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VEGETATION OF ALDABRA, A REASSESSMENT

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INTRODUCTION

Aldabra's vegetation has been described and communities or types of vegetation distinguished for a part or all of the atoll on several occasions (Fryer, 1911-12; Vesey-Fitzgerald, 1942; Stoddart & Wright, 1967; Stoddart 1968b; Fosberg, 1971; and Grubb, 1971). The classifications of Vesey-Fitzgerald and Stoddart & Wright are essentially modifications of that of Fryer (1911-12, p 414) who recognized four major units: Mangrove Swamp, *Pemphis* Bush, Varied or Open Bush, and Shore Zone (table 1). Vesey-Fitzgerald (1942, p 7) added a "Spray Zone Community" and a "Herb Mat Community" while Stoddart and Wright (1967, p 26) included "Man induced vegetation". Stoddart (1968b, Fig. 1) included "*Casuarina*" as a separate unit. He also made important distinctions within the shrub dominated communities by using what appears as a combination of floristic and geomorphologic criteria. However, in his descriptions of the "Platin with open woodland" he did not specifically note the occurrence of tortoise turf although reference to *Dactyloctenium pilosum* and *Eragrostis* sp. clearly indicates he was aware of its presence.

Grubb (1971, p 351) produced a detailed map of the east end of Grande Terre showing 10 "vegetation types" as distinguished on aerial photos with some ground control, but since he includes units called "champignon" and "mud flats", he is concerned with "habitats" and not only "vegetation". However, he has come closer to understanding the complexity of the scrub types than many of the other workers have. Fosberg's (1971) classification is by far the most detailed to date, recognizing 63 vegetation types almost exclusively on the basis of vegetation and floristic criteria. Only in the distinction of "swamp" does he overtly use habitat data in his definition of a type (Fosberg

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Table 1. A comparison of classifications of the vegetation of Aldabra.

FRYER (1911)	VESEY-FITZGERALD (1942)	STODDART & WRIGHT (1967)	GRUBB (1971)	FOSBERG (1971)	HNATIUK & MERTON (this paper)
Mangrove Swamp	M. Communities	M. Communities	<i>Avicennia</i> Swamp	15,16,17,18,19,35,36,38,47,48	(4) M. Vegetation
<i>Pemphis</i> Bush	P. Thicket	P. Thicket	P. Scrub	21,46	(3) P. Scrub
Varied & Open Bush	Mixed Scrub	Mixed Scrub	Mixed Scrub Scrub Forest Coastal Woodland	2,3,4,5,7,8,9,11,12,13,23,25,30,32,34,39,42,43,45,50	(6) Mixed Scrub (1) <i>Casuarina</i> Groves
			Pool Vegetation	6,20,31,37,52,53,58	(<i>Lumnitzera-Thespesia populneoides</i> Scrub (10) <i>Bacopa-Mollugo</i> Meadows.
			Grass Sedge Swards	33,44,45,50,51,54,56,57	(9) Tortoise Turf
Shore Zone	Psammophilous Associations Spray Zone Communities Dune Scrub	Psammophilous Associations	<i>Sporobolus</i> Swards (Coastal Woodland)	10,14,22,29,43a,57,59,60,61,62	(7) <i>Sclerodactylon</i> Tussock Grassland (8) <i>Sporobolus virginicus</i> Coastal Turf (11) Pioneer Vegetation of Beaches
		Man-induced Vegetation		24,28,40	(1) <i>Casuarina</i> Groves (2) Coconut Groves (13) Gardens
	Herb Mat Community				(12) Herbaceous Meadows of Lagoon Islets
				27,41,63	(15) algal
				49	(14) <i>Acrostichum</i> Stands
				26,55 (Submerged marine meadows)	

1967, p 120).

Four vegetation maps, or maps which at least portray vegetation units, for the whole of the atoll are known to exist (Baker, 1963, Stoddart 1968a, b, and Directorate of Overseas Surveys D.O.S. 6001 Vegetation Overlay, 1969). All maps appear to be drawn from an interpretation of aerial photographs taken in 1960. Baker's map was primarily intended as a geological map with some vegetation notes appended and thus criticism of his vegetation notes need to be tempered with this in mind. Both the D.O.S. map and Baker's suffer from what appears to be lack or insufficient use of ground control. Because of certain errors in photo-interpretation found on these maps caution is advised in attempting to use them. Stoddart's 1968b map clearly shows the distribution of the major landforms and some vegetation units for Aldabra. The only major unit missing on the scale of his map is dense shrub on medium champignon.

Fosberg has applied the classification scheme which he devised for the International Biological Program (Fosberg, 1967). It is a general purpose scheme that is able to be applied in many places of the world. It uses a hierarchical structure so that, for instance, his 63 ultimate units on Aldabra may be grouped into 24 units at the next highest and six units at the top of the classification.

With so much work already done on the vegetation of the 155 square kilometres of dry land on Aldabra, why is yet another study necessary? The reason is, that despite the past work, there is still only a rudimentary understanding of the atoll's vegetation. The earliest works gave the basic outline of much of the vegetation but did not specifically consider several important units such as the "tortoise turf" (Grubb 1971, p 359) or "mixed orthophyll 'tortoise pastures'" (Fosberg 1971, p 223). Grubb's work was not intended to be comprehensive for the atoll, and certain specific problems, treated below, have limited the use of Fosberg's classification. It is the objective of the current work to present both a comprehensive classification and a synthesis of Aldabra's vegetation such as has not been possible before.

Before discussing our classification it is instructive to make a closer examination of Fosberg's detailed classification (1971). His primary subdivision criterion of "spacing" of plants, and his ultimate criterion of "floristic" composition have made it difficult to use on Aldabra. Of lesser importance but still contributing to the overall difficulty of use are the criteria of leaf size, and evergreenness. These latter two criteria have been found to be dependant upon the amount of water available during a particular year or growing season. Thus the plants on one piece of ground may appear "evergreen" and "mesophyllous" one year but the same plants deciduous and "microphyllous" another year, because of the unpredictable and very variable climatic regime found on Aldabra (see Stoddart & Mole, 1977). Such a characteristic is undesirable in a vegetation classification and the solution (of Asprey & Loveless 1958) to a similar problem encountered in Jamaica, that of using the phenological state prevailing under "average"

