GIANT TORTOISE AND VEGETATION INTERACTIONS ON ALDABRA ATOLL—PART 1: INLAND

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ABSTRACT

A very large endemic population of giant land tortoises, which are the major terrestrial herbivores, survives on the western Indian Ocean atoll of Aldabra. Tortoise densities are highest in the inland areas of the south-east where the habitat is being greatly modified by tortoise activity. In particular, they are responsible for considerable soil erosion and the death of many trees and shrubs with the resultant reduction in the amount of shade cover, which is so important to tortoise survival. There are also signs that food resources may be limiting: the low vegetation is intensively cropped; there are pronounced browse lines on most tree species and tortoise growth rates are reduced. A reduction in tortoise numbers is therefore a distinct possibility.

INTRODUCTION

The interactions between plants and animals within a community can often play an important role in determining the distribution and abundance of the species concerned. On Aldabra atoll in the western Indian Ocean (46°20′ E.Long., 9°24′ S.Lat., Fig. 1) it appears that in certain areas the vegetation is being modified by the activity of the large endemic population of giant land tortoises, *Geochelone* (*Testudo*) *gigantea* Schweigger. Hnatiuk *et al.* (this issue) consider the changes

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that have occurred in the coastal vegetation, while here we present evidence to support the hypothesis that in the past tortoises have had, and continue to have, a marked effect on the inland vegetation in the south-east of the atoll.

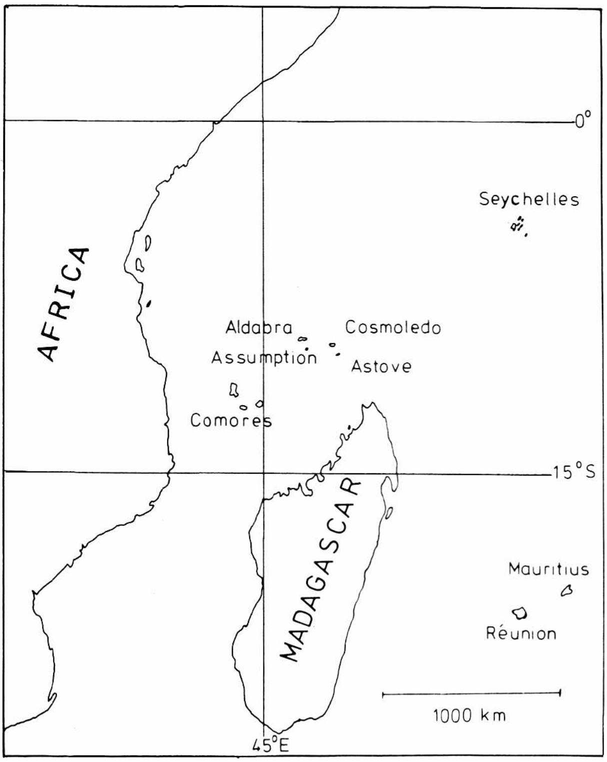

Fig. 1. Situation of Aldabra atoll in the West Indian Ocean.

Aldabra is a large, raised, coral atoll, with a land area of 155 km^2 (Fig. 2), situated 420 km north-west of Madagascar and 640 km east of Tanzania. In comparison with other island groups in the region, it has largely been spared from the deleterious effects of human exploitation. The setting and geography of the atoll have been discussed by Stoddart (1967), the geology by Braithwaite *et al.* (1973), the geomorphology by Stoddart *et al.* (1971), the vegetation by Stoddart & Wright (1967), Fosberg (1971) and Grubb (1971), and the tortoise population by Gaymer (1968), Grubb (1971) and Frazier (1972). Grubb's account of the vegetation is particularly accurate and perceptive. Some repetition of these descriptions is

