

The Primary Production of Aldabra Atoll, with Reference to Habitats Used by Giant Tortoises

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THE PRIMARY PRODUCTION OF ALDABRA ATOLL, WITH REFERENCE TO HABITATS USED BY GIANT TORTOISES

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This paper reports on the seasonal changes of standing crop and production in habitats used by a high-density population of giant tortoises on Aldabra atoll.

The study had two main aims: first to investigate the primary production of a raised coral atoll (to our knowledge the first such study) and secondly to provide base data for a study of the interactions of a large reptilian herbivore (the giant tortoise) with its food supply and environment.

Environmental heterogeneity made it necessary to measure separately the standing crop and the above-ground net production of different components of the vegetation; these components were usually single species or small groups of species of plants. Measurements of these components were then combined with cover data for the same components in selected places to illustrate the seasonal and spatial variability of primary production on Aldabra.

Standing crop biomasses were estimated from harvest samples. Methods for production estimates varied with the component studied, but included harvest difference methods, repeated clipping of the same plots and direct measurement of leaf turnover rates on marked shoots. These methods are compared where appropriate.

Net annual above-ground production varied between plant types from 3165 kJ per square metre of plant for 'tortoise turf' to 47700 kJ m⁻² for *Cyperus ligularis*, a robust perennial sedge. Total above-ground annual net production of different habitat types (bare ground and rocks between plants being taken into account) varied from 9100 kJ m⁻² in a thinly wooded area with high tortoise turf cover ('open mixed scrub') to 28200 kJ m⁻² in an area of thick scrub forest ('groves'). The seasonality of production and standing crop also varied considerably between habitats, owing to the role of different components of the ground layer and shrub cover.

These results are discussed in terms of the roles of environmental and structural heterogeneity in setting primary production and of the tortoises themselves in their interactions with the vegetation via trampling and grazing. The effect of this heterogeneity on sampling strategies and results is also assessed.

INTRODUCTION

The islands of Aldabra (figure 1) form a large (156 km²) raised coral atoll some 400 km north-west of Madagascar. The climate is a tropical seasonal one, with most rain falling during the northwest monsoon (approximately November–April). Because of differences in the timing of the monsoon, and of the southeast trade wind season (April–November) with its occasional rainy periods, annual rainfall exhibits considerable variation; range during 1949–1978, 349–1467 mm. This fourfold or more difference in annual precipitation leads to the presumption that the net primary production of Aldabra will vary markedly from year to year.

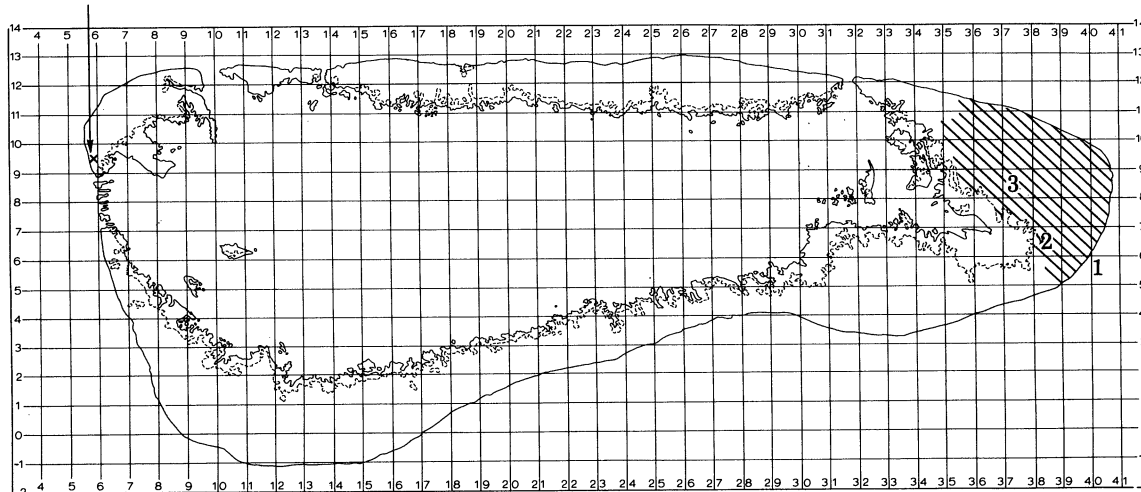
Since 1973, intensive studies have been made on the giant tortoise (*Geochelone gigantea* Schweigger) populations of Aldabra, some 150 000 animals in total (Bourn & Coe 1978), forming the largest concentration of giant tortoises in the world. A high density subpopulation of 90 000 individuals lives in an area of 34 km² at the eastern end of the atoll at and to the northwest of Cinq Cases (figure 1). Coe *et al.* (1979) are of the opinion that the growth and reproduction of this subpopulation are limited by food availability.

With the supposition of a varying food supply and the proposition of at least one subpopulation of giant tortoises being limited by food availability it is clearly of importance to investigate interactions between the tortoises and the vegetation. One element in this process is an evaluation of the relations of above-ground net primary production to vegetation type, and annual and seasonal changes in climate.

Detailed descriptions of the climate, physical environment and vegetation of the atoll can be found in Braithwaite *et al.* (1973), Farrow (1971), Stoddart & Mole (1977), Hnatiuk & Merton

(1979) and Gibson & Phillipson (1983). The main purpose of this paper is an examination of seasonal variations in the availability of potential food and shade for the eastern (Cinq Cases) high density subpopulation of giant tortoises. Estimates of the seasonal changes in standing crop and above-ground net primary production of the vegetation available to the tortoises are presented. The results are examined in the context of the potential quality of three major vegetation types as seasonal tortoise habitats. Additionally a comparison of the above-ground net primary production of Aldabra with that of other semi-arid tropical habitats emphasizes the role of environmental and vegetational heterogeneity in governing the absolute level and variability of potential tortoise food on Aldabra. The comparison also permits a preliminary assessment of the part played by the tortoises themselves in setting the levels of food availability via vegetational heterogeneity.

research station



KEY

- 1 Cinq Cases hut (field base), enclosure 1 and litter traps
 - 2 enclosures 2 and 3, and associated litter traps
 - 3 groves study site, enclosure 4 and litter traps
- ▨ approximate extent of major habitat zones used by the Cinq Cases subpopulation of giant tortoises

FIGURE 1. For details of litter traps see figure 2; for other study site details see tables 1–5 and text.

METHODS

(a) Study sites and treatment of samples

Four study sites were chosen to cover the three habitat types most used by tortoises in the high density subpopulation at Cinq Cases (figure 1). These habitat types were (i) *Sporobolus virginicus* coastal turf, (ii) 'open mixed scrub' (Gibson & Phillipson 1983) and (iii) 'groves' (Gibson & Phillipson 1983).

In 'open mixed scrub' two sites were chosen, one in an open part of the area with mixed tortoise turf-sedge plant cover, and the other in a small thicket.

At each of the study sites a 10 m × 10 m enclosure was constructed. The enclosures were made from posts of 2 m high scaffolding poles set in concrete and 2 inch (5.1 cm) mesh chain-link fencing, providing structures that were proof against tortoises and feral goats and yet open enough to minimize the edge effects from the fence. The 1 m wide strips of ground around the insides of the fences were not sampled.

In general, samples were taken at monthly intervals from November 1977 to December 1978. Any deviation from this sampling régime is dealt with under the specific sampling methods below.

All samples of plant material were sun-dried at the Cinq Cases field hut before being returned to the research station (figure 1), where they were sorted and weighed. Dried subsamples of different plant types were sealed separately in plastic bags and stored in an air-conditioned room until March 1979, when they were transported to the U.K. for determination of energy equivalents in a Phillipson micro-bomb calorimeter.

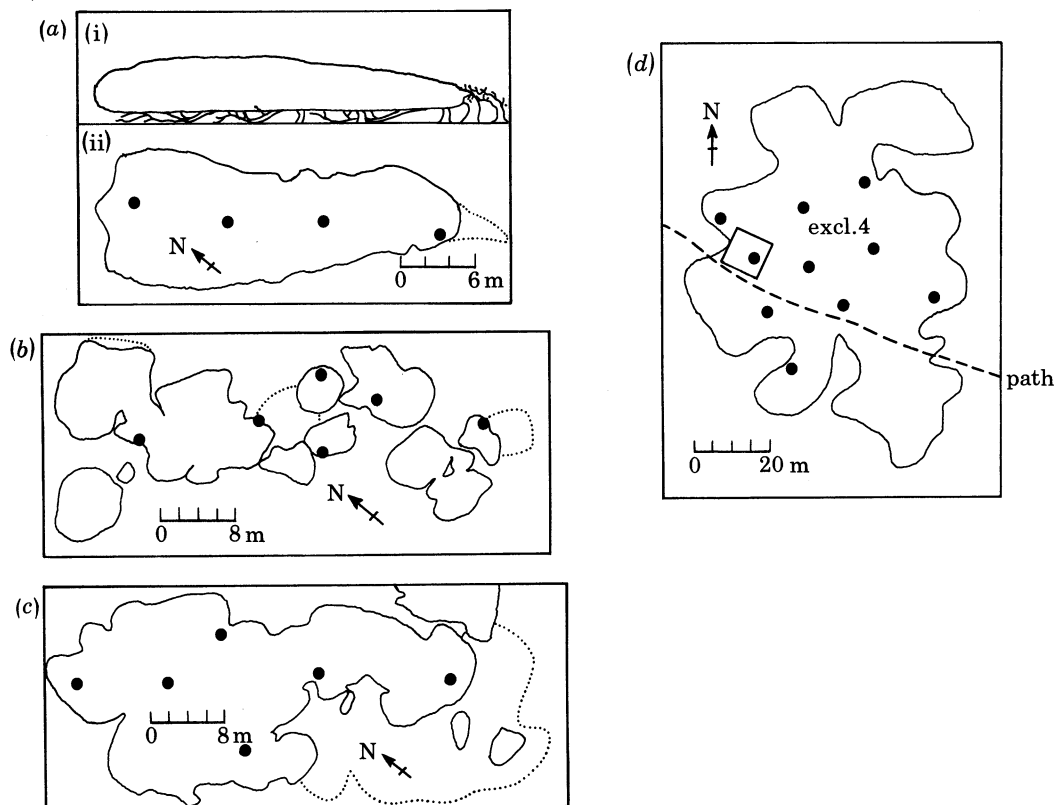


FIGURE 2. Canopy maps of thickets and grove of woodland, to show positions of litter traps (●). Only canopies of contiguous tree cover surrounding litter traps are shown. Solid lines denote living canopy; dotted lines show further extent of dead leaves, tree trunks, branches etc. (a) Profile (i) and plan view (ii) of *G. speciosa* thicket at Cinq Cases. (b) Plan of goat browsed thicket near enclosure 2. (c) Plan of other thicket near enclosure 2. (d) Plan of groves litter trap sites. (a-c) Mapped by direct ground survey; (d) from aerial photo-survey of Aldabra (D.O.S.).

(b) Methods specific for sample types

(i) Litter fall

Traps for assessing fruit and litter fall were made from half 45 gal (170 l) oil drums, perforated at the bottom and fitted with a removable inner bucket of alloy mosquito screening (effective catching area, 0.212 m²).

Four different sets of four to ten litter traps were used. One set was in the single species *Guettarda speciosa* L. (Rubiaceae) thicket beside the *S. virginicus* coastal turf site (four traps), one was at the 'groves' study site (ten traps) and two were in the 'open mixed scrub' study site

(six traps each). Of these last two sets, one was in a thicket regularly browsed by feral goats and one was in a thicket usually avoided by these animals but used by giant tortoises for shade.

Southeast trade winds affected both thicket structure and the likelihood of windblown loss of litter at different places. In an attempt to reduce errors from these sources litter traps were placed in a stratified pattern (figure 2).

Litter collections were sorted into leaves and fruits of different species and other material (i.e. woody material and dust) after drying. These components were weighed and their energy equivalents were determined separately. Results were expressed in kilojoules per square metre of ground covered by woody plants.

(ii) *Woody vegetation: species studied*

Although the flora of Aldabra includes at least 83 indigenous species of woody plant (Fosberg & Renvoise 1980), five species made up over half of the woody plant vegetation by number of plants in the Cinq Cases area (Gibson & Phillipson 1983). These species were *Apodytes dimidiata* F. Ney (Icacinaceae), *Polysphaeria multiflora* Hiern. (Rubiaceae), *Ochna ciliata* Lan. (Ochnaceae), *Maytenus senegalensis* Exell (Celastraceae) and *Mystroxydon aethiopicum* Loes. (Celastraceae). *P. multiflora* is a small understorey shrub and numbers probably overestimate its importance. The four species *O. ciliata* (obligate deciduous with short bursts of growth), *M. senegalensis* (facultative deciduous with continuous growth), *M. aethiopicum* (evergreen with continuous growth) and *A. dimidiata* (evergreen with short bursts of growth) covered the major types of phenology found in the woody vegetation of Aldabra. These four species were therefore selected for study. A fifth species, *Guettarda speciosa*, was added as it is an important shade tree for tortoises (Grubb 1971) in coastal mixed scrub and *S. virginicus* coastal turf. In the latter habitat it was effectively the only shade tree species (Gibson & Phillipson 1983).

