The problem of maintaining large herbivores in small conservation areas: deterioration of the grassveld in the Addo Elephant National Park

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Changes in vegetation cover and species composition in a grassland community during a six year period are reported. The grass *Themeda triandra* and the dwarf shrub *Helichrysum rosum* decreased in abundance, whereas the grass *Eragrostis obtusa* increased. Comparison of grazed plots with fenced plots revealed large herbivores were responsible for the increase in abundance of *E. obtusa*. The abundance of *T. triandra* was influenced by large herbivores, but rainfall fluctuations apparently also played a role. The decline in relative abundance of *H. rosum* was evidently not caused by large herbivores. Grass cover was closely determined by rainfall. A drought-induced decline in forage abundance evidently caused the buffalo population to crash.

Key words: herbivory, Addo, plant species composition, stocking rates, vegetation cover.

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Introduction

The maintenance of large wild herbivores in small conservation areas poses some management problems. Boundary fences limit dispersion and migration, forcing the animals to forage continuously in a limited array of vegetation communities, supposedly increasing the risk of range deterioration (Macdonald & Brooks 1982; Sinclair & Fryxell 1985). The artificial confinement of herbivores characteristic of most southern African wildlife reserves is regarded as being one of the main justifications for culling (Pienaar 1983). Despite the potential seriousness of herbivore impact in small conservation areas there have been few detailed long-term studies.

The Addo Elephant National Park (AENP), one of the smallest national parks in southern Africa (8 995 ha), carries populations of large herbivores that are potentially destructive of vegetation: elephant *Loxodonta africana* (Blumenbach, 1797), black rhinoceros *Diceros bicornis* (Linnaeus, 1758), and buffalo *Syncerus caffer* (Sparrman, 1779). These species are either rare (rhinoceros) or of considerable aesthetic appeal (elephant and buffalo), and have therefore been awarded priority status in the conservation objectives of the AENP. In order to successfully maintain such a spatially confined plant-herbivore system it is essential to understand the impact of herbivory on vegetation composition.

The objectives of this study were (i) to determine the nature of long-term changes in plant species composition and cover in the grassland in the AENP, (ii) to assess the role played by rainfall and grazing in influencing these changes, and (iii) to assess the potential effect of vegetation changes on the large herbivore populations.

Study Area

The Addo Elephant National Park is situated about 60 km north of the city of Port Elizabeth in the eastern Cape Province. Rainfall in the region is relatively low (annual mean 480

mm) and largely non-seasonal. The vegetation is a dense evergreen thicket termed the Addo bush by Acocks (1975). The thickets are almost devoid of grass, but small, scattered patches of grassland occur in a vegetation community known as the Bontveld (Archibald 1955; Grobler & Hall-Martin 1982). The grassland patches are dominated by perennial tufted grasses, with forbs, succulents and dwarf shrubs as secondary components.

The park was proclaimed in 1931 to protect a remnant population of 11 elephants in the Addo bush. A small population of buffalo was also present, more because the dense Addo bush afforded protection against hunting than because of the suitability of the habitat. Rhinoceros, as well as eland *Taurotragus oryx* (Pallas, 1776) and red hartebeest *Alcelaphus buselaphus* (Pallas, 1776) were later introduced into the park. Other species which occur naturally in the area include kudu *Tragelaphus strepsiceros* (Pallas, 1776), bushbuck *Tragelaphus scriptus* (Pallas, 1776), grey duiker *Sylvicapra grimmia* (Linnaeus, 1758), Cape grysbok *Raphicerus melanotis* (Thunberg, 1811) and bushpig *Potamochoerus porcus* (Linnaeus, 1758).

This study concerns the grassland patches in the Bontveld, and also those large herbivore species that utilise the grass: elephant, buffalo, eland and red hartebeest (the remaining species in the park being browsers).

Before 1984 the elephant, rhinoceros and red hartebeest were excluded from the Bontveld by fences, but the other species had access to the area. In March 1984 the elephant enclosure was expanded to include most of the Bontveld, except for an area of 410 ha (referred to in this paper as the Botanical Reserve) which remained fenced to provide an indication of the impact of large herbivores on the vegetation. The fence surrounding the Botanical Reserve prevented access by elephants, rhinoceros and red hartebeest, but the other species occasionally entered by going through or over the fence. Although the Botanical Reserve did not fully exclude all herbivores the grazing pressure was significantly lower inside than outside (Novellie 1988).