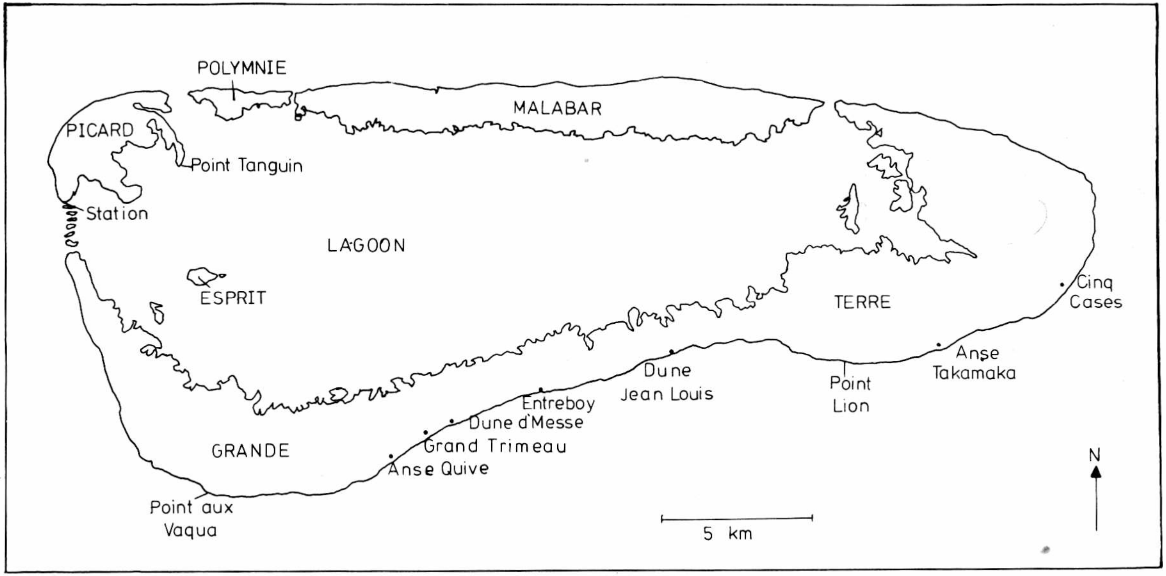

Fig. 2. Aldabra atoll.

necessary here, either to amplify or modify them or to make discussion more readily intelligible.

The vegetation consists for the most part of scrub of varying height, either continuous or in a mosaic with open rocky ground carrying a variable cover of grasses and sedges (Fig. 3). Several authors have commented on the very large number of dead or dying trees and shrubs in the south-east of the atoll, particularly near the coast and most prominent in the Cinq Cases area, but also continuing westwards to Dune Jean Louis and Dune d'Messe. A number of suggestions have been made to account for their death, including storm damage (Fosberg, 1971), long-term climatic changes (Grubb, 1971), and hurricane damage (Stoddart, 1971). It is our contention that the widespread death of the woody vegetation in this area is the most obvious expression of a series of changes in the environment that can be attributed to the effects of the presence of high tortoise densities.

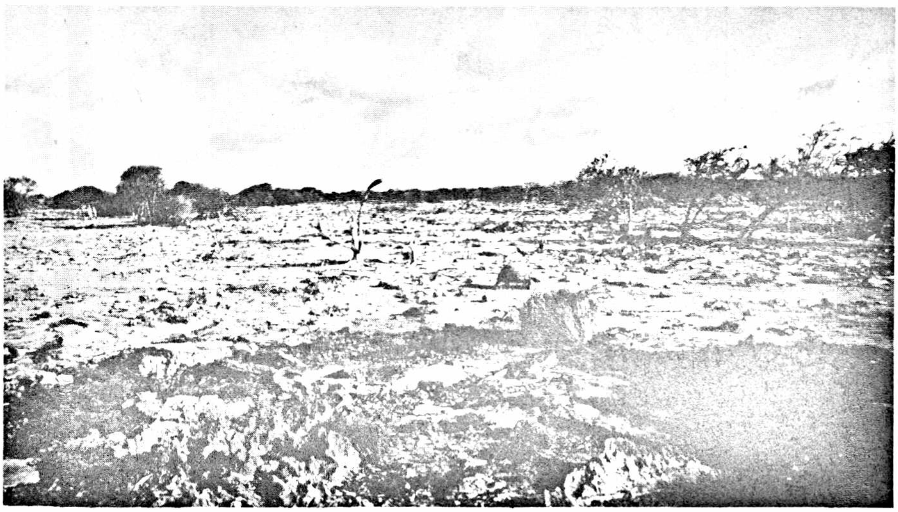

Fig. 3. Flat, platin and pavé terrain inland from Cinq Cases covered by thin soil with tortoise turf. Shrubs grow in scattered clumps. (Photo D.M.B.).

