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Author(s): G. C. Stuart-Hill

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Effects of elephants and goats on the Kaffrarian succulent thicket of the eastern Cape, South Africa

G.C. STUART-HILL*
Dohne Research Station, Department of Agriculture, Stutterheim, South Africa

Summary

1. Kaffrarian succulent thicket is a dense, semi-succulent, thorny vegetation which is rapidly being eliminated under current pastoral systems. To understand why this occurs, the effect of defoliation by wild herbivores (mostly elephant) was compared with that of domestic ungulates (mostly goats) from surveys inside and outside the Addo Elephant National Park.
2. Both elephants and goats reduced canopy cover and increased shrub density in relation to control areas. Goats reduced the number of dominant shrub species per quadrat.
3. Replacing elephants with goats resulted in a fundamental change in the shrub community to one dominated by small, unpalatable shrubs with a few scattered umbrella-shaped trees. Removing elephants and not replacing them with goats resulted in the sites becoming more dissimilar, possibly because the vegetation reacted to the unique climatic and edaphic potential of each site.
4. Goats reduced the percentage frequency of the dominant tree-succulent *Portulacaria afra* by 40% and its density by 71% causing a 91% decline in the total area rooted by this plant.
5. It is argued that Kaffrarian succulent thicket (in particular *P. afra*) is adapted to elephant utilization but not to utilization by small domestic ungulates stocked at equivalent biomass. Some implications for land managers are discussed.

Key-words: browse, co-evolution, mega-herbivores, shrubs, species response.

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Introduction

The Kaffrarian succulent thicket (Cowling 1984) occurs on the eastern seaboard of South Africa in hot, dry (rainfall 225–500 mm), frost-free areas at low altitudes, usually below 500 m but never above 1000 m (Acocks 1975; Cowling 1984; Everard 1987; Palmer 1990; Agmet. records 1991). It is a dense, semi-succulent, thorny thicket *c.* 2–3 m high in which succulents contribute in excess of 20–30% relative cover (Cowling 1984). Grasses are present, but sparse (10 000–30 000 plants ha^{-1}) and mostly non-perennial (Acocks 1975). In a 'pristine state' this vegetation is dominated by the tree-succulent *Portulacaria afra*[†], representing over half of the total phytomass (data from Penzhorn *et al.* 1974; Aucamp 1979). It is considered to be the most important plant for production of goat forage (Aucamp 1979).

This vegetation is currently farmed with goats and supports a large proportion of the mohair industry of South Africa. It is sensitive to utilization and is rapidly being eliminated under current pastoral systems (Hoffman & Everard 1987; Hoffman 1989; Hoffman & Cowling 1990). This is serious because it represents an irreversible loss of a unique vegetation type; and the community which replaces it is unstable, allowing soil erosion and supporting fewer stock (Stuart-Hill & Danckwerts 1988). Clues to understanding the lack of persistence of this vegetation could be found by examining recent (past 200 years) developments, notably the replacement of indigenous herbivores (in particular elephants) by small domestic ungulates.

Accounts from early travellers and hunters in the region reported large numbers of elephants (Barrow 1801; Lichtenstein 1811; Pringle 1966; Skead 1989). As the plants in this vegetation are largely evergreen and highly nutritious (Aucamp 1979), and perennial rivers are always in close proximity, elephants would

* Present address: Chief Ecologist, BOP National Parks, PO Box 4124, Rustenburg, 0300, South Africa.

† Nomenclature follows Gibbs Russel *et al.* (1987) for plants, and Smithers (1983) for animals.

have been neither nutrient- nor water-limited and the early reports of large numbers were probably accurate. It follows that elephants would have had a major impact on the evolution of this vegetation and especially the dominant plant *P. afra* which, in 1835, was noted as the '. . . .favourite food of the elephant. . . .' (Pringle 1966), an observation since confirmed by research (Archibald 1955; Penzhorn, Robbertse & Olivier 1974).

The objective of this investigation was to contrast the effect of elephants and goats on the shrub component, in order to understand why this vegetation was able to tolerate the impact of many elephants, but not the current utilization by goats. Comparisons were made at three levels. At the first two of these, hypotheses were generated from the responses of the community of individual plants. The third was a test of the specific hypothesis that elephants and goats differentially affect the physiognomy of the dominant shrub, *P. afra*.

Adaptation of P. afra *to defoliation: a conceptual model*

Sexual reproduction of *P. afra* is of limited importance because seeds are small and short-lived (B. Whiting, personal communication); and because germination and seedling establishment are extremely rare (personal observation). This plant is, however, able to reproduce vegetatively from side branches which, as they grow, bend downwards, eventually rooting at regions where the nodes touch the ground (Fig. 1a). Undisturbed plants are characterized by having a 'skirt' or 'apron' of rooted side branches. With time, the plants become multi-stemmed and spread horizontally, eventually forming new individuals as the connecting branches become detached.

On farmland, *P. afra* is being eliminated (Stuart-Hill *et al.* 1986; Hoffman 1989). It is here suggested that this is because goats defoliate the lower portions of the canopy and effectively prevent the development of the 'skirt' of rooted branches (shown in Fig. 1a and b). If goat browsing is severe, the shrubs take on an umbrella shape (Fig. 1c), eventually collapsing as the weight of the succulent canopy becomes too great for the relatively weak stem to support. The plant then dies.

Elephants, by contrast, browse from the 'top downwards' and consequently severely damage the upper portions of the canopy. The lower rooted branches, however, escape defoliation; and vegetative reproduction is allowed to continue regardless of the damage to the upper canopy (Fig. 1b).

In summary then, the conceptual model proposes that *P. afra* is chiefly dependent on asexual reproduction which continues under utilization by elephants, but not under heavy browsing by small animals such as goats.