Table 2. A vegetation classification for Aldabra based upon canopy plants

WOODY	HERBACEOUS	ALGAL
Single-Species Dominant	Monocot Herbs	15. "Cyanophycean film and boring algae vegetation" (little studied but see Fosberg 1971, p 224; also A. Donaldson, Botany Dept. Durham has worked on these communities (unpublished).
(1) Coconut Groves	Single-Species Dominants	
(2) <i>Casuarina</i> Groves	(7) <i>Sclerodactylon</i> Tussock Grassland	
(3) <i>Pemphis</i> Scrub	(8) <i>Sporobolus virginicus</i> Coastal Turf	
Species-Groups Dominant	Species-Groups Dominant	
(4) Mangrove Vegetation	(9) Tortoise Turf	
(5) <i>Lumnitzera-Thespesia populneoides</i> Scrub		
(6) Mixed Scrub	Dicot Herbs (Species Group)	
variants:	(10) <i>Bacopa-Mollugo</i> Meadows	
a. Dune Scrub	(11) Pioneer Vegetation of Beaches	
b. Beach Scrub	(12) Herbaceous Meadows on Lagoon Islets	
c. <i>Sideroxylon</i> Scrub	Mixed woody & herbaceous Community (man induced)	
	(13) Gardens	
	Other	
	(14) " <i>Acrostichum</i> stands" (of limited extent, see Fosberg 1971, p 222).	

conditions is not feasible because the "average" condition on Aldabra is not known (Hnatiuk & Merton, 1979).

The use of spacing of plants as the primary basis of division in classification (Fosberg, 1967, p 69) may appear at first sight to be a straightforward description of a feature of the plants, independent of the surrounding physical environment. "Closed" vegetation poses little problem but the "open" and "sparse" spacing groups used by Fosberg (1967, 1971) include space which on Aldabra is not part of the individual plants making up the vegetation. The unoccupied space between plants is part of the physical environment that Fosberg wishes to exclude from the classification criteria. Such a distinction may appear as "hair splitting" but two fundamentally different situations are being grouped under Fosberg's application of his "spacing" criteria. To take the extreme case of sparse vegetation in which there is more than twice the individual plant diameter between plants (Fosberg 1967, p 79), on the one hand plant cover may be sparse but the actual place where each plant grows in the sparsely vegetated area is usually assumed to be independent of the substrate (i.e. the plants could grow at any site within the area). On the other hand plant cover may be sparse because the sites where the plants can potentially grow are themselves sparsely distributed in a matrix of uninhabitable space. If plant cover is "closed" in the habitable areas then the vegetation should be seen as closed even though the "habitat" is open. The situation is somewhat analogous to plants growing in soil in pots on a bench. The spacing of plants is then easily seen as a two-level characteristic dependent upon firstly how close together plants can grow in a pot and secondly upon how closely spaced are the pots. We believe that it is the first of these levels of spacing which should be considered on Aldabra where this two-level distinction is to be found, for example at the east end of Grande Terre and along much of the south coast of Grande Terre inland of the "8-metre ridge".

Floristic data have often been effectively used to define vegetation units because the presence or abundance of particular species or species groups are known to be good indicators of environmental conditions. Studies of species distribution patterns on Aldabra (S. & R. Hnatiuk, unpublished) have suggested that colonization patterns may be a prominent feature of the atoll's plants, and these patterns are made complex through the interaction of developing interspecific and species-environment interactions leading to establishment of species niches. Fosberg (1971) has been generally cautious in his use of floristics as criteria for classification, but even so he has used such units as *Acalypha* scrub, *Guettarda* scrub, and *Scaevola* scrub that subsequent observations have found to be too heterogeneous to be called single types. Fosberg's classification may thus indicate the potential vegetation that could develop on Aldabra, but it does not adequately portray the present vegetation.

Our classification has been based upon features of the canopy plants only, understorey plants are not considered in the classification but are noted in the descriptions. Plant nomenclature follows that of Fosberg and Renvoize (1979).

(1) COCONUT GROVES

Location: planted at many sandy places but particularly on the west coast of the atoll, on Ile Esprit and Ile Michel. Small groves can be found on other beaches.

Vegetation: the coconut palm, *Cocos nucifera* is the dominant plant. It is evergreen and often reaches over 20 m, but also much less in poor sites. *Casuarina* is frequently found with and usually somewhat taller than the palms. The cover of the coconut palm canopy varies from greater than 75% in densely reproducing groves to less than 25% where planting was sparse. The largest plantation with over 1000 trees is found at Settlement while small plantings of less than a dozen trees can be found at Grande Cavalier. The distribution patterns of mature plants often reflects the ordered rows of the original planting. The understorey is variable depending somewhat upon the degree and recentness of maintenance of the groves. Thus the better maintained groves tend to have a grass understorey about 5-20 cm high. The grass species are usually either *Eragrostis sub-aequiglumis*, *Paspalum distichum*, or *Sporobolus virginicus*. The sedges *Cyperus ligularis*, *Cyperus niveus*, and *Fimbristylis cymosa* may also occur in locally dense patches. In some groves there may be much self seeding of coconuts resulting in very dense groves as on parts of Ile Michel. The Anse Mais grove is developing similarly (R.J.H. unpublished work). Species from the Mixed Scrub (6) are commonly found in the understorey of the neglected groves.

Soil: The calcareous mineral arenaceous soil of Trudgill (1979), also called the Farquhar Series (Piggott 1968), is the most common soil found, but sand of the Shioya Series (Piggott 1968) may be found in parts of the Ile Esprit Grove.

Phenology: Seasonal changes in the coconut trees are limited to a reduction in crown size and a slowed development of leaves, flowers and fruit during the dry season, at which time the understorey herbs also become brown and dry. Flowering of understorey plants is largely restricted to periods of sufficient rain.

Notes: The coconuts are not thought to be native to Aldabra and primarily occur in areas where they were introduced by man, although now they have become naturalized in some areas. Whereas formerly, maintenance of the groves kept the understorey clear of scrub and coconut regeneration, now that maintenance has essentially lapsed, except for sections of the Settlement grove, scrub species can be found invading some parts of groves, while in other places the development of coconut thickets with litter accumulations exceeding 1.5 m deep is occurring. There are no indications as yet that the groves will spread beyond the areas of deep sandy soil, though they may be extending into a few formerly scrub-dominated areas with sandy soil on the west coast of Grande Terre. It appears from simple transplant studies with *Carica papaya*, that competition for water may be an important limiting factor for the vegetation of these plantations.

(2) CASUARINA GROVES

Location: *Casuarina* Groves are found primarily on the north and west sea coasts of Aldabra, and on some lagoon-facing sandy beaches.