CLIMATE

Farrow (1971) described the climate of the atoll as being semi-arid. Two seasons may be distinguished: from May until October the prevailing south-east trade winds blow, temperatures are relatively low, and little rain falls; between November and April the lighter, more variable winds of the north-west monsoon bring rain, and temperatures are higher.

GEOMORPHOLOGY

The distribution of the various types of vegetation depends largely upon the geomorphology of the atoll. The atoll is elevated in relation to the present sea level and has been subject to karstic erosion; the surface is seldom more than 3 m above mean sea level and frequently much less. In the south-east of the atoll, with which we are chiefly concerned, there are extensive areas with little surface relief where shallow 'platin' basins occur (Fryer, 1911; Stoddart *et al.*, 1971). The floors of these basins are covered with a more or less shallow layer of soil. They are widely flooded during the wet season, and semi-permanent bodies of fresh water are not infrequent here, although rare elsewhere. Two other forms of limestone surface may be distinguished: 'pavé', which has a more irregular surface than 'platin' but with a generally rounded appearance and a surface relief usually less than 0·5 m; and 'champignon', which has an extremely jagged surface with deep pits and pinnacles and a relief of up to several metres (Stoddart *et al.*, 1971).

The sea coasts of Aldabra are formed from low, eroded, limestone cliffs interrupted at intervals by coves with sandy beaches. For much of the perimeter of the atoll, the cliffs themselves form the seaward edge of a narrow, perched, wave-cut terrace 4 m above sea level. Behind this a belt of limestone with a surface some 4 m higher separates the coast from the more sheltered and altitudinally lower terrain inland.

INLAND VEGETATION

The vegetation inland from Cinq Cases is a complex of different communities, the species composition of which is given by Fosberg (1971) and Grubb (1971). The ground consists of expansive areas of platin and pavé with numerous sink holes or sump-like depressions. The hollows support a shrub vegetation and may sometimes have pools of water from the summer rains. The intervening areas support a vegetation of grasses, sedges, and broad-leaved herbs, together with barren ground. Changes in the vegetation from place to place appear related to the degree of flooding and the salinity of the water. The most saline (but not sea water influenced) areas support *Lumnitzera* and *Thespesia* shrubs, and *Bacopa* and *Glinus* herbaceous pastures while the least saline sites are dominated by groves of mixed shrubs and a low 'tortoise turf' of grasses and sedges, or a taller herbaceous vegetation of coarse sedges (*Cyperus ligularis* L. and *Fimbristylis obtusifolia* Kunth). Low ridges of champignon running from the coast inland transect the area in several places and these ridges bear a more continuous, markedly wind-sculptured scrub.

TORTOISES

Stoddart (1971) presented evidence which suggested that the size of the tortoise population had been greatly reduced by the end of the 19th century, as a result of extensive collections by man. Grubb (1971) estimated the population size to be about 100,000 and one of us (D.M.B.), after a wide-ranging census, obtained a figure of some 141,000. It seemed probable, therefore, that the tortoise population had increased dramatically in the last seventy-five years. Ninety-seven per cent of the tortoises occurred on Grande Terre, but the distribution was uneven with 100,000 concentrated in the south-east of that island at a mean density of 27/ha. A typical animal weighed 24 kg and had a curved length of 70 cm. The highest tortoise densities occurred where low herbaceous vegetation was abundant (Table 1). Most of the low grasses, sedges and herbs within this habitat were intensively grazed and some shrubs provided shade. Where low vegetation represented more than 50% of the ground cover, tortoise densities were higher than in areas where much limestone rock was exposed and low vegetation represented less than 50% of the ground cover. Considerably fewer tortoises were found in the tall herb and scrub habitats.

