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A perspective of the vegetation of Aldabra

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1. Introduction

Several accounts are now available about the vegetation, or portions of it, of Aldabra (Fryer 1910–12; Vesey-Fitzgerald 1942; Stoddart & Wright 1967; Stoddart 1968; Fosberg 1971; Grubb 1971 and Hnatiuk & Merton 1979). Most of these reports derive from short periods of observation, which, while adequate for general description, are generally insufficient to permit much synthesis. The work of Grubb (1971) is an exceptional case in so far as it shows fine perception of the factors affecting vegetation within his particular study area. The presence of the Royal Society Aldabra Research Station has been fundamentally important in permitting many researchers the opportunity to study Aldabra both in detail and for extended periods of time. The result has been that a more complete understanding of the vegetation is now possible. It is our objective to present some of this synthesis, even if in doing so we largely highlight the voids in our knowledge.

2. Mosaics in the vegetation patterns

One of the most striking features of the vegetation of Aldabra is the complex spatial patterning it shows. A large part of this mosaic pattern appears to be due to the fragmentated nature of the habitats for plants provided by the underlying limestone substrate. The origin of the pattern must lie in the combined effects of the pattern of growth shown by the original organisms producing the limestone and the subsequent erosional and depositional patterns superimposed on these structural ones after the coral and algae had died. The parallel rows and fields of more or less circular patterns of various sizes that can be similarly seen in living parts of the reefs on Aldabra and on other atolls as on dry land on Aldabra, lend support to the idea that the present day vegetation patterns are controlled by the patterns found on the original reefs.

In our classification of Aldabra's vegetation (Hnatiuk & Merton 1979), the patterns of the vegetation that are related to spatial distribution and fragmentation of the vegetation have not been used as criteria as they were in the classification of Fosberg (1971). We believe that a clearer understanding of the vegetation is to be had by excluding the spatial pattern from the classification and only bringing it in in the descriptive notes. Our units may be subdivided by using criteria of spatial pattern if, for example, plant density or spacing were of importance to habitat studies.

Another aspect of the mosaic nature of the vegetation is that caused by changes that occur to only selected elements of the vegetation. For example, if *Cyperus niveus* can develop as a continuous mat only under a scrub canopy and then the scrub dies and decays, leaving the

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Cyperus, which having become established, persists, then the usual association of this sedge as an understorey to scrub is seen to have an apparent exception at such a site if little trace of the original scrub remains. Many other examples of this sort could also be given.

The distribution patterns of individual species across the atoll add yet another dimension to the vegetation mosaic. Some of the species patterns appear to be substrate controlled (e.g. *Pemphis*, and many of the Tortoise Turf species) while others, especially in relation to their frequency of occurrence, appear to be related to colonization patterns (e.g. *Passiflora*, *Scaevola*, *Polysphaeria*, *Coptosperma nigrescens*, *Sophora tomentosa*). Vigorous, opportunistic species that invade certain disturbed habitats (e.g. *Cyperus ligularis*, *Sporobolus virginicus*) add yet more complexity to the mosaic of species and vegetation.

3. Stratification of the vegetation

The classification of Aldabra's vegetation presented by Hnatiuk & Merton (1979) is based upon criteria of the overstorey only. In general, understorey vegetation is not very well developed on Aldabra with a few important exceptions: herbs beneath *Cocos* and *Casuarina* (partly maintained by plantation management); shrubs beneath *Cocos* and *Casuarina* (a slow invasion of coconut groves by Mixed Scrub and an invasion of Mixed Scrub by *Casuarina* are the important immediate causes); the 'Mixed Scrub' understorey in Takamaka Grove where it appears that sufficiency of water has permitted some scrub species to overtop others that is not generally seen elsewhere on the atoll (e.g. *Dracaena* and *Polysphaeria* in the understorey); and extensive *Cyperus niveus* and *C. dubius* mats beneath some areas of Mixed Scrub.

4. Dynamic interrelations in the vegetation

That vegetation is a dynamic element in the landscape is hardly questioned by anyone, but the inclusion in a classification of variability due to the passage of time is difficult and little agreement is to be found on criteria or methods for doing so. Nevertheless, its existence cannot be ignored if the units of the classification are to be understood and evaluated. While the present paper does not allow a detailed presentation of the information now accummulating, a few of the findings will be summarized here because they help to build a synthetic view of part of the Aldabran ecosystem.