Standing crop and production of leaves, flowers and fruits of the five selected species were estimated by a combination of monitoring tagged shoots at monthly intervals through the year and taking clipped quadrats from the bushes at the time of peak standing crop (April 1978). By combining these measurements, estimates per shoot were converted into estimates per square metre. These were then used to calculate the total standing crop above ground and net production per unit area of land after taking into account ground-layer vegetation and bare substrate. The methods used for estimating standing crop and production were as follows.

(iii) *Leaf standing crop of woody vegetation*

Table 1 gives the number and position of marked shoots on each of the five shrub species studied. Once each month from December 1977 to December 1978 (*G. speciosa*) or from January to December 1978 (the other species) all marked shoots were located and observations were made on shoot position, number and order of side branches and further-order branching produced since the beginning of observations. The observations and measurements made on each individual shoot/subshoot were:

- (1) length of shoot/subshoot from initiation point to tip;
- (2) number of leaves per shoot;
- (3) length of longest measurable leaf on shoot/subshoot (leaves with missing tips or damaged/senescing along midrib were scored 'unmeasurable' because of possible shrinkage);
- (4) length of shortest measurable leaf;

- (5) condition of each leaf as a percentage of pristine leaf to nearest 10 % by eye (senescence and herbivore damage were not distinguished);
- (6) position of each leaf for future identification;
- (7) presence/absence of reproductive subshoots, their length and the number and condition of flowering sites present i.e. bud, flower, dead flower, fruit or fallen;
- (8) fate of disappeared or dead shoots.

To convert the number of leaves per shoot to the standing crop of leaf biomass per shoot in each month, 50 intact leaves of each of the five shrub species were sampled to establish relations between length, area and dry weight. The leaves were chosen to cover the complete size range for each plant species and area was measured by outlining fresh leaves on graph paper and weighing the graph paper. Individual dried leaves were weighed on a torsion balance and the weight was related to leaf area.

TABLE 1. NUMBERS AND POSITIONS OF MARKED SHOOTS ON WOODY PLANT SPECIES

	location	position†	height‡	number of shoots
<i>A. dimidiata</i>	outside E2§	NW	0.8–3.0	6
		SE	0.8–3.0	6
<i>O. ciliata</i>	outside E2	NW	0.8–3.0	6
		SE	0.8–3.0	6
<i>M. aethiopicum</i>	outside E2	NW	0.1–3.0	6
		SE	0.8–3.0	6
<i>M. senegalensis</i>	outside E2	NW	0.8–3.0	6
		SE	0.8–3.0	6
<i>G. speciosa</i>	397059	NW	0.8–2.8	9
		NE	0.8–2.8	9
		SW	0.8–2.8	9
		SE	0.8–1.8	6
		top	3.5–4.5	6

† Position refers to aspect within a thicket. Prevailing wind direction was SE.

‡ Height of shoot above ground level.

§ The first four species were sampled in a thicket 30 m from enclosure 2.

|| Map reference refers to figure 1.

The standing crop biomass of leaves per shoot was calculated by using the resultant length: dry weight relations, the mean leaf length and the number of leaves for the relevant shoot.

Such estimates still needed conversion to the standing crop biomass per area of ground covered by bush (i.e. per square metre of plant). To ascertain the number and hence biomass of leaves per unit area of ground covered by shrubs, vertical quadrat clips were taken at the time of peak standing crop in April. A bush is a three-dimensional object, and so any quadrat sample from it must take account of this and be a three-dimensional sample. This can be done either by assuming that the canopy is homogeneous with respect to distance from the trunk and taking all leaves that are vertically above a particular area of ground (method 1) or by taking the spheroidal nature of the canopy into account (method 2). Method 2 requires the use of sample units on the surface of the canopy and all leaves inward from them (towards the centre of the bush); in addition, estimates of the area of the *ground* covered by the bush and total canopy area *on the bush* are required for the estimation of standing crop biomass *per area of ground that the bush covers*. The structure of the bush species concerned determined the method used. Method 1 was used for the four species *A. dimidiata*, *O. ciliata*, *M. senegalensis* and *M. aethiopicum* and method 2 was used for *G. speciosa*.

For the first four species, a 50 cm × 50 cm metal quadrat was mounted on a telescopic pole

so that it was parallel to the ground surface. Plumb lines, marked at 1 m intervals, were suspended from the corners of the quadrat. This gave a sample unit of a series of boxes 1 m deep by 50 cm × 50 cm square, starting at the canopy top and progressing towards the ground. Each shoot originating within each box was clipped back to the beginning of the current season's growth, which was still easily identifiable in April by a change in stem colour and texture. From each of the four species, ten of these canopy samples were taken, covering a range of compass aspects.

G. speciosa had much larger leaves than the other species, but its canopy was shallower. This necessitated the use of a 1 m × 1 m quadrat with smaller (50 cm) depth increments. Here the quadrat was laid parallel to the canopy surface, not the ground, and stiff wires instead of plumb lines were attached to the corners, so that the three-dimensional quadrat could be followed down into the bush. Otherwise clipping procedure was the same as for the other four species. Curvature of the canopy was such that errors due to the difference between the quadrat 'boxes' and a true 'slice section' of the canopy were considered negligible.

To minimize damage to the essential shade tree for the Cinq Cases tortoises only four *G. speciosa* clip quadrats were taken, one from each cardinal compass point.

All samples were sun-dried, separated into living leaves, flowering material and shoots, and weighed, and the number of separate shoots was counted.

(iv) *Leaf production by woody vegetation*

Information on the fates of individual leaves on the tagged shoots (see (iii), standing crop) was used to calculate leaf turnover rates for the five shrub species and hence leaf production per shoot. New leaves produced between monthly sampling visits were almost always the smallest on a shoot/subshoot, and production of new leaves could be estimated directly. Growth of the older leaves present was inferred if any increase of mean leaf size on the shoot had occurred. These two measurements were combined to estimate the minimal production of leaves on a shoot in each month. The position of each leaf on each sampling occasion being known, the position of leaves produced after one month's measurement but lost before the next month's could be identified by the position of leaf scars. This event was so rare that it was considered unnecessary to develop a means for quantifying it.

Production in numbers of leaves and/or length of leaves was converted to dry weight production of leaf per shoot by using the relations between length and dry weight of leaves. Net production by leaves was also estimated per unit area of ground covered by bush.

(v) *Herbaceous vegetation: plant types studied*

The structure of the ground vegetation was highly heterogeneous in *S. virginicus* coastal turf, open mixed scrub thicket and open mixed scrub tortoise turf-sedge. Figure 3 shows a plan view of an area, 8 m × 4 m, of the thicket enclosure when it was built (November 1977) and illustrates the mosaic of vegetation set in a matrix of standing leaf litter and bare rock.

Despite this heterogeneity, the ground vegetation in and around the enclosures could be characterized into a number of distinct components: single plant species or mixtures of species, which could be easily identified. The sampling régime was built up around the following components.

(1) *Sporobolus virginicus* formed a monospecific coastal turf or grew in association with *Sclerodactylon macrostachyum* A. Camus. Estimates in this paper are from the monospecific stands.

(2) *S. macrostachyum*. A large coarse perennial grass on coastal turf, sometimes growing with *S. virginicus*. Single species stands or stands with a very small admixture were sampled.

(3) Tortoise turf (Grubb 1971). Very short (usually less than 5 mm) turf, composed of an intimate mixture of several species, some of which are genetically dwarfed (Merton *et al.* 1976). Intensively grazed by tortoises. Samples taken regardless of species composition.

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FIGURE 3. Part of enclosure 3 (thicket in open mixed scrub) to show patchy and discrete nature of ground-layer vegetation. Each symbol represents a 10 cm x 10 cm square. The central part of the area was under shrub cover. Key to symbols: 1, tortoise turf; 2, *F. cymosa*; 3, *Cyperus* spp.; 4, *C. ligularis*; 5, bare ground (soil); *, bare rock; blank, litter. This map was made in November 1977, immediately after the area was fenced.

(4) *Fimbristylis cymosa* R. Br. Perennial sedge. Single species samples.

(5) *F. ferruginea* Vahl. Perennial sedge. Single species samples.

(6) *Cyperus* spp. A mixture of *C. niveus* Retz and other species, nearly always *C. bigibbosus* Fosberg. This mixture was not separable into species without bruising the plants, except when they were flowering. Samples were taken as a mixture but the species were effectively separable

as enclosure 2 (in the open) was dominated by *C. niveus* and enclosure 3 (thicket) was dominated by *C. bigibbosus*.

(7) *C. niveus*. A perennial sedge growing in the open or in light shade. See (6).

(8) *C. bigibbosus*. A perennial or occasionally an annual sedge, growing in deep shade. See (6). Single species samples taken when flowering. Occasionally small amounts of *C. dubius* Rottb. may have been present.

(9) *C. ligularis* L. A large (to over 1 m) perennial sedge. Single species samples.

(10) Grasses. Various grasses over 10 cm high. Extremely rare in the study areas owing to tortoise grazing.

(11) 'Mosaic rock' (Gibson & Phillipson 1983). Coral rock containing a patchwork of small holes (defined by having all holes less than 10 cm across), in some of which plants grew. These plants were usually tortoise turf species, but other small herbs and sedges sometimes occurred.

(12) Herb. All other dicotyledonous herbs. Extremely rare in the vegetation types studied, owing to tortoise grazing.

Sampling régimes for the above cover types were organized according to their relative abundances in the vegetation types studied: it was considered more important to have a large number of samples for those cover types that were either extremely common in the vegetation or known to be important as tortoise foodplants than for those that were rare or unimportant to tortoises as either food or shade.

(vi) *Standing crop samples of herbaceous vegetation*

Two levels of harvesting were used for estimating above-ground standing crop. At the first level, a 25 cm × 25 cm square patch of a cover type was clipped down to the level of living leaf bases: such samples contained only living leaves, attached leaf litter and reproductive material and were taken to be an index of the amount of material that could be removed by a grazing tortoise. These are henceforth called 'clip' samples.

At the second harvesting level, a 10 cm × 10 cm square of a cover type was dug up. Below-ground standing crop could not be measured as roots often disappeared into cracks in the rock, but this harvesting level removed all material except roots, i.e. all reproductive material, living leaves, attached leaf and other litter, and basal leaf sheaths (sedges) or stolons (some grasses). These samples are henceforth called 'dig' samples, and represent total above-ground standing crop.

The cover components *S. virginicus*, tortoise turf, *F. cymosa* and *Cyperus* spp. were common enough in one or more enclosures for samples to be taken each month from November 1977 to November 1978. Samples were taken at random both within and outside the enclosures. Table 2 gives details of the places and numbers of the clip and dig samples for these cover types.

The components *S. macrostachyum* and *C. ligularis* were not sufficiently abundant in the enclosures for this sampling régime, and a reduced programme was applied (table 2). Five clip samples of each of these two components were taken each month from January to December 1978.

The remaining components were still rarer in the study areas, and a single harvest at the estimated time of peak standing crop (April 1978) was employed (table 2) for *F. ferruginea*, 'grasses' and pure stands of *C. aromaticus*. The other components were ignored initially, but by September 1978 it was clear from studies of tortoise feeding (Gibson & Hamilton 1983) that 'mosaic rock' was an important component of tortoise diet in one vegetation type (coastal mixed scrub (Gibson & Phillipson 1983)). Observation suggested that its growth pattern was

likely to be different from that of tortoise turf. Accordingly a special series of 50 cm × 50 cm clip samples was taken in November–December 1978 (table 2).

All the samples were sorted into leaf, litter, stolon/base and flower/fruit after drying and these different plant parts were weighed separately and converted to estimates of standing crop biomass *per square metre of ground covered by plant*. This unit or its energy equivalent is used throughout when production and standing crop of single plant components are discussed. Such measurements were combined later with estimates of the percentage cover of different plant and bare substrate types to give figures per area of land.