Vegetation: The canopy is evergreen and dominated by *Casuarina equisetifolia* that may reach more than 20 m above ground. The *Casuarina* may occur together with *Cocos* and the vegetation type may then be referred to as "*Casuarina* and *Cocos* Grove". The understory of *Casuarina* Groves is various and can be *Cocos*, Mixed Scrub (tall or low), grass, or barren.

Soil: Two soil types have been found under *Casuarina*: Farquhar Series (Piggot, 1968), and organic brown calcareous soils (Trudgill, 1979). Occasionally a shallow, rendzina-like soil consisting largely of organic matter with a small amount of sand over rock is all that is found. In most places, the soil under *Casuarina* has a thick (2-10 cm) layer of *Casuarina* 'needles'.

Phenology: There is still some doubt about how *Casuarina* reached Aldabra. Fryer (1911, p 416) and Fosberg (1971, p 215) believe *Casuarina* to be definitely introduced by man, but Ridley (1930, p 316-17) believes it to be widely distributed by the sea. Wickens (1979) gives further information. What ever may have been its method of introduction, it is now well established and apparently spreading (as are other species) as seen in the small, dense groves of young saplings and seedlings at the periphery of some groves (e.g. west end of Passe Houareau grove, and south of Anse Var). Young plants are to be seen growing up through Mixed Scrub on both sides of Passe Houareau. The effect of the overtopping of scrub by *Casuarina* is variable. In some instances it appears that the scrub may either die out (Fosberg 1971, p 216) or may continue to thrive apparently little affected by the *Casuarina* as for example just north of Settlement. In some areas *Acalypha claoxyloides* is found to form a dense understory shrub stratum to *Casuarina* (e.g. between Anse Owen and Anse Grande Poche, north west end of Ile Polymnie, part of the grove on the west side of Passe Houareau) as also does *Plumbago aphylla*. We would repeat Fosberg's statement that this is a "good problem for an ecological investigation" (1971, p 216).

Heavy infestations of *Casuarina* by the woolly coccid, *Icerya seychellarum*, are associated with reduction in photosynthetic canopy, reduced or halted growth, and, in small plants at least, death.

(3) PEMPHIS SCRUB

Location: *Pemphis* Scrub is one of the widespread and common vegetation types found on the atoll.

Vegetation: *Pemphis* Scrub as defined here includes those areas where *Pemphis acidula* grows in pure or virtually pure stands, and excludes those areas where *Pemphis* is merely one of many scrub species — such latter areas being classed Mixed Scrub (6). Most of the *Pemphis* in

the *Pemphis* Scrub occurs as multi-stemmed plants although large, single-stemmed, tree-like *Pemphis* also occur. Other plant species are rare in this type but the most common include *Vernonia grandis*, *Acalypha claoxyloides*, and *Scaevola taccada*. Certain Mixed Scrub species are often found growing in a mosaic with *Pemphis* Scrub, and it appears from observations that two vegetation types are involved (see notes below and discussion on 'Mosaics').

The height of *Pemphis* Scrub ranges from about 0.5 m to more than 6 m. Mature *Pemphis* growing in nearly pure stands less than 1 m high, is common along parts of the trade-wind-exposed, south coast of Grande Terre. There is some evidence (D. Lewis, pers. comm.) that such plants may be genotypically dwarfed and often prostrate. That they have only been found on the seaward edge of scrub may suffice to distinguish them as a sub-type, which is part of Fryer's "Shore Zone" (Table 1).

The canopy of tall *Pemphis* is very deep, often reaching 4 to 5 m. The "surface" of the canopy is very irregular with narrow, conical branches that are leafy to near their bases. Foliage density does not appear to be exceptionally high and direct sunlight penetrates to the ground; however, there is virtually no understory development.

Soil: The soil appears very poorly developed. It may consist of "shallow organic soil" (Trudgill, 1979) over solid rock (and is thus a very shallow rendzina-like soil) or no soil may be visible at all. Surface feeding roots may be abundant in the small pockets of organic accumulation but all that is generally visible is the tops of roots that pass down into crevices in the otherwise barren rock.

Phenology: *Pemphis* is evergreen, its stems form no resting buds, and it can grow throughout the year, producing leaves, flowers, and fruits. Growth may decline or cease in periods of severe drought, particularly in plants that do not appear to have direct contact with sea water. Leaf fall is stimulated by the onset of dry conditions and by heavy infestations of the woolly coccid, *Icerya seychellarum*.

Notes: As noted by Fosberg (1971, p 221) past estimates of the abundance of *Pemphis* have been exaggerated. This is particularly noticeable in the maps of Baker (1963) and the Directorate of Overseas Surveys (Vegetation overlay 6001, 1:25,000, 1969) where Mixed Scrub and *Pemphis* Scrub have been misinterpreted from the aerial photographs (see notes under Mixed Scrub (6)).

The correlation between the occurrence of *Pemphis* Scrub and very rough limestone (champignon) has been noted since the earliest reports, but caution is necessary in using this relationship. For example, Braithwaite *et al.*, (1973, p 337) found a high correlation between '*Pemphis* dominated scrub' on the D.O.S. vegetation map and the occurrence of 'dissected areas of the Takamaka limestone' and used this correlation in their extrapolation of geological boundaries from interpretation of vegetation as seen on aerial photographs. The geological map is probably a fair representation of the surface geology, but the designation "*Pemphis* dominated scrub" is very much in error in several

large areas. In our experience it would appear that *Pemphis* is the dominant plant on sites where the surface is sufficiently dissected to allow salt water to penetrate into the rooting zone, and also to prevent any substantial amount of soil from accumulating at the surface. Areas such as this can extend over several square kilometres (e.g. parts of south west Grande Terre) but most of the *Pemphis* Scrub occurs in a mosaic with a subdivision of the Mixed Scrub. *Pemphis* Scrub occupies the low ground, while Mixed Scrub occupies the knolls that rise 0.5 to 1.0 m above the low ground. These knolls may be only 5 to 10 m across so that if a larger unit of area is taken as the basis of study, the distinction between these types disappears. However, it appears useful in understanding the vegetation to recognize the elements as separate vegetation types because there does not seem to be a dynamic, vegetational relationship between the two types — each occurs in its own distinct habitat.

From circumstantial evidence, it seems that *Pemphis* may be able to utilize salt water as a water source: live roots are often seen extending into the tidally inundated portions of pot holes; the canopy is evergreen with somewhat succulent leaves; measurements show growth to be continuous throughout the dry months on sites apparently devoid of soil when other shrub species nearby have long lost their leaves.