The source regions for the Aldabran flora have been determined by Renvoize (1971, 1975) as primarily the surrounding land areas flanking or lying within the Indian Ocean. The unpublished work of one of us (R.J.H.) indicates that viable propagules of a large number of species (about 50) not found on Aldabra are washed onto its beaches in a period of 20 months and others are accidentally or deliberately introduced by man. Many germinate, but only a few produce viable seed and spread. Thus there is a potential for continual accretion of new species to the flora. Most of these potential additions to the flora, even excluding those brought in by man, appear to arrive on the west coast of the atoll. Studies of local distribution maps for each species in the Aldabran flora (S. H. Hnatiuk & R. J. Hnatiuk, unpublished) show that within the atoll there is a geographic variation unrelated to vegetation type, represented by areas adjacent to passes (and also facing the north and west) being rather different from the rest of the atoll, perhaps reflecting the preferential sites of introduction of many species. Dispersal within Aldabra appears to be readily accomplished for many species with the aid of seed-eating animals such as birds and tortoises (S. Hnatiuk, personal communication). The animals themselves appear to be helping to shape the vegetation as for example the apparent destruction of shrubs and spread of grassland in the south and east of the atoll caused by the activities of the large tortoise population (Hnatiuk *et al.* 1976, Merton *et al.* 1976). And finally, the variation in climate from year to year (Stoddart & Mole 1977) with periods of exceptionally dry years broken by relatively wet ones, must severely affect the kinds of plants that can establish on Aldabra.

The interaction between all these factors means that the vegetation of the atoll is in a constant state of flux, as new disturbances destroy part of the existing vegetation. The vegetation that follows disturbances such as a cyclone, drought, or excessive grazing and browsing, may bear little relation to what existed before because new species may be present that were not there when the previous vegetation became established. Thus a new balance between species will be struck that will not necessarily be the same across the whole atoll. Chance factors like the distribution of viable seed and the state of the climate during and following a disturbance, may play a very large rôle in determining the pattern of species and vegetation. The hypothesis of catastrophic events being the main driving force in shaping vegetation may apply to Aldabra with the added nuance that the 'raw materials' for rebuilding following each catastrophe may be continually changing.

The relevance of these ideas on change to Aldabra's vegetation is that we shall be unlikely ever to produce a satisfactorily complete classification of Aldabra's vegetation that is entirely understandable in terms of the then existing physical environment, and that is neither a classification of habitats nor of floristic distribution patterns. Thus the rapid spreading of such species as *Casuarina* and *Passiflora* that can drastically alter the structure of the vegetation soon make obsolete a necessarily static image of vegetation in a classification based solely upon the plants as seen at one time. This does not negate the value of the classification, because if it is found 'good' it will greatly help in understanding the functioning of the Aldabran ecosystem as it currently exists, and may even help to predict some of the changes that will occur if certain habitat factors are changed (e.g. if grazing pressure increases or decreases).

5. Life forms in the Aldabran flora

Fosberg's classification of Aldabra's vegetation finds particular use in indicating some of the potential vegetation types that could develop on Aldabra and thus the vegetation of the atoll can readily be compared to that of other atolls. Another system of classification which can be usefully applied to show the relationship of Aldabra to other areas of the world is the life-form system of Raunkiaer (1934). Table 1 shows the life-form spectrum for Aldabra in comparison with Raunkiaer's 'Normal Spectrum' for the whole world, and also for some other atolls, and tropical islands.

Aldabra's spectrum differs from the Normal Spectrum by a relatively high proportion of chamaephytes, low proportions of hemicryptophytes, and cryptophytes, and about the same amount of phanerophytes as in the Normal Spectrum. In Raunkiaer's terms then, the 'plant climate' of Aldabra is a chamaephyte climate. His findings indicate the chamaephyte climate to occur in cold, polar regions. However, in none of his data for the chamaephyte type is there an example that also has relatively high values for phanerophytes.

In order to assess the significance of the Aldabran spectrum, a survey was made of some other atolls for which species lists were available and for which life forms could be determined. The results are listed in table 1 together with spectra from the Seychelles and coastal Jamaica. From these data it can be seen that the coral atoll spectra differ from those of the large tropical islands in that chamaephytes predominate in the former and not the latter. Among the atolls, the one with the most similar spectrum to that from Aldabra is Diego Garcia, also a 'raised' atoll. The sand cay atolls of the Hawaiian Islands have high proportions of chamaephytes but somewhat lower levels of phanerophytes although this latter life form is still the second most common one on the sandy cays.