In addition to the Botanical Reserve a small exclosure (30 m x 25 m) is present in the Bontveld. The date of establishment of this exclosure has been lost from the records but it was known to be at least 17 years old at the start of the study in February 1984. As far as can be established, the fence surrounding this exclosure has been successful in excluding all large herbivores.

Procedure

Determining vegetation trends in heavily grazed patches

Changes in vegetation composition and cover were monitored in six permanently marked plots in the Bontveld. The intention was to determine vegetation trends in grassland patches that were particularly favoured by grazers. The plot localities were therefore chosen in areas that showed signs of heavy use (as indicated by accumulations of dung and heavily defoliated plants). The plots were first surveyed in February-March 1984, just before the elephants were allowed access to the Bontveld. Follow-up surveys were conducted in January of each of the years 1985 to 1990. Since the plots were marked with iron fencing standards each follow-up survey was conducted at the same place as the first survey.

Plant species composition was determined by means of nearest plant point surveys (Mentis 1984). In each year's survey one hundred points were examined at each of the six plots, and the plant species rooted nearest to each point was recorded. From these results the relative abundance of the different plant species was calculated.

In addition, canopy spread cover of grass,

dwarf shrubs and forbs was determined by the descending point method of Roux (1963). A canopy spread strike was recorded if a point fell within an imaginary line drawn around the perimeter of the canopy of a plant. Canopy spread strikes were recorded only as either 'grass' or 'other plant', without distinction between species. In the 1984 surveys only nearest plants were recorded, but in the remaining surveys both nearest plants and canopy strikes were recorded. Further details of the survey procedures are given by Novellie (1988).

The effect of grazing on plant species composition

The effect of grazing was evaluated by comparing the inside and outside of the Botanical Reserve. Six matched pairs of plots were laid out, one member of each pair being inside the Botanical Reserve and the other outside. The plots were situated so that the members of each pair resembled one another as closely as possible with regard to slope, aspect and degree of shading by trees. In each plot a 100-point survey was conducted. The nearest plants to each point, and the canopy spread cover of grass and other plants were recorded as described above. These surveys were first conducted in January 1987 and then repeated in January 1990.

A 100-point survey was also conducted in the 30 m by 25 m exclosure in January of each year of the study period (1984 to 1990) with

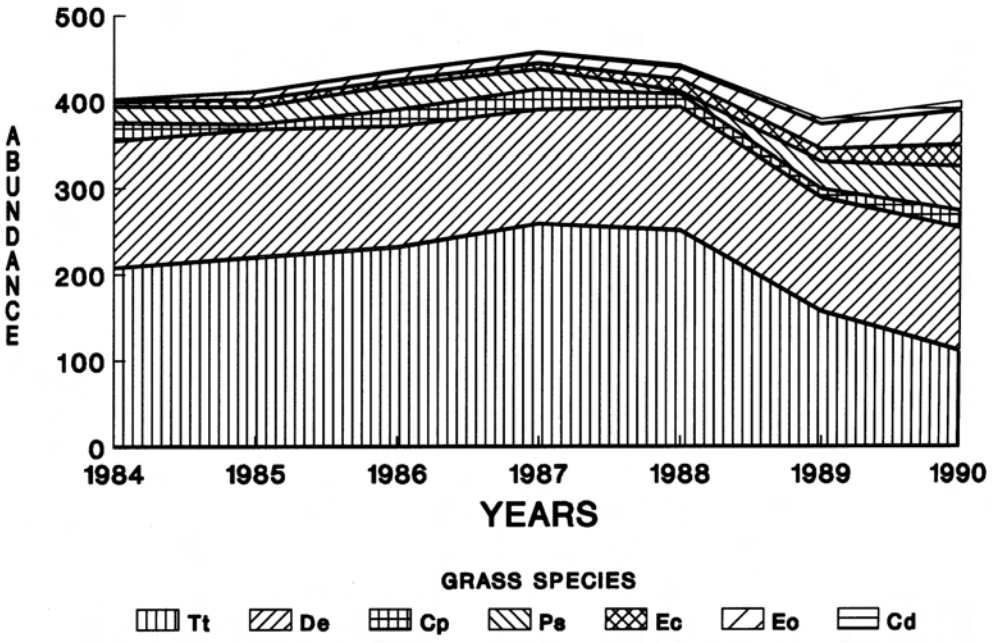

Fig. 1. Changes in the relative abundance of some common grasses in the Bontveld from 1984 to 1990, based on the pooled results from six plots surveyed using the nearest plant method (a total of 600 points were observed in each year). Tt = *Themeda triandra*; De = *Digitaria eriantha*; Cp = *Cymbopogon plurinodis*; Ps = *Panicum stapfianum*; Ec = *Eragrostis curvula*; Eo = *Eragrostis obtusa*; Cd = *Cynodon dactylon*.