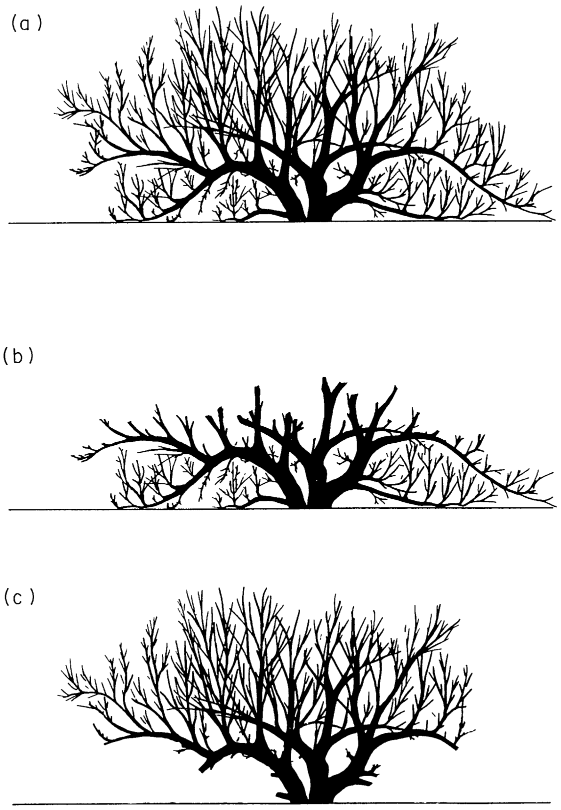

Fig. 1. Effect of (a) no browsing, (b) elephant browsing and (c) goat browsing on the growth habit and vegetative propagation of *Portulacaria afra*.

Study area

The study was undertaken in and around the Addo Elephant National Park (33°31′S, 25°45′E): the reserve for the last remaining elephants in the Cape province of South Africa (Fig. 2). Elephants were at their lowest densities (approximately 10 animals left) just prior to 1931 when the park was finally proclaimed and the eradication programme which culminated in 120 elephants being shot in a 'few months', was halted (Penzhorn *et al.* 1974). Before 1954 the elephants wandered throughout the region; but they have since been confined. Initially the fenced area was 2270 ha and the elephant population rapidly increased to 60, so that by 1971, Penzhorn *et al.* (1974) reported that they had begun to over-utilize the vegetation. Subsequently, the fenced area was progressively enlarged, while the population had grown to 166 by September 1990. The park is currently some 8600 ha in extent, but the elephants only have access to 8200 ha, the rest being set aside as botanical reserves (Fig. 2).

Topographically the park environs form a series of low undulating hills (altitude between 76 and 341 m). The soil is a light-red clay-loam (Archibald 1955) derived from sandstone and mudstone of the Sundays River Stage, Uitenhague Series, Cretaceous System (Toerien 1972).

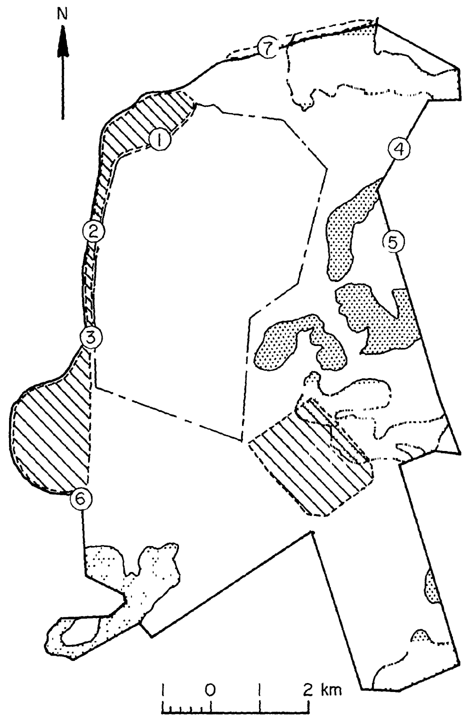

Fig. 2. Addo Elephant National Park showing: Kaffrarian succulent thicket (□), other plant communities (□) (after Archibald 1955), botanical reserves (▨), original elephant-proof fence (—·—), and seven sampling areas (numbered).

Mean annual rainfall (27 years) is 436 mm and falls throughout the year with small peaks in late summer (February–March) and spring (October–November). Mean daily temperature is 32·4 °C in January and 13·5 °C in July, but temperatures greater than 40 °C are frequently recorded in summer. Mean minimum temperature is 16·4 °C in January and 5·0 °C in July with frosts being extremely rare (Agmet records).

Archibald (1955) described five plant communities, the most extensive being Kaffrarian succulent thicket (Fig. 2) which covered more than 90% of the park (Penzhorn *et al.* 1974).

Methods

TREATMENTS

Three treatment areas were identified: (i) those in the park to which elephants have access ('elephants'); (ii) those outside the park where goats are the dominant browser ('goats'); and (iii) botanical reserves from which both elephants and goats have been excluded (control). In all three of these treatment areas, kudu, bushbuck, grysbok and duiker were present, although probably at different stocking rates. The park areas were stocked with various herbivores at a rate of approximately 50 kg livemass ha^{-1} (Table 1). Of this, elephants contributed 78% and it is realistic to attribute most of the defoliation effect in the park to them. It is important to note that, at two animals km^{-2}, the elephants were heavily stocked in comparison to that recommended in other areas of Africa with similar rainfall (Glover 1963; Van Wyk & Fairall 1969; Penzhorn *et al.*

Table 1. Approximate stocking of herbivores on 8200 ha in the Addo Elephant National Park (Park records)

Species	Feeding class*	Assumed mean mass† (kg)	Numbers	Total biomass (kg)	Relative contribution (%)
Elephant (*Loxodanta africana*)	G/B	1931	166	320 546	78·4
Kudu (*Tragelaphus strepsiceros*)	B	128	>180‡	23 040	5·6
Bushbuck (*Tragelaphus scriptus*)	B	26	>150‡	3 900	1·0
Grey duiker (*Sylvicapra grimmia*)	B	18	>250‡	4 500	1·1
Black rhinoceros (*Diceros bicornis*)	B	1350	21	28 350	7·0
Eland (*Taurotragus oryx*)	G/B	300	25	7 500	1·8
Grysbok (*Raphicerus melanotis*)	G/B	10	>50‡	500	0·1
Buffalo (*Syncerus caffer*)	G	390	46	17 940	4·4
Hartebeest (*Alcelaphus buselaphus*)	G/B	90	21	1 890	0·5
Total				408 166	100·0

* Browser (B) or grazer (G).
† 0·75 of mean female mass (Smithers 1983).
‡ Estimated from counts.

1974). The stocking rate of the farmland (goat) treatments could not be assessed accurately because farmers tend to avoid divulging this information, fearing that it could be used to prosecute them for overstocking. Whereas some of the farms were stocked relatively conservatively, others appeared to exceed the recommended 36–50 kg livemass ha^{-1} (Stuart-Hill 1990).

