Biodiversity and Conservation **6**, 1203–1217 (1997)

The impact of large herbivores on floral composition and vegetation structure in the Naukluft Mountains, Namibia

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Received 25 October 1995; revised and accepted 5 March 1996

Floral composition and vegetation structure were investigated on the Naukluft Mountain Plateau to determine (i) whether or not grazing has had an impact on the flora of the Naukluft Mountains during the last two decades and (ii) if so, whether vegetation recovery is influenced by the nature of the rainy season. Vegetation subjected to grazing to large herbivores and vegetation excluded from grazing for 18 and 19 years was compared. Based on classification (TWINSPAN) and ordination (detrended and canonical correspondence analysis) of 20, 10 × 10 m stands within and outside exclosures in two seasons, a clear difference in floristic composition between grazed and not grazed areas was indicated. Although neither the height of the vegetation, not the growth form spectrum differed significantly between grazed and not grazed sites, leaf-succulents were much more abundant when grazing was excluded. This suggests that changes in the vegetation due to grazing pressure have occurred in the last two decades, but the degree of grazing impact is not severe and may be part of the natural savanna ecosystem of the Naukluft Mountains. Whether this trend also occurs in other vegetation types in the Naukluft Mountains remains to the investigated.

Keywords: grazing pressure; Namib fringe; rangeland management; semi-arid; savanna vegetation.

Introduction

How many herbivores can be supported by vegetation in confined conservation areas on a sustainable basis is one of the most frequent questions park managers put to rangeland researchers (Ben Shahar, 1993). However, even in parks where data describing long-term vegetation changes in response to different grazing pressures are available, this question is a debated issue. In the past, rangeland researchers were pressed to give one-off figures for carrying capacity or stocking rates in a particular park or rangeland. At the same time there is a realization that in semi-arid and arid regions with highly variable and unpredictable climatic conditions over years, such figures can only be very crude estimates and may not reflect the true situation (Westoby, 1980).

Timing, amount and intensity of rainfall in the Namib Desert has shown a marked influence on population dynamics as well as floral composition of desert plants (Günster, 1993; Jürgens *et al.*, 1996). Savanna vegetation in Namibia is expected to show a similar response which would particularly affect the recovery potential of vegetation under grazing pressure. A study in North American desert shrubland, for example, showed that the grazing season had a more pronounced effect on floristic composition than grazing

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intensity (Whisenant and Wagstaff, 1991). Similarly, recovery of African savanna vegetation might also be influenced by seasonal effects (Novellie and Bezuidenhout, 1994).

The present study investigates the floral composition and vegetation structure of enclosed and comparable sites subjected to grazing by large herbivores to determine (i) whether or not grazing has had an impact on the flora in the Naukluft Mountains during the last two decades and (ii) if so, whether vegetation recovery is influenced by the nature of the rainy season. This study may thus contribute to future management decisions in the park.

Materials and methods

Study area

The study site is situated on the eastern plateau of the Naukluft Mountains in the Namib Naukluft Park (24°12′S, 16°17′E) at an altitude of 1940 m (Fig. 1). The topography is level and dolomite is exposed in most areas (Hartnady, 1980), sometimes covered by calcrete crusts. Thin layers of lithosol are only found in depressions and cracks. The climate in this region is semi-arid with rainfall averaging 50–100 mm annually. Average daily maximum temperatures reach 33°C, usually in January, while the average daily minimum lies at 4°C, the coldest month being July (van der Merwe, 1983). Due to the high altitude, frost occurs regularly during the winter months and wind blows strongly from varying directions all year round. The vegetation is classified as 'semi desert and savanna transition zone' (Giess, 1971) and is dominated by dwarf shrubs on the plateau.