TABLE 2. GROUND-COVER STANDING CROP AND PRODUCTION SAMPLING RÉGIME

species	place†	sampling‡	sample area	number of	time	
			cm ²	samples per month		
<i>F. cymosa</i>	inside E2	dig	100	5–7	Nov 1977–Nov 1978	
	inside E3	dig	100	5–7	Nov 1977–Nov 1978	
	outside E2	clip	625	5	Nov 1977–Nov 1978	
	outside E3	clip	625	5	Nov 1977–Nov 1978	
	outside E2	dig	625	5	April 1978	
	outside E3	dig	625	5	April 1978	
	inside E2	P 1 month	625	3	Nov 1977–Nov 1978	
	inside E3	P 1 month	625	4	Nov 1977–Nov 1978	
<i>Cyperus</i> spp.	inside E2	dig	100	2–5	Nov 1977–Nov 1978	
	inside E3	dig	100	5	Nov 1977–Nov 1978	
	outside E2	clip	625	5	Nov 1977–Nov 1978	
	outside E3	clip	625	5	Nov 1977–Nov 1978	
	outside E2	dig	625	5	April 1978	
	outside E3	dig	625	5	April 1978	
	inside E2	P 1 month	625	2	Nov 1977–Nov 1978	
	inside E3	P 1 month	625	4	Nov 1977–Nov 1978	
	tortoise turf	inside E2	dig	100	5	Nov 1977–Dec 1978
		outside E2	clip	625	5	Nov 1977–Dec 1978
outside E2		dig	625	5	April 1978	
outside E4		clip	625	5	April 1978	
inside E2		P 1 month	625	6	Nov 1977–Dec 1978	
<i>S. virginicus</i>	inside E1	clip	625	5	Nov 1977–Dec 1978	
	outside E1	clip	625	5	Nov 1977–Dec 1978	
	inside E1	dig	625	5	Nov 1977–Dec 1978	
	outside E1	dig	625	5	Nov 1977–Dec 1978	
	inside E1	P 1 month	625	5	Nov 1977–Dec 1978	
	inside E1	P 2 month	625	5	Nov 1977–Dec 1978	
<i>C. ligularis</i>	396059	clip	625	5	Dec 1977–Nov 1978	
<i>S. macrostachyum</i>	400064	clip	625	5	Dec 1977–Nov 1978	
<i>F. ferruginea</i>	395058	clip	625	5	April 1978	
<i>C. aromaticus</i>	outside E4	clip	625	5	April 1978	
	outside E2	clip	2500	6	Nov–Dec 1978	
	inside E5	P 1 month	2500	6	Nov–Dec 1978	
mosaic rock	outside E2	clip	2500	6	Nov–Dec 1978	
	inside E5	P 1 month	2500	6	Nov–Dec 1978	
	outside E5	P 1 month	2500	10	Nov–Dec 1978	

† Six-figure map references refer to figure 1. E5 was a dry stone wall enclosure at 397059.

‡ P 1 month refers to sample plots repeatedly clipped every month; P 2 month refers to plots clipped every other month.

(vii) *Production by herbaceous vegetation*

Clearly, an absolute, minimal estimate of above-ground production could be gained from monthly changes in standing crop, or a very crude estimate from twice the peak value of the live standing crop (Hughes 1971). More accurate measurements of the above-ground production

were needed, especially of the commonest cover components and those regularly used by tortoises. In particular, a method was needed for assessing the impact of tortoise grazing and for estimating the net production when tortoise grazing was prevented.

The best method with the equipment available would have been to estimate turnover directly by following marked tillers (Williamson 1975) as we did for the woody plants. Unfortunately, tags were removed by land crabs, which could not be kept out of the exclosures. Attempts were therefore made to mimic tortoise grazing. A randomly located series of 25 cm × 25 cm plots of the cover component in question was chosen at the beginning of the study in November 1977. The same plots were then clipped to leaf base level (as for clip samples) each month. These samples are henceforth called 'production' samples. A full year's series of production samples was obtained of tortoise turf, *F. cymosa*, *Cyperus* spp. and *S. virginicus*, inside the exclosures. An additional series of production samples of *S. virginicus* was clipped every two months. Details of this sampling régime are given in table 2.

Other cover components were not included in the production samples, except mosaic rock, from which a single series of production samples was obtained in November–December 1978 (table 2).

Results were expressed in kilojoules per square metre of ground covered by plant type for later conversion to net production per unit area of land.

RESULTS

The full results are available through the authors. A summary of results has been deposited in the archives of the Royal Society and in the British Library, Lending Division.†

(a) Energy equivalents of plant material

Table 3 shows the energy equivalents of different types of plant material sampled in July 1978, and table 4 shows the seasonal patterns of change in energy equivalent of selected materials (tortoise turf, *Terminalia boivinii* Tul leaf litter, *S. virginicus* leaf and *Cyperus* spp. leaf). Ash contents are given when measured.

In general the values obtained for different materials were within the range reported by other authors (e.g. Cummins & Wuychek 1971; Golley 1960; Lieth 1975). Samples of tortoise turf, however, had much lower energy equivalents than other plant material. This is evident in the seasonal samples (table 4), where *Cyperus* spp. and *S. virginicus* showed a slight seasonal pattern with energy equivalents being lowest at the time of growth initiation in the early wet season (December–March). This pattern was obscured in tortoise turf by the higher variability between months.

A probable reason for this was the greater chance of contamination of the samples with soil when the standing crop was lowest (note the high ash content of January tortoise turf). Such contamination could not be avoided completely when clipping turf less than 5 mm high. For this reason, measures of tortoise turf production and standing crop in grams per square metre of plant were probably overestimated by about 10–15%, making correction for each month's energy equivalent imperative.

† 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 10042).

TABLE 3. ENERGY EQUIVALENTS OF ALDABRAN PLANT MATERIALS

plant type	energy equiv. kJ (g dry wt) ⁻¹		ash content (%)	ash-free e.e.	number of samples
	mean	s.d.			
sedge leaves					
<i>Cyperus</i> spp.	16.952	0.420	7.00	18.228	3
<i>F. cymosa</i>	17.839	0.366	4.38	18.656	3
<i>C. ligularis</i>	18.066	0.260	5.86	19.191	3
sedge litter					
<i>Cyperus</i> spp.	18.200	0.148	4.81	19.119	2
<i>F. cymosa</i>	18.007	0.307	2.04	18.382	2
<i>C. ligularis</i>	17.488	0.169	2.49	17.935	3
sedge basals					
<i>Cyperus</i> spp.	18.291	0.161	4.10	19.073	3
<i>F. cymosa</i>	17.678	0.515	4.80	18.569	3
sedge flowers					
<i>Cyperus</i> spp.	16.388	0.192	9.535	18.115	3
<i>F. cymosa</i>	16.384	0.746	6.08	17.445	3
<i>C. ligularis</i>	16.830	0.503	5.49	17.807	3
grass leaves					
tortoise turf†	15.503	0.493	12.03	17.632	3
<i>S. macrostachyum</i>	16.132	0.229	8.43	17.617	3
<i>S. virginicus</i> †	18.460	0.566	n.d.		
other grasses	17.468	0.678	3.85	18.160	3
grass litter					
<i>S. macrostachyum</i>	17.365	0.389	5.80	18.721	2
<i>S. virginicus</i>	18.023	0.337	10.732	20.167	2
miscellaneous herb layer plants and grass parts					
tortoise turf flowers	14.248	0.265	n.d.		3
<i>S. virginicus</i> stolons	18.219	0.102	2.70	18.724	3
herb (October)	16.799	0.561	n.d.		2
<i>C. bigibbosus</i> litter (April)	17.460	0.399	9.425	19.277	3
shrub species: leaf litter falling into litter traps each month and April clips					
<i>G. speciosa</i> litter	19.249	0.068	5.39	20.345	3
<i>G. speciosa</i> clip, fresh leaves	17.753	0.228	6.28	18.943	3
<i>A. dimidiata</i> litter	19.991	0.422	5.99	21.264	2
<i>A. dimidiata</i> clip, fresh leaves	19.461	0.609	5.97	20.697	2
<i>M. aethiopicum</i> litter	18.269	—	10.48	20.409	1
<i>M. aethiopicum</i> clip, fresh leaves	18.643	0.040	11.49	21.064	3
<i>M. senegalensis</i> litter	16.712	0.181	10.406	18.654	3
<i>M. senegalensis</i> clip, fresh leaves	16.547	0.192	9.99	18.384	3
<i>O. ciliata</i> litter†	17.486	0.706	5.25	18.454	2
<i>T. boivinii</i> litter	18.664	0.383	12.398	21.305	3
<i>F. ramontchii</i> litter	20.781	0.543	9.29	22.910	3
<i>Ficus</i> litter	17.761	0.160	9.08	19.534	3
<i>T. populneoides</i> litter	17.084	0.491	n.d.		
<i>P. multiflora</i> litter	20.299	0.106	7.37	21.915	3
<i>M. hildebrandtii</i> litter	18.670	0.232	8.48	20.399	1
shrub species: flowers and fruit falling into litter traps					
<i>G. speciosa</i> (flowers)	16.695	0.473	10.28	18.608	3
<i>M. aethiopicum</i> (fruit)	18.785	0.228	4.09	19.586	3
<i>A. dimidiata</i> (fruit)	19.917	0.297	3.18	20.571	3
twigs of mixed species falling into litter traps					
other	16.697	0.215	7.37	18.025	3

† Materials chosen for determination of calorific values each month throughout the year, as shown in table 4.

PRIMARY PRODUCTION OF ALDABRA

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TABLE 4. SEASONAL CHANGES IN ENERGY EQUIVALENTS OF SELECTED PLANT MATERIALS

(Conventions as for table 5.)

month	energy equivalent kJ (g dry wt) ⁻¹		ash content (%)	ash-free	number of samples
	mean	s.d.			
tortoise turf					
Jan	13.208	0.351	19.43	16.170	3
Feb	n.d.				
Mar	14.265	0.473			2
Apr	11.769	0.502			2
May	13.957	0.180			2
Jun	n.d.				
Jul	15.503	0.493	12.03	17.623	2
Aug	16.349	—			1
Sep	15.786	—			1
Oct	16.200	0.451			2
Nov	15.505	0.605			2
Dec	15.997	0.414			2
<i>Terminalia boivinii</i> litter					
Jan	no leaf fall				
Feb	no leaf fall				
Mar	18.248	—			1
Apr	17.819	0.163			2
May	18.981	0.120			2
Jun	n.d.				
Jul	18.664	0.383	12.40	21.305	3
Aug	n.d.				
Sep	18.124	0.197			2
Oct	17.619	0.112			2
Nov	n.d.				
Dec	17.537	0.130			2
<i>Sporobolus virginicus</i> leaf					
Jan	16.534	0.736			2
Feb	17.229	—			1
Mar	16.949	—			1
Apr	18.398	0.462			2
May	18.620	0.445			2
Jun	17.301	0.118			2
Jul	18.460	0.566			3
Aug	16.811	0.111			2
Sep	17.317	0.066			2
Oct	17.045	0.279			2
Nov	18.065	0.279			2
Dec	17.459	—			1
<i>Cyperus</i> spp. leaf					
Jan	16.425	0.063	6.40	17.548	2
Feb	16.315	0.182	5.55	17.273	2
Mar	17.701	0.141			2
Apr	n.d.				
May	16.768	0.190			2
Jun	n.d.				
Jul	16.952	0.420	7.00	18.228	3
Aug	n.d.				
Sep	16.826	0.093	5.595	17.762	2
Oct	n.d.				
Nov	17.282	0.162	5.05	17.762	2
Dec	17.256	0.437			2