SAMPLING

From 1:10 000 aerial photographs, seven sampling areas were identified (Fig. 2) ensuring that, as far as possible: (i) they were spread along the perimeter of the park but confined to Kaffarian succulent thicket; (ii) they included a portion of a botanical reserve or were in positions where the three treatments were in close proximity; (iii) they were not in areas which had been previously cultivated; (iv) they represented different farms and, in the park, various histories of elephant usage.

Field location of the three treatment sites within each of the sample areas was achieved by driving along the elephant fence until the fifth iron fence post was encountered within the designated sampling area. This post was then used as the reference point from which the treatment sites were located. The first point in the elephant treatment site was always positioned perpendicular to the fence and 10 m from the reference point. The site on the opposite side of the fence (either farmland or botanical reserve) was located in a similar manner except that it was 15 m from the fence to accommodate the service road. The third treatment site in a sampling area was, on occasion, some distance from the reference point, in which case sites were located on the same altitude and aspect as the other two sites. At two of the sampling areas there was no botanical reserve and the control was unavoidably omitted, contravening condition (ii) above. It follows that there was an unequal number of replications for each treatment (elephants = 7, goats = 7, control = 5).

MEASUREMENTS

To determine the response of the vegetation to elephant and goat defoliation, the occurrence of 23 of the common shrub species (see Appendix) was recorded in seven circular quadrats (radius = 2·3 m) at each treatment site. Presence was recorded even if only part of a plant's canopy fell within the quadrat since this proved to be more efficient and repeatable than recording only rooted individuals. Percentage frequency, per treatment site, was determined for each species from these data. The percentage canopy cover in each quarter of the circular quadrat was estimated and the mean used as the cover estimate for the quadrat as a whole.

To test the conceptual model (Fig. 1), the profile of each plant was visually assigned to one of three categories: triangular with base on the ground, inverted triangle (umbrella-shaped), or box-shaped (or undecided). The degree of development of the 'skirt' of rooted branches was also recorded in one of three categories: well developed, absent, or poorly developed. To limit bias, these variables were recorded by operators who were unaware of the hypothesis being addressed. In addition, the following variables were measured on the first 10 *P. afra* plants encountered from the starting point: canopy height, maximum canopy radius, height of maximum canopy radius, radius of the rooted area, and height of the lowest leaf-bearing twigs. The last two measures were incorporated as an objective test of the visual classification made by the operators when assessing canopy shape and degree of 'skirt' development.

To obtain an index of density of *P. afra*, the distance from the centre of the plant being measured to the centre of the nearest neighbouring *P. afra* was recorded. An index of density of all trees and shrubs was obtained in a similar manner, except that the distance to the centre of the nearest neighbour, regardless of species, was recorded.

ANALYSIS

Because the park had been opened up in stages, different parts of the reserve had different histories of elephant usage. Similarly, the surrounding farms, having been farmed by different land owners, represented different intensities of goat utilization. Since this investigation involved comparing usage by goat with that by elephant, the approach was to sample throughout the area, with the variation due to different intensities of usage being allocated to error. This permitted more stringent testing of hypotheses because, if they held over all these situations, they could be accepted with greater confidence.

The measurements (on each plant or in each quadrat) within each treatment site were considered to be subsamples and their means were used as the variate values for that site. In consequence, degrees of freedom were drastically reduced (e.g. from 69 to 6 for the elephant and goat treatments), but this was preferred since it avoided pseudo-replication and allowed rigorous tests of significance.

Confidence limits (95%) were calculated (and are displayed in Figs 3, 4, 6 & 9–11) for each mean. In addition, the significance of treatment differences was evaluated using Student's *t*-test. Significance was set at the 95% level ($P < 0·05$).

The floristic data were initially subjected to principal component analysis (PCA). The responses of the individual species to the treatments were evaluated using *t*-tests in the manner described above. In addition, the responses of the species common to both sides of each fence were evaluated for consistency, using the Fisher's exact probability test in an approach similar to that adopted by Noy-Meir *et al.* (1989). In this study, a consistent response was assumed if at least three of the fence line comparisons had significant ($P < 0{\cdot}05$) responses in the same direction and had no significant response across the fence in the opposite direction.

Results

GROSS COMMUNITY CHANGE

Both elephants and goats had a marked effect on density and cover of trees and shrubs in the community. Each increased the density of the shrub community, i.e. the distance between woody plants was significantly ($P < 0{\cdot}05$) less under goats and elephants than in the control (Fig. 3a). On the other hand, each reduced ($P < 0{\cdot}05$) the canopy cover of the woody community (Fig. 4a); but only goats reduced ($P < 0{\cdot}05$) the number of woody species per quadrat (Fig. 4b).

The first two axes of the PCA accounted for 66% of the floristic variation. The first axis appeared to represent a goat degradation gradient similar to that quantified by Stuart-Hill *et al.* (1986), and had *Porticulacaria afra*, *Euclea undulata*, *Capparis sepiaria* and *Schotia afra* located on one end and *Lycium oxycarpum* and *Zygophyllum morgsana* on the other (Fig. 5a). The second axis had *Azima tetracantha* and *Protasparagus* spp. on one end and *Maytenus* spp., *Rhigozum obovatum* and *Grewia robusta* on the other, and separated sampling areas 6 and 7 from the rest (Fig. 5a,c,d). *Grewia robusta* was abundant in areas 6 and 7; but this species was absent or rare at the other sampling areas although generally common in the vegetation as a whole. Given this, and results from a previous gradient analysis (Stuart-Hill *et al.* 1986) where *A. tetracantha*, *R. obovatum* and *G. robusta* were indicators of differences between sites, the second axis appeared to represent inherent site-dependent differences.

