic rock	litter	bare soil	cover type prostrate shrubs
Sporob./Sclerod. coastal swards	0.01	1.85	—	—	1.05	0.23	1.82	—	15.9	26.5	—	0.73	16.8	1.09	3.57
Picard/Polymnie pastures	0.04	3.23	0.34	—	25.8	14.3	0.21	0.02	0.03	—	—	0.28	20.0	2.39	6.58
tortoise turf/sedge	33.4	—	1.1	0.1	0.6	—	—	—	—	—	—	—	17.35	18.55	—
('open mixed	22.4	5.3	11.6	—	0.22	0.65	9.33	—	3.48	—	—	0.97	32.4	0.12	—
scrub') range of	15.8	11.35	4.94	0.09	0.04	0.31	1.22	0.89	—	—	—	2.01	18.2	4.22	0.02
variation in	15.5	14.3	—	0.6	—	0.07	—	1.53	—	—	—	0.4	21.9	7.63	—
agglomerated sites shown	11.0	6.8	—	—	0.8	2.8	3.33	—	—	—	—	0.43	3.85	0.29	0.37
sedge mixtures under mixed scrub	—	9.4	3.25	0.1	0.325	—	2.4	0.2	—	—	—	—	13.8	2.2	—
sedge mixtures in groves	0.36	7.09	4.92	1.19	—	0.16	0.76	4.75	—	—	—	—	34.2	4.92	—
Takamaka open	10.99	7.85	0.29	0.06	1.88	0.22	0.49	—	—	—	0.21	32.9	2.36	1.03	
coastal mixed scrubs	24.6	1.32	—	—	0.28	0.01	5.43	—	—	—	0.07	20.2	4.54	2.38	2.93
	2.41	3.61	0.175	—	1.05	—	7.125	—	0.025	—	3.85	55.3	5.36	0.35	—
fern-pocket *Pemphis*	0.07	3.97	—	3.1	0.03	0.27	—	—	3.67	—	5.33	0.2	22.2	5.1	—
pool vegetation with *Thesp./Lum.*	0.72	6.45	—	6.97	—	—	0.08	—	—	—	—	0.46	31.2	16.3	1.08

plant cover was always dominated by *Polysphaeria multiflora*, *Ochna ciliata*, *Mystroxylon aethiopicum*, *Maytenus senegalensis* and *Apodytes dimidiata*. A wide range of other woody species was present. The commoner ones were *Erythroxylum acranthum*, *Canthium bibracteum*, *Flacourtia ramontchii*, *Terminalia boivinii* and the climber *Secamone fryeri*.

Subtype (A): '*open mixed scrub*' (column 11 in table 2). Woody plants were at low density and often grew in small clumps orientated along the axis of the trade winds (Grubb 1971). Species numbers per segment were low. Ground layer vegetation had a high percentage cover of tortoise turf, with varying amounts of *Fimbristylis cymosa* (often co-dominant), *Cyperus ligularis* and *C. niveus*. Dicotyledonous herbs and long grasses were rare and restricted to cracks where the large number of giant tortoises using this vegetation type could not reach them.

Subtype (B): '*mixed scrub*' (column 10 in table 2 gives subtypes (B)–(D) combined). This differed from (A) in being much thicker woodland; the boundary between the two was unclear in places (see Discussion) but (B) is defined by having ground cover (table 3) dominated by *Fimbristylis cymosa* and *Cyperus niveus*, with tortoise turf rare or absent. Under very close canopy, *F. cymosa* disappeared and the only ground layer species were *C. niveus*, *C. bigibbosus* and occasionally other *Cyperus* species. In subtypes (A), (B) and (C), *F. ferruginea* was occasionally included in transect segments that also crossed the edge of freshwater/brackish pools (§ix) below).

Subtype (C): '*groves*'. The commonest woody plants were the same as in the other subtypes, but the ground cover (table 3) contained more of the deep-shade *Cyperus* species such as *C. bigibbosus* and generally less tortoise turf. This subtype was considerably different from the rest of Aldabra's vegetation in height of woody plants, in structure, and in the rarer plant species found. It contained patches of woodland, usually from 0.5 to 2.0 ha in area, separated by lower, more open, scrub. In the centres of the groves tree and shrub layers were often evident. The tree layer was formed by plants growing up to 10 m high emerging through the layer of bushes at the more typical height (for Aldabra) of up to 5 m.

One of these woodland patches is well known as 'Takamaka grove' (Fryer 1911; Fosberg 1971). It is by no means unique and the greatest extent of these woodlands occurs at the northwest end of the 'airport trace' transect (figure 1).

The more usual tree layer species were *Calophyllum inophyllum* (Takamaka grove only), *Ochna ciliata*, *Apodytes dimidiata*, *Guettarda speciosa*, *Ficus nautarum*, *Mystroxylon aethiopicum* and *Malleastrum leroyi*.

Four individuals of *Operculicarya gummifera* and two of *Macphersonia hildebrandtii* were seen elsewhere on Aldabra; otherwise the following species were restricted to the groves: *O. gummifera*, *M. hildebrandtii*, *Pandaca mauritiana*, *Carissa edulis*, *Pisonia aculeata*, *Psychotria pervillei* (not seen in this study), *Maillardia pendula*, *Calophyllum inophyllum*, *Ludia myrtina*, *Eugenia elliptica* and *Pandanus aldabrensis*.

The following species were restricted to the northwest corner of the atoll and the groves and subtype (D): *Tarenna supra-axillaris*, *Abrus precatorius* (a climber), *Dichrostachys microcephala*, *Dracaena reflexa*, *Jasminium elegans* and *Malleastrum leroyi*.

Most of the above species were rare; any one grove only contained one or two of them and many were found only by ground search outside the transects. However, we believe that this search was extensive enough in other vegetation types to discount the possibility that these species occurred elsewhere, except in very low numbers.

Subtype (D): '*Cyperus park-woodland*'. This subtype was distinguished from (C) by being

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more open, having ground cover only of *Cyperus* spp. but containing many of the woody plant species otherwise restricted to the groves. The rock on which this subtype grew was noticeably more crenellated and brittle than that on which (A)–(C) grew.

(ii) '*Picard mixed scrub*' (column 15 in table 2)

At the northwest end of the atoll, this type of vegetation lay at the opposite extreme to (i) on a gradient of changing species composition and richness. Species richness was the highest on Aldabra, and the dominant woody plants were *Acalypha claoxyloides*, *Dichrostachys microcephala*, *Polysphaeria multiflora*, *Tarenna supra-axillaris*, *Euphorbia pyrifolia* and the climber *Gouania scandens*. Of the eastern Grande Terre dominants, *P. multiflora* was common in both types, *O. ciliata* was less common on Picard but regularly present, as was *M. aethiopicum*, *M. senegalensis* was rare and *A. dimidiata* was very rare.

In open areas other than disturbed ground near the settlement, usually on the '8 m ridge' (Stoddart *et al.* 1971), pastures similar to those on Île Polymnie were present. The dominant cover types here were (table 3) dicotyledonous herbs and long grasses. Where tortoises grazed relatively intensively on Île Picard, a turf lusher than the southeast Grande Terre 'tortoise turf' had developed, often dominated by grasses of more robust growth form than the 'tortoise turf' species (e.g. *Daknophobis boivinii*).

The remaining 'mixed scrub' and 'mixed *Pemphis*' associations described below lay between (i) and (ii) in species composition and richness; boundaries were often uncertain and discontinuities may have been made artificially obvious by the distance between transects.