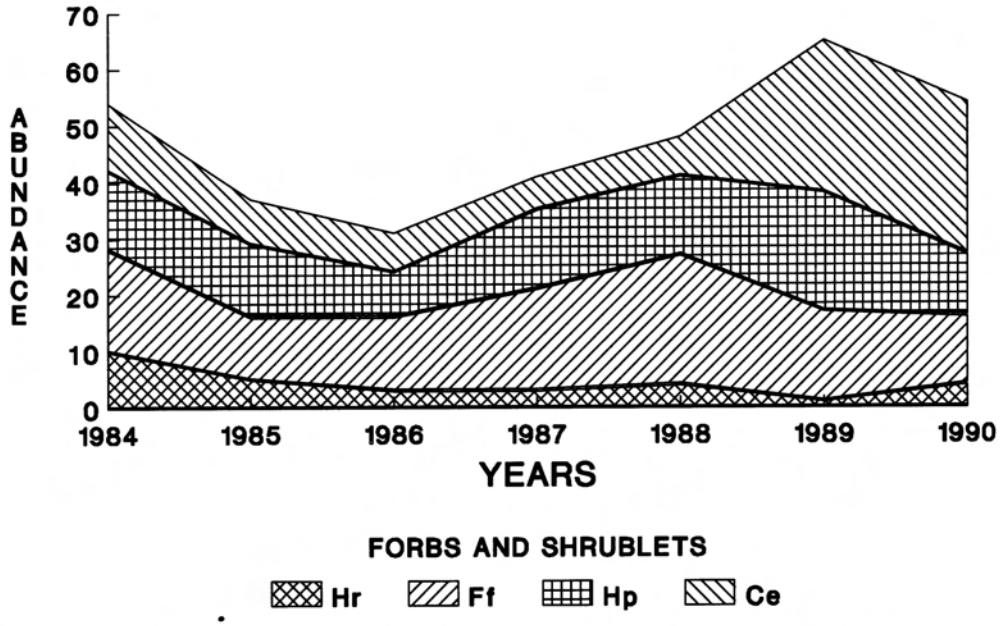

Fig. 2. Changes in the relative abundance of some common forbs and dwarf shrubs in the Bontveld from 1984 to 1990, based on the pooled results from six plots surveyed using the nearest plant method (a total of 600 points were observed in each year). Hr = *Helichrysum rosum*; Ff = *Felicia fascicularis*; Hp = *Hibiscus pusillus*; Ce = *Crassula ericoides.*

the exception of 1985.

Statistical analysis

The null hypothesis of no difference between the inside and outside of the Botanical Reserve was tested by analysis of variance. Each follow-up survey was done at the same site as the previous one, and therefore the analysis was conducted as for a split plot design where successive observations are made of the same unit over a period of time (Little & Hills 1978). The angular transformation was applied to the data. Relationships between plant cover and rainfall were determined by means of Pearson's correlation coefficients.

Herbivore populations

Herbivore numbers in the park were determined by means of an annual helicopter census which followed the procedure described by Hall-Martin (1988).

Results

The relative abundance of the most common grass species in the six monitoring plots changed markedly from 1984 to 1990 (Figure 1). From 1984 to 1988 *Themeda triandra* was the dominant species, followed in abundance by *Digitaria eriantha.* Thereafter *Themeda triandra* declined, and by 1990 *D. eriantha* was dominant. Three other grasses, *Eragrostis obtusa*, *Eragrostis curvula* and *Cynodon dactylon,* progressively increased over the study period, reaching a peak in 1990. The abundance of *Panicum stapfianum* fluctuated: it declined abruptly in 1988, then recovered in 1989 and 1990.