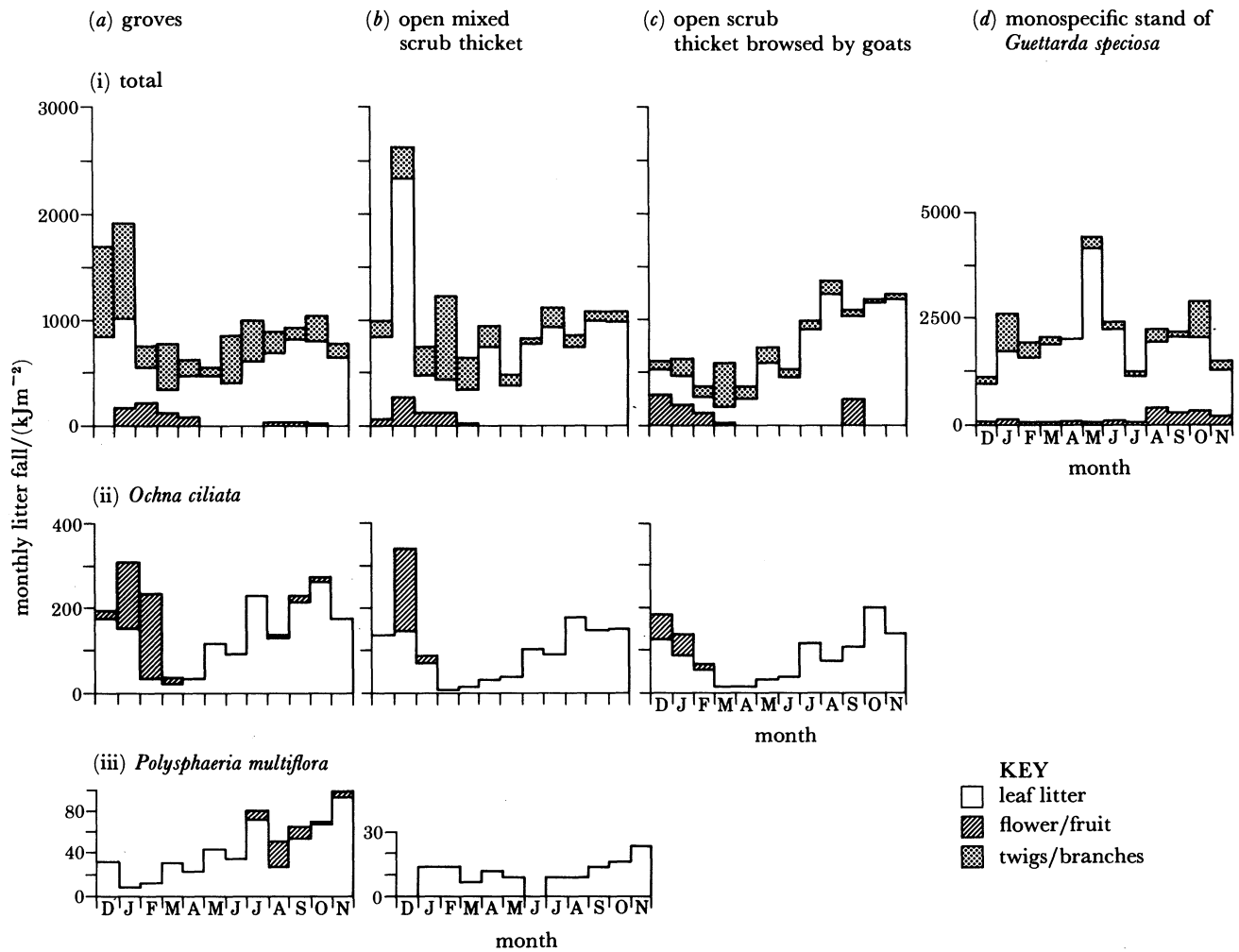


FIGURE 4. Seasonal patterns of litter fall (in kilojoules per square metre of bush per month) in the four sets of litter traps whose positions are shown in figures 1 and 2. The first row of histograms (i) shows total litter fall into the traps, by components of leaves, flowering/fruited material and twigs/branches. The second row (ii) shows *O. ciliata*, one of the species chosen for turnover studies and one of the dominants in the Cinq Cases area mixed scrub. The bottom row (iii) shows *P. multiflora*, another common mixed scrub species of different phenology to *O. ciliata*. Since (d) shows results from litter traps placed under a monospecific stand of *G. speciosa*, *G. speciosa* litter fall equals the total.

S. virginicus presented a similar clipping problem, being often less than 5 mm high, but, as it was growing in coarse sand rather than fine soils, substrate and sample were much easier to separate.

(b) Litter fall from woody plants in different areas

Except in the monospecific stand of *G. speciosa*, litter fall in any one area resulted from a variety of species with different phenologies. Given the heterogeneity in plant composition of Aldabra it follows that the seasonal pattern of litter fall, and hence availability of woody plant material to tortoises, is likely to differ from place to place. Figure 4 provides an illustration of this and shows the seasonal patterns of (i) total fruit and litter fall in the four study sites (effectively *G. speciosa* litter fall in the coastal site), (ii) litter fall of one of the dominant species in the inland sites, namely *O. ciliata*, and (iii) litter fall from a common inland species of

strikingly different leaf fall phenology (*P. multiflora*). Clearly, there was considerable variation in fruit and litter fall between sites. The general trend is one of decreasing litter fall from the coastal *G. speciosa* (9.178×10^6 g per hectare of bush per year) through the open mixed scrub to the groves site some 3 km inland (4.02×10^6 g ha⁻¹ a⁻¹). A possible explanation of this pattern can be attributed to the phenology of leaf production and is discussed fully later.

It should be noted that the results in table 4 are expressed as kilojoules per square metre of plant cover and are thus directly comparable with the figures for leaf production and standing crop outlined in the following section.

(c) *Leaf production and standing crop*

Raw data on the size and condition of leaves in each shoot/subshoot were converted to biomass per shoot/subshoot by using the length:area and length:dry weight relations described on p. 172 and shown in table 5. These estimates were converted to values per square metre of ground covered by bush by the method described before, with use of the results from the peak standing crop of April 1976 obtained by 'vertical quadrat' clips and shown in table 6.

Leaf turnover and production were calculated as described in Methods. The resulting estimates of the standing crop and production of leaves are shown in figures 5 and 6, and the phenology of flower and fruit production in figure 7.

The timing and seasonability of leaf production and the timing of peak standing crop varied considerably between species and, for *G. speciosa*, between different parts of the same stand. Each species being considered separately, the principal features of production and the phenology of the standing crop were as follows. (All production figures are per square metre of ground covered by plant.)

(i) *Apodytes dimidiata* (Total production, 29 053 kJ m⁻² a⁻¹; peak standing crop 22 214 kJ m⁻²; production/peak standing crop, 1.31.)

Although this species is usually evergreen on Aldabra, the leaf standing crop was very low during the dry season compared with the peak standing crop (figure 5), and leaf production (figure 6) was concentrated during the early wet season, with only a small response to the unseasonable high rainfall in July (figure 8). Flower and fruit production were likewise concentrated in a short period with an additional dry season peak.

(ii) *Ochna ciliata* (Total production 16 248 kJ m⁻² a⁻¹; peak standing crop, 11 158 kJ m⁻²; production/peak standing crop, 1.46.)

This was the only completely deciduous species studied. Flowers appeared before the leaves and all production was concentrated at the beginning of the wet season, with only a minute response to rain in the dry season. This last response on the deciduous trees was much more conspicuous than important in terms of leaf dry weight produced.

(iii) *Guetarda speciosa* (Total leaf production, 24 000 kJ m⁻² a⁻¹; peak standing crop, 9 263 kJ m⁻²; production/peak standing crop, 2.59.)

The mean time of peak standing crop was March (figure 5). The patterns of leaf production varied considerably with the height and aspect of shoots (figure 6). The experimental stand was exposed to the southeast trade winds and the low production in the exposed sites (windward, northeast and southwest) compared with the relatively sheltered ones (lee and canopy top) reflected this; indeed a visible rime of salt spray was sometimes deposited on the exposed leaves. When this happened, leaves died quickly and new growth was of a heavy cristate form, apparently more resistant to salt spray. The effect of exposure on flowering (figure 7) was even

TABLE 5. CALIBRATIONS USED TO CONVERT NUMBERS AND SIZES OF LIVING LEAVES ON SHRUBS TO DRY WEIGHT

(a) Length (L): area (A) relations

species	regression equations	correlation coefficients	number of leaves
<i>G. speciosa</i>	$A = 0.805 L^2 - 0.313$	0.993	49
<i>O. ciliata</i>	$A = 0.514 L^2 + 0.214$	0.961	50
<i>A. dimidiata</i>	$A = 0.546 L^2 + 0.381$	0.984	50
<i>M. aethiopicum</i>	$A = 0.683 L^2 + 0.032$	0.986	49
<i>M. senegalensis</i>	$A = 0.639 L^2 - 0.552$	0.959	49

(b) Dry weights per unit area of leaf

(Figures for different size classes of leaves are given for all species save *O. ciliata*: small leaves are more likely to be immature and lighter per unit area than large ones. In *O. ciliata* leaf expansion was fast and seasonally synchronized and so all size classes were combined.)

species	size class	mean weight/area	s.d.
	mm	mg cm ⁻²	
<i>G. speciosa</i>	≤ 50	6.80	3.04
	≤ 239	5.33	0.835
	≥ 240	7.79	0.861
<i>O. ciliata</i>	all	6.15	1.06
<i>A. dimidiata</i>	< 50	7.37	3.71
	< 80	9.65	2.89
	> 80	9.99	1.55
<i>M. aethiopicum</i>	< 30	5.35	0.922
	< 60	10.73	2.62
	> 60	11.3	2.23
<i>M. senegalensis</i>	< 37.5	6.45	1.33
	> 37.5	10.87	3.56

TABLE 6. APRIL STANDING CROP OF SHRUB SPECIES (IN GRAMS PER SQUARE METRE OF GROUND COVERED BY BUSH)

(There was no flowering or fruiting material save a trace in *M. aethiopicum*.)

	leaf		twig		total	
	mean	s.d.	mean	s.d.	mean	s.d.
<i>A. dimidiata</i>	1134	208	146	34	1281	237
<i>O. ciliata</i>	638	163	85.9	33.5	724	189
<i>G. speciosa</i>	390	126	111	46.9	501	126
<i>M. senegalensis</i>	1001	241	530	124	1531	353
<i>M. aethiopicum</i>	1111	246	260	73.2	1371	301

more dramatic: although success of fruit set peaked in the trade wind season, virtually the only fruits set were on lee and canopy top shoots, and the only fruits in litter traps came from the two westernmost traps. Only the sheltered shoots produced a flush of new growth after unseasonable July rain (figures 6, 8).

Shoots less than 1 m above ground at the start of measurements also fared badly; at the end of the study most had been removed by tortoises or goats and their net production was low.

An important result of this pattern of production within stands was that lee and top shoots elongated much more rapidly than the others. Such asymmetric growth results in the tree becoming top heavy, and individual shoots were observed to have sunk through the canopy towards the ground by about 50 cm vertical height per year. Thus new growth is constantly being

produced at the top and lee of the tree and being exposed to herbivores as it falls slowly towards the ground. Provided that production exceeds herbivore damage, the tree continues to elongate, producing the curious shape shown in figure 2.

The sheltered shoots were capable of continuous growth through the year and could respond very rapidly to increased rainfall, although the peak of growth was at the beginning of the wet season. Although the trees never lost all their leaves, the peak standing crop of leaves in the wet year of 1977–1978 was over six times the minimal standing crop of leaves in the dry season. *G. speciosa* is capable of losing all its leaves and subsequently recovering (own observation).

(iv) *Maytenus senegalensis* (Total leaf production, 28 120 kJ m⁻² a⁻¹; peak standing crop, 18352 kJ m⁻²; production/peak standing crop, 1.53.)

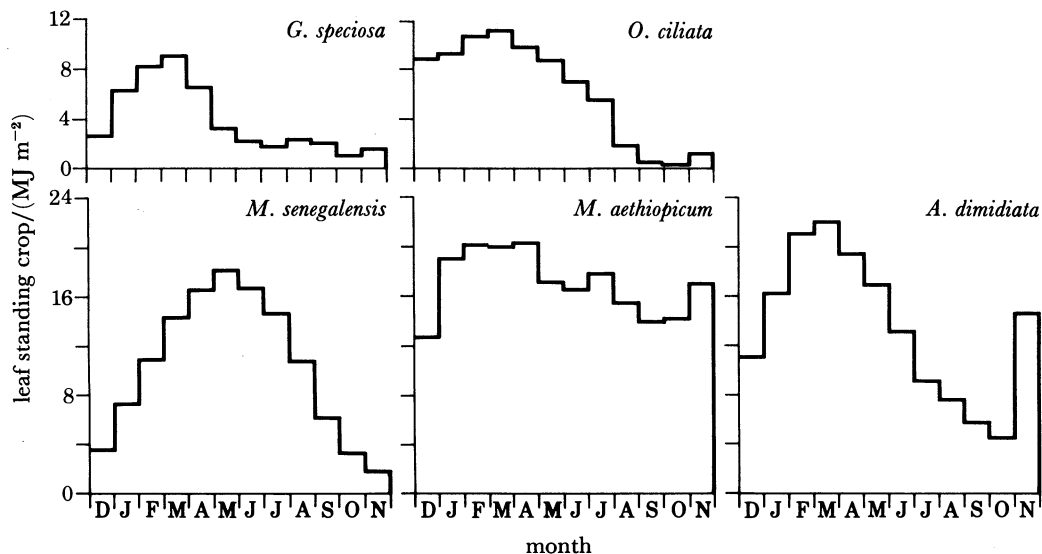


FIGURE 5. Seasonal changes in leaf standing crop (in megajoules per square metre of plant) for the five species chosen for turnover studies, based on results from tagged shoots.

In this species new leaves are produced only in the wet season; the species does not respond to July rain. It rarely loses all its leaves in the dry season, but the minimal standing crop of leaves was less than 10% of the maximum for the years, and there was extensive die-back of shoots from the newest growth. Fruit production (figure 7) was very low and concentrated in the late wet season. Total shoot production was the highest of all species, however, and up to five orders of branching were produced in the one season.

(v) *Mystroxydon aethiopicum* (Total leaf production, 40 142 kJ m⁻² a⁻¹; peak standing crop, 20 176 kJ m⁻²; production/peak standing crop, 1.94.)