(iii) *Gionnet and Polymnie mixed scrubs and mixed Pemphis* (columns 14 and 16 in table 2)

These were extremely thick mixed scrubs lying between the *Pemphis* coastal hedge (figure 10) and the lagoonward *Pemphis*, near Gionnet channel (figure 1) and on Île Polymnie. The Gionnet vegetation has been described previously by Prŷs-Jones (1979) as the only known habitat for the endangered endemic warbler *Nesillas aldabranus*. It stands out in comparison with other Aldabra vegetation by its high species richness, the thickness of twigs and canopy right down to ground level at Gionnet, and the dominance of the Gionnet vegetation by *Pandanus tectorius* and *Dracaena reflexa*. A very wide range of other woody taxa are present, including *Cassipourea thomasseti* and *Asparagus umbellulatus*, which are restricted to the northwest of Aldabra.

(iv) *Malabar mixed scrub* (column 13 in table 2)

This type was intermediate between (iii) and (i) in species richness and composition. Dominants were *Acalypha claoxyloides*, *Polysphaeria multiflora* and *Maytenus senegalensis*. Other 'northwest' species such as *Tarenna supra-axillaris* were rare, and some such as *Gouania scandens* were absent. In more open areas, where ground cover was present, it was more similar to the 'open mixed scrub' high tortoise turf areas of southeast Grande Terre than it was to the Picard and Polymnie pastures.

(v) *Dune Jean-Louis mixed scrub* (column 12 in table 2)

The odd species composition here interrupted the otherwise smooth progression in species composition and richness of woody plants from northwest to southeast across the atoll.

The dominant woody plant in the mixed scrub was *Euphorbia pyrifolia*, otherwise a northwestern species. 'Coastal' species (see (vi)) such as *Colubrina asiatica* and *Scaevola taccada* were occasionally very abundant, even several hundred metres from the dune coast. The transect ran across the narrowest part of Grande Terre, but ground search showed that this odd vegetation type extended for more than a kilometre on either side of the transect. Further work will be needed to understand the difference between this vegetation and the general mixed scrub pattern on Aldabra. Causes might include topographical patterns, the effects of high dunes on small scale wind and salt spray patterns or even past disturbance by man (Dune Jean-Louis was a major turtling station and fuel was needed for its boilers).

Inland the ground layer vegetation was similar to that under the mixed scrub (i, *B*) of southeast Grande Terre, a mixture of sedges. However, at Dune Jean-Louis the grass *Sclerodactylon macrostachyum* was present further inland than usual.

(vi) *Formations on the coastal fringe: the first* 50 m *or less of the seaward coast*

(*A*) *Pemphis coastal hedge* (column 8 in table 2). When a woody plant fringe was present on the Aldabra coast, on the north and west sides, the first bush encountered inland was nearly always *Pemphis acidula*. The first impression of the vegetation from the sea was of a line of this species broken only by the vegetation of sandy beaches and the occasional *Pandanus tectorius*. The mixed vegetation inland was rarely visible. However, the *Pemphis* hedge was often only one bush thick, receiving the bulk of the salt spray in the northwest monsoon storms. Vegetation such as that in (vi, *C*) and (vii) usually replaced it inland.

(*B*) *Sporobolus virginicus/Sclerodactylon macrostachyum* coastal series (table 3). Along the southern and eastern coasts of Aldabra, there is a virtually continuous raised beach of deposited coral sand (Stoddart *et al.* 1971). On these exposed coasts, woody plants were rare; in some places prostrate forms of *Pemphis acidula* were found, contorted by wind and salt spray; in a very few other places isolated clumps of *P. acidula*, *Guettarda speciosa* and *Pisonia grandis* were found.

Over most of this area, the only vegetation was in the ground layer, nearly all the plant cover being the grasses *Sclerodactylon macrostachyum* and *Sporobolus virginicus*. *S. macrostachyum* is much disturbed by tortoises seeking shade and/or nest sites, and it has been suggested that *S. virginicus* takes over where tortoise and/or nesting green turtle activity is highest (Hnatiuk *et al.* 1976). However there are large areas on the south coast where tortoise density was high and *S. macrostachyum* was dominant; so the picture may be more complicated than this. On the scale of 50 m transect segments, there was a continuous grade from pure *S. virginicus* to pure *S. macrostachyum*; only one vegetation type could be identified, but on a smaller scale the grasses formed largely discrete patches rather than an intimately mixed turf.

(*C*) *Sand-based coastal fringe* (column 2 in table 2). Along the sheltered north and west coasts, raised beach deposits are rare, but a large number of small pocket beaches are found. These pocket beaches could not be distinguished from (vi, *D*) on the composition of woody plants generally common on Aldabra, but each site had some of the following rarer species: *Colubrina asiatica*, *Cordia subcordata*, *Salvadora angustifolia*, *Scaevola taccada*, *Suriana maritima* and *Tournefortia argentea*. *Thespesia populnea* was also present behind the south coast dunes. The ground layer vegetation was dominated by the grasses of (vi, *B*) and occasionally by the sprawling perennial *Ipomoea pes-caprae* and the sedge *Cyperus conglomeratus*.

(*D*) *Rock-based coastal fringe* (column 9 in table 2). Sites from this area were also difficult to classify, but usually contained an impoverished version of the local mixed scrub flora, with either *Scaevola taccada* or *Sophora tomentosa* often present as well. The commonest woody plants were generally *Guettarda speciosa* and *Maytenus senegalensis*. Ground layer vegetation was a mixture of sedges, often containing small amounts of *Sclerodactylon macrostachyum*.

(vii) *'Coastal mixed scrubs' on the* 8 m *ridge, and other nearby formations*

The above area title covers a broad range of distinct vegetation, classified as shown below. On the sheltered coasts, 'coastal' shrubs and shrubs known to be tolerant to salt spray did not extend beyond the fringe described in (vi). On the more exposed coasts, this 'coast influence' extended further inland, as follows.

(*A*) *Coastal mixed scrubs: general* (columns 3–5 in table 2). These sites fell into small discrete groups from different areas. Ground search suggested that these formed points on a continuous spectrum of variation from Aux Vacoas in the west to Point Hodoul in the far northeast. Places slightly sheltered from the trade winds, either by coast aspect or by being on the lagoonward slope of the 8 m ridge, tended to produce a thick woodland dominated by *Guettarda speciosa* (in the southwest, south and southeast) or *Pandanus tectorius* (in the east). *Scaevola taccada* was common throughout, and *Cassytha filiformis* occurred at the eastern end of this vegetation type. Species from the local mixed scrub variants were also found, notably *Maytenus senegalensis* and *Polysphaeria multiflora*.

The woodland became more open on a gradient from west to east. In the western areas, ground layer vegetation was sparse, but in the more open areas a characteristic mix of mosaic rock and tortoise turf dominated the ground layer (table 3), with the fern *Acrostichum aureum* and the sedge *Cyperus ligularis*.

(*B*) *Dune Jean-Louis variant* (column 7 in table 2). The oddity of the mixed scrub in this area was repeated at the sea-coast end of the transect. Besides an admixture of the mixed scrub species in (v), *Colubrina asiatica* and *Scaevola taccada* characterized this type. The ground layer vegetation was dominated by a mixture of sedges with *Sclerodactylon macrostachyum*, as for (vi, *D*).

(*C*) *Ridge foreslope*. On the very exposed southeast coast, there was no woody vegetation at all on the seaward slope of the 8 m ridge. Ground layer vegetation was sparse. Lack of shade for giant tortoises reduced their grazing activities here.