TABLE 1
GIANT TORTOISE DENSITIES IN DIFFERENT HABITATS IN THE SOUTH-EAST REGION OF ALDABRA

Habitat type	*Mean tortoise density/ha*	*Standard error of mean*	*Number of* 1-*ha samples*
Scrub	18·3	±1·8	107
Tall herb	18·2	±2·3	6
Low herb >50% cover	62·3	±7·6	11
Low herb <50% cover	41·9	±6·5	44

Tortoises, being poikilothermic animals, are active and feed during the cooler times of the day: from dawn until mid-morning and from mid-afternoon until dusk. During the heat of the day they must find protection from direct solar radiation and usually shelter in the shade of trees or shrubs or cool themselves in pools and mudwallows. Those unable to find suitable shelter suffer from heat stress and often die. This is particularly true during the hotter summer months.

Effects of tortoises on inland vegetation

In the south-east of the atoll there were widespread signs of overgrazing by tortoises, particularly in the vicinity of Cinq Cases where densities were highest. Grubb (1971) and Frazier (1972) have shown that tortoises are extremely catholic in their

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choice of food and few species remain untouched. They are primarily grazers, although browsing is common. The highest tortoise densities occurred in habitats where 'tortoise turf' (see later) and various perennial plants, growing in small soil pockets in otherwise rocky ground, were most abundant. These plants were heavily grazed and had low, well-cropped forms except in the few places where the terrain made them inaccessible to tortoises. 'Tortoise turf' seldom exceeded 5 mm in height, but was still intensively grazed and, by the middle of the dry season, much of the underlying soil had been exposed and was susceptible to erosion by tortoises, wind, and rain.

A conspicuous browse line 0·6 m above ground level occurred on many trees and bushes (Grubb, 1971, p. 358), but the fact that many branches, now mostly dead, curved below this line suggested that the canopy was at a lower level in the past. During the heat of the day, it was not uncommon to see between 20 and 30 tortoises sheltering in the shade of a small thicket. The presence of tortoises and their daily movement effectively cleared undergrowth, greatly disturbed the top 5 cm of soil, and exposed the larger roots. In disturbing the soil, the fine feeding roots which bound it were broken up, while the exposed bark on the upper root surface was scarred and eventually worn away by the abrasion of tortoise plastrons. By the end of each dry season, the soil under shade trees could be reduced to a fine dust which was easily blown away. The exposure of large roots was widespread where tortoises were common and was clearly due to soil loss (Fig. 4). However, in some instances roots may have been raised above their original position when the trees were tilted by the wind. In many other cases, though, large roots, now some centimetres above a rock surface, could not have grown into that position in the absence of a deeper soil. Numerous measurements of the heights of root axes above the present ground surface, even assuming that the axes were eccentric and nearer the lower side, strongly suggested that 10–15 cm of soil have been lost over much of the area.

Many dead trees, mostly *Guettarda speciosa* L. and *Thespesia populneoides* (Roxb.) Kost., were to be found in the south-east; some were still standing but many had fallen. We suggest that the death of these trees was due to tortoise-induced soil erosion which (a) exposed the roots to tortoise abrasion and de-barking and (b) made the trees unstable and more likely to be blown over.

Tortoises feed on freshly fallen leaves of certain species and thus, where densities were high, comparatively little leaf litter accumulated. Despite the lack of litter and disturbed surface soil, seedlings of various scrub species could be found in the south-east, especially after the rains, *e.g. Ochna ciliata* Lam., *Ficus* spp., *Polysphaeria multiflora* Hiern. However, tortoises frequently fed on the leaves of young plants, many were trampled, and most of the remainder appear to have been unable to withstand the long, dry season. Certainly saplings were comparatively rare and the regeneration of many scrub species seemed to be severely restricted.

Fig. 4. Dead tree (? *Guettarda speciosa*) with root system exposed by removal of soil. A living *Ficus reflexa*, with partially exposed root system, provides mid-day shade for tortoises behind the dead *Guettarda* (Photo: S. R. J. Woodell).

Tortoise turf

Although we have presented evidence which suggests that the tortoise population is not at present in equilibrium with its environment, at least in the south-east of the atoll, one feature indicated that the relationship is of long standing and has resulted in the modification of certain plant species. That feature is 'tortoise turf' (Fosberg, 1971; Grubb, 1971) which was conspicuous in areas of high tortoise density and was heavily grazed. The turf is a complex of twenty-one grass, sedge, and herb species, of which more than half are plants of a dwarfed form (see Table 2). Observations on Aldabra of transplanted sods which were ungrazed and regularly watered for a year, and of plants grown from seed, showed that 52% of the species were genetically dwarfed, although some (*e.g. Eragrostis decumbens* Renv.) are genetically plastic, in that plants grown from the seed of dwarf plants may themselves be dwarfed or very much larger.