The dynamic status of *Pemphis* Scrub is not clear. Seedling and sapling size individuals are very rarely reported for *Pemphis*. As noted above, a few large, tree-like individuals with diameters of about 0.3 m and extending above ground for 2 to 2.5 m before branching, can be found throughout the atoll, but most *Pemphis* occurs as a prolifically, low-branching shrub. Until more is known about this species, further interpretation of these observations would be premature. The autecology and population structure of *Pemphis* is another good problem for ecological research.

(4) MANGROVE VEGETATION

Location: around most of the lagoon coast including on many of the numerous islets in the lagoon, and occasionally at isolated, inland places.

Vegetation: The four most common species are *Avicennia marina*, *Bruguiera gymnorrhiza*, *Ceriops tagal*, and *Rhizophora mucronata*. Three less abundant species of mangrove are *Sonneratia alba*, *Xylocarpus granatum* and *X. moluccensis*. The trees range in height from 1 m to greater than 10 m, and canopy cover ranges from less than 25% to virtually 100%. A zonation of mangrove species relative to distance inland or nearness to tidal streams is not obvious on Aldabra as it is in continental areas (Macnae, 1971). Without knowing more about the reason why the mangrove species are distributed as they are on Aldabra, division of this vegetation on floristic bases seems premature. Macnae recognized two variants on the basis of the height of the trees: 'high forests' (greater than about 6 m) being found mostly on the north, west and east lagoon shores and only sporadically on the south, while

the second 'thickets and low forests' being 1 to 6 m high predominate on the south shore of the lagoon.

Soil: ranges from light grey, silty marl with only stunted mangrove (e.g. Dune Jean Louis landing) to deep, highly organic muds with tall mangrove forests (e.g. Cinq Cases Creek) (Macnae, 1971).

Phenology: The trees are evergreen and for *Bruguiera*, *Ceriops* and *Rhizophora*, flowers and fruits can be found at all times of year, but not necessarily on the same plant at all times. The cycle of events for an individual is not known. *Avicennia* appears to have a seasonal response and to be more synchronized for all populations than are the former three species. Generally it appears that *Avicennia* produces leaves during the wet season, and flowers and fruits during the dry season but more observations are needed.

Notes: The mangroves, especially the tall ones, have been cut for timber at many places and regeneration is abundant in some places and absent in others. Macnae (1971) comments on the relatively old trees on the north lagoon shore of Grande Terre where soils are poor and the trees, though stunted, have large root systems. The detailed dynamics of this vegetation are not known and would repay study.

(5) *LUMNITZERA-THESPESIA POPULNEOIDES* SCRUB

Location: appears restricted to the east end of the atoll, in and around summer-flooded basins.

Vegetation: The major canopy species are *Lumnitzera racemosa* and *Thespesia populneoides*. *Pandanus tectorius* occurs around some of the basins, forming large dense clumps. These three species commonly occur in pure stands but may be inter-mixed. Canopy cover ranges from 100% beneath closely growing shrubs to less than 25% where shrubs are few and branches not numerous. The canopy ranges in height from about 1.5 m to more than 5 m above ground.

The understorey is generally barren of plants but tussocks of the sedge *Fimbristylis ferruginea* are common beneath breaks in the shrub canopy and are largely, but not exclusively restricted to these sites. *Cyperus ligularis* is also occasionally found here.

Soil: The soil is classed as mineral sediments: SM in Trudgill's system (1979). The soil is light to dark grey, fine-textured, saline, and commonly contains mollusc shells. The surface may have a litter layer and organic matter appears well mixed into the upper layers. Water logging is common during the rainy season, whilst during the dry months, the water table may fall below soil surface allowing the surface soil to become quite dry and powdery. The extent of the drying is dependent upon the amount and distribution of rainfall in any particular year.

Phenology: *Lumnitzera* and *Pandanus* are essentially evergreen but the quantity and size of leaves present appears to be much greater during the wet season than during the dry. *Thespesia* may lose most if not all leaves during prolonged dry season drought. Flowers can be found at most times of year on *Lumnitzera* but they become very scarce during drought periods and very abundant with the return of the rainy season. Flowers on *Thespesia* and *Pandanus* are largely confined to the late wet season although occasional exceptions do occur. Ripe fruits are common in late wet and early dry season, and become more scarce as the dry season advances.

Notes: It appears that *Lumnitzera* occurs most abundantly and luxuriantly beside pools and in soils that are more saline than those favoured by *Thespesia*, while *Pandanus* is at its best in the least saline conditions. However, the species are often found intermixed at one and the same site. Although *Pandanus* often occurs near fresh water pools (cf. Stoddart & Wright 1967, p 27) it is found sufficiently often in equally large and luxuriant groves or as isolated individuals in locations far from such pools (e.g. Anse Var, coastal scrub east of Passe Gionnet, Passe Houareau camp, and Point Vacqua) that the general value of *Pandanus* as an indicator of fresh water pools or of a particular vegetation type is largely restricted to the east end of Grande Terre.

The dynamic status of this vegetation type is not known. However, it appears to have experienced change as evidenced by the apparently uniform size of most individuals around a pool although different pools appear to have different populations. About 1.3 km south west of Takamaka Grove, conspicuously "two-aged" stands of *Lumnitzera*, as judged by shrub height and stem diameter, are to be found but the reasons for this structure are not known.

(6) MIXED SCRUB

Location: widespread throughout the atoll.

Vegetation: No single taxon characterizes this community, but some of the most common ones are: *Apodytes*, *Canthium*, *Erythroxylum*, *Euphorbia pyrifolia*, *Ficus* spp., *Maytenus*, *Mystroxyton*, *Ochna*, *Polysphaeria*, *Sideroxyton*, and *Terminalia boivinii*. Less abundant or locally common taxa are: *Acalypha claoxyloides*, *Allophyllus*, *Clerodendrum*, *Dracaena*, *Flacourtia*, *Guettarda*, *Jasminum*, *Operculicarya*, *Pandanus tectorius*, *Phyllanthus casticum*, *Margaritaria cheloniphorbe*, *Scaevola*, *Scutia*, *Secamone*, *Tarenna trichantha*, *Tarenna supra-axillaris*, *Tricalysia*, and *Triainolepis*. Many other taxa also occur. The understorey is generally barren, but dense to open patches of *Cyperus niveus* or *Lomatophyllum aldabrense* locally occur.