(*D*) *Pinnacle zone* (column 6 in table 2). This heavily fretted and pot-holed area contained a flora growing in the potholes distinct from any other on the island. On the basis of common woody species, the flora was most similar ($r_s = 0.6$) to that of a site on Île Picard at the opposite end of Aldabra. Few pits contained more than one or two plant species, but the deeper ones allowed shrubs to grow to 5 m high before being blasted by the dry season salt spray or browsed by tortoises or feral goats reaching from the pit edges. Several plant species were found nowhere else; these were the shrubs *Brexia madagascarensis* and *Ehretia cymosa*, the perennial herbs *Hypoestes aldabrensis* and *Melanthera biflora* and the fern *Nephrolepis biserrata*.

Within this zone, most species had distributions clustered in adjacent pits rather than spread throughout (14 out of 17 species common enough for the test showed significant clumping ($p < 0.01$) on the runs test (Siegel 1956)).

(viii) *Takamaka open ground* (table 3 only)

In the southern half of the Takamaka transect (figure 1), there was a large area with virtually no woody plant species. Ground layer vegetation was intermediate between that of coastal mixed scrubs and that of open mixed scrub, being dominated by mosaic rock, tortoise turf and *Fimbristylis cymosa*.

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(ix) *Pool vegetation* (column 1 in table 2)

Brackish and freshwater pools of eastern Grande Terre had a distinct vegetation (Fosberg 1971) dominated by the shrubs *Thespesia populneoides* and *Lumnitzera racemosa*, with the sedge *Fimbristylis ferruginea* often present in the ground layer. Occasionally species of the surrounding mixed scrub were present in segments of pool vegetation but this is likely to have been an artefact of the constant size of the transect segments. *Flacourtia ramontchii* was the commonest additional species. Disturbance of areas around the pools by tortoises seeking water in the dry season, and the violently fluctuating water levels in the pools (in March 1978 some rose 2 m overnight after 200 mm of rain) created areas of continually disturbed ground. The dwarf-plant meadows described by Fosberg (1971) as a separate vegetation type (*Bacopa*, *Mollugo* and *Bryodes*) were characteristic of this transition zone around the pools.

(x) *Vegetation associated with Pemphis acidula*

Previous workers have identified '*Pemphis*' scrub and 'mixed' scrubs as the most distinct vegetation types on Aldabra (Vesey-Fitzgerald 1942; Fosberg 1971). The data reported here show that the relationship between '*Pemphis* scrub' and the mixed scrubs was extremely complex and difficult to disentangle. To test cause and effect behind these relationships would require experimental work outside the scope of this study; one can only speculate that complex patterns of topography and of tolerance to salt groundwater are involved. The closest approximation to a classification and understanding based on the present observations is given below. In the transition mentioned below, the mixed scrub ends of the spectrum have already been described under the appropriate mixed scrub.

(*A*) *Lagoon Pemphis–mixed scrub transition* (columns 12, 14 and 16 in table 2 include this transition). At the lagoon end of this spectrum the scrub was of low species richness with characteristic species composition and spectacular impenetrability. The dominant species was always *P. acidula*, regularly associated with *Acalypha claoxyloides* and *Vernonia grandis*. The perennial herb *Achyranthes aspera*, the climber *Ipomoea macrantha* and the shrubs *Sideroxylon inerme*, *Maytenus senegalensis* and *Scutia myrtina* were also present in many places.

As the land level rose further from the lagoon, more and more of the woody species of local mixed scrub appeared, until eventually the vegetation was similar to that near the sea coast, with no *P. acidula* (see, for example, figure 6). When sharp boundaries occurred, they were usually associated with visible change in rock level.

The only cover plants of the ground layer were seedlings of woody plants and the climber/sprawler *Pleurostelma cernuum*, except in some areas of eastern Grande Terre where the *P. acidula* scrub was open enough to allow a ground layer dominated by *Fimbristylis cymosa* to develop.

Thus the trend was for a gradual change from the open sea coast inland to the lagoon shore, from mixed scrub of relatively high species richness to *P. acidula* scrub of low species richness. Change was usually continuous, both along sea–lagoon radii and between them, causing sites containing *P. acidula* to chain and merge in an unclear manner in the classification (figure 7).

(*B*) *Fern-pocket Pemphis: closed and open* (column 17 in table 2). Few transect segments crossed this eastern Grande Terre vegetation type. Ground search confirmed its characteristic nature; woody plant cover was dominated by *P. acidula*, usually appearing from deep pits in the rock, mingled with mixed scrub species growing elsewhere. Ground layer vegetation (table 3) was dominated by the fern *Acrostichum aureum*, with the sedge *Fimbristylis cymosa*. The grass *Sporobolus* *virginicus* was abundant in some sites. Ground search and air photographs showed that some areas of this type had a nearly closed shrub canopy while others were virtually free of woody plants.

(xi) *Other definitely indigenous vegetation*

(*A*) *Tidal pools*. Not strictly a 'vegetation' type but easily visible on air photographs and identifiable on the ground by a fringe of mangrove or *P. acidula* and the lack of any vegetation in the pools.

(*B*) *Single species Scaevola stand*. A single large (*ca.* 2 ha) monospecific stand of *S. taccada* near the east end of Île Malabar, with virtually no ground layer vegetation, was mapped solely because of its large size.

(*C*) *Avicennia mangrove and mudflats*. This type was composed of single species stands of *A. marina* varying from 'thicket-in-parkland' appearance to open mudflats with scattered mangrove trees.

(*D*) *Closed-canopy mangrove woodland*. This type included all other mangrove vegetation. Macnae (1971) discusses the patterns of species composition in Aldabra's mangroves in specific places.

(xii) *Possibly or certainly introduced vegetation*

(*A*) *Casuarina and coconut groves*. It is uncertain whether *C. equisetifolia* is native to Aldabra or introduced (Wickens 1979). Except for single-species stands, sites containing this species tended to agglomerate with those adjacent to them without *Casuarina*, but the *Casuarina* sites usually had a lower number of species. *Cocos nucifera* was probably introduced to the atoll, and many of the extant stands are known to have been planted. Sites containing it tended to behave in the same way as the *C. equisetifolia* sites; often the two species grew together. Ground layer vegetation varied from virtually nil to a rich sward of grasses and herbs under the more open groves on Île Picard.

(*B*) *Gardens and other disturbed ground*. A great variety of plant species, mostly introduced weeds but some indigenous, grew here. This type is probably maintained in its several states by continued human disturbance.

(*e*) *Construction of the vegetation map*

The map was constructed by linking knowledge of the vegetation with air photographs, as described in Methods.

The easiest boundaries to identify on the photographs were those accompanied by major changes in texture of the vegetation or, in open vegetation, by changes in the underlying rock or other ground cover. Thus the groves (figure 11, 2C, 2D) could easily be identified as patches of tall woodland in a matrix of lower, sparser scrub. The boundary changes in figure 11, 2A, could readily be seen from changes in rock texture and slope.

Two types of boundary proved difficult to identify from photographs and these have already been pointed out as boundaries difficult to identify floristically. These were those boundaries where the odd species composition at Dune Jean-Louis gave way to the more usual mixed scrub vegetation, and those involving the *Pemphis*–mixed scrub transition.