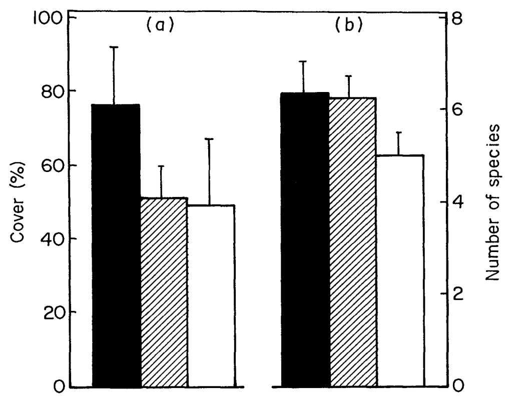

Fig. 4. Effect of neither elephants nor goats (■), elephants (▨) and goats (□) on (a) the canopy cover of woody plants, and (b) on the number of woody species per quadrat (upper 95% confidence limits of the mean).

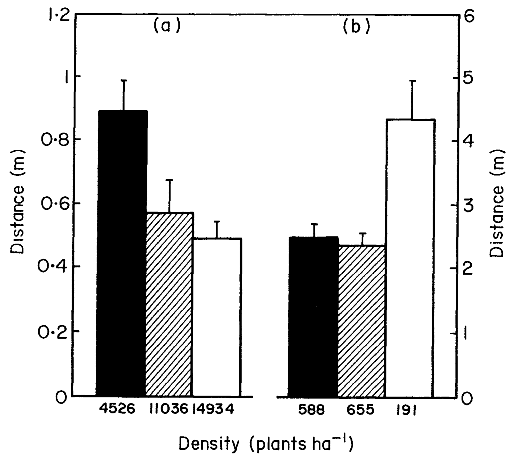

Fig. 3. Effect of neither elephants nor goats (■), elephants (▨) and goats (□) on the nearest neighbour distance between (a) woody plants of any species, and (b) *Portulacaria afra* plants. The values at the base of each column are approximate densities from a formula in Bonham (1989) (upper 95% confidence limit of the mean).

All the elephant and control sites were situated towards the right on axis 1 while most of the goat sites were situated towards the left (Fig. 5b), indicating that *P. afra*, *C. sepiaria*, *E. undulata* and *S. afra* were associated with elephants and the control, and *L. oxycarpum* and *Z. morgsana* with goats (Fig. 5a, b). Although the botanical reserves are referred to as the control, one could also argue that this is a treatment (i.e. elimination of elephant as the natural dominant browser without goat replacement) and the sites within the park are the 'control'. This means that the reults can be interpreted from different viewpoints, which becomes especially relevant when considering treatment trajectories (Fig. 5c,d) in ordination space. I present both interpretations and from these it appears that elephant browsing drew the community (Fig. 5c) into a relatively small domain situated towards the right on axis 1 and in the centre on axis 2 (Fig. 5b). Removal of elephants without replacement by goats (i.e. the botanical reserves) caused the vegetation to drift away from the centre of this domain (Fig. 5d), the sites becoming increasingly different.

RESPONSE OF INDIVIDUAL SPECIES

The effect of elephants and goats on frequency of 23 trees and shrubs is presented in Fig. 6. From the low frequencies, it is evident that the quadrat was too small for reasonable assessment of the less common species and these were eliminated from further analysis. The following species were retained because they were either: adequately sampled (*Protasparagus* spp., *A. tetracantha*, *Capparis sepiaria*, *Euclea undulata*, *G. robusta*, *Maytenus* spp., *P. afra*, *S. afra* and *Euphorbia mauritanica*); not well sampled but nevertheless showing significant

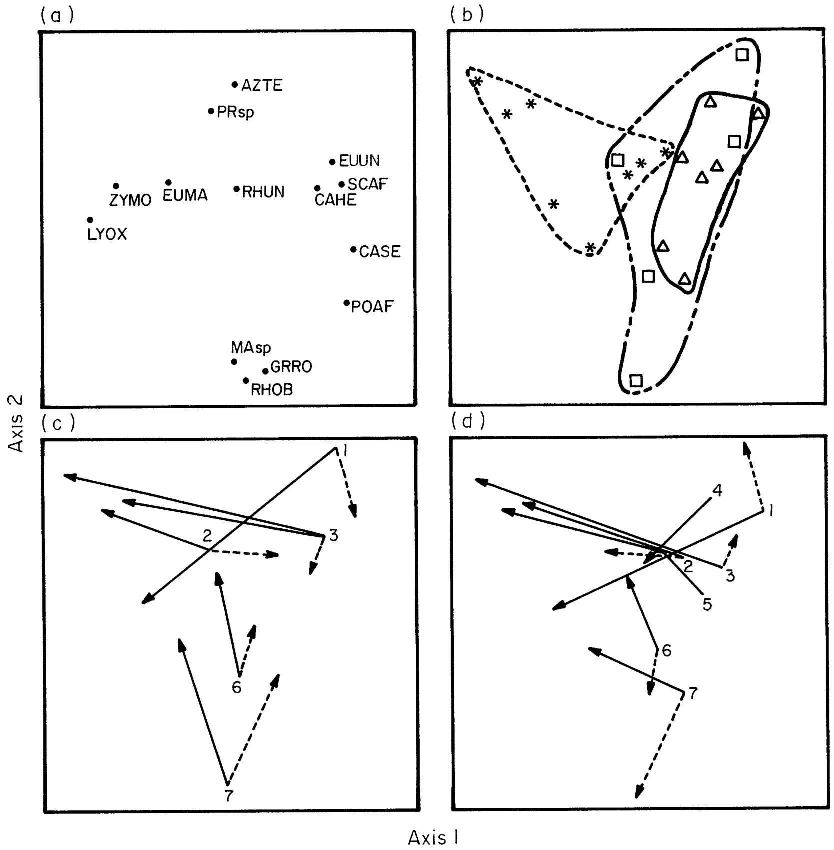

Fig. 5. Principal component analysis of floristic data from sites in and around the Addo Elephant National Park showing: (a) plot of diagnostic species; (b) domains of the control (□), elephant (▽) and goat (*) sites; (c) the treatment trajectories where the control acts as the anchor; (d) trajectories where 'elephant' acts as the anchor. Solid arrows indicate change by goats; broken arrows indicate change by elephants (c) or by removal of elephants without replacement with goats (d). Numbers in (c) and (d) indicate sites; absence of trajectories for sites 4 and 5 is due to lack of controls for these sites. See Appendix for species codes.

($P < 0{\cdot}05$) responses (*Z. morgsana* and *R. obovatum*); or marginally sampled and showing consistent trends (*Carissa haematocarpa* and *L. oxycarpum*). For each of these species, absolute changes in frequency are presented in Figs 7 and 8, and the changes relative to the control are summarized in Table 2.