The Mixed Scrub varies greatly in height from site to site. It is at its greatest in Takamaka Grove, reaching about 12 metres and at its least (less than 1 m) in some of the areas of shallow soil. In some of the most extensive areas of Mixed Scrub (e.g. west of Bassin Frigate) the height is about 3-5 m.

Soil: The Organic Brown Calcareous Soil (CMD) (Trudgill, 1979) is the most common found under Mixed Scrub. It often occurs in pits 5-20 cm deep and in some areas is overlain by leaf litter or even several centimetres of arthropod frass (mostly from a millepede). The latter is called a Shallow Organic Soil, Pellet Type (OSP) by Trudgill.

In some areas the soil is sandy and belongs to the Farquhar Series. In a few places, sand has become mixed with the upper layers of the CMD. Shallow Organic Soil (OS) (Trudgill, 1979) may also be found.

Phenology: With such a large number of species, the phenological status of this type is complex at any time of year. However, certain generalizations are possible. Firstly, there are evergreen and deciduous species and a few which are neither entirely one nor the other depending upon just how dry it becomes. Flowering and fruiting is in general most prolific during the rainy season. For any particular species the peak may be at the start, middle or end of the wet period. A very few species flower most profusely during the dry months (e.g. *Capparis cartilaginea*). Some taxa are very opportunistic, flushing new leaves and flowers after any moderate rainy period and just as rapidly losing them when it dries up (e.g. *Allophyllus*, *Erythroxylum*).

Notes: This vegetation type is perhaps the most complex on Aldabra and the one about which the least is known. As a type it extends into a wide variety of habitats defined on species dominance, canopy height, plant spacing, and substrate type. For the time being it is being left as a single, heterogeneous unit although variants are recognised below as sub-types on the basis of certain conspicuous features. However, the status of these sub-types is very uncertain and requires detailed study.

sub-type a. Leeward Scrub

Recognised primarily by its location in the lee of the trade winds on or at the base of dunes.

Location: mostly associated with the large dunes on the south coast of Grande-Terre.

Notes: As a habitat it is extensively used by both tortoises and birds as a cool, shadey place to avoid the heat of midday. As a vegetation category, it is essentially an extension of the Mixed Shrub.

sub-type b. Dune Scrub

Recognised by its location on dunes and by floristic composition.

Location: primarily on large dunes (e.g. Dune Jean Louis).

Vegetation: dominated by woody plants from 1 metre to about 7 m high in open or closed communities. Understorey plants usually absent. The common species are *Tournefortia argentea*, *Scaevola taccada*, and *Thespesia populnea*.

Notes: The species are characteristically, widespread, coastal, tropical taxa.

sub-type c. Beach Scrub

Recognised by its location and floristic composition.

Location: at the head of small beaches.

Vegetation: as for Dune Scrub but the common species are usually *Cordia subcordata*, *Casuarina equisetifolia*, *Hibiscus tiliaceus*, *Scaevola taccada*, *Suriana maritima*, and *Tournefortia argentea*.

Notes: Resembles Dune Scrub closely, but the nearness to the sea and less deep sandy soil may account for the somewhat different species composition. Otherwise the two sub-types have much in common.

sub-type d. Sideroxylon Scrub

Recognised primarily on the basis of species composition.

Location: Generally on knolls of limestone rising 0.5 to 1.0 m above the surrounding rough champignon terrain.

Vegetation: *Sideroxylon inerme* dominates these knolls as relatively large single-stemmed plants with broadly spreading crowns and fairly dense, evergreen canopy. *Maytenus* and *Scutia* may be common associates in the canopy while *Cyperus niveus* often occurs in the understorey.

Notes: This sub-type is one of the important variants of the Mixed Scrub in that it is common and widespread in a mosaic with the extensive areas of *Pemphis* Scrub. Because *Sideroxylon* Scrub occurs consistently in habitats distinct from those of *Pemphis* Scrub, although in a fine mosaic with it, it seems valid and useful to classify the *Sideroxylon* Scrub separately from the *Pemphis* Scrub.

The dynamic status of the sub-type is not clear. Most *Sideroxylon* on Aldabra are large and no seedling or sapling individuals have been reported despite prolific fruit production that is known to be fertile at least in part. How this sub-type relates to Mixed Scrub is not clear, as the two merge imperceptibly in some areas.

The distribution patterns of Mixed Scrub in some areas of Aldabra are very conspicuous, particularly when seen on aerial photographs. In the present classification, the various distinct patterns are not classified separately, but some comments seem pertinent because of the very different habitats they create.

Firstly, there is a conspicuous arrangement of shrubs in rows oriented more or less north west to south east. Fosberg (1971, p 218, and Grubb 1971, p 357) have suggested that the prevailing south east trade wind may be involved in the origin of this pattern. The present day trade winds may be ruled out as the immediate cause by noting that several areas of pronounced row-pattern are sharply demarcated from surrounding scrub which shows no such pattern. Examination on the ground showed that shrubs in areas of row-pattern are almost always growing in pits, depressions or on broken ground separated by smooth to undulating regions with very shallow pits and virtually no soil. The smaller the depression in which the shrubs grow, the more dwarfed were the shrubs. Thus the immediate cause of the rows would appear to be patterning of the habitable substrate and not to the direct influence of the wind. It is noteworthy that very similar patterns can be seen on aerial photo 42 SY 15 no. 031 where they occur not only on dry land but also on the wave cut platform of the south east coast of Grande Terre. The trade winds do result in regular die-back of the previous seasons growth on shrubs. This die-back is most pronounced on the windward sides of shrubs and eventually may result in very windswept crowns. Some plants with such crowns do lean down wind, but whether this tilt is directly caused by the force of the wind or the stress resulting from the very asymmetric crowns is not clear, but this situation of wind shaping of crowns is not directly related to that of arranging the positions of individuals into a pattern of parallel rows.

The second conspicuous pattern is that of "clumps" of shrubs throughout large areas of *platin* and *pavé* at the east of Grande Terre. Field observations again have shown the shrubs to be associated with patches of rough ground in an otherwise little broken terrain of limestone. The rough ground may be (as noted by Grubb 1971, p 357) in the form of depressions or sump holes. Such places accumulate soil and thus hold moisture, providing adequate rooting conditions for shrubs, or they may be local patches of moderately deeply pitted *champignon* or fissured rock. In all cases it seems that where adequate rooting by shrubs is possible, they occur, and where sufficient rooting conditions are not met, there is only low vegetation or bare rock. Takamaka Grove is the superlative development of one such shrub clump on Aldabra. The distribution of space habitable by shrubs in these areas relates to the origins of the substrate pattern Hnatiuk & Merton (1979).