Both have been drawn in roughly on the map (pullout 1) to give an indication of where species composition might be expected to change. For the *Pemphis* transition, the first appearance of

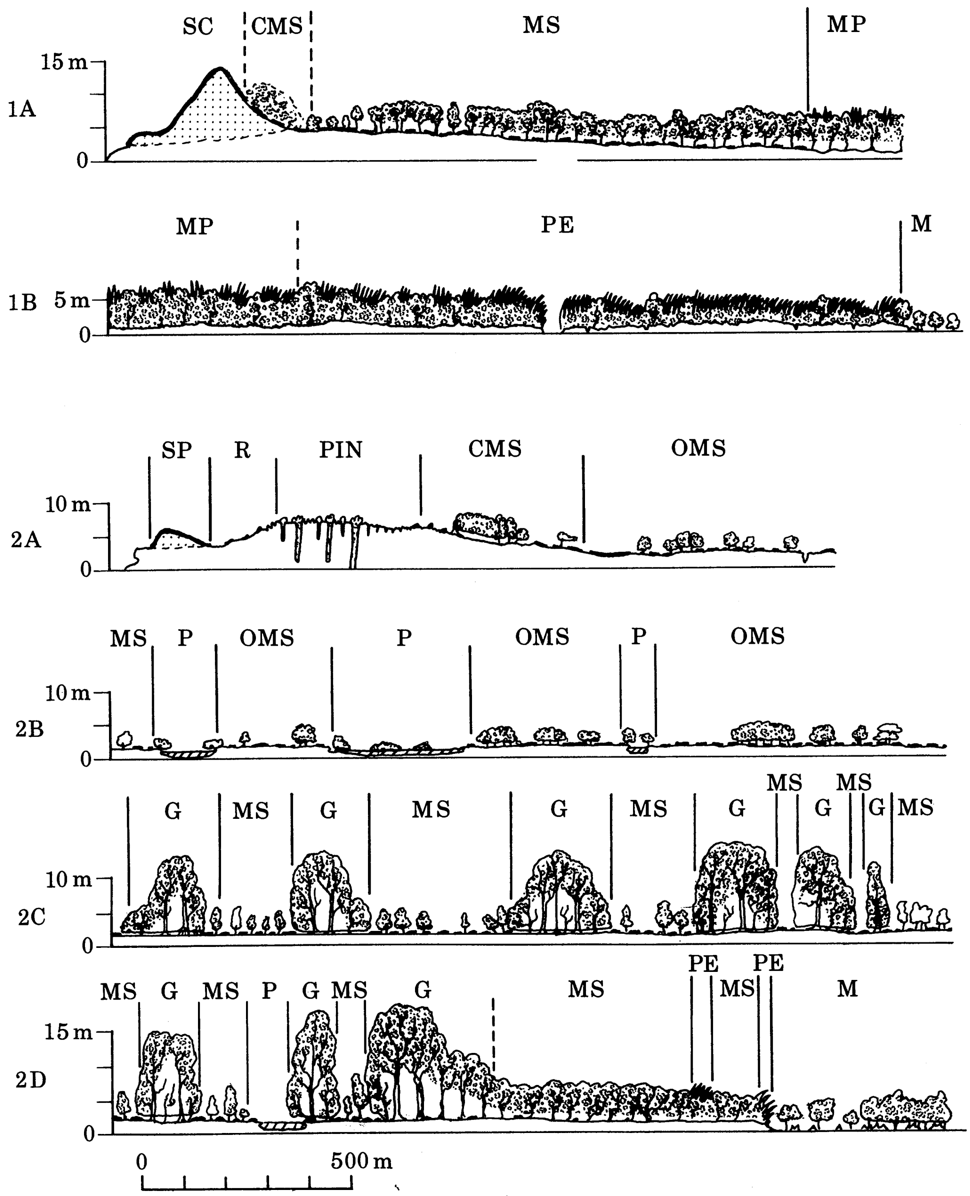

Figure 11. Appearance of the vegetation on a coast–lagoon transect and across southeast Grande Terre. Both transect sections start from the coast and end at the lagoon. Section 1A is directly followed by 1B, but in series 2 there are gaps between the sections. Height above sea level is real in 1A, 1B and 2A (from Stoddart *et al.* 1971), and conjectured in the other sections. Presence of ground vegetation is indicated by heavy lines demarcating the ground surface. Mixed species canopy is denoted by shading, *Pemphis acidula* canopy by jagged lines. Sections 1A and 1B form transect 8 in figure 1, 2A is near transect 13, 2B is the north–south segment of 14, 2C is the southeast 1 km of 15, and 2D runs from near the end of 15 to the lagoon coast at the west. All except 2D are based on quantitative data. Section 2D is based on air photographs and visiting the sites. The double '*Pemphis* hedge' in 2D is due to a mangrove creek abutting the section. Dashed boundaries are arbitrarily imposed on a continuum and/or flexible from place to place. Key: SC, *S. macrostachyum* with some *S. virginicus*; CMS, coastal mixed scrub; MS, mixed scrub; MP, mixed scrub with *Pemphis acidula*; PE, low diversity *P. acidula* scrub; M, mangroves; SP, *Sporobolus virginicus*; R, rocky foreslope of the 8 m ridge; PIN, pinnacle zone; OMS, open mixed scrub with tortoise turf and sedges; G, groves; and P, *Thespesia populneoides*/*Lumnitzera racemosa* pool vegetation.

P. acidula in the vegetation was usually marked by a change in texture of the vegetation and often accompanied by a change in topography. This boundary could often be drawn with some confidence, but remains one of 'convenience' rather than of 'community structure'. This was not always so; notable exceptions were the area west of the Takamaka transect and that west of the airport trace transect in eastern Grande Terre. Here the vegetation had been represented previously as single species *Pemphis* or even mangrove (Jenkin 1967) in places where it was found to be devoid of either type. Subsequent to this study, another, previously inaccessible, area in southwest Grande Terre, previously thought to contain single-species *Pemphis*, has been found to carry mixed vegetation (D. Cowx & C. Peet, personal communication). This emphasizes that the *Pemphis*–mixed scrub boundary, even if floristically real, cannot be identified with certainty without visiting each area on the ground.

Some of the vegetation types described above have been given the same shading on the map because of problems in representing extremely narrow zones on the scale of the map and with the limited number of distinct black-and-white shading patterns. These were the single-species *S. taccada* patch on Île Malabar (which was given the same shading as the open coastal mixed scrubs in southeast Grande Terre, but which can be identified from its position), the *S. virginicus*–*S. macrostachyum* coastal grasslands (which were shaded with wooded coastal sands, but which can be identified from their position on the south and east coasts), and the *P. acidula* coastal hedge and coastal fringe. The hedge (vi, *A*) was usually only one or two bushes thick, and was always on the side towards the sea coast.

The Malabar and Gionnet mixed scrubs were mapped together (a boundary probably lies some 4 km from the west end of Île Malabar) and all possibly introduced vegetation was shaded together; gardens were only present on a small area of southern Île Picard. Thus these poolings of vegetation types can readily be separated by their positions on Aldabra.