Effect of goats

Relative to the control, goat browsing resulted in a decrease ($P < 0{\cdot}05$) in the percentage frequency of *G. robusta*, *P. afra* and *R. obovatum*. Goats also resulted in relatively large (>50%) decrease in *C. sepiaria*, *C. haematocarpa*, *E. undulata* and *S. afra* (Table 2) and, although these were not significant given the efficiency of sampling, they were consistent across fences (Fig. 7a).

Z. morgsana was the only species which increased significantly ($P < 0{\cdot}05$) in response to goats but the large relative increase (88%) in frequency of *L. oxycarpum* (Table 2) is a trend worth noting, as is the response of *E. mauritanica*, because both these species consistently increased across fences (Fig.7a).

Effect of elephants

Relative to the control, elephant browsing resulted in a significant ($P < 0{\cdot}05$) decrease of only a single species, the succulent climber, *E. mauritanica*

Table 2. Increase (%) in frequency of 14 common trees and shrubs in circular quadrats ($r = 2{\cdot}3$ m) due to goat and elephant utilization, relative to the frequency measured in areas where goats and elephants had been excluded. Statistical analysis and symbols described in Fig. 7

Species	Goat	Elephant
Azima tetracantha	11	4
Capparis sepiaria	−50	17
Carissa haematocarpa	−55	33
Euclea undulata	−50	38
Euphorbia mauritanica	25	−82*
Grewia robusta	−70*	−21
Lycium oxcycarpum	88	−41
Maytenus spp.	− 5	1
Portulacaria afra	−39*	− 1
Protasparagus spp.	7	5
Rhigozum obovatum	−90*	−80
Rhus undulata	4	19
Schotia afra	−56	25
Zygophyllum morgsana	100*	0

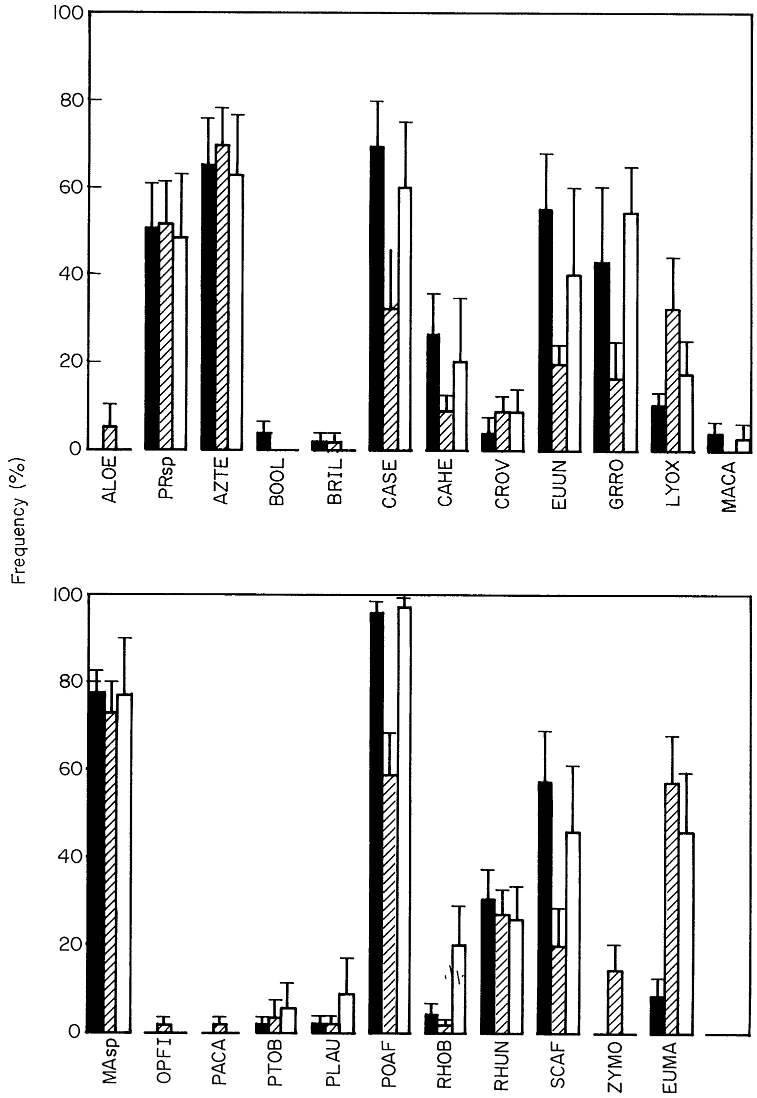

Fig. 6. Effect of elephants (▨), goats (□), and neither elephants nor goats (■) on the frequency of 23 trees and shrubs (upper 95% confidence limit of the mean). See Appendix for species codes.

(Table 2, Fig. 7b). *R. obovatum* was the only other species which showed a relative decrease greater than 50% (Table 2) in response to the influence of elephant, but this was neither significant nor consistent (Fig. 7b).

Elephants did not cause large, significant or consistent increases in any species (Table 2, Fig. 7b).

Relative effect of elephants and goats

Relative to elephant, goat browsing resulted in higher frequencies of *Z. morgsana* and *Euphorbia mauritanica* ($P < 0{\cdot}05$) and a large and nearly significant ($P < 0{\cdot}05$) increase in frequency of *L. oxycarpum* (Fig. 8).

Elephant browsing, on the other hand, resulted in more *P. afra*, *Euclea undulata*, *Capparis sepiaria* and *S. afra* in comparison with goats ($P < 0{\cdot}05$). *Carissa haematocarpa* and *G. robusta* were also higher under elephant than goat browsing and while not significant these trends were consistent across fences (Fig. 8). It should be realized that elephants did not actually increase the frequency of these species; rather these species were able to maintain themselves under elephant but not under goat browsing (see previous sections).

PORTULACARIA AFRA

The distance between *P. afra* plants was greater ($P < 0{\cdot}05$) on farmland than in the control or the elephant browsing areas (Fig. 3b), i.e. *P. afra* density was lowered by goat browsing. Because of the non-linear relationship between distance and density (Bonham 1989) it was not possible to evaluate significance on the basis of plant density.