This species showed a similar phenology of leaf production to *G. speciosa*. *M. aethiopicum* has much smaller leaves than *G. speciosa* and a higher weight/area for mature leaves (table 5); it lost a smaller proportion of its leaves during the dry season (figure 5), and perhaps for this reason was able to respond to July rain more than any other species studied (figures 6, 8). Flowering was erratic and continuous, with a small number of fruit set overall: however, differences in fruiting between the species may have been characteristic of year rather than of species and it is not possible to generalize about the relative contributions of different species to the seed rain on Aldabra (except in species such as *O. ciliata* and *A. dimidiata*, which produced a conspicuous and short-lived fruit fall in all three years for which it was observed (1977–1979)).

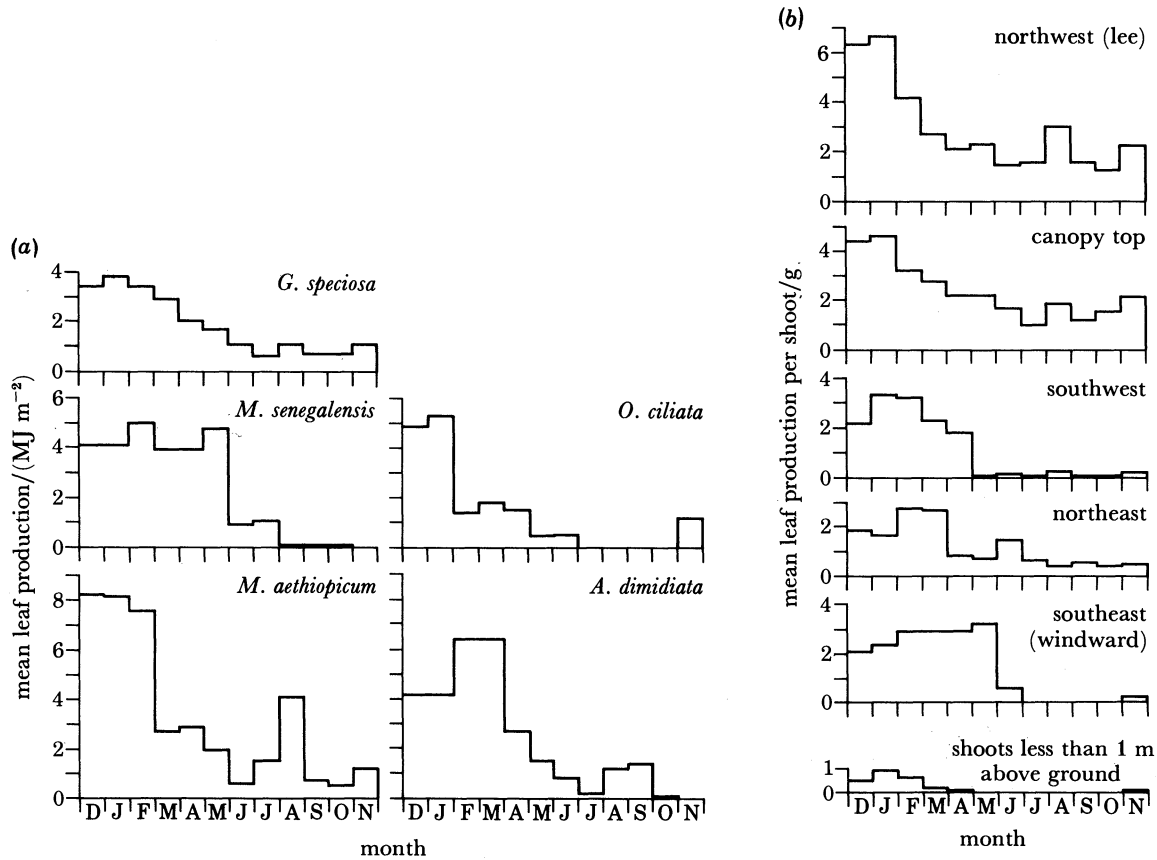


FIGURE 6. Mean leaf production in each month for the five shrub species chosen for turnover studies. (a) Leaf production for all shoots of a particular species, expressed in megajoules per square metre of plant. (b) Production of shoots at different sites within the monospecific stand of *G. speciosa*, expressed as grams per shoot.

(d) *Ground vegetation standing crop and production*

(i) *Tortoise turf* (exclosure 2)

The standing crop of tortoise turf outside the exclosure (figure 9*a, b*) was low at all seasons (peak in May at 67.5 g per square metre of plant ≈ 942 kJ per square metre of plant) and varied in a manner that did not follow rainfall patterns (figure 8). Part of the explanation for this lies in seasonal variations in tortoise activity and is dealt with elsewhere (Gibson & Hamilton 1983). Grazed areas of tortoise turf were less than 0.5 cm high throughout the year; in contrast (figure 9*a*), tortoise turf protected from grazing grew into a thick mat of fine vegetation still under 10 cm high but reached a peak standing crop in September of 544 g (7590 kJ) per square metre of plant, over eight times the value for grazed turf. Production samples from inside the exclosure (figure 9*c*) gave a total annual production of 3165 kJ per square metre of plant, less than half the peak standing crop of ungrazed turf.

In most cases where the production of grass swards under different grazing régimes has been studied (see Kelly & Walker (1976) and McNaughton (1979) for tropical grassland examples), it has been found that production by ungrazed turf is somewhat less than that by lightly grazed swards. However, as grazing pressure increases, production drops off again until a point of degradation and eventual erosion and death of the sward is reached. Since repeated clipping

of the same plots each month for production samples gave rise to a turf similar in appearance and height to the grazed sward outside, it is likely that the clipping was a reasonable mimic of tortoise grazing. If the general grazing–production model outlined above applies to tortoise turf on Aldabra, then the tortoises were ‘overgrazing’ in the sense that they were depressing the production of their food well below its maximum (values from production samples were less than half the absolute minimum (peak standing crop minus minimum standing crop) production of ungrazed turf.

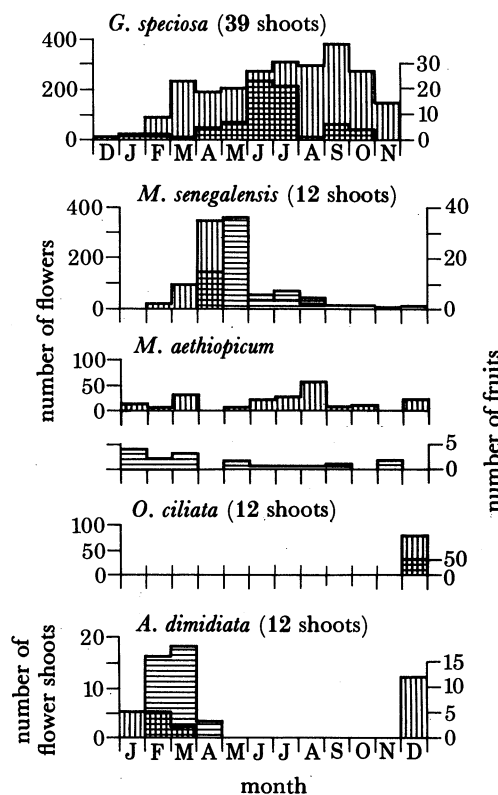


FIGURE 7. Phenology of flowering and fruiting in the tagged shoots of the five shrub species chosen for turnover studies, expressed as the numbers of flowers/fruits or flower sites/fruits in each month of the study. Histograms of flowers and fruits for each species are plotted separately, not additively.

Note. Flowering of *O. ciliata* only occurs once in the study period. This is caused by the marking method: in this species flowers are produced before the new shoots at the end of the dry season; hence flowers from 1977 were not recorded with the new shoot growth.

(ii) *Sporobolus virginicus* coastal turf (enclosure 1)

In contrast to the habitat provided by open mixed scrub with a high percentage of tortoise turf cover, *S. virginicus* coastal turf is only grazed heavily by tortoises for a short time at the beginning of the wet season (Voeltzkow 1897; Swingland & Lessels 1979). This is likely to account for the observed seasonal pattern of standing crop.

Figure 10 shows the seasonal changes in standing crop of clip samples from outside the enclosure and the seasonal changes in production of monthly and bimonthly production samples of *S. virginicus* from inside the enclosure. Comparison of figure 10a with figure 8 indicates that the standing crop of *S. virginicus* outside the enclosure was inversely related to rainfall. Peak

standing crop was attained at the end of the dry season, when tortoise grazing was at a minimum, and standing crop leaf and leaf litter fell to a minimum of 553 kJ per square metre of plant in January, 1 month after the peak in tortoise grazing (Gibson & Hamilton 1983).

The monthly clip production samples are directly comparable with the tortoise turf production samples. In contrast to the tortoise turf (3165 kJ per square metre of plant per year), they produced only 1360 kJ m⁻² a⁻¹. The bimonthly clip production samples were slightly higher, 1940 kJ m⁻² a⁻¹. If a similar type of grazing–production model to that suggested for tortoise turf applies, this means that *S. virginicus* was showing a quantitatively different response to tortoise grazing than was tortoise turf. In particular, *S. virginicus* was less tolerant of extremely heavy grazing than the tortoise turf. If the *Sporobolus* had been grazed at the intensity represented by monthly clips for the whole year instead of for only two months, the turf would probably have been degraded or even destroyed.

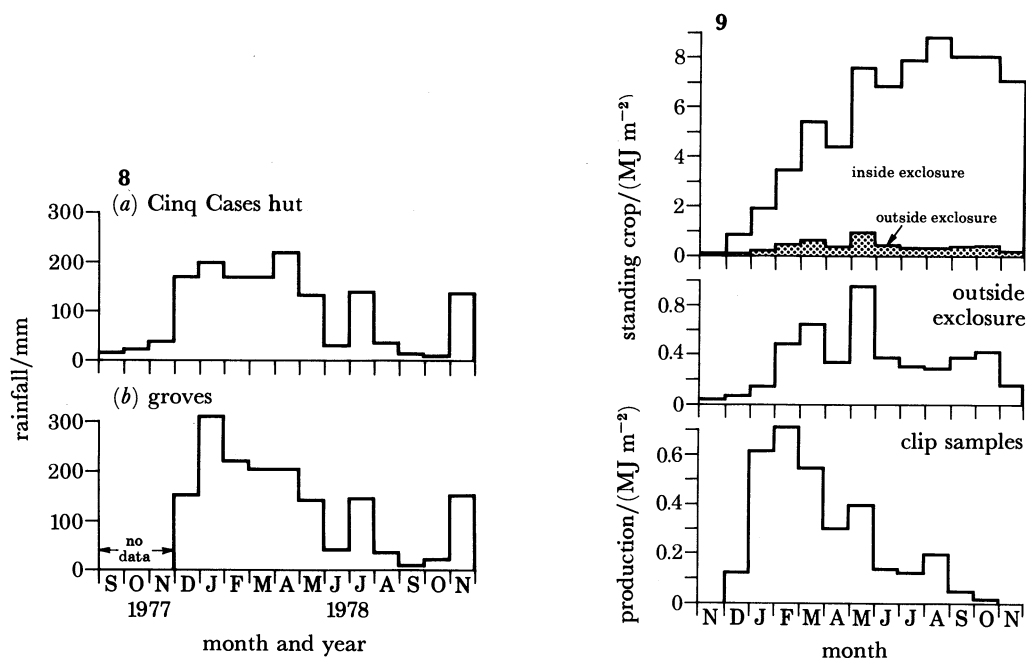


FIGURE 8. Rainfall at two sites in the Cinq Cases region, recorded in standard Meteorological Office copper rain gauges, from September 1977 to November 1978 inclusive. 'Months' run from the 22nd of one month to the 21st of the next, to tie in with the sampling programme for vegetation. Positions of sites are given in figure 1.

FIGURE 9. Seasonal changes in production and standing crop of tortoise turf (expressed in kilojoules per square metre of plant). Histograms are plotted separately, not additively.

It is clear that clips taken at regular intervals are unlikely to give a good estimate of production by *S. virginicus* over the whole year under irregular natural grazing. Other methods must be used to estimate this.

Two possibilities were available, with use of the results from (1) dig samples or (2) clip samples. If the year's minimal standing crop of leaf and attached litter from dig samples inside the enclosure is subtracted from the year's peak standing crop from the same sample type, this gives an absolute minimal estimate of production of 4388 kJ per square metre of plant. The same exercise for dig samples from outside the enclosure provides an estimate of 4822 kJ m⁻².

It is surprising that the estimate from inside the enclosure was not greater than that from outside, as material removed by grazing outside was not taken into account in this type of estimate. Only examining the progress of succession inside the enclosure over several years (in progress) will indicate whether this was due to sampling error, stimulation of production outside by the short period of tortoise grazing (see grazing–production relations in ‘tortoise turf’ section) or limits from the soil where long-term removal of biomass from an area of deep sand may have produced a nutrient-poor environment dependent on tortoise activities such as defaecation for growth to occur. Areas of *S. virginicus* topographically protected from tortoise grazing elsewhere on the atoll produced a considerably greater biomass (Hnatiuk *et al.* 1976).