Among the plants other than grasses the dwarf shrub *Helichrysum rosum* declined in abun-

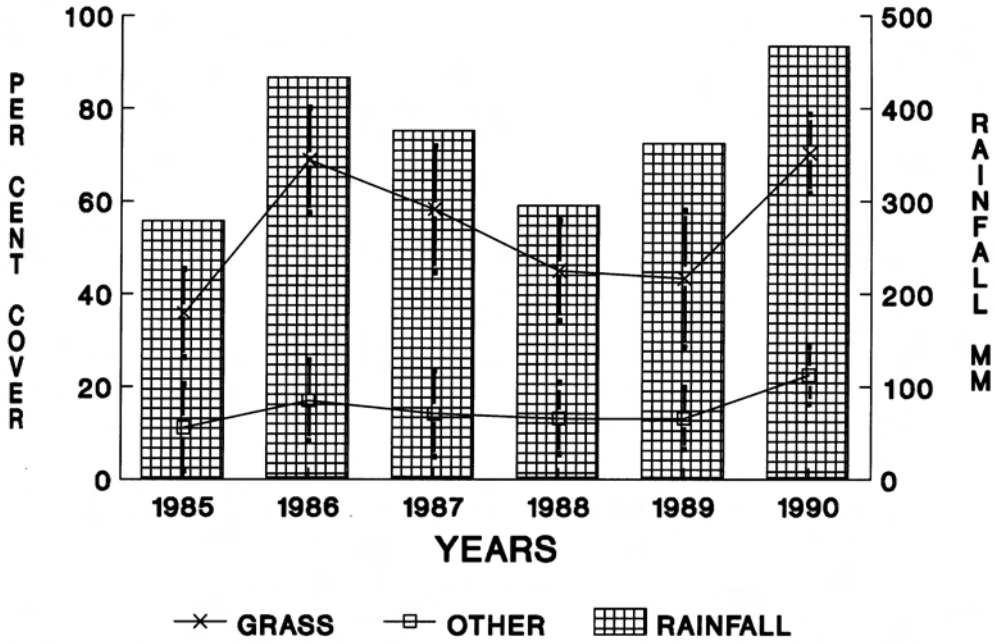

Fig. 3. Changes in canopy spread cover of grasses and plants other than grass from 1985 to 1990, compared with the rainfall over the 12 months preceding the surveys. For the cover values means are presented with 95% confidence limits (n = 6 plots surveyed in each year).

dance over the study period. The succulent *Crassula ericoides* remained stable from 1984 to 1988, then increased in 1989 and 1990 (Figure 2).

Between-year fluctuations in the canopy spread cover of both grass and other plants (Figure 3) were closely correlated with the amount of rain that fell during the 12 months preceding the surveys (r = 0,93 for grasses, r = 0,90 for other plants; $P < 0,05$).

There were marked differences in plant species composition between the inside and outside of the Botanical Reserve (Figure 4). There is also evidence of changes from 1987 to 1990, both inside and outside the Reserve.

Themeda triandra was significantly more abundant inside the Botanical Reserve than outside ($F = 15.72$, df 1 and 5, $P < 0,01$). This species also declined significantly in abundance from 1987 to 1990 ($F = 25.57$, df 1 and 10, $P < 0,001$). The analysis of variance for *Themeda triandra* showed no significant years X situation (inside vs outside) interaction ($F = 0.01$ df 1 and 10). This shows that the magnitude of the decline in abundance from 1987 to 1990 did not differ significantly between the inside and outside the Botanical Reserve (see Figure 4).

Inside the Botanical Reserve the abundance of *Eragrostis obtusa* changed relatively little from 1987 to 1990. In contrast, outside the reserve it increased sharply (Figure 4). This difference is substantiated by the significant years X situation interaction ($F = 11,44$, df 1 and 10, $P < 0,01$).

Both inside and outside the Botanical Reserve the dwarf shrub *Helichrysum rosum* declined in abundance from 1987 to 1990. For this species the difference between years was sig-