Previously used for sheep farming, the farm Naukluft was proclaimed a conservation area for Hartmann's mountain zebra (*Equus zebra hartmannae* Matschie) in 1968. Neighbouring farms were added steadily in the following decade until almost the entire mountain range was included in the game park. Today the Naukluft Mountains are linked to the dune areas of the Namib by a corridor allowing free movement of game in an area of nearly 5 million hectares. Hartmann's mountain zebra, springbok (*Antidorcas marsupialis* Zimm.) and kudu (*Tragelaphus strepsiceros* Pallas) are the most prominent herbivores, while steenbok (*Raphicerus campestris* Thun.) and klipspringer (*Oreotragus oreotragus* Zimm.) occur occasionally (Joubert, 1979).

A programme to monitor possible vegetation changes in the Namib Naukluft Park was set up in 1976 by Nel (Bridgeford, pers. comm.), but unfortunately never followed up. For this programme, exclosures were erected at several sites throughout the park.

Surveys for this study were conducted in the rainy reason 1994 and 1995 (March–April). In southern Africa, a meteorological year is measured from July to June to include the entire rainy season which usually extends from November to May (Lancaster *et al.*, 1984). In the Namib Desert the rainy season is often confined to a few rain events during the period of January to April. In 1993/1994, 8 mm fell in January and 34 mm in February totalling 42 mm for the entire season in the Naukluft Mountains (measured at Arbeid Adelt). In the period 1994/1995 45 mm were recorded in February and 18 mm in March, totalling 63 mm (Bridgeford, pers. comm.).

Field survey

To determine possible vegetation changes in response to grazing by large mammals, a 100 × 125 m exclosure was erected in 1976 by Nel with a 1.5 m high diamond mesh fence