All *P. afra* plants growing without goat or elephant defoliation were either box-shaped or triangular in profile (Fig. 9). Elephants reduced the fraction of box-shaped plants, thereby increasing the fraction of

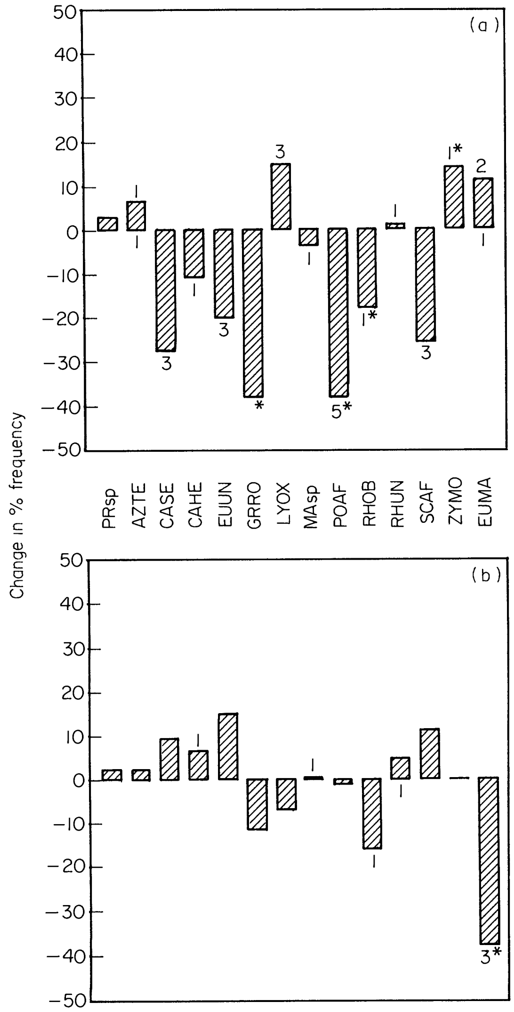

Fig. 7. Change in percentage frequency, compared with control, of 14 common trees and shrubs as a result of browsing by (a) goats and (b) elephants. Asterisks indicate significant ($P < 0{\cdot}05$; df = 6) differences between treatments, using *t*-tests where fence-lines were used as replications. Numerals indicate the number of individual fence-line comparisons (out of 7) where significant ($P < 0{\cdot}05$) changes were recorded using Fisher's exact probability tests. Tests were performed on actual frequencies recorded. See Appendix for species codes.

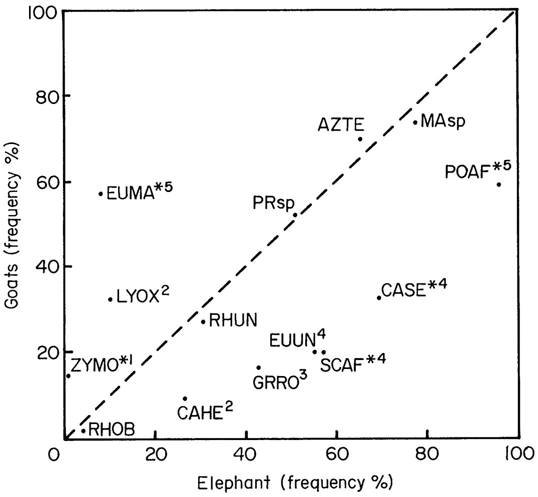

Fig. 8. Comparison of the effect of browsing by goats and elephants on the percentage frequency of 14 common trees and shrubs. Statistical analysis and symbols described in Fig. 7; see Appendix for species codes.

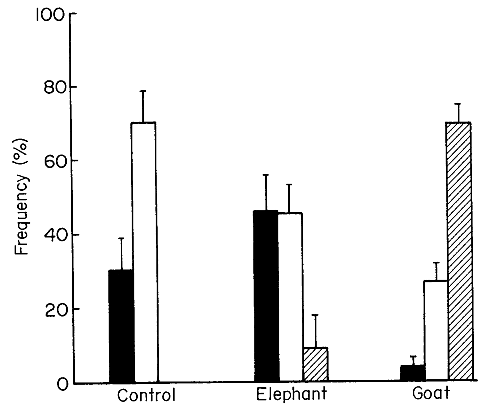

Fig. 9. Population frequency distributions of canopy profiles for *P. afra* plants growing under the impact of elephants, goats and neither elephants nor goats (control). Triangular canopies with bases on the ground (■), box-shaped canopies (□) and umbrella-shaped canopies (▨) (upper 95% confidence limit of the mean).

plants with triangular and umbrella-shaped canopies. Goats eliminated almost all of the triangular canopies ($P < 0{\cdot}05$) and drastically increased ($P < 0{\cdot}05$) umbrella-shaped plants so that 70% of all *P. afra* plants had umbrella canopies.

Most of the control plants had well developed 'skirts' of rooted branches, only 8% having none (Fig. 10). Elephants increased the fraction of 'full-skirts' in relation to the control but this was not significant. Goats on the other hand, reversed the frequency distribution ($P < 0{\cdot}05$) by eliminating almost all of the 'full-skirts'.

P. afra plants growing under the influence of elephants were shorter than both the control plants and the plants growing on the farmland ($P < 0{\cdot}05$) (Fig. 11a). Plants browsed by goats were the tallest

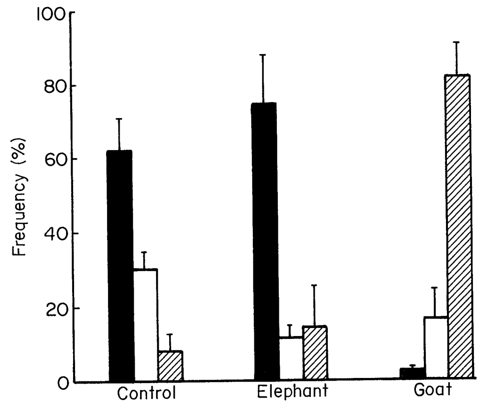

Fig. 10. Population frequency distributions characterizing the development of 'skirts' of rooted side branches for *Portulacaria afra* plants growing under the impact of elephants, goats and neither elephants nor goats (control). Fully developed (■), poorly developed (□) and absent (▨) (upper 95% confidence limit of the mean).