(7) *SCLERODACTYLON* TUSSOCK GRASSLAND

Location: primarily around the sea coasts of the whole atoll although its greatest extent is along the south coast of Grande Terre. Occasional patches can be found well inland (e.g. 1.3 km south west of Takamaka Grove).

Vegetation: One species, *Sclerodactylon macrostachyum* dominates this vegetation type. This grass grows in tussocks from 0.05 m in height where grazing is heavy to over 0.5 m in height where grazing is absent. The crowns of the tussocks usually interdigitate with each other and produce virtually 100% canopy cover, but where grazing occurs, cover may be considerably less. There is no understorey vegetation, but a variant with *Cyperus ligularis* as dominant may occur (see notes below).

Soil: The sandy Farquhar Series (CMA of Trudgill, 1979), is the most common soil found in this vegetation type, but stoney soils and occasionally the fine Organic Brown Calcareous soil (Trudgill, 1979) form the substrate of the tussocks.

Phenology: Seasonal changes are slight. The tussocks are evergreen and individual leaves appear to remain green throughout their length and then die rapidly, thus the canopy never appears brown from dead leaf tips as occurs in some tussock grasses. The leaves do turn pale grey from salt and fine calcareous deposits during long dry spells with strong onshore winds and ocean swell. Flowering occurs almost exclusively during the rainy season and can be prolific.

Notes: The dynamic status of the community is complex. It would seem that under heavy grazing pressure and shade seeking activity of tortoises, the tussocks are killed and replaced by *Sporobolus virginicus* (Hnatiuk et al., 1976). Where extensive stands of *Sclerodactylon* occur, the plants often appear to belong to distinct clones, 10 to 50 m across, being distinguished on the basis of leaf colour (blue, brown, light green). In some places that are little disturbed by grazing, the *Sclerodactylon* grow in a mosaic, closed-canopy community with low, coastal Mixed Scrub on rocky, shallow, soil. *Cyperus ligularis* also forms tussocks and dense, one-species stands in habitats identical to those of the *Sclerodactylon*. The *Cyperus* appears to be an invasive species of disturbed habitats. It is only grazed by tortoises when it is producing new growth. Its loose tussocks and flexible leaves are not as susceptible to mechanical damage from trampling as are tussocks of *Sclerodactylon*. Until more is known about the sedge, it seems best not to classify it as a separate vegetation type.

(8) *SPOROBOLUS VIRGINICUS* COASTAL TURF

Location: Widespread on sandy deposits around the sea coast of the atoll, but most abundant along the south and east coast of Grande Terre.

Vegetation: One species, *Sporobolus virginicus*, dominates this vegetation type, but several other species also are to be found: *Euphorbia stoddartii*, *Fimbristylis cymosa*, *Launaea sarmentosa*, *Lepturus repens*, *Portulaca mauritiensis*, and *Sida parvifolia*. All but *Lepturus* occur most frequently with the *Sporobolus* where tortoise grazing is intense; *Lepturus* tends to be found on stonier soil than is *Sporobolus*. The short turf of *Sporobolus* (less than 1 to 2 cm in height) with cover of less than 50% in places, found under intense grazing conditions,

becomes a tall sward (10 - 20 cm in height) with 100% cover and with a dense accumulation of litter (Hnatiuk *et al.*, 1976).

Soil: The type appears largely restricted to the Farquhar Series sand (CMA of Trudgill, 1979) of the low perched beaches but in some places Shioya sand is the substrate.

Phenology: *Sporobolus virginicus* is evergreen. It produces most new growth during the rainy season. It appears to flower most prolifically during the late wet and early dry season, but relatively heavy rains during the dry season can stimulate sporadic flowering. The leaves may become grey on the windward trade coast from fine, air-borne, calcareous deposits during the trade wind season. The vegetation takes on a brownish cast during the dry months as the leaves begin to slowly die back from the apex.

Notes: The dynamics of this vegetation type appear to be closely linked with that of the *Sclerodactylon* Tussock Grassland. The *Sporobolus virginicus* Coastal Turf may at some time in the past have been confined to unstable sandy soil at beach crests but appears to have become widespread through the feeding and shade seeking activity of tortoises at the expense of both low Mixed Scrub and the Tussock Grassland. However, having once become established over large tracts, it seems to persist (Hnatiuk *et al.*, 1976). Its long term status in these places is not known.

(9) TORTOISE TURF

Location: primarily on the plain and pavé terrain at the east end of Grande Terre although rather small, often poorly developed patches are found on Ile Picard (e.g. Back Path, near Bassin Cabri, and near Anse Var) and on Ile Polymnie.

Vegetation: Tortoise Turf is an assemblage of many species that change in relative dominance from place to place. The following dwarf grasses and sedges are most common: *Bulbostylis basalis*, *Dactyloctenium pilosum*, *Eragrostis decumbens*, *Fimbristylis cymosa*, *Panicum aldabrense*, *Cyperus pumilus*, and *Sporobolus testudinum*. The most common dicot herbs are *Euphorbia stoddartii*, *Phyllanthus maderaspatensis*, *Sida parvifolia*, and *Tephrosia pumila*. A thallose liverwort, *Riccia*, is common on heavily grazed ground. The intensely grazed turf is mostly less than 1 or 2 cm in height and the canopy cover less than 20%. In lightly grazed conditions, cover can approach 100% and height, depending upon which species is dominant, can reach 10 - 15 cm. There does not appear to be any development of strata within the community.

Soil: The Organic Brown Calcareous Soil (Trudgill, 1979) is almost all that is found in this type. The soil is only a pale coloured representative of this soil type, perhaps because the dark horizon only forms under a shrub canopy or perhaps the former, darker horizon has been eroded in recent years (Merton *et al.*, 1976).

Phenology: The summer rains bring a slow greening of the turf and the onset of dry conditions brings a gradual browning as many of the plants die. Flowering and fruiting is largely done during the late rainy period and early dry period. Most of the species appear to be short lived perennials or facultative annuals during years of severe drought. Seed production can be high judging from the abundance of seedlings that can be found once the wet season is well established.