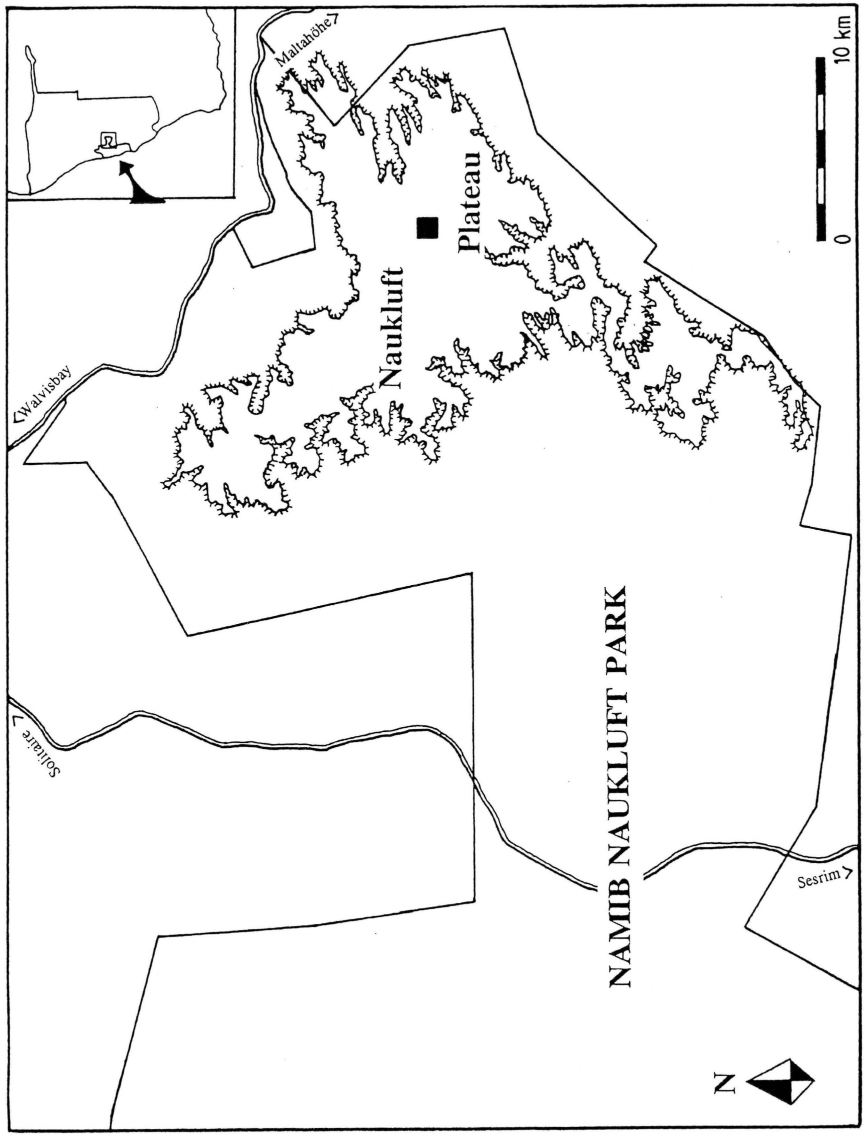

Figure 1. Location of the study area in the Namib-Naukluft Park (— park boundary; ═ road, ┬┬┬ escarpment; ■ study site).

extended by three horizontal wires to a total height of 2 m. This exclosure was revisited after 18 (1976–94) and 19 (1976–95) years.

The vegetation was surveyed in randomly placed 10 × 10 m stands within and outside the exclosure. Because the exclosure was already in place when the study was conducted, it was not feasible to intersperse different grazing treatments as suggested by Hurlbert (1984) to avoid pseudoreplication. However, the fences were not erected along a natural ecotone, thus it is unlikely that any differences existed between the sites prior to exclusion of herbivores.

In each stand, vegetation cover was estimated according to Braun-Blanquet (Müller-Dombois and Ellenberg, 1974) and each species was assigned a height class (0–25 cm, 26–50 cm, 51–100 cm), which was an average for all individuals of a species within a particular stand. Species identifications followed the nomenclature of Kolberg *et al.* (1992) and Arnold and de Wet (1993). All plant species were assigned to one of seven growth form categories (herb; grass; stem-succulent; leaf-succulent; evergreen; deciduous; geophyte and hemicryptophyte). Because of their rare occurrence, geophytes and hemicryptophytes were lumped in one category. In addition, the percentage rock, stone and soil cover was estimated visually in each stand and notes were taken to describe total vegetation cover, habitat type, altitude, aspect and slope.

Soil sampling and analysis

Soil depth was measured randomly three times in each stand by hammering a metal rod into the soil until bed-rock was reached. About 50 g of soil was sampled at the same three locations from the top 5 cm and pooled for later laboratory analysis. Soil pH was measured with a 1:2.5 soil KCl ratio on a mass basis. Exchangeable cations of calcium, magnesium, potassium and sodium were released from the soil with ammonium acetate, while phosphorus was released using sodium carbonate. Atomic absorption spectrophotometry (Reynolds and Aldous, 1970) was used for measurement of soluble phosphorus and exchangeable calcium, magnesium, potassium and sodium. Sand content was measured with sieving, while silt and clay content was determined with hydrometer analysis (Bouyoucos, 1962). Soil analyses were carried out by the Ministry of Agriculture and Rural Development.

Data analysis

Three units of measurement: floristic composition, height class and growth form spectrum (the last two resemble vegetation structure) were used to determine the dual effect of grazing and the nature of rainy season on the vegetation. The nature of the rainy season encompasses, besides total amount of rainfall, intervals between rain events and the intensity of rainfall.

To test whether there were differences in soil parameters between inside and outside the exclosure, the 1995 soil data with non-parametric distribution were subjected to Mann-Whitney U-tests, while those with parametric distribution were subjected to Student's *t*-tests (Fowler and Cohen, 1992).

To explore the effect of fencing on growth form diversity and height of the vegetation, the total cover per height class and growth form was calculated in each plot and subjected to two-way ANOVA for 1994 and 1995 data separately, because of possible pseudoreplication.