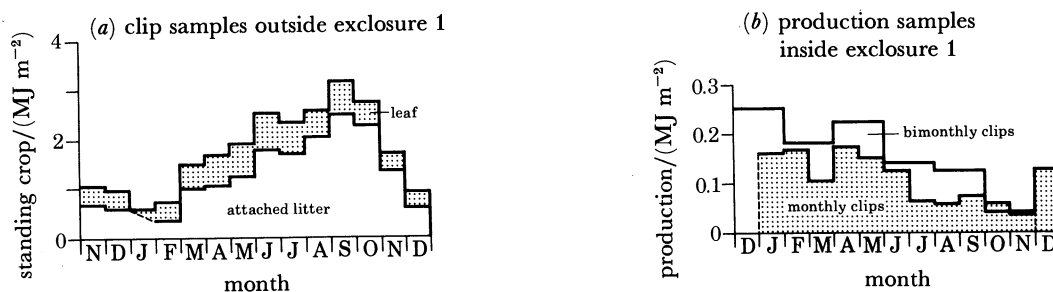


FIGURE 10. Seasonal changes in standing crop and production of *S. virginicus* turf (expressed in megajoules per square metre of plant).

TABLE 7. ABOVE-GROUND PRODUCTION OF SEDGES (IN KILOJOULES PER SQUARE METRE OF SEDGE PER YEAR)

method of estimation and sample type	in open	in shade
<i>(a) F. cymosa</i>		
(A) total of production samples	3494	4221
(B) clip samples outside enclosures; year's peak standing crop of leaf and attached leaf litter, minimum during the year	6836	4380
(C) total above ground in dig samples in enclosures, calculated as in (B)	25100	25000
(D) 2 × peak leaf standing crop inside enclosures	10632	20514
<i>(b) Cyperus spp.</i>		
(A) as above	10639	3335
(B) as above	7378	4914
(C) as above	49800	22080
(D) as above	36640	16374

A better estimate of the production available to grazing tortoises can be obtained by subtracting the year's minimal standing crop from clip samples outside the enclosure (figure 10) from the year's peak standing crop in the same sample set, and then adding production (from the bimonthly production samples) for the period before peak standing crop in 1978 when tortoises were removing material. This gives an estimate of 'tortoise-usable production' of 3223 kJ per square metre of plant per year, similar to the 3165 kJ m⁻² a⁻¹ reported above for tortoise turf.

(iii) *The commoner sedges: Fimbristylis cymosa and Cyperus spp.* (enclosures 2 and 3 and areas outside them)

Figure 11*a* shows seasonal changes in standing crop and figure 11*b* gives the phenology of flowering in *F. cymosa* and *Cyperus* spp.

Estimates of production are complicated in these species by the persistence and variability of attached leaf litter. The compact, mat-like growth form of some plants of *F. cymosa* allows several seasons' growth to be still attached to the shoots, but in other plants first-year tussocks already had much leaf litter attached and in yet others trampling by tortoises outside the enclosures had removed some or all of the attached leaf litter. The problem was less acute with *Cyperus* spp.; nevertheless, more than one year's leaf litter may still have been attached and there was no way of assessing how many seasons' growth was in a particular sample.

Harvest methods were nevertheless useful as the appearance of production sample sites after several months' clipping showed that the régime represented a far heavier grazing pressure on these sedges than they actually suffered from tortoise grazing.

Table 7 shows four ways in which real above-ground production in these sedges can be estimated. The first method (A) is the total of clipped production samples for the year, and shows what the probable production would be if tortoises grazed these sedges as heavily as they do tortoise turf. The second method gives a minimal estimate of what was available to the tortoises under the grazing régime that the sedges actually suffered. This method (B) involved subtracting the year's minimal standing crop from clip samples outside the enclosures from the peak standing crop for the same sample series. The third method (C) gives a minimal figure for total above-ground production if there was no tortoise grazing or trampling. It was calculated by subtracting the year's minimal above-ground standing crop in dig samples from the year's peak standing crop in dig samples (inside the enclosures). The fourth method (D) ignores dead material completely, but assumes a turnover rate such that production for the year was twice the peak standing crop of living leaves. Like method (C) it gives an estimate of production without tortoise grazing or trampling.

The results from method (A) are clearly too low for what is required, an estimate of production available to tortoises under the current grazing régime. Method (B), again, provides a minimal estimate because it takes no account of turnover. The same criticism applies to method (C), which if used as an index of herbivore-available production, would overestimate consumption by including plant parts unlikely ever to be taken by tortoises (leaf bases and older attached litter). Method (D) gives lower estimates relative to (C) in the open than in the shade; this could be either because production is lower or because turnover rate is higher in the open. Despite this, method (D) seems to be the most reliable for estimating leaf production available to tortoises.

In fact tortoises rarely ate the sedge leaves but did take the flowers in the wet season (Grubb 1971; Gibson & Hamilton 1983). Figure 11*b* shows that flowers and fruiting material were only available for a short period in the wet season (January–April). This means that doubling the peak standing crop of flowers would probably greatly overestimate production as flowering in the sedges was much more of a single-cohort event than was leaf production. Thus the peak standing crop of flowers minus the minimal standing crop for the year (i.e. 0), is probably nearer a true estimate of total production of flowering material. When two distinct flowering periods took place in the year, they were counted as separate episodes and added together to give the figures shown in table 8.

It is apparent that flower production by *F. cymosa* was lower in the open while that of *Cyperus* spp. was lower in the shade. Since leaf production followed a similar pattern (table 7) and

PRIMARY PRODUCTION OF ALDABRA

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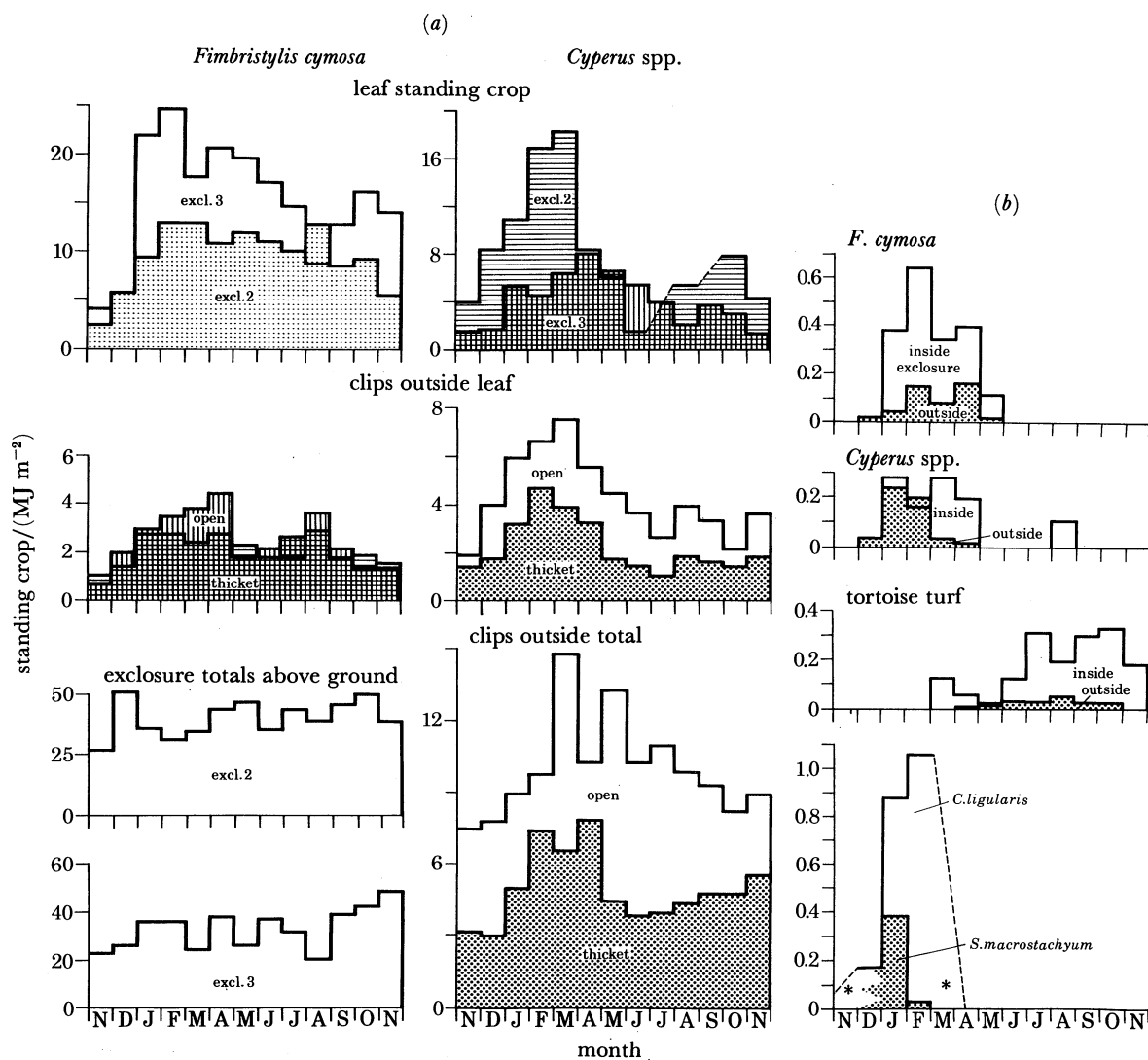


FIGURE 11. (a) Changes in standing crop of sedge species. (b) Flowering phenology of ground cover. (Standing crop expressed in megajoules per square metre of plant. Asterisk indicates 'data missing'.)

TABLE 8. PRODUCTION OF FLOWERS BY SEDGE SPECIES (IN KILOJOULES PER SQUARE METRE OF SEDGE PER YEAR)

species and sample	inside exclosure, A	outside exclosure, B	A - B	(A - B)/A
<i>F. cymosa</i> in open	639	241	398	0.62
<i>F. cymosa</i> in shade	1049	91	958	0.91
<i>Cyperus</i> spp. in open	1114	590	524	0.47
<i>Cyperus</i> spp. in thicket	528	244	284	0.54

F. cymosa generally grows in the open while *Cyperus* spp. are usually shade species, this might seem a paradox. However, the distribution of the plants was such that one is comparing *F. cymosa* in the open with *F. cymosa* in light shade, while comparing *C. niveus* production in the open with a mixture of a small amount of *C. niveus* in light shade and a large amount of *C. bigibbosus* in deep shade. Thus the comparison is not simply between shade and open conditions: degree of shade and species distributions must be taken into account.

Table 8 also shows that the production of sedge flowers was much greater inside a particular enclosure than outside. We cannot attribute this difference to tortoise grazing by itself, as trampling is likely to have had as great an effect on the relatively fragile flowering stems; we can regard the difference, however, as a general 'index' of tortoise effect (table 8, columns 3 and 4).

In general, estimates of the production of sedge species outside the enclosures, where there was natural grazing and trampling, showed that these species were capable of much greater production than tortoise turf or *S. virginicus* turf accessible to tortoises. Despite this, sedges do not replace tortoise turf in the open mixed scrub vegetation. Possible explanations require knowledge of further details of tortoise movements, feeding patterns and nesting behaviour.

TABLE 9. ESTIMATES OF PRODUCTION FOR OTHER COVER TYPES: *C. LIGULARIS*, *S. MACROSTACHYUM* AND 'MOSAIC' ROCK VEGETATION

(a) Production of *C. ligularis* and *S. macrostachyum* (in kilojoules per square metre of plant per year)

method	<i>S. macrostachyum</i>	<i>C. ligularis</i>
peak leaf and attached litter standing crop during year (minimum)	25 555	57 300
2 × peak leaf and flower standing crop	41 298	47 658

(b) Relation between standing crop and production of tortoise turf and mosaic rock in November–December 1978

samples	'mosaic'	tortoise turf	$\frac{\text{'mosaic'}}{\text{tortoise turf}}$
November standing crop outside enclosure†	320	153	2.09
November standing crop inside enclosure	561		
production Nov–Dec	143	294	0.49

(c) *F. ferruginea* and 'grasses' (in kilojoules per square metre of plant per year)

	<i>F. ferruginea</i>	grass (excl. 3)
2 × April standing crop	38 200	5639

† For studies on 'mosaic' an existing dry-stone wall enclosure at map reference 396060 was renovated for use in production studies (see also Methods). For tortoise turf the usual plots in enclosure 2 were used.

(iv) Standing crop and production of the rarer sedges and mosaic rock vegetation

The restricted nature of sampling limits the methods available for calculating production.

For *S. macrostachyum* and *C. ligularis* monthly clip samples were available. These species were not important food for tortoises, except perhaps as flowers (Grubb 1971), but did suffer disturbance from tortoises seeking shade (Hnatiuk *et al.* 1976) and nesting (own and I. R. Swingland's observations). The only production estimates that can be made are from peak standing crop or year's minimum standing crop from twice peak leaf standing crop (table 9). The latter is used in the rest of the paper for compatibility with measurements of the other components of ground cover.