Notes: Tortoise Turf, first named by Grubb (1971, p 359), is a community that appears well developed to withstand moderate to intense grazing. In fact, its species richness may in part be possible because grazing keeps the more vigorously growing members from overtopping the less vigorous ones. Exclosure plots have only recently been set up but strong species interactions appear to be possible as the various species grow to much greater stature when not or little grazed than when heavily grazed. The Tortoise Turf has been seen to be invaded by the large sedge *Cyperus ligularis* where grazing has been restricted. It does not appear that the turf survives under a shrub canopy. Thus where shrubs are prevented from growing by continual browsing and abrasion as for example with *Ficus* spp., and *Ochna*, the Turf thrives where it would otherwise be shaded out. In the absence of at least moderate grazing, the Tortoise Turf could well become much less extensive than it is today.

The status of broad leaf herbs in the Turf is not clear. They are all readily eaten by the tortoises and some of these herbs are restricted to pits and crevices where the tortoises cannot reach. Many of these herbs appear capable of growing more rapidly and much larger than most of the dwarf grasses and sedges in the Turf. Thus, whether the dicot herbs would completely dominate the Turf if grazing were reduced is a matter of conjecture.

Two sub-types may be recognized:

sub-type a. Herbaceous pasture

It is characterized by a dominance of broad leaved herbs. It occurs in areas little grazed by tortoises (e.g. pits in champignon near Cinq Cases, on the 8 m ridge south of Anse Var, along part of Back Path, and near Bassin Cabri). The major taxa vary with geographic location but include: *Asystasia*, *Euphorbia stoddartii*, *Evolvulus*, *Hypoestes*, *Lagrezia*, *Nesogenes*, *Hedyotis*, *Portulaca mauritiensis*, *Ruellia*, and *Tephrosia*. Although quite distinct communities of Herbaceous Pasture can be found, because it grades into Tortoise Turf in some places, it here will be only distinguished as a sub-type.

sub-type b. *Fimbristylis cymosa* Turf

It is dominated by a single species and occurs over extensive areas of plain and pavé. It does not appear to be as readily grazed by tortoises as the other Turf

species although enclosure sites indicate that there must be some degree of grazing of new leaves and inflorescences during the rainy season. *Fimbristylis cymosa* appears somewhat more abundant in the northern part of the plain-pavé at the east end of Grande Terre while the other monocot Turf community is more common further south, but the two ranges overlap considerably. Until more is known about the interrelationships of the various Turf communities, it seems best to recognize only subtypes of the main Tortoise Turf vegetation.

(10) *BACOPA-MOLLUGO* MEADOWS

Location: It has been found only at the east end of Grande Terre on summer flooded basins.

Vegetation: The dwarf, succulent herbs, *Bacopa monnieri* and *Mollugo oppositifolius*, are the most common species found. They generally grow as very prostrate plants, less than 1.5 cm high and rooting at the nodes. Where protected from grazing *Mollugo* has been found to grow very much larger, reaching 20 cm in height, but *Bacopa* does not respond so vigorously. Cover is variable from greater than 75%, to less than 10% where grazing is intense or soil sparse.

Soil: A "mineral sediment (SM)" of Trudgill, (1979). It is a fine grey, generally saline silt, that may crack on drying. Algal sediments (SA of Trudgill, 1979) may also occur here. An algal surface layer is not uncommon. The soil is periodically submerged when the basins fill after rain, and then slowly dries out. Depending upon the extent of the droughts each dry season, the soil may or may not completely dry out.

Phenology: The plants are short lived perennials that remain green for as long as there is sufficient moisture available. Several weeks inundation does not halt either leaf or flower production although competition from algal blooms may eventually retard their growth. When the water recedes, the herbs flourish. Flowering and fruiting can thus occur at any time of year when moisture conditions permit.

Notes: *Bacopa-Mollugo* Meadows are closely associated with *Lumnitzera-Thespesia* Scrub. However, since the former does not grow under the latter nor are they always present at the same basin, it seems best to classify these two very different structural units as separate vegetation types.

The particular conditions favoured by each of the two dominant herbs is not clear. *Bacopa* may be more common in shallow soil and rock crevices while *Mollugo* may be more common on the deeper soil of the basin, but more observations are needed.

sub-type a. Bryodes Meadow

A dicot herb community dominated by one species, *Bryodes micrantha*. It appears to form in some places, a zone which is transitional between *Bacopa-Mollugo* Meadow and Tortoise Turf. The soil is often inundated by water during the wet season, but as the colour of the soil is brown, the duration of water logged conditions must be brief. The *Bryodes* community is ephemeral, appearing for a brief period only after prolonged rainy periods and dieing out as the soil dries out. Flowering and fruiting occur readily during this brief, active season. If artificially watered, the individual plants can live at least a year. Because only a very few patches of this community have been seen, its status is uncertain.

The pools occupied by both *Bacopa-Mollugo* Meadow and *Lumnitzera Thespesia populneooides* Scrub are found in depressions with impeded drainage in the hardened platin and pavé. The basins may fill with 0.5 m to 1.5 m of water during the rainy season, and slowly dry during the trade wind season. A complex succession of algae parallels the seasonal changes in water levels (A. Donaldson pers. comm.), and fish are occasionally to be found in the flooded pools. When pools dry out they are left with a hard, cracked crust that is matted by algae, or may be colonized by *Bacopa* and *Mollugo*.

(11) PIONEER VEGETATION OF BEACHES

Location: at the crest of most beaches around the atoll.

Vegetation: A mixture of herbs common on the strand line throughout much of the tropics forms this type. The most common species are *Cyperus conglomeratus*, *Dactyloctenium ctenoides*, *Ipomoea pes-caprae*, and *Sporobolus virginicus*. The community may consist of several or only one of these species. The canopy height is dependent on the species but is usually less than 0.2 m except for *Cyperus* which rises to 0.6 m. The canopy cover is generally less than 25% but locally denser patches do occur.

Soil: The soil is undeveloped beach sand.

Phenology: Vegetative growth, flowering, and fruiting are prolific during the wet season and much reduced or halted during the dry months.

Notes: This vegetation type is a pioneer on disturbed beach crests. It can vanish overnight if the beach is eroded by a storm, or may gradually disappear as tall woody plants of the Mixed Scrub sub-type Beach Scrub become established on places of extended stability.

(12) HERBACEOUS MEADOWS ON LAGOON ISLETS

Location: on some of the islets in the lagoon, particularly off the north shore of Grande Terre (e.g. Champignon des Os).