Discussion

(*a*) *Vegetation on Aldabra*

The limits of definition in this study must be established before coming to conclusions about the nature and structure of Aldabra's vegetation. Two problems of methodology emerge. The first concerns the use of classification *per se* and the choice of a similarity measure. Most similarity measures between sites were excluded as possible bases for classification either because they sacrificed quantitative information or because the structures of different parts of the data set were not comparable (e.g. the *P. acidula* complex and 'open' and 'closed' mixed scrub sites). Bouxin (1975), comparing the use of quantitative and qualitative data for an ordination of African savanna vegetation (the nearest equivalent to Aldabra's vegetation that we know in the quantitative literature), came to the conclusion that qualitative data alone were inadequate for the understanding of complex vegetation. The complexity of Aldabra's vegetation also meant that we were attempting to understand relationships between vegetation of similar cover abundance but different species composition, and those between vegetation of the same species composition but different cover abundance in the same analysis. This directed the division of the analysis into a hierarchy of steps.

The second methodological problem concerns the simple clustering algorithms used. Eventually we hope to use the Aldabra data set for comparison of a variety of ordination and classification techniques, but this complexity of analysis was considered inappropriate for the construction of a large-scale vegetation map, and so only a small number of simpler techniques were used. Specific areas of interest emerge from this; the 'chaining' problem in single-linkage clustering of the ground layer data probably reflected the range of scales on which Aldabra's vegetation is organized, determined by environmental heterogeneity and heterogeneity of effects from giant tortoises; this set of problems is being investigated.

The analysis used gives a description of the large-scale characteristics of Aldabra's vegetation which can be used to make hypotheses about within-island patterns and the relationship of Aldabra's vegetation to that of other areas in the semi-arid tropics. On this large scale, we suggest three possible determinants of spatial vegetation change: topographical changes varying from sea coast to lagoon shore; extent of shelter from the dry, salt-laden southeast trade winds; and the effect of giant tortoise grazing and trampling on the ground layer plants and seedlings. The first two factors are similar to those suggested in the ordination, by Newbery & Hill (1981), of a subset of mixed scrub sites.

Figure 11, 1, shows effects likely to arise largely from the topographical changes between the open sea and the lagoon shores. On a large scale, the greatest effect was the gradual replacement of the mixed scrub species by *P. acidula* as level of the land changed and the groundwater became more salty with decreasing height above sea level (Fosberg 1971; Stoddart *et al.* 1971; Hnatiuk & Merton 1979). Changes in topography on a smaller scale are likely to be equally important, but experimental work would be needed to clarify this. Microtopography is likely to be just as important in determining the scales of pattern in the vegetation of the ground layer; definite conclusions must await a full pattern analysis of the data from the ground layer.

Grande Terre also has the largest and widest land area of the Aldabra islands. This adds another dimension to topographical effects through the establishment of a freshwater lens (Whitehead & Jones 1969; Wiens 1962), which is permanent in areas far removed from the sea. The larger is the land area, the deeper and more extensive is the freshwater lens. This lens may be a major reason for the diversity of Aldabra's flora when compared to lower atolls, although it is difficult to distinguish the effects of area *per se* from more complex hypotheses about island diversity (Connor & McCoy 1979). The freshwater lens may also account for the development of higher woodland in the groves, which contain many species not found on continental sand islands or debris-based atoll islands.

Table 4 shows a qualitative estimate of the distribution of some of the woody plant species over the atoll. Most species restricted to particular areas within the atoll show patterns suggesting either topographical determination or shelter from the trade winds. Occasionally, as with *P. suberosa*, a northwest distribution can be accounted for by recent introduction via Île Picard, but many other species have distributions restricted in this manner, and the only environmental variables known to be correlated with this northwest–southeast axis are the trade winds and features of topography.

Many ground layer species show markedly different patterns from the above. Grubb (1971) lists some of the species restricted to 'tortoise turf' and Renvoise (1971*b*) has described others. In most cases these species are restricted to areas of intense tortoise grazing, but the persistence of tortoise turf on Île Polymnie, where there have been no tortoises for at least 90 years, suggests either that the plants' extinction times are long or that the right conditions for their growth can arise edaphically alone.

Many more species of the ground layer flora are restricted to areas with little tortoise grazing (e.g. *Hypoestes aldabrensis* and *Melanthera biflora* in the 'pinnacle zone'). Still others are extremely

Table 4. Woody plant species with restricted distributions on Aldabra (excluding mangroves)

(Only those species that were extremely common and highly skewed in their distribution and those completely restricted to one or two vegetation types are shown.)

species	restriction pattern
Abrus precatorius	northwest and groves
Abutilon angulatum	Picard and Polymnie (introduced?)
Acalypha claoxyloides	northwest and *P. acidula* scrub
Apodytes dimidiata	southeast centred
Asparagus umbellulatus	northwest only
Brexia madagascarensis	pinnacle zone
Calliandra alternans	southeast only
Calophyllum inophyllum	groves only
Carissa edulis	groves only
Cassipourea thomasseti	northwest only
Cassytha filiformis	southeast coastal mixed scrub only
Colubrina asiatica	sheltered coastal strand
Cordia subcordata	northwest coastal strand
Dichrostachys microcephala	northwest and groves
Dracaena reflexa	northwest and groves
Ehretia cymosa	pinnacle zone
Eugenia elliptica	groves only
Flacourtia ramontchii	southeast centred
Gouania scandens	northwest only
Ipomoea macrantha	northwest *P. acidula* scrub
I. pes-caprae	northwest strand
Jasminium elegans	northwest and groves
Ludia myrtina	groves only
Maillardia pendula	groves only
Malleastrum leroyi	northwest and groves
Macphersonia hildebrandtii	groves
Ochna ciliata	southeast centred
Operculicarya gummifera	groves
Pandaca mauritiana	groves only
Pandanus aldabrensis	groves only
Passiflora suberosa	northwest only (introduced)
Pisonia aculeata	groves only
P. grandis	coastal strand
Pleurostelma cernuum	northwest and *P. acidula* scrub
Psychotria pervillei†	groves only
Scaevola taccada	coast centred
Secamone fryeri	southeast centred
Sophora tomentosa	coastal fringe
Tarenna supra-axillaris	northwest and groves
Terminalia catappa	coastal strand
Thespesia populneoides	southeast pools only
Tournefortia argentea	coastal strand
Vernonia grandis	*P. acidula* low diversity scrub

† Not seen alive in this study.

rare where tortoises graze or have completely different growth forms in grazed and ungrazed situations (e.g. *Lagrezia oligomeroides* (Fosberg 1974)).

(*b*) *Aldabra in context: parallels with other vegetations*

Historically Aldabra is unlikely to have been unique. Other raised atolls exist and some (e.g. Assumption) are close to Aldabra. Even now, remnants of vegetation types pertinent for comparison exist in the Caribbean, Pacific and Indian oceans and along the raised reef deposits on tropical continental margins. However, direct comparison is made difficult by the lack of quantitative data and by human disturbance before plant ecologists could study these areas.

The most relevant comparison with other quantitative data could be with continental savanna vegetation. Continental savannas often have the same two-layered vegetation structure and are frequently heavily grazed by large herbivores (Coupland 1979). Such comparison, however, only highlights the distinctness of Aldabra's vegetation. The only large indigenous herbivore on Aldabra is primarily a grazer: browsing above 1 m comes only from the relatively small population of feral goats. Also, the range of environmental heterogeneity provided by the reef rocks of Aldabra is set by karst-form erosion processes (Stoddart *et al.* 1971) and is completely different from the soil base found in most savannas and dry forests of continents. Aside from inland karst formations, we must examine existing studies on raised reef vegetation to put Aldabra in context.