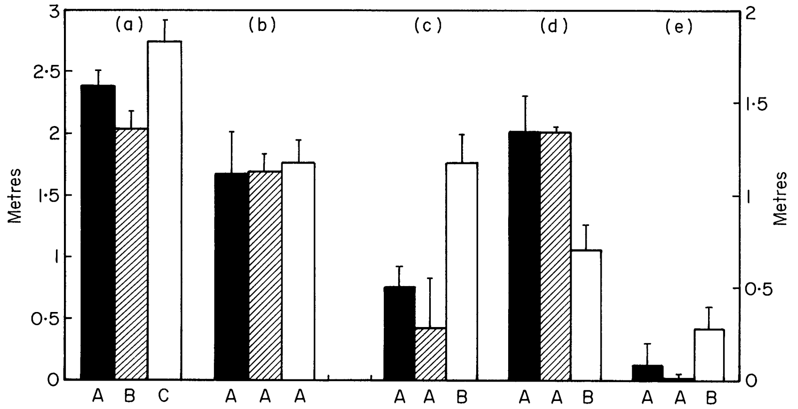

Fig. 11. Effect of elephants (▨), goats (□), and neither elephants nor goats (■) on: (a) height, (b) maximum canopy radius, (c) height of maximum canopy radius, (d) radius of the rooted area, and (e) height of the lowest leaf-bearing twigs of *Portulacaria afra* (upper 95% confidence limit of the mean); items with the same letters below the column do not differ significantly ($P < 0{\cdot}05$).

of all plants ($P < 0{\cdot}05$). In addition to the lack of top-defoliation, this result reflects elimination of many smaller individuals by goats (Fig. 3b).

The maximum canopy radius did not differ between treatments (Fig. 11b) but *P. afra* plants growing on farmland had their maximum canopy radius at a greater height ($P < 0{\cdot}05$) than undefoliated plants or plants defoliated by elephants (Fig. 11c).

Goats reduced ($P < 0{\cdot}05$) the radius of the rooted area of *P. afra* in comparison to that of plants not browsed by goats (Fig. 11d). Although this reduction is only 48%, it represents a 73% reduction in rooted area per plant.

The lowest leaf-bearing twigs of *P. afra* on farmland were higher ($P < 0{\cdot}05$) than those of plants growing under the influence of elephants (Fig. 11e).

Discussion

THE COMMUNITY

Elephants, in contrast to goats, did not reduce the number of shrub species (Fig. 4b) but limited the variation in floristic composition to a relatively small domain characterized by high amounts of *P. afra*, *C. sepiaria*, *E. undulata* and *S. afra* (Fig. 5). The removal of elephant without goat replacement (i.e. the control), increased floristic variation between sites causing the 'envelope' in ordination space to increase in size in all directions away from the centre of the domain of the elephant sites (Fig. 5b, d). Perhaps this is because, once elephants are no longer present, the shrub community is able to respond to the unique combination of edaphic and micro-climatic conditions prevailing at each site, leading to increased spatial variation. This result implies that elephants maintain succulent thicket in a relatively uniform state, and it is important to note that this state corresponds to that which has been found to have highest forage potential for goat farming (Aucamp 1979; Stuart-Hill & Danckwerts 1988; Stuart-Hill 1990).

Goats, on the other hand, caused a significant decline in *P. afra*, *C. sepiaria*, *E. undulata* and *S. afra* (Fig. 7a), reduced the number of species per unit area (Fig. 4b), increased *L. oxycarpum*, *Z. morgsana* and *E. mauritanica* (Figs 7a & 8), and moved the sites in ordination space towards a new domain (Fig. 5) corresponding to a state of low goat-forage productivity (Aucamp 1979; Stuart-Hill & Danckwerts 1988; Stuart-Hill 1990). Some of the goat-sites (sites 4 and 5), however, were within the domains of the elephant and the control sites (Fig. 5b) and this may be because these sites experienced relatively low goat utilization. By contrast, the sites which moved furthest in the ordination space (goat-sites 1, 2 and 3) were situated close to homesteads, and had consequently been subjected to heavy goat usage (Fig. 5). It is possible therefore, that goats do not inevitably cause a change in floristics but the community response depends on the intensity of goat browsing. Equally, however, it could be argued that the goat sites within the elephant and control domains are in the process of moving towards the goat domain (Fig. 5c & d), and that consequently all farmland will eventually end up in the area towards the left on axis 1.

The decrease in number of species per quadrat (Fig. 4b), the increase in apparent density (Fig. 3a), and the increase in *Z. morgsana*, *E. mauritanica* and *L. oxycarpum* (Fig. 7a), means that the farmland areas are becoming invaded by these unpalatable shrubs (Stuart-Hill & Danckwerts 1988) and this is corroborated by data from Stuart-Hill *et al.* (1986). On the other hand, the increase in the density with elephant defoliation (Fig. 3a) is due to an increase in the density of all species (see Figs 3a & 4b). This probably results from the elephants breaking down trees (the decline in cover, Fig. 4a), thereby promoting coppicing. However, elephants may also promote seedling establishment because they churn the soil, which together with large amounts of rotting litter (elephant dung, leaves, twigs, and broken branches), makes an excellent seedbed. A further possibility is that the flightless dung beetle (*Circellium bacchus*), which depends on coarse dung and locally has become almost confined to the Addo Elephant Park (Grobler & Hall-Martin 1982), could also promote seedling establishment. These insects bury balls of elephant dung which could also contain viable shrub seed.

SPECIES RESPONSE

All the species which were adequately sampled (Table 2) were able to tolerate fairly heavy levels of elephant utilization, except for the succulent scrambler *E. mauritanica* (Figs 6 & 7). Other workers have noted that there are other species which may also be harmed by elephants. Penzhorn *et al.* (1974) measured no *Aloe africana* in the park but recorded it as relatively abundant outside. J. Midgley (personal communication) noted, in time-sequence photographs, that another tree-succulent (either *Euphorbia tetragona* or *Euphorbia triangularis*) was one of the first plants to be eliminated by elephants. A 50% reduction (non-significant) of *Crassula ovata* was recorded here in response to browsing by elephants (Fig. 6). Interestingly, all these plants are succulents and none appear to coppice if cut at ground level. Conversely, all the non-succulent species have the ability to coppice either from stem bases or from the roots. This attribute enables plants to recover from catastrophic events (e.g. fire or breakage by large herbivores) where the aerial portions of a plant are killed. It could be argued, given that fires do not burn in this vegetation, that the woody plants in this community are adapted to tolerate defoliation by elephants. The succulents, apart from *P. afra*, have probably either 'adopted' an escape strategy (Feeny 1980), growing in inaccessible areas, or else are very rare.