Two-way indicator analysis (TWINSPAN, Hill, 1979a) was used to investigate whether or not differences in floral composition occurred between stands under grazing pressure and those protected from grazing in two subsequent seasons. TWINSPAN classifies plant communities on the basis of co-existence and abundance of plant species in different stands. The final result is a hierarchical tabulation of species and stands according to their similarities, which can be presented in a dendrogram. For further detail see Kent and Coker (1992). To aid the interpretation of the species and stand groupings produced in the TWINSPAN analysis, the data were also ordinated. Species cover data and environmental data were ordinated using indirect (detrended correspondence analysis) and direct (canonical correspondence analysis) gradient analysis. In detrended correspondence analysis (DCA) (Hill, 1979b), species or stands are organized along DCA axes which are extracted from the species data alone. Environmental data are superimposed subsequently to explain the derived DCA axes. Canonical correspondence analysis (CCA), in turn, is designed to detect patterns in species composition which are best explained by the measured environmental variables (Ter Braak, 1986, 1987). The final ordination diagram thus presents species distributions and their relationships with environmental variables. To find out how much of the variation in the species data is accounted for by the environmental data, Ter Braak (1986) suggested using DCA and CCA together. If the results of these analyses do not differ greatly, then the environmental data measured account for much of the variation in species data. A Monte Carlo permutation test was used to test the significance of the first CCA axis.

The following environmental variables were included in the initial analyses: soil depth, slope angle, aspect, rockiness, exposure, altitude, pH, phosphorus, potassium, calcium, magnesium, sodium, sand, silt, clay, grazing impact and year. The data analyses showed negligible variance in some variables (slope angle, aspect, exposure and altitude) and detected multi-collinearity with clay content (Ter Braak, 1987). Those variables were thus removed from the final analyses.

Results

Floristic composition

Total species richness was higher in 1995 (81 species) than in 1994 (52 species).

The TWINSPAN analysis of the pooled data showed that most stands were grouped according to position inside and outside the exclosure and according to year. Division one separated all grazed stands in 1994 and one grazed stand in 1995 (21 to 25 and 81) from the remaining stands (Fig. 2). On the next level all stands within the exclosure (26 to 30 and 76 to 80) and one stand from the grazed area in 1995 (84) were separated from the remaining grazed stands of 1995 (82, 83 and 85). On the same level, stand 81 was also separated from the grazed stands in 1994 (21 to 25). The last presented division separated the stands within the exclosure between different years (Fig. 2). The indicator species for the grazed stands in 1995 (species group A) are *Tribulus zeyheri* and *Ursinia nana*, while for the stands within the exclosure (groups B and C) the indicator species is *Crassula* species. The indicator species for stands within the exclosure in 1995 is *Enneapogon desvauxii* (group B), while that for the grazed stands in 1994 (group D) is *Lycium cinereum*. The four groups of stands of the first two levels of the TWINSPAN analysis also emerged clearly in the DCA ordination diagram (Fig. 3), indicating that these might be the most important