The relationship between tortoises and the turf is thought, for the following reasons, to be an old one. Firstly, eight of the species within the tortoise turf complex are thought to be endemic to Aldabra and the neighbouring islands, *i.e.* 40% of the turf species may be endemic compared with 10% endemism for the whole flora. Secondly, Braithwaite *et al.* (1973) consider that the tortoises may

TABLE 2

TORTOISE TURF SPECIES. THOSE MARKED * ARE THOUGHT TO BE ENDEMIC TO THE ALDABRA GROUP OF ISLANDS. THOSE MARKED † ARE GENETICALLY DWARFED

Grasses
*†*Dactyloctenium pilosum* Stapf.
*†*Eragrostis decumbens* Renv.
*†*Panicum aldabrense* Renv.
**Sporobolus aldabrense* Renv.
*†*Sporobolus testudinum* Renv.
Stenotaphrum clavigerum Stapf.
Sedges
*†*Fimbristylis* sp. indet.
†*Pycreus pumilus* (L.) Domin.
*†*Scirpus* sp. indet.
Herbs
†*Bacopa monieri* (L.) Wett.
†*Bryodes micrantha* Benth.
**Cassia aldabrensis* Hensley
†*Euphorbia prostrata* Aiton
Euphorbia sp. indet. (cf. *E. prostrata*)
Evolvulus alsinoides (L.) L.
Glinus oppositifolius (L.) A.DC.
Justicia procumbens L.
Oldenlandia corymbosa L.
†*Phyllanthus* sp. indet. cf. *P. maderaspatensis* L.
Sida parvifolia Burm. f.
Tephrosia pumila (Lam.) Pers.

have been on Aldabra for the past 80,000 years. We therefore believe that the tortoise turf complex evolved under, and is certainly well adapted to, grazing pressure from tortoises. In fact, the large areas of tortoise turf found today may be the result of selective removal of other potentially competitive plant species by tortoise activity. In some plots of tortoise turf which were fenced off to eliminate or reduce tortoise grazing, it was apparent after only one year that the turf was rapidly being encroached upon by vigorous, tall growing sedges like *Cyperus ligularis*, as well as by shrubs of the genus *Ficus*.

COMPARISON WITH OTHER ISLANDS ON ALDABRA

Areas of platin, with their associated plant community, did not occur outside Grande Terre apart from a few very small sites on Ile Picard and Ile Polymnie that were not comparable with the Cinq Cases region. The phenomenon of extensive root exposure and removal of bark did not occur on Ile Polymnie or Ile Esprit where tortoises were absent, although the upper surface of large roots may sometimes be uncovered in very shallow soils. A few tortoises have recently been tortoises. The turf on which the tortoises feed is well adapted to heavy grazing and has probably increased in areal extent at the expense of some shrubs and larger sedges. However, under extremely high tortoise densities, the turf is now being seriously degraded.

The tortoise population obviously cannot increase in size indefinitely. It is already apparent that food resources are limiting the growth rates of tortoises on Grande Terre. The overall reduction in the amount of shade cover available to tortoises, most apparent in the south-east, is, in our opinion, a factor likely to lead to high rates of mortality. So, too, is the recent spread of the woolly coccid *Icyera sechellarum* which is attacking and killing many shade-giving species throughout the atoll. The death of numerous trees in the Cinq Cases area in the past is not thought to have been caused by the woolly coccid because the area involved is of limited extent.

Whether or not the tortoise population is going to 'crash' in the near future is open to debate. Acting to hasten the decline would be a continuing, rapid decrease in the amount of shade available due to the activities of both the tortoises and the woolly coccid. This decline in shade could be accelerated by a series of drought years. However, the decline in tortoise numbers is slowed down by their ability to withstand adverse conditions, with little or no growth taking place for a number of years; and there is evidence to suggest that the reproductive potential of the population is reduced at high densities. It is possible, therefore, that the expected decline in tortoise numbers may occur over a period of many years and may have already started.

ACKNOWLEDGEMENTS

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