The most directly relevant studies that we know are those of Birch (1963) on the raised reef deposits of the Kenya coast and of Robins (1976) on the Josani forest, Zanzibar Island. Birch (1963) lists 146 woody species from approximately 290 km^2 of coral based vegetation on the Kenya coast. The range of vegetation types that he found parallels that in this work, but the rainfall range in space (940–1400 mm a^{-1}) was probably greater than that on Aldabra (Hnatiuk 1979). Strict exclusion of all woody species suspected of having been introduced to Aldabra leaves 83 indigenous woody species on 156 km^2. Exclusion of species restricted to low diversity *Pemphis* scrub, covering about half the land area of Aldabra, leaves 82 species on approximately 80 km^2 compared with the 146 species on 290 km^2 from the Kenya coast. One needs no assumptions about the precision of species–area relations to suggest that the Aldabra flora appears to be astonishingly rich for an isolated atoll. Many of the woody species of Aldabra are held in common with the Kenya coast coral, and the range of physiognomy of the vegetation from open scrub through scrub forest to the occasional higher patch of woodland is similar.

Many of the woody plants of Aldabra are restricted to a few vegetation types (table 4). Attention is naturally focused on two particular areas of high species richness: the groves, and Îles Picard and Polymnie. Except for a few coastal species, these areas between them contain nearly all Aldabra's woody species. The high richness of the northwest islands may be accounted for by shelter from the trade winds alone, but the groves pose a different problem.

Robins (1976) noted that the Josani forest (37 woody plant species listed) was probably formed on a mature solution basin, allowing a deep soil to develop on the coralline deposits. He was also struck by the similarity of Josani to the 'Takamaka grove' on Aldabra in species composition. The appearance of the groves on Aldabra suggests that they also may be based on old solution basins from 0.5 to 2.0 ha in area. This provides a possible explanation for some of Aldabra's species richness. The depth of the freshwater lens, as in Josani, would allow a deep, salt-free soil to accumulate in solution basins. The large extent of Aldabra may have meant that problems of soil eutrophication from seabird nesting and attendant guano accumulation were avoided, unlike on other raised atolls, like Assumption, and islands with seabirds, where low diversity *Pisonia grandis* forests are often found in otherwise comparable areas (St John 1951). The net result is a type of environment probably unique in the world, certainly a unique survivor among raised atolls.

The vegetation of Aldabra contains a set of plant associations that are probably extremely rare worldwide; one can speculate that they were once characteristic of raised reef deposits around the world, whether on continental coasts or on raised atolls, and they may still be characteristic of such areas where they have not been disturbed catastrophically by human activity. Life form analysis of Aldabra's vegetation (Hnatiuk & Merton 1979) supports this view: the closest life form spectrum to that of Aldabra was that of Diego Garcia, another raised atoll (Fosberg & Bullock 1971).

Aldabra has been fortunate in the relative lack of human disturbance though enough has taken place for over 40 plant species to be introduced (Renvoise 1971*a*; Fosberg & Renvoise 1980), probably as many as to the neighbouring island of Assumption. However, only a few of these plant species have become established as components of any vegetation type other than 'gardens and disturbed ground' (*Stachytarpheta jamaicensis*, *Cocos nucifera*, *Passiflora suberosa*, *Agave sisalana* and *Casuarina equisetifolia*), in stark contrast to Assumption (Stoddart *et al.* 1970; Renvoise 1975). *S. jamaicensis* was often associated with disturbance by human paths and tortoise nesting sites (own unpublished data). Introduced plant species on Aldabra may have succeeded only where they could establish themselves in long-standing plant associations, whereas on Assumption guano mining destroyed the original plant associations and recolonization by indigenous and introduced plant species started from virtually bare ground.

Conclusions

(i) The vegetation of Aldabra is immensely varied, ranging from open areas of coral rock with sparse vegetation to structured forest over 10 m high.

(ii) The vegetation is unusually species-rich for an isolated atoll.

(iii) Changes within the vegetation are correlated with a wide range of scales of topographical change, with relative shelter from the southeast trade winds and with variations in tortoise grazing pressure.

(iv) Environmental heterogeneity and tortoise grazing produce mosaic patterns in the vegetation whose scales range from decimetres to kilometres.

(v) Aldabra's vegetation structure may once have typified that developed on raised reef deposits throughout the world. Human disturbance and the lack of quantitative studies in appropriate places limit present-day comparisons: Aldabra's vegetation may be the last surviving example of its kind. No other locality is likely to support vegetation that has developed in interaction with a large reptilian grazer.

This work was done at the request of the Royal Society while one of us (C.W.D.G.) was working under contract to that body at the Aldabra Research Station.

We are indebted to Julie Hamilton for her untiring help with field recording and to many of the Aldabra Seychellois who made the work possible, notably Harry Charles, Bernard Legae and Eluc Constance. C.W.D.G. was able to become familiar with the Aldabra flora quickly owing to the many people who have contributed to the Aldabra herbarium, and in particular to G. E. Wickens, who generously made his unpublished key to the flora freely available to those working on Aldabra. Michael Young, Department of Geography, University of Cambridge kindly provided a base map of Aldabra for figure 1 of this paper.

Appendix. List of plant species mentioned in the text

This is not a complete species list for Aldabra. Nomenclature follows Fosberg & Renvoise (1980).

Polypodiaceae	*Acrostichum aureum* L.
	Nephrolepis biserrata (Sw.) Schott
Capparidaceae	*Capparis cartaliginea* Decne
	Maerua triphylla A. Rich
Flacourtiaceae	*Flacourtia ramontchii* L'Hér, var. *renvoisei* Fosberg
	Ludia mauritiana Gmel.
Guttiferae	*Calophyllum inophyllum* L. var. *takamaka* Fosberg
Malvaceae	*Abutilon angulatum* (Guill. & Perr.) Masters
	Thespesia populnea (L.) Sol.
	T. populneoides (Roxb.) Kostel
Erythroxylaceae	*Erythroxylum acranthum* Hemsley
Surianaceae	*Suriana maritima* L.
Ochnaceae	*Ochna ciliata* Lam.
Meliaceae	*Malleastrum leroyi* Fosberg
Icacinaceae	*Apodytes dimidiata* F. Mey.
Celastraceae	*Maytenus senegalensis* (Lam.) Exell.
	Mystroxylon aethiopicum (Thunb.) Loes.
Rhamnaceae	*Colubrina asiatica* (L.) Brogn.
	Gouania scandens (Gaertn.) R. B. Drummond
	Scutia myrtina (Burm.f.) Kurz.
Sapindaceae	*Allophylus aldabricus* Radlk.
	Macphersonia hildebrandtii G. Hoffm.
Anacardiaceae	*Operculicarya* (*Poupartia*) *gummifera* (Sprague) Capuron
Leguminosae	*Caesalpinia bonduc* (L.) Roxb.
	Calliandra alternans Vahl. ex Benth.
	Dichrostachys microcephala Renvoise
	Abrus precatorius L.
	Sophora tomentosa L.
Brexiaceae	*Brexia madagascarensis* (Lam.) Ker-Gawl.
Rhizophoraceae	*Cassipourea thomassetí* (Hemsley) Alston
Combretaceae	*Lumnitzera racemosa* Willd. var. *racemosa* F.T.E.A.
	Terminalia boivinii Tul.
	T. catappa L.
Myrtaceae	*Eugenia elliptica* Lam. var. *levinervis* Fosberg
Lythraceae	*Pemphis acidula* Forst.
Passifloraceae	*Passiflora suberosa* L.
Molluginaceae	*Mollugo oppositifolia* L.
Rubiaceae	*Canthium bibracteum* (Baker) Hiern.
	Guettarda speciosa L.
	Polysphaeria multiflora Hiern.
	Psychotria pervillei Baker
	Tarenna supra-axillaris (Hemsley) Bremekamp
	T. trichantha (Baker) Bremekamp
	T. vedcourtiana Fosberg
	Triainolepis africana Hook subsp. *hildebrandtii* Verde.
	Tricalysia sonderana Hiern.
Compositae	*Melanthera biflora* (L.) Wild.
	Vernonia grandis (DC) J. Humb.
Goodeniaceae	*Scaevola taccada* (Gaertn.) Roxb.
Sapotaceae	*Sideroxylon inerme* L. subsp. *cryptophlebia* Hemsley
Oleaceae	*Jasminium elegans* Knobl.
Salvadoraceae	*Azima tetracantha* Lam.
	Salvadora angustifolia Turrill
Apocynaceae	*Carissa edulis* Vahl.
	Pandaca (*Tabernaemontana*) *mauritiana* (Poir.) Markgraf & Boiteau
Asclepiadaceae	*Pleurostelma cernuum* (Decne.) Bullock
	Sarcostemma viminale (L.) R.Br.
	Secamone fryeri Hemsley