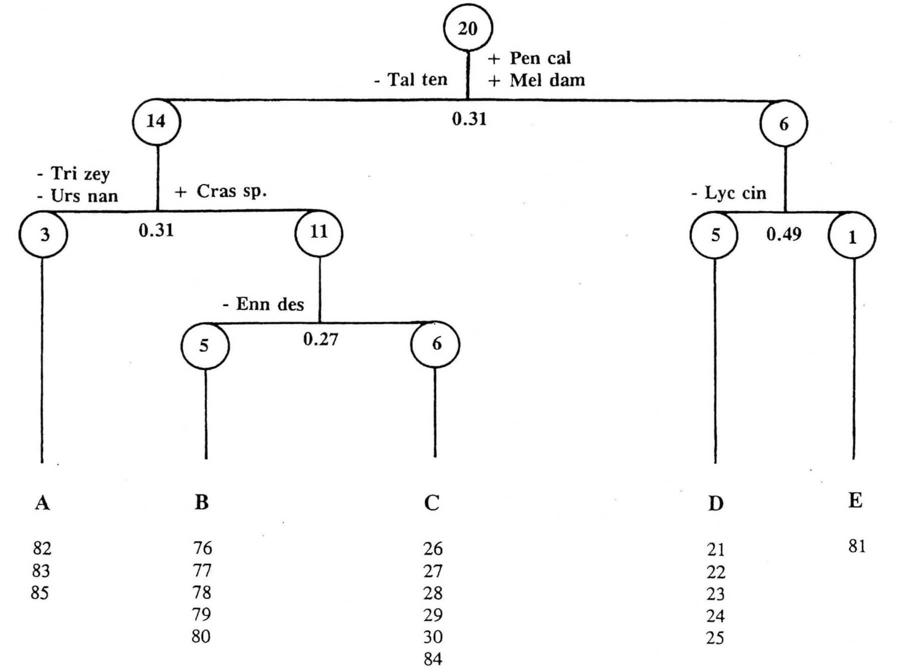

Figure 2. Hierarchical classification of stands derived from TWINSPAN. Encircled values represent the number of stands in groups on different levels, while non encircled values are eigenvalues of each division (Indicator species: Pen cal = *Pentzia calva*, Mel dam = *Melhania damarana*, Tal ten = *Talinum tenusissimum*, Tri zey = *Tribulus zeyheri*, Urs nan = *Ursinia nana*, Cras sp. = *Crassula* sp., Enn des = *Enneapogon desvauxii*, Lyc cin = *Lycium cinereum*). Stands and species groups are indicated at the bottom of the diagram.

divisions. Stand 81 appeared removed from all other stands. Further divisions of the TWINSPAN analysis were not supported by the DCA ordination.

The geophytes *Dipcadi longiflora* and *Oxalis purparescens*, the succulents *Ebracteola candida* and *Othonna protecta* and the grass *Fingerhutia africana* were only found in the exclosure in both seasons.

Floristic composition and environmental variables

The environmental data, slope angle, aspect, exposure and altitude, showed such low variation between stands that they were removed from the CCA analysis. Although the measured quantitative environmental variables did not show significant differences between grazed stands and those within the exclosure (Table 1), the variation between stands was sufficient for inclusion in the CCA analysis.

When comparing eigenvalues, inter-set correlations and cumulative variance of the DCA and CCA analysis, it was evident that the values of the first axis were almost identical, while those of the second axis showed less than 20 % difference (Table 2). The

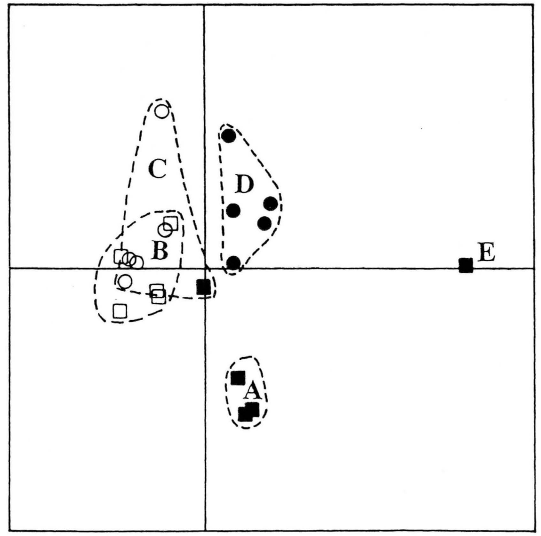

Figure 3. Detrended correspondence analysis (DCA) biplot of stands for axis 1 and 2 (○ not grazed 1994, ● grazed 1994, □ not grazed 1995, ■ grazed 1995). The stands are grouped according to TWINSPAN divisions (A–E).

eigenvalues of axis 3 were within a 10 % difference, but the other variables showed higher discrepancies.