Goats reduced a number of woody shrubs including the succulent *P. afra* (Table 2; Figs 6, 7 & 8). These, with the exception of *E. undulata*, all have leaves which are highly acceptable to goats (Stuart-Hill, unpublished data). *Zygophyllum morgsana* and *L. oxycarpum* increased with goat defoliation, a finding consistent with that of Stuart-Hill *et al.* (1986), probably because these plants are avoided by goats (Stuart-Hill, unpublished data). *Euclea undulata*, however, remains an enigma because it is consistently found to disappear under heavy utilization by goats (this study & Stuart-Hill *et al.* 1986) but does not itself seem to be utilized by goats (Stuart-Hill, unpublished data).

Portulacaria afra

The lower density of *P. afra* under goats (Fig. 3b) confirms that this species is harmed by goats but not elephants, even when the latter are at high densities (Table 1). None of the results (Figs 9–11) refute the conceptual model (Fig. 1). 74% of plants under elephant defoliation had well developed 'skirts' of rooted branches, whereas 82% of plants on farmland had no 'skirts' (Fig. 10). This is corroborated by the larger radius of rooted area and the lower height of the lowest leaf-bearing twigs (Fig. 11). The apparent persistence of some triangular plants under goat grazing (Fig. 9), was due to the collapse of a number of large, formerly umbrella-shaped *P. afra* plants. Multiplying the average rooted area per plant with the densities of *P. afra* (Fig. 3b) for the respective treatments, gives the rooted area of this plant ha^{-1}: i.e. 3694, 3316 and 294 $m^2 ha^{-1}$ for the elephant, control and goat treatments, respectively. Goats, therefore, caused a 91% decline in the area rooted by *P. afra*.

It may be argued that because of its vegetative reproductive strategy, *P. afra* is adapted to utilization by elephant. However, this strategy also renders it vulnerable to utilization by goats: a principle of importance because land managers need to ensure that all *P. afra* plants have a healthy 'skirt' of rooted branches.

It was noticed that a number of *P. afra* plants had been pulled out by elephants, but the lack of any differences in density and rooted area between the elephant and control treatments indicates that this activity has minimal impact.

LIMITATIONS OF THIS INVESTIGATION

The impression could be created that goats *per se* are harmful to the vegetation and in particular *P. afra*. Aucamp (1979) found, however, that *P. afra* was stimulated by light goat defoliation (25% leaf removal), if followed by an extended period of rest (approximately 12 months), a phenomenon recorded in a number of other browse species (Garrison 1953; Lay 1965; Ferguson & Basile 1966; Teague 1987). Stuart-Hill *et al.* (1986) reported that the composition of the shrub community was not adversely affected by goats provided these are lightly stocked. In this study, some of the goat sites were within the plant sociological domains of the control and the elephant sites (notwithstanding the possibility that these sites were moving away from these domains) (Fig. 5b) and, on the basis of the foregoing and of sightings on some goat farms of *P. afra* plants with well developed 'skirts', it would appear that this vegetation is able to tolerate browsing by goats, provided this is lenient. It is probably true, however, that few commercial farms are stocked at such low levels.

A further limitation of this work is that the influence of elephants is not separated from that of the other indigenous browsers such as black rhinoceros, kudu, eland, bushbuck, grysbok and duiker. Bearing always in mind that elephants are the dominant browser, it is nevertheless worth discussing how these other species may have influenced the results, despite their low densities (Table 1). Kudu and eland are taller than goats and would be expected to forage at a higher level. It is suggested, however, that they would have a similar effect on *P. afra* because goats readily stand on their hind legs to browse. Bushbuck, grysbok and duiker browse lower than goats and less intensively and while not preventing the development of the 'skirt', give it a hedge-clipped appearance. Because black rhino feed at a low height and reportedly do not break or tear branches as do elephants (Goddard 1968), one expects them to have a similar effect on the vegetation to goats. However, these animals push over shrubs and young trees to feed on the upper portions of canopies (Smithers 1983), and this would have similar effects to elephant browsing.

CONCLUSION

It appears that a mixture of indigenous herbivores, dominated by elephants and stocked at similar biomass to that of goats on farmland, is not as detrimental to Kaffrarian succulent thicket as goats stocked at current levels. It is doubtful whether this vegetation can be economically farmed with goats at the low stocking rates which would ensure its persistence. As an alternative, the larger land owners (>2000 ha) might consider reducing goats in favour of game and in particular elephant; because tourism, hunting and the products of game can be extremely lucrative.

With the current ban on elephant products (Anon 1989), no production-orientated land-owner is going to bring elephants onto his property if he cannot eventually sell the products of these animals or use his surplus for trophy hunting. Given this, landowners will probably continue to farm with goats, and elephants will have to stay confined to the limited National Parks. The consequence for farmland will be continuing desertification; and elephants in excess of the carrying capacity of the National Parks will be culled with no financial benefit accruing to those countries and agencies which conserve these animals. This poses obvious problems for a continent populated by poor people, who perceive National Parks as unproductive land set aside as a playground for privileged tourists.

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Appendix

List of woody and succulent plant species recorded in this study with their codes.

Species	Code
Aloe spp.	ALOE
Azima tetracantha	AZTE
Boscia oleoides	BOOL
Brachylaena ilicifolia	BRIL
Capparis sepiaria	CASE
Carissa haematocarpa	CAHE
Crassula ovata	CROV
Euclea undulata	EUUN
Euphorbia mauritanica	EUMA
Grewia robusta	GRRO
Lycium oxycarpum	LYOX
Maerua caffra	MACA
Maytenus spp.	MAsp
Opuntia ficus-indica	OPFI
Pappea capensis	PACA
Plumbago auriculata	PLAU
Portulacaria afra	POAF
Protasparagus spp.	PRsp
Ptaeroxylon obliqum	PTOB
Rhigozum obovatum	RHOB
Rhus undulata	RHUN
Schotia afra	SCAF
Zygophyllum morgsana	ZYMO