Boraginaceae	*Cordia subcordata* Lam.
	Ehretia cymosa Thonn.
	Tournefortia argentea L.f.
Convulvulaceae	*Ipomoea macrantha* Roem & Schultes
	I. pes-caprae (L.) R.Br. subsp. *brasiliensis* van Ooststr.
Solanaceae	*Solanum indicum* L. var. *aldabrense* (C. H. Wright) Fosberg
Scrophulariaceae	*Bacopa monnieri* (L.) Fennell
	Bryodes micrantha Benth.
Acanthaceae	*Hypoestes aldabrensis* Baker
Verbenaceae	*Avicennia marina* (Forssk) Vierh.
	Clerodendrum glabrum E. Meyer var. *minutiflorum* Fosberg
	Lantana camara L.
	Premna obtusifolia R.Br.
	Stachytarpheta jamaicensis (L.) Vahl.
Nyctaginaceae	*Pisonia aculeata* L.
	P. grandis R.Br.
Amaranthaceae	*Achyranthes aspera* L.
	Deeringia polysperma (Roxb.) Moq.
	Lagrezia oligomeroides (C. H. Wright) Fosberg
Lauraceae	*Cassytha filiformis* L.
Euphorbiaceae	*Acalypha claoxyloides* Hutch.
	Euphorbia pyrifolia Lam.
	Margaritaria anomala (Baill) Fosberg (= *Phyllanthus cheloniphorbe* of other Aldabra authors)
	Phyllanthus casticum Willem f.
	Ricinus communis L.
Moraceae	*Ficus avi-avi* Bl.
	F. nautarum Baker
	F. reflexa Thunb.
	Maillardia pendula Fosberg
Casuarinaceae	*Casuarina equisetifolia* L.
Dioscoraeaceae	*Dioscorea bemarivensis* Jum. & Perr.
Liliaceae	*Agave sisalana* (Perrins ex Engelm.) Drummond & Prain
	Asparagus umbellulatus Bresler
	Dracaena reflexa Lam.
	Lomatophyllum aldabrense Marais
Palmae	*Cocos nucifera* L.
Pandanaceae	*Pandanus aldabrensis* St John
	P. tectorius Park
Cyperaceae	*Cyperus bigibbosus* Fosberg
	C. conglomeratus Rottb.
	C. ligularis L.
	C. niveus Retz. var. *leucocephalus* (Kunth) Fosberg
	Fimbristylis cymosa R.Br.
	F. ferruginea (L.) Vahl.
Gramineae	*Daknophobis boivinii* (A. Camus) W. D. Clayton
	Sclerodactylon macrostachyum (Benth.). A. Camus
	Sporobolus virginicus (L.) Kunth.