For the sedge *F. ferruginea* and long grasses (table 9), estimates only from twice the live standing crop in April were possible. Over all ground and shrub cover components, April was the commonest month for the standing crop to reach its peak (figures, 5, 9, 11). Although March and May were periods of peak standing crop for some cover components, the error resulting from use of April values for estimates of total standing crop and production was small because of the rarity of such components.

Mosaic rock vegetation (table 9*b*) had a higher standing crop than tortoise turf but a lower production. As mosaic rock was measured in areas of cover type including bare rock, this is to be expected. Much of the plant cover within mosaic rock was in holes up to 20 cm deep but less than 10 cm wide. Such holes could never be grazed as intensively as tortoise turf patches, even by the smallest tortoises. Thus standing crop remained high but production per square metre of mosaic was relatively small owing to the low percentage plant cover within areas of mosaic rock vegetation.

ABOVE-GROUND STANDING CROP AND PRIMARY PRODUCTION OF THE ATOLL: SYNTHESIS OF COMPONENT RESULTS AND THEIR APPLICABILITY TO DIFFERENT AREAS OF ALDABRA

So far, we have estimates of the standing crop and production of different cover components, expressed as dry weight and energy equivalents per unit area of plant cover. To assess the potential quality of an area of Aldabra for giant tortoises, we need to know not only the production and standing crop of different cover components, but also the relative proportion of total ground area taken up by each cover component, and to use these two parameters to estimate the seasonal patterns of production and standing crop in particular places.

Such an exercise is complicated on Aldabra by the great heterogeneity of the ground: the patchwork of vegetation is set in a matrix of bare coral rock. In some places bare rock covers all the ground surface and, even in the thickest closed-canopy scrub forests, soil rarely covers patches of more than a few hundred square metres, interspersed with bare rock.

Thus any synthesis of the component measurements outlined in the previous sections must take this heterogeneity into account. This study was restricted also to those areas known to be important for the tortoise population and no attempt has been made in this paper to assess productivity of other vegetation types such as *Pemphis acidula* scrub or mangroves (Gibson & Phillipson 1983).

Estimates of production and standing crop were made for those vegetation types important to tortoises, i.e. containing only the cover types studied. Such vegetation types cover most of the Cinq Cases tortoise subpopulation area and range from the coastal *S. virginicus* swards, through mixed scrub types, to the thick scrub forest of the groves.

Estimates of production and standing crop per unit of ground area were made for three separate places at the ends and in the middle of the range from open mixed scrub to thick woodland in the groves. Since the *S. virginicus* turf forms patches of single-species swards on the coast, this exercise of synthesis was not necessary for the Cinq Cases coastal grasslands. They constituted a fourth locality at map reference 397059 (see figure 10, where grams per square metre of plant is equivalent to grams per square metre of ground).

The first three sites were at map references 383070 (intermediate), 387066 (open mixed scrub) and 364089 (groves) (see figure 1). The open mixed scrub site measured 50 m × 20 m, the intermediate site 50 m × 10 m and the site at the groves 50 m × 4 m. The numbers of all woody plant species had been recorded and the ground cover in each sequential 10 cm of a 50 m × 1 cm line transect along the centre of the strip had been assigned to a cover component and shade cover (Gibson & Phillipson 1983). Table 10 shows the combined data for cover components at the three sites.

Since the object of the synthesis was to provide an estimate of the potential quality of different

areas for giant tortoises, the measures of standing crop were from clip samples outside the exclosures for all cover types. Production estimates were taken from production samples for tortoise turf, from the 'tortoise-usable production' outlined for *S. virginicus*, and from twice the peak of living above-ground standing crop for the remaining cover components except mosaic rock vegetation. The standing crop and production of mosaic rock vegetation were assumed to bear the same relation to those of tortoise turf for the rest of the year as they did in November, as mosaic rock vegetation contained mostly tortoise turf plant species.

TABLE 10. COVER COMPOSITION (AS PERCENTAGES) FOR THE EXAMPLE SITES FOR WHICH TOTAL PRODUCTION AND STANDING CROP WERE ESTIMATED

site map reference ...	387066 (open mixed scrub)	383070 (intermediate)	364089 (groves)
cover type			
tortoise turf	31.4	7.0	0
'mosaic' rock	10.2	0	0
<i>F. cymosa</i>	1.8	10.2	0
<i>F. ferruginea</i>	0	0.2	0
<i>Cyperus</i> spp.	0	0	9.8
<i>C. bigibbosus</i>	0	4.4	14.2
<i>C. ligularis</i>	6.4	0	0.6
long grasses	0	0.2	0
<i>A. dimidiata</i> type shrubs	4.3	13.4	34.7
<i>M. senegalensis</i> type	0	1.1	0
<i>M. aethiopicum</i> type	4.3	4.5	12.5
<i>O. ciliata</i> type	10.0	14.5	29.2
<i>G. speciosa</i> type	0	1.1	1.4
total ground cover	49.8	22.0	32.0
total shrub cover	18.6	34.6	69.8
total vegetation	68.4	56.6	101.8†

† Can be over 100% as a single point may have both ground layer and shrub cover.

When shrubs of species other than the five on which production estimates were made were present, these other species were assigned to the phenological type of one of the five species studied and were assumed to have the same production and phenology of the standing crop.

The results of this exercise are shown in figures 12–14. Figure 12 shows seasonal changes in estimated total standing crop of ground-cover leaves, attached leaf litter and flowering material plus shrub leaves and flowering material (figure 12*a*), ground-cover standing crop alone (figure 12*b*) and ground-cover standing crop as a percentage of the total (figure 12*c*). Figure 10 shows that the production and standing crop of *S. virginicus* swards were lower than at any of the mixed scrub sites.

The three mixed scrub sites differed not only in the total amount of material present but also in the seasonal pattern of relative availability of different components. Although the groves site had the greatest standing crop at all seasons, most of this was living shrub leaves and thus not directly available to tortoises. A greater proportion of standing crop was in the ground layer in the dry season at all sites, owing to the persistence of attached leaf litter on perennial sedges and lower variability in seasonal leaf standing crop in these sedges than in all but the most evergreen of the shrubs (*M. aethiopicum* type). Ground-cover vegetation also responded more to the unseasonable July rain than did the shrubs (figure 12*b*).

Annual production also varied considerably between sites (figure 13). Even in the site with a high cover of tortoise turf (open mixed scrub), this accounted for only a small proportion of ground-cover production: most ground-cover production here was by the sedge *C. ligularis*, of which the leaves, like those of the other sedges, formed only minor components of the tortoises' diet (Gibson & Hamilton 1983).

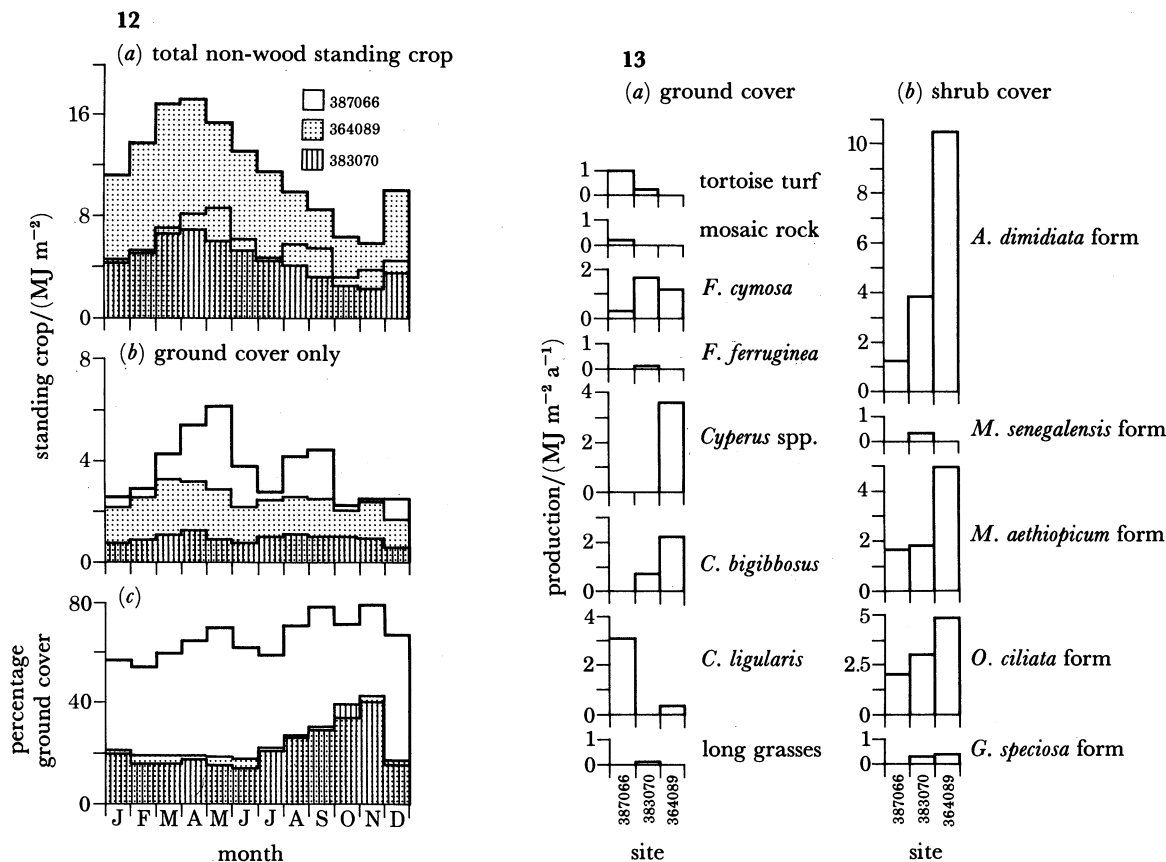


FIGURE 12. Seasonal changes in total above-ground standing crop per square metre of ground, for the three sites described in the text. Histograms are plotted separately, not additively.

FIGURE 13. Contribution of different cover types to annual production at three sites on Aldabra.

Total production (figure 14a) was three times greater in the groves site than in the open mixed scrub high tortoise turf site. This demonstrates the effect of the patchy and variable nature of vegetation cover on Aldabra on its production ecology. All three selected sites had a vegetation cover that was high compared with that in some vegetation types (Gibson & Phillipson 1983) but there was much variation even within this narrow range of vegetation sites. This variation was also evident in the ratios of production to peak standing crop in the three sites (figure 14b). A site dominated by woody plants (groves) had a much higher rate of turnover of non-wood material than either the open mixed scrub site or the intermediate site. This was another consequence of the persistent attachment of leaf litter on the perennial sedges compared with the high turnover of leafy material on the woody plants.

These three sites represent the two ends and the middle of a vegetation change within the mixed scrub (Gibson & Phillipson 1983). Although extrapolation from these sites to the whole spectrum will not give a highly accurate assessment of the tortoise habitat that the spectrum

represents, the three sites can be used to give a rough guide to the extent of different parts of the spectrum (wooded, intermediate and open areas). Of the approximately 34 km² over which the Cinq Cases tortoise subpopulation ranges (Coe *et al.* 1979), ca. 11–12 km² are thick forest comparable with groves, 3 km² are intermediate and 4 km² are open mixed scrub. The remainder of the area is under vegetation such as mangroves and *Pemphis* scrub, which are much less used by tortoises, and smaller parts are under other vegetation types used by them (Gibson & Phillipson 1983), such as the *S. virginicus* coastal sward (< 1 km²). Thus not only is the tortoise population more concentrated than is apparent at first sight, but also the open mixed scrub and *S. virginicus* swards, on which it is likely that the tortoises and the vegetation interact most strongly, together account for only about 10% of the area used by the Cinq Cases subpopulation.

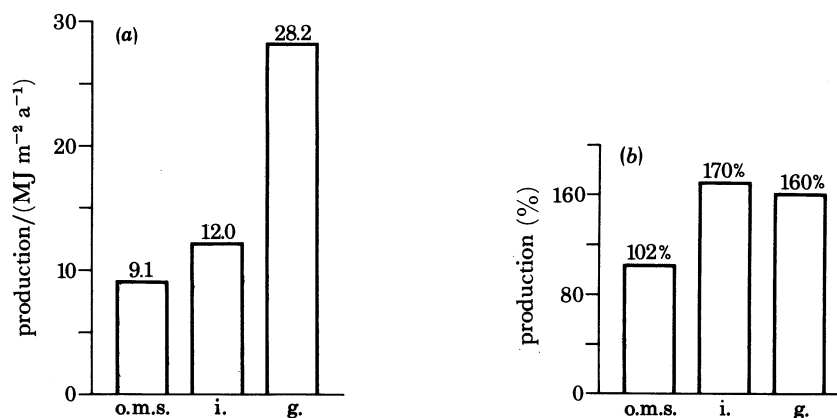


FIGURE 14. Total non-wood production of the three sites, 'open mixed scrub' (o.m.s.), 'intermediate' (i.) and 'groves' (g.), expressed in (a) absolute terms per square metre of ground and (b) as a percentage of peal standing crop.