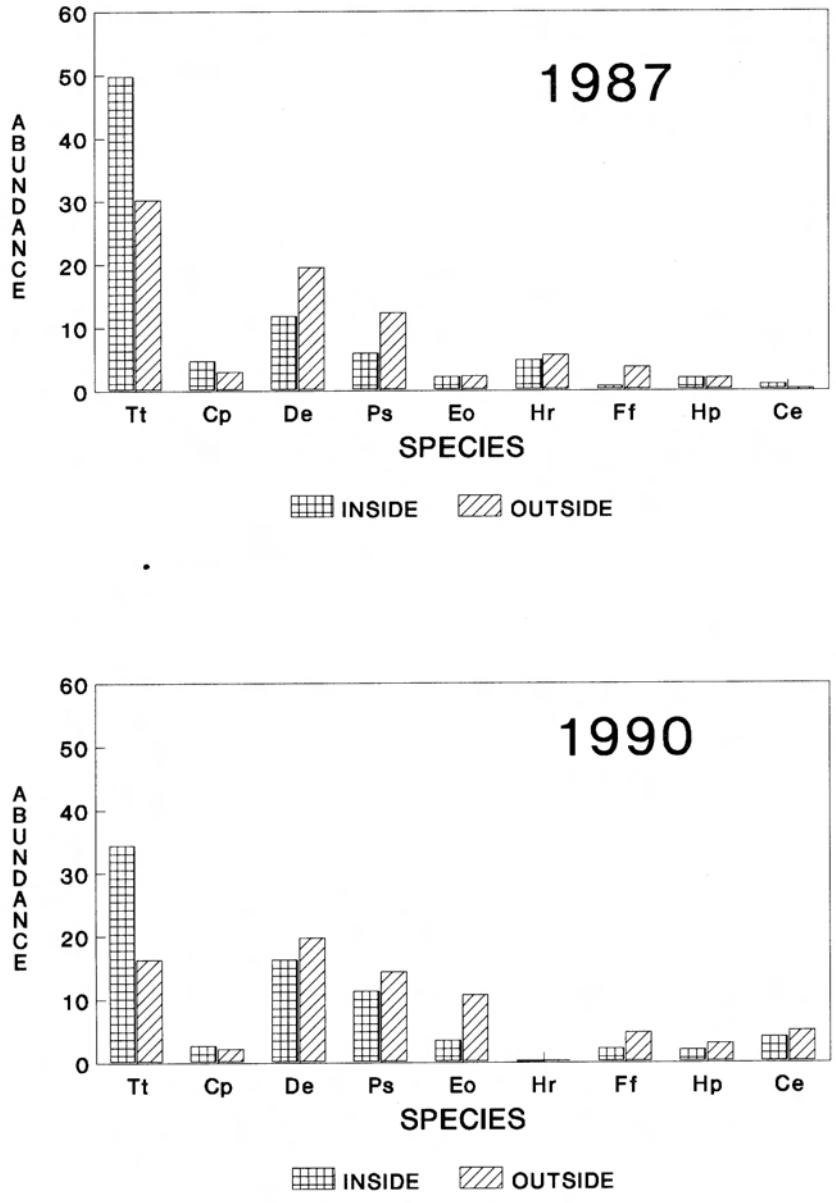

Fig. 4. The abundance of some common plant species compared between (i) the inside and outside the Botanical Reserve and (ii) the years 1987 and 1990. Tt = *Themeda triandra*; Cp = *Cymbopogon plurinodis*; De = *Digitaria eriantha*; Ps = *Panicum stapfianum*; Eo = *Eragrostis obtusa*; Hr = *Helichrysum rosum*; Ff = *Felicia fascicularis*; Hp = *Hibiscus pusillus*; Ce = *Crassula ericoides*.

Table 1
Changes in the population sizes of four herbivore species in the Addo Elephant National Park, 1983-1989. (No census was conducted in 1984)

	1983	1984	1985	1986	1987	1988	1989
Elephant	116	—	120	127	133	140	151
Buffalo	157	—	42	53	53	50	48
Hartebeest	24	—	23	26	37	42	23
Eland	37	—	49	54	50	35	22

nificant (F = 18,29, df 1 and 10, $P < 0,01$). Neither the difference between the inside and outside of the Botanical Reserve (F = 0,1 df 1 and 5) nor the interaction (F = 0,04, df 1 and 10) were significant.

For the grasses *Digitaria eriantha*, *Panicum stapfianum*, *Cymbopogon plurinodis*, the dwarf shrub *Felicia fascicularis* and the forb *Hibiscus pusillus* neither the differences between years, nor the difference between the inside and the outside of the reserve were significant. The succulent *Crassula ericoides* showed a marked increase from 1987 to 1990, both inside and outside the Botanical Reserve. This species was, however, largely confined to only one pair of plots and so no analysis of variance could be conducted.