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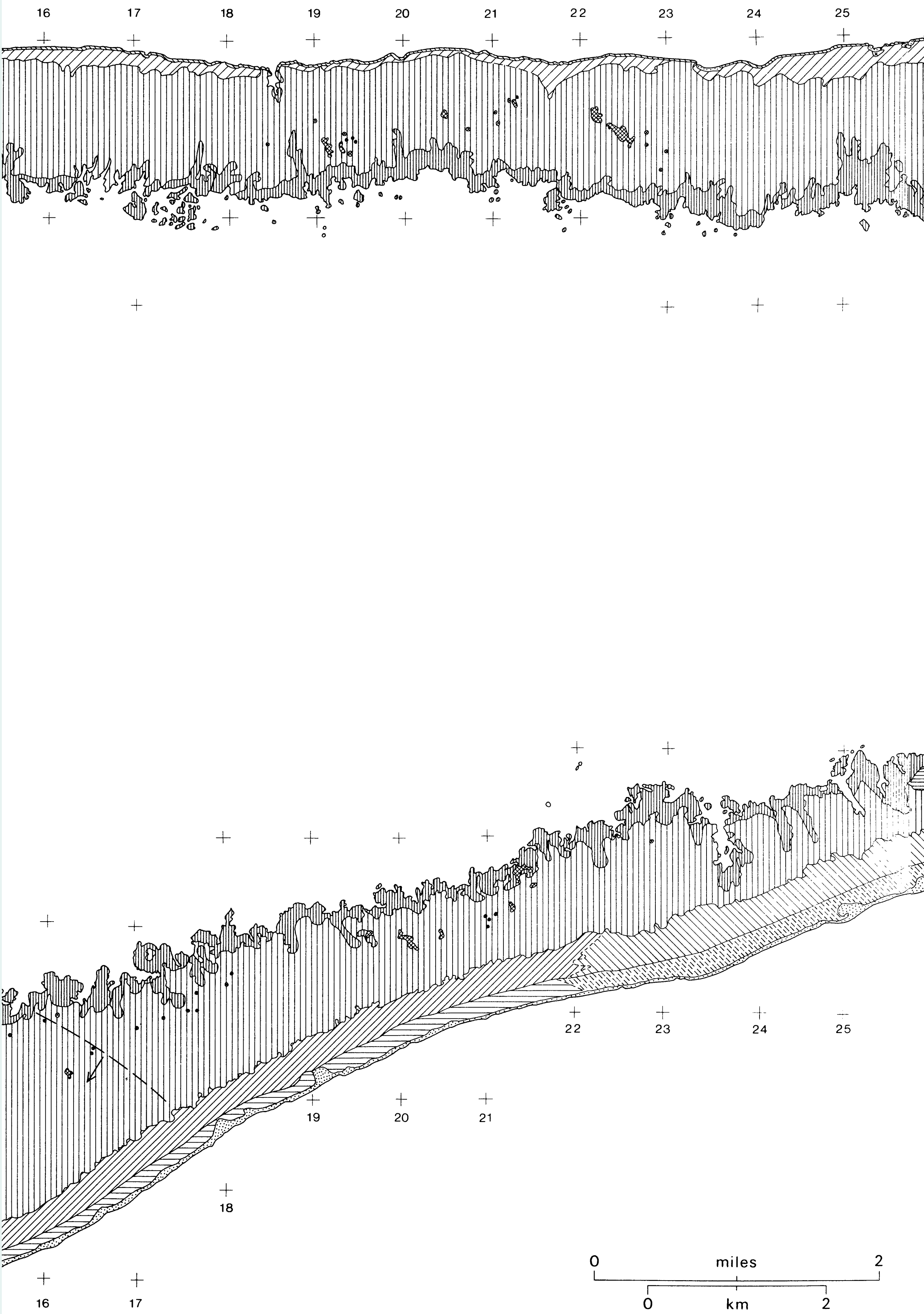
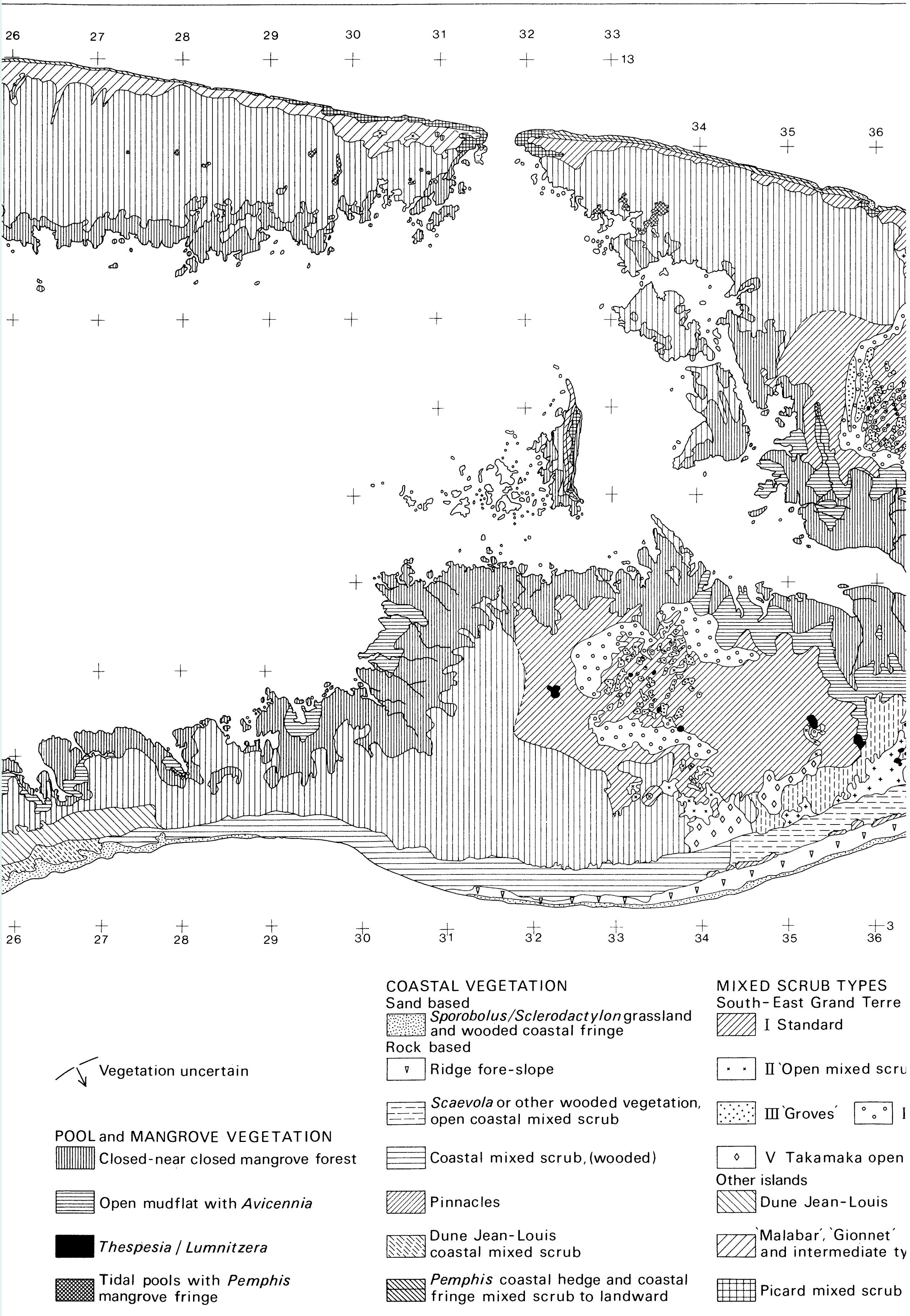
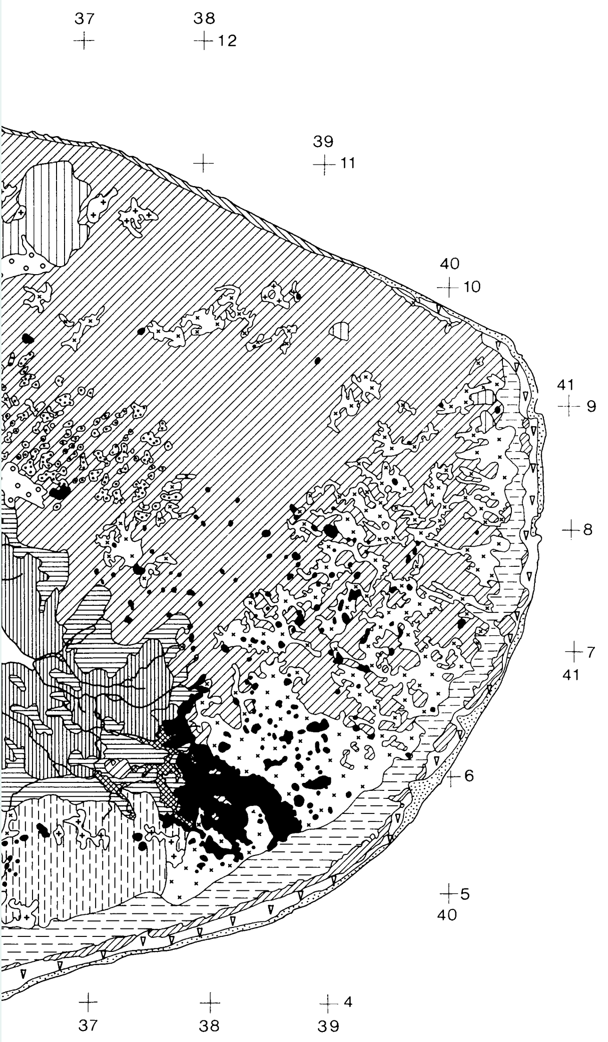


The vegetation of Aldabra atoll.



26 27 28 29 30 31 32 33 34 35 36
13
3
COASTAL VEGETATION
Sand based
Sporobolus/Sclerodactylon grassland and wooded coastal fringe
Rock based
Ridge fore-slope
Scaevola or other wooded vegetation, open coastal mixed scrub
Coastal mixed scrub, (wooded)
Pinnacles
Dune Jean-Louis coastal mixed scrub
Pemphis coastal hedge and coastal fringe mixed scrub to landward
MIXED SCRUB TYPES
South-East Grand Terre
I Standard
II 'Open mixed scru
III 'Groves'
V Takamaka open
Other islands
Dune Jean-Louis
'Malabar', 'Gionnet' and intermediate ty
Picard mixed scrub
Vegetation uncertain
POOL and MANGROVE VEGETATION
Closed-near closed mangrove forest
Open mudflat with Avicennia
Thespesia / Lumnitzera
Tidal pools with Pemphis mangrove fringe



ub'

IV *Cyperus* Park-woodland

'PEMPHIS SCRUB'

Grade from local mixed type to *Pemphis*, open and closed

Fern-pocket *Pemphis*/mixed scrub

Open

ypes

Closed

MISCELLANEOUS

Casuarina, *Cocos*, gardens

The vegetation of Aldabra atoll.