DISCUSSION AND CONCLUSIONS

(a) *Patterns of production on Aldabra*

The level and pattern of primary production on Aldabra can be illustrated best by comparison with other areas in the semi-arid tropics (semi-arid defined here as being limited by rainfall–evapotranspiration for most of the year in most years). Such a comparison is rendered difficult by those very features that appear to determine the production of vegetation types studied on Aldabra. The difficulty is highlighted by the threefold variation in net production of material above ground level (excluding wood) between the three types of site. These sites (figure 14) did not cover the whole range of variability of vegetation on Aldabra, yet encompassed half the range of production found in tropical 'raingreen forests' of the world (7000–44 000 kJ m⁻² a⁻¹ (Lieth 1975)). The production of individual components of Aldabra's vegetation was even more variable (3165 kJ per square metre of plant per year for grazed tortoise turf and 3220 kJ m⁻² a⁻¹ for *S. virginicus* to 47 700 kJ m⁻² a⁻¹ for *C. ligularis*).

Part of the difficulty in comparison arises from the lack of standardization of methods between studies: different studies are made for different purposes and with different equipment and support. Thus comparisons are limited to those studies with compatible methods; this cannot be avoided. The other major constraints on comparison arise directly from the nature of Aldabra, in particular from the range of scales on which this raised atoll provides much

greater heterogeneity than that reported in savanna woodlands on continents, the main basis for comparison. The likely effects of these two factors, methods of study and structural heterogeneity, are discussed in detail below.

Turnover has rarely been measured directly in studies of productivity. Williamson (1975) provides a classic example of the measurement of turnover on chalk grassland, and he (1976) and Coupland (1979) assess other studies where this has been done. In the present study such measurements could only be made with the woody plant species and revealed a range of ratios of production to peak standing crop from 1.31 (the single-growth-peak, semi-evergreen *A. dimidiata*) to 2.59 (the continuously growing, exposed-site *G. speciosa*).

Net primary production of the ground cover could only be estimated from harvest-difference methods or by following the production of the same plots clipped every month. The results of these methods showed that only vegetation adapted to heavy grazing (tortoise turf) responded to repeated clipping of the same plots in an enclosure by producing a sward similar to that outside the enclosures. Results from *S. virginicus* turf suggested that this grass, although grazed very heavily by tortoises for 2 months of the year, could not stand such pressure for the whole year and probably relied for survival on the intense grazing period being short. The perennial sedges presented a different pattern again; most species were tough and resinous, their leaves were usually very little grazed and they could not withstand the artificial grazing régime imposed by repeated clips without above-ground production being drastically reduced. This régime was probably a realistic imitation of heavy tortoise grazing. Grunow *et al* (1980) discuss the error involved in measuring total production from a standard stubble-height clip and the realism of estimates from such a clip. Tortoises are very different grazing machines from the large ungulates that Grunow *et al.* (1980) were concerned with: the precise and close cut of tortoise jaws can more easily be imitated by a human being with nail scissors cutting to the base of green leaf material.

Most estimates of leaf production by woody plants have been made from litter fall or harvest methods alone (Whittaker & Marks 1975) or sometimes with small-scale studies of turnover (see, for example, Tanner 1980). In such studies between-site homogeneity of loss before litter deposition must be assumed and has been shown to be justified in particular cases (see, for example, Tanner 1980). In the present study there are strong grounds for assuming that this was not so. The decline in litter production from the coastal site through to thick woodland inland could have been assigned to real and large (2.5-fold) variation in shrub production if actual leaf production had not been measured. The greatest decline between sites was that between the coastal *G. speciosa* thicket (9.8×10^6 g per hectare of bush by leaves) to the first inland thicket (5.2×10^6 g ha⁻¹). At both these sites production was measured from the turnover of marked shoots, giving a value of 24 000 kJ m⁻² of bush per year for the *G. speciosa* thicket and 26 200 kJ m⁻² a⁻¹ for the inland thicket. Thus the difference in litter fall is unlikely to be due to real differences in production. The most likely cause for the observed discrepancy is ultimately the effect of salt exposure on the coastal thicket. This could have acted either by reducing the amount of herbivory on leaves of *G. speciosa*, or by reducing the amount of material that the tree was able to resorb during leaf senescence by rapid leaf death during the southeast trades, or by reducing the amount of decomposition taking place between senescence and leaf fall into the litter traps, or through a combination of these factors. Previous authors have reported between 10 and 30% difference between leaf production and litter fall (Bray & Gorman 1964; Edwards 1977). Yet more than 50% loss must have occurred to account for the difference between

G. speciosa and the inland thickets, and so it is likely that more than one factor was involved. The thick intertwined nature of the Aldabra shrub canopy meant that the fall of much leaf litter was delayed for several months by branches: some decomposition probably occurred above ground. It is unlikely that wind reduced the total amount of litter caught by the inland traps because wind exposure was highest at the coast.

Few environments are homogeneous at all scales, but Aldabra illustrated special problems in the degree of environmental heterogeneity and its range of scales. Besides division into shrub and herb layer (a characteristic of any wooded savanna), the most striking component of cover diversity was the pattern of pockets of vegetation set in bare rock. This pattern varied on all scales from the tiny patches of forbs growing in holes a few centimetres across (mosaic rock vegetation), to variations in total vegetation cover on a scale of kilometres (Gibson & Phillipson 1983).

The other major generator of heterogeneity was the pattern of tortoise grazing. Most of the tortoises' food supply came from a narrow range of cover types, which were heavily grazed, while the perennial sedges, for instance, were virtually untouched except for the removal of flower and fruit and trampling (Gibson & Hamilton 1983).

These patterns set both the sampling methods used and the pattern of primary production and seasonal changes in the standing crop. Although the total primary production per square metre of plant was well up in the range expected from Aldabra's rainfall (Rosenzweig 1968), the environmental heterogeneity outlined above meant that different places varied considerably in their standing crop, production and seasonal patterns of availability of different components per square metre of ground. The feeding preferences and grazing patterns of tortoises would accentuate this pattern of heterogeneity. The effect of these patterns of standing crop and production on the tortoises' food supply and their responses to them are dealt with elsewhere (Gibson & Hamilton 1983).

(b) *Choice of approaches for production studies*

The implications of the results here reported, environmental heterogeneity being taken into account by building up a picture of production from a large number of components, must be considered in terms of the methodology of production studies in general. Two questions are relevant here: first, is the heterogeneity of Aldabra typical of a wide range of ecosystems or is it special to the atoll?; and secondly, how much effect would ignoring this heterogeneity have on the production estimates for the island?

The first of these questions has already been specifically considered in terms of the Aldabra system, and in particular in terms of the effects of tortoise grazing in maintaining it. To examine the question in a wider context, however, we need to point out both the biotic and abiotic contributions to Aldabra's heterogeneity of production. The biotic contributions are such as might be expected in a wide range of places: differences in the performance of different individuals/clumps of the same plant species or cover type, differences in production ecology of different cover types and the impact of a large grazing herbivore on the production of specific cover types. The balance between within-component variation and between-component variation should determine whether component-by-component or random-sample approach should be made in a particular case. Few studies have tested both approaches; as a particular example Grunow *et al.* (1980) considered that variation between tussocks of the same grass species was so great as to negate the value of a tussock-by-tussock approach to primary produc-

sion. However, they did not have the complication of the high grazing intensity on specific cover types that we encountered on Aldabra and indeed suggested that a component-by-component approach would be best organized on a 'forage–non-forage species' axis rather than a species-specific one when such grazing intensities are encountered.

It must be emphasized that our treatment of biotic heterogeneity as found on Aldabra is not the same as approaches based on species sorting in a homogeneously structured sward as reviewed by Singh *et al.* (1975). Such approaches are usually attempting to correct for differences in timing of peak standing crop and/or production between different species, while the present study must take into account variations in these factors as well as the grazing and genetically (tortoise turf) programmed differences in growth pattern between cover types.

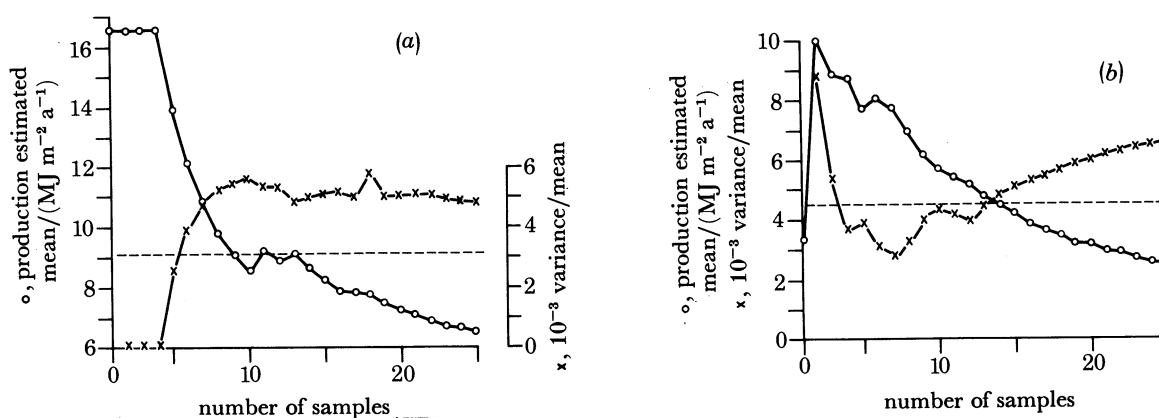


FIGURE 15. The effect of increasing number of samples on the accuracy of estimates of ground cover production for open mixed scrub sites. The data used in generating this figure were taken from the area around the open mixed scrub site discussed in the text and shown in figures 12–14. Figure 15*a* was generated by starting at a random point on a line transect and taking 25 1 m samples at random intervals along the transect, non-vegetation cover being ignored; i.e. the first metre of vegetation cover after a random interval was taken for each sample. The dashed line shows the estimated mean production per square metre of plant cover for the open mixed scrub site discussed in the text ($9030 \text{ kJ m}^{-2} \text{ a}^{-1}$). Figure 15*b* was generated in the same way except that the samples are the first metre of ground after a random interval; i.e. including rocks and other non-vegetative ground cover. The dashed line shows the estimated mean ground cover production per square metre of ground for the open mixed scrub site discussed in the text ($4500 \text{ kJ m}^{-2} \text{ a}^{-1}$).

All these factors being taken into account, the biotically generated heterogeneity at Aldabra is likely to be unusual in its complexity but, not unique; any environment that is grazed as severely and made up of components that vary both in their accessibility (i.e. shrub as compared with ground cover) and apparent palatability (i.e. the perennial sedges as compared with tortoise turf) to the major herbivores is likely to vary as much. In such cases the component-by-component approach to production studies will yield the best production estimates and those most likely to be useful for examining the interaction of primary consumers with the producers.

Where Aldabra is unique, or at least extremely unusual, is in the abiotic determinants of heterogeneity (i.e. the proportion of rock or other substrate covered by vegetation). An analogue can be found in deserts, where component-by-component production studies have been recommended and made (Goodall & Perry 1979), but even most deserts probably lack the range of scales of heterogeneity found on Aldabra. One would have to seek other raised atolls or raised coastal reefs to encounter this range of scales from centimetres to kilometres. Vegetation studies (see, for example, Birch 1963) have been made in such areas, but production studies are not known to us.

It is this variation in vegetation cover that suggests an answer to our second type of question about how much difference the component-by-component approach makes. Figure 15 illustrates the manner in which estimates of production for one of our 'synthesis' sites (open mixed scrub) would vary with the number of random samples taken if we ignored variations in the type of plant cover but accounted for differences in the amount of plant cover (figure 15*a*) or if we ignored both the biotic and abiotic generators of heterogeneity (figure 15*b*). In both cases the answer given by random sampling is unacceptable. The mean estimates at a sample number of 25 are still very different from the component-by-component estimates, and the errors are vast, indeed still growing in figure 15*b*. This is because under the artificial sampling régime we are ignoring, and crossing, patch boundaries. The decreasing means after 25 samples in figure 15 signify only that at the end of sampling we are in a low-production patch; extending the sample number would probably include other high-production patches and bring the mean up again; the number of samples needed for a reliable estimate for the whole area would be vast.

Thus the component-by-component approach adopted in this study was essential for the particular problem of Aldabra, and in general should be adopted in areas where there is a large amount of variation in the pattern and amount of plant cover in the substrate, or where an intense and variable pattern of herbivore pressure dictates a between-species patchiness of production and/or standing crop among the plants.

We are extremely grateful to all the Seychellois and others on Aldabra who gave technical help there, among them Antonio Constance who organized the heavy work and Andrew Quatre, Eluc Constance and Julie Hamilton who helped with the sorting of samples. M. Young, University of Cambridge, provided the base map for figure 1.

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