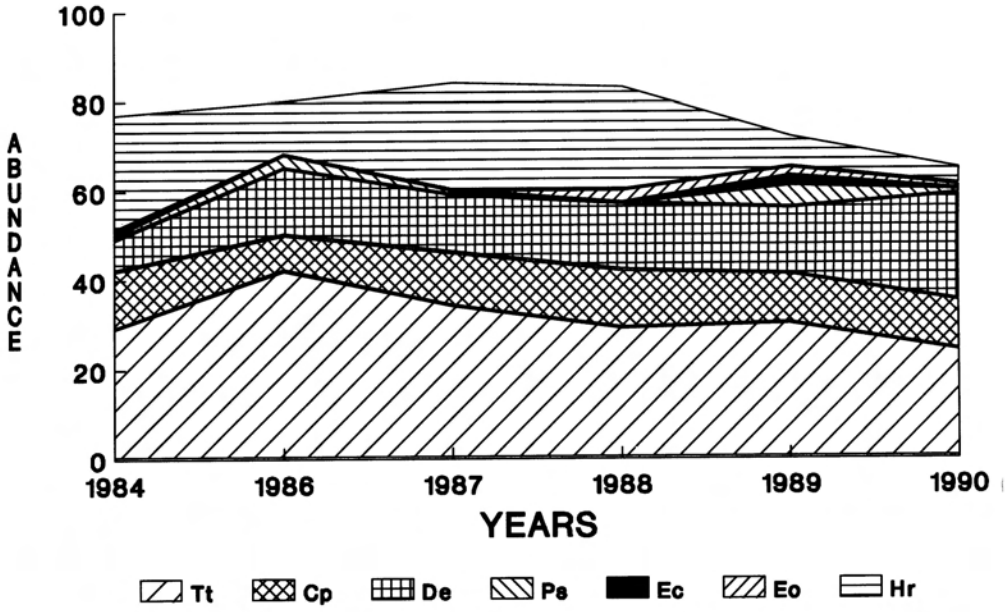

Fig. 5. Changes in the relative abundance of some common plant species in a 30 m by 25 m exclosure in the Bontveld from 1984 to 1990 (excluding 1985). Based on results from nearest plant point surveys (a total of 100 points were observed in each year). Tt = *Themeda triandra*; Cp = *Cymbopogon plurinodis*; De = *Digitaria eriantha*; Ps = *Panicum stapfianum*; Ec = *Eragrostis curvula*; Eo = *Eragrostis obtusa*; Hr = *Helichrysum rosum*

Changes in the relative abundance of the different plant species within the 30 m x 25 m exclosure (Figure 5) were similar to those described for the other plots in that both *Themeda triandra* and *Helichrysum rosum* declined over the study period.

Fluctuations in the numbers of grazers and mixed grazer/browsers during the study period are shown in Table 1. Before 1983 buffalo numbers were maintained at between 150 and 200 by regular harvesting, excess animals being captured and translocated to other conservation areas. In 1984 rainfall was particularly low (279 mm), and a number of buffalo were observed to be in poor condition. A total of 68 animals were harvested during 1983 and 1984, but this failed to prevent a die-off. Thirty-four buffalo carcasses were observed during the census of April 1985, the population having declined from 157 in 1983 to 42 in 1985.

After 1985 it was decided to reduce the stocking rate of the buffalo population. Numbers were maintained at between 40 and 55 by harvesting 10 to 15 individuals per year.

The elephant population expanded during the study period, probably at least partly because of the increase in the size of the available area (see above). The hartebeest population also expanded up to 1988, after which they were reduced by management to relieve the pressure on the grazing (Table 1).

Discussion

The results show that large herbivores had an important influence on plant species composition. In particular, *Eragrostis obtusa*, which showed a much greater increase in relative abundance in unfenced than in fenced plots, appears to have been promoted by grazing. This is substantiated by other studies: increases in abundance of *Eragrostis obtusa* are regarded as being symptomatic of severe overgrazing (Willis & Trollope 1987; Danckwerts & Stuart-Hill 1988).

The grasses *Eragrostis curvula* and *Cynodon dactylon* increased from 1984 to 1990 in the six monitoring plots (Figure 1). These two species were absent from the paired plots on the boundary of the Botanical Reserve, so it was not possible to determine the extent to which they were influenced by large herbivores. *E. curvula* and *C. dactylon* are, however, also widely regarded as being promoted by grazing (e.g. Vorster 1982; Willis & Trollope 1987; Danckwerts & Stuart-Hill 1988).