Table 1. Life-form analysis for the flora of Aldabra

leaf size ...	lepto	nano	micro	meso	macro	mega	sum	% of total	Normal Spectrum[1]
life-form									
phanero-	3	8	38	36	6	0	91	48	46
chamae-	8	18	11	6	1	0	44	23	9
hemicrypto-	0	4	3	6	0	0	13	7	26
liane	0	2	5	6	0	0	13	7	—
thero-	3	7	11	4	0	0	25	13	13
parasite	0	1	0	1	0	0	2	1	—
crypto-	0	0	1	0	0	0	1	0.5	6
sum	14	40	69	59	7	0	**189**		
% of total	7	21	37	31	4	0			

	Diego Garcia[2]	Laysan[3]	Lisianski[4]	South East[5]	North[5]	Grass[5]	Seal[5]	Little N.[5]	'combined'[5]	Seychelles[6]	coastal Jamaica[7]
life-form											
phanero-	41	32	33	25	18	20	20	25	22	61	75
chamae-	43†	54	61†	60†	82†	70†	80†	75†	71†	6	10
hemicrypto-	—	3	—	—	—	—	—	—	—	12	2
liane	—	—	—	—	—	—	—	—	—	—	7
thero-	9	11	6	10	0	10	0	0	5	16	5
parasite	—	—	—	—	—	—	—	—	—	—	—
crypto-	5	—	—	—	—	—	—	—	—	5	0
sum	121	37	18	20	11	10	10	4	55	—	—

References: (1) Raunkiaer (1934), p. 428; (2) Fosberg & Bullock (1971), spp. list, data are percentage of total; (3) Ely & Clapp (1973), spp. list, data are percentage of total; (4) Clapp & Wirtz (1975), spp. list, data are percentage of total; (5) Amerson, Clapp & Wirtz (1974), data are percentage of total; (6) Raunkiaer (1934), p. 428, data are percentage of total; (7) Asprey & Loveless (1958), data are percentage of total.

† Chamaephytes and hemicryptophytes combined because of difficulty in distinguishing them from available information.

Raunkiaer attributes a predominance of chamaephytes to a plant response to unfavourable conditions, particularly water supply and temperature. The tropical atolls may generally have an unfavourable water supply owing to either low rainfall or porous soil and thus the chamaephyte form may be selected for. The absence or low level of geophytes contrasts the atoll's spectra with those often found in continental semi-arid areas. The relatively high phanerophyte proportions, especially on the raised atolls, may indicate the relation of the atolls to the tropical region where phanerophytes are supposed to be predominant if moisture permits.

The evergreen and deciduous nature of the vegetation is an important element in its characterization, especially on a world-wide scale. However, in the semi-arid tropics the characteristic feature in this respect is variability, in response to the irregular oscillations of wet and dry years.

Asprey & Loveless (1958) attempted an analysis of coastal vegetation in Jamaica on the basis of the plant response under 'average' conditions. Not enough is known of Aldabra's climate to state what conditions are average. However, after 21 months' continuous observation including two dry seasons it has been possible to tentatively classify the flora in terms of 'evergreen', 'deciduous', and 'intermediate' (table 2). From this analysis it is seen that over half of the flora is evergreen, while less than a third is deciduous and only a small proportion falls in the intermediate category. Evergreenness and deciduousness are distributed between leaf-size categories more or less in proportion to that in the whole flora, for example, there are nearly half of the species in each leaf size class that are evergreen and under a third are deciduous. Among the life-form classes, however, the proportions are different from those in the whole flora, e.g. 67 % of phanerophytes are evergreen and only 22 % are deciduous.

Table 2. An estimate of evergreenness and deciduousness in the Aldabran flora

(Numbers represent percentages of total flora.)

leaf size ...	lepto	nano	micro	meso	macro	sum
evergreen	4	11	22	20	2	50
deciduous	2	6	12	8	0.5	28.5
indeterminate	2	5	3	3	1	14

life-forms ...	phanerophyte	chamaephyte	hemicryptophyte	liane	therophyte	parasite	cryptophyte
evergreen	32	14	6	3	0	1	0
deciduous	11	2	0	3	12	0	0.5
indeterminate	5	7	0.5	1	0	0	0

Only 18.5 % of the flora has divided leaves and of these 63 % are phanerophytes, 17 % lianes, 11 % chamaephytes, 6 % therophytes, and 3 % hemicryptophytes. Of the 35 species with divided leaves, 57 % have microphyllous leaflets, 26 % nanophyllous, 23 % mesophyllous, 11 % leptophyllous, and only 3 % megaphyllous leaflets.

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