Vegetation: The dominant species are different on different islets and even on different parts of the same island. But taken as a whole they form an assemblage quite distinct from anything else on the atoll and therefore they are recognized as a separate vegetation type. The commonest species are *Achyranthes aspera*, *Boerhavia* sp., *Dactyloctenium pilosum*, *Lagrezia oligomeroides*, *Lepturus repens*, *Portulaca oleracea*, *P. mauritiensis*, *Sida parvifolia*, and more rarely *Sesuvium portulacastrum*. The shrubs *Acalyphyta claoxyloides* and *Pemphis acidula* are not uncommonly present though in a stunted form. Cover is generally high (greater than 75% during the wet season). Average height to the top of the canopy is less than 0.75 m and often less than 0.3 m.

Soil: Generally very little and composed of coarse sand with a few silty patches presumably both blown or washed up from the lagoon floor by wind and wave action. Bird dung and remains are locally abundant and in such areas the soil may be of the Desnoeuvs Series (the organic soil, guano variety, OSG of Trudgill, 1979).

Phenology: Vegetative growth, flowering and fruiting are largely confined to the wet season and early dry season until fresh water supplies are exhausted and then most of the community goes dormant. These islands can thus be bright green in January to March, and dull brown in August to November.

Notes: The dynamic status of this vegetation is uncertain but since some islets are currently used as roosts and nesting sites, while others appear to have been so used in the past, they may have been modified from shrub to herb cover by the activities of the birds. Some dead shrubs can be seen on some of the islets which are now entirely covered by Herbaceous Meadow.

(13) GARDENS

Location: near current or old sites of habitation, primarily at Settlement but also near Anse Var, Anse Mais, Anse Malabar, Ile Michel and Passe Houareau camp.

Vegetation: Many species of both cultivated and "weed" status are used to define this type. The commonest cultivated species are *Ipomoea batatas*, *Moringa oleifera*, *Capsicum frutescens*, *Phaseolus* sp., *Datura metel*, *Tamarindus indicus*, *Cymbopogon*, *Solanum melongena*, *Carica papaya*, *Panicum maximum*, *Cucurbita* spp., *Agave sisalana*, and *Pedilanthus tithymaloides*. Common weeds and ornamentals are *Stachytarpheta jamaicensis*, *Tridax procumbens*, *Synedrella nodiflora*, *Catharanthus roseus*, and *Sida acuta*.

Canopy height and cover is very variable depending upon the degree of cultivation, disturbance, and species composition.

Soil: Primarily of the Farquhar Series although some phosphate rich soil has been reported (Baker, 1963, p 107).

Phenology: Variable, depending upon the species concerned. However, most of the species are active during the wet season and early dry season, becoming dormant during the driest months. Some species such as *Carica* produce most leaves during the rains, and ripen their fruits only during the mid to late dry season.

Notes: Although the vegetation can be recognized on the basis of its floristic composition, certain special features can be noted. The species are all probably either deliberately or accidentally introduced by man. Some of the species do not appear able to spread either because all viable seed seems to be eaten by animals (e.g. *Moringa*), or no flowers are produced and vegetative spread is extremely limited (e.g. *Cymbopogon*, *Bambusa*). Other species have become naturalized and are spreading into the native vegetation (e.g. *Stachytarpheta*, *Passiflora*, *Agave*).

REFERENCES

- Baker, B.H. 1963 Geology and mineral resources of the Seychelles Archipelago. *Geol. Surv. Kenya Mem.* 3.
- Braithwaite, C.J.R., Taylor, J.D., & Kennedy, W.J. 1973 The evolution of an atoll. *Phil. Trans. R. Soc. Lond. B.* 266: 307-340.
- Fosberg, F.R. 1967 A classification of vegetation for general purposes. In G.F. Peterken, *IBP Handbook No. 4 Guide to the Check Sheet for IBP areas.* Blackwell Scientific Publ. Oxford & Edinburgh.
- Fosberg, F.R. 1971 Preliminary survey of Aldabra vegetation. *Phil. Trans. R. Soc. Lond. B.* 260: 215-227.
- Fosberg, F.R. & Renvoize, S. 1979 *Flora of Aldabra.* Royal Botanic Gardens, Kew.
- Fryer, J.C.F. 1910-12 The structure and formation of Aldabra and neighbouring islands with notes on their flora and fauna. *Linn. Soc. (Lond.) 2nd series (Zoology)*, 14: 397-442.
- Grubb, P. 1971 The growth, ecology and population structure of giant tortoises on Aldabra. *Phil. Trans. R. Soc. Lond. B.* 260: 327-372.
- Hnatiuk, R.J. & Merton, L.F.H. 1979 A perspective of the vegetation of Aldabra. *Phil. Trans. R. Soc. Lond. B.* 286: 79-84.

- Hnatiuk, R.J., Woodell, S.R.J., & Bourn, D.M. 1976 Giant tortoises and vegetation interactions on Aldabra atoll. II. Coastal. *Biol. Conserv.* 9: 305-316.
- Macnae, W. 1971 Mangroves on Aldabra. *Phil. Trans. R. Soc. B.* 260: 237-248.
- Merton, L.F.H., Bourn, D.M., & Hnatiuk, R.J. 1976 Giant tortoises vegetation interactions on Aldabra atoll. I. Inland. *Biol. Conserv.* 9: 293-304.
- Piggot, C.J. 1968 A soil survey of Seychelles. *Tech. Bull. No. 2.* Land Research Division, Directorate of Overseas Surveys, Tolworth.
- Ridley, H.N. 1930 *The Dispersal of Plants throughout the World.* L. Reeve and Co. Ashford.
- Stoddart, D.R. 1968a The Aldabra affair. *Biol. Conserv.* 1: 63-69.
- Stoddart, D.R. 1968b The conservation of Aldabra. *Geogr. J.* 134: 471-486.
- Stoddart, D.R. & Wright, C.A. 1967 Geography and ecology of Aldabra atoll. *Atoll Res. Bull.* 118: 11-52.
- Stoddart, D.R. & Mole, L.U. 1977 Climate of Aldabra Atoll. *Atoll Res. Bull.* 202: 1-21.
- Trudgill, S.T. 1979 The soils of Aldabra. *Phil. Trans. R. Soc. Lond. B.* 286: 67-77.
- Vesey-Fitzgerald, L.D.E.F. 1942 Further studies on the vegetation of islands in the Indian Ocean. *J. Ecol.* 30: 1-16.
- Wickens, G.E. 1979 Speculations on seed dispersal and the flora of the Aldabra Archipelago. *Phil. Trans. R. Soc. Lond. B.* 286: 85-97.