Themeda triandra typically tends to decrease in abundance as a result of overgrazing (Vorster 1982; Willis & Trollope 1987; Danckwerts & Stuart-Hill 1988). The fact that this species was significantly more abundant in fenced than in unfenced plots shows that this was also the case in the AENP.

However, the decrease in *T. triandra* from 1987 to 1990 was evident in all plots, fenced and unfenced. This suggests that grazing may not have been the main factor determining its decline during the latter part of the study period, rainfall fluctuations probably played a role. The year 1988 was dry with little grass cover. Rainfall improved over the two following years, and this evidently stimulated an increase in grass cover in 1990 (Figure 3). Thus the drought of 1988 may have caused tuft mortality among *Themeda triandra*. The improved rainfall which followed is likely to have promoted *Digitaria eriantha* and *Eragrostis obtusa*, which characteristically recover more rapidly after drought than *T. triandra* (Danckwerts & Stuart-Hill 1988).

The sharp decline in relative abundance of *Panicum stapfianum* in 1988 may also have been due to the drought during that year (Figure 1). Unlike *T. triandra* this species readily establishes itself on denuded soil, in the AENP (pers. obs.) and elsewhere (Roberts 1973), and this characteristic may have assisted its recovery in 1989 and 1990.

Themeda triandra is favoured by the herbivore community in the AENP over *Eragrostis obtusa* and *Digitaria eriantha* (Novellie 1988). *E. obtusa* is in fact little utilized. The observed increase in relative abundance of *E. obtusa* in plots subjected to grazing is therefore deleterious in terms of one of the priority conservation objectives of the AENP, which is to maintain an expanding buffalo population. If the increase in unpalatable grasses at the expense of more palatable ones is allowed to continue the capacity of the Bontveld to sustain buffalo and other grazers will decline.

The decline in relative abundance of the dwarf shrub *Helichrysum rosum* was evidently not caused by large herbivores as it was evident in all plots, fenced and unfenced. The reason for its decline is unknown - it could be due to either rainfall fluctuations or invertebrate herbivores. The succulent forb *Crassula ericoides* increased in certain plots in 1989 and 1990 (Figure 2, Figure 4). The plants encountered in the 1989 surveys were almost all small seedlings, so the increase of this species was apparently due to an episode of seedling establishment.

The decline of the buffalo population in 1984 illustrates the difficulty of managing large herbivores in confined areas that are subject to marked environmental fluctuations. The dry conditions prevailing in 1984 led management to anticipate a die-off among the buffalo. Between 40 and 50 % of the population was harvested in an effort to forestall a crash, but this failed to prevent a substantial number of deaths.

It seems likely that a drought-induced shortage of forage was largely responsible for the decline in buffalo numbers. In January 1985, just after the population crash, mean canopy spread cover of grass in the monitoring plots was only 36 % (Figure 3). The following year mean grass cover increased to 69 % under the influence of improved rainfall. Figure 3 indicates that variations in rainfall can result in wide fluctuations in grass cover.

On several occasions in the past die-offs of the buffalo population in the AENP have occurred during droughts (Schultz & De Graaff 1970). De Graaff *et al.* (1973) found that the rumens of Addo buffalos that had died during a drought contained a large proportion of browse. Hofmann (1989) showed that the digestive system of buffalos is typical of bulk and roughage grazers, and is unsuited to a diet of browse. The animals were thus evidently forced by the scarcity of grass to accept a diet to which they were not adapted.

The normal response of wild grazing herbivores to localized droughts is to move in search of better grazing (McNaughton 1979; Sinclair & Fryxell 1985), but this option is not open to the Addo buffalo.

The buffalo population at Addo is one of the few in southern Africa that is free of foot-and-mouth and corridor disease, and hence they are much in demand for re-establishment in other conservation areas. It is therefore desirable to optimize harvests and to minimise mortality. However, the wide rainfall-induced fluctuations in the food supply make it difficult to set realistic stocking and harvesting rates. Even if stocking rates are set at conservative levels there is always the possibility that a run of dry years will decimate the population.

In view of the observed deleterious changes in plant species composition it appears advisable to set the herbivore stocking rates at levels below those which prevailed during the study period. The following management measures are planned in order to take the pressure off the grazing in the AENP:

- The stocking rates of species that compete with buffalo for grass (eland and hartebeest) will be substantially reduced.

- Planted pastures have been established

on recently acquired agricultural land adjoining the AENP, and the buffalo will be allowed access to these in the near future.

- The size of the AENP will be expanded.

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