Grazing impact showed the highest correlation with axis 1 and axis 2, while the difference in year was most highly correlated with axis 3 (Table 3). Rockiness was the most

Table 1. Means and standard deviations and statistical analysis of soil physical and chemical data from five 10 × 10 m stands within and outside of exclosures at Kapokvlakte, Naukluft Mountains

	Exclosure	Grazed	Significance
Soil depth (cm)	11.0 ± 4.2	12.9 ± 6.1	NS^U
% rockiness	14.0 ± 8.2	11.0 ± 8.9	NS
pH	6.2 ± 0.7	6.0 ± 1.0	NS
P (ppm)	15.0 ± 6.3	13.8 ± 6.4	NS
K (ppm)	169.6 ± 71.5	169.8 ± 25.8	NS
Ca (ppm)	1288 ± 1188	1827 ± 1129	NS^U
Mg (ppm)	204.4 ± 18.9	170.0 ± 49.9	NS
Na (ppm)	14.6 ± 3.9	14.8 ± 2.3	NS
% sand	78.6 ± 8.2	89.6 ± 7.1	NS^U
% silt	12.4 ± 6.6	4.6 ± 4.8	NS
% clay	9.0 ± 1.7	5.8 ± 2.5	NS^U

^{U} Mann whitney U-test, all other variables are tested with *t*-tests; $^*p < 0.05$; NS not significant.

Table 2. Comparison of DCA + CCA data. Monte Carlo permutation test: *significant at 0.01 level

	axis 1	axis 2	axis 3	axis 4
eigenvalues				
DCA	0.599	0.393	0.307	0.212
CCA	0.592*	0.480	0.333	0.249
inter-set correlations				
DCA	0.992	0.860	0.772	0.897
CCA	0.995	0.986	0.974	0.979
% cumulative variance				
DCA	21.7	32.3	30.9	45.3
CCA	21.7	39.3	51.6	60.7

important determinant of axis 4. The first two axes of the CCA analysis accounted for 39.3 % of the variance in the species data (Table 2, Fig. 4). A Monte Carlo permutation test showed that the first axis was highly significant. Thus variation in species abundances was related to variation in environmental data, in this case to a grazing gradient which separated grazed and not grazed stands along the first canonical axis. Other important environmental factors were calcium, % sand, % silt, pH and soil depth (Fig. 4, Table 3).

Vegetation structure

No plants above 1 m height were encountered in this survey. Total cover was highest in the height class 25–50 cm, while the height class 51–100 cm showed the lowest cover values (Table 4). The height class distribution differed significantly in both seasons, but there was no significant difference between grazed and not grazed areas (Table 5). Although there was no interaction between height class and grazing pressure in 1994, there was an interactive effect between these two parameters in 1995.

Of seven identified growth forms, evergreens, leaf-succulents and grasses were most frequently encountered (Fig. 5). Evergreen shrubs and stem-succulents contributed comparatively evenly to the growth form spectrum in grazed and not grazed areas and in different seasons (Fig. 5), but there was significant variation in the contribution of other growth forms (Table 4). Although the cover values for leaf-succulents were remarkably higher and those for grasses remarkably lower within the exclosure in both seasons, no obvious trends were found in any other growth form category. Thus there was no significant difference between grazed and not grazed areas in both seasons, but there were interactions between growth form and the effect of fencing (Table 5).

Table 3. Correlations of environmental variables with canonical axes of CCA analysis

	axis 1	axis 2	axis 3	axis 4
Soil depth	0.034	−0.478	−0.334	−0.522
% rockiness	0.238	0.033	0.327	**−0.582**
pH	0.450	0.262	0.622	−0.047
Phosphorus	−0.091	0.033	−0.127	−0.151
Potassium	0.201	−0.099	0.022	−0.237
Calcium	0.697	0.218	0.248	0.077
Magnesium	0.090	0.038	0.004	−0.487
Sodium	−0.341	0.383	−0.023	0.187
% sand	0.493	−0.147	−0.419	0.145
% silt	−0.504	0.144	0.336	−0.182
Grazing impact	**0.716**	**−0.549**	0.159	0.195
Year	0.039	−0.001	**−0.788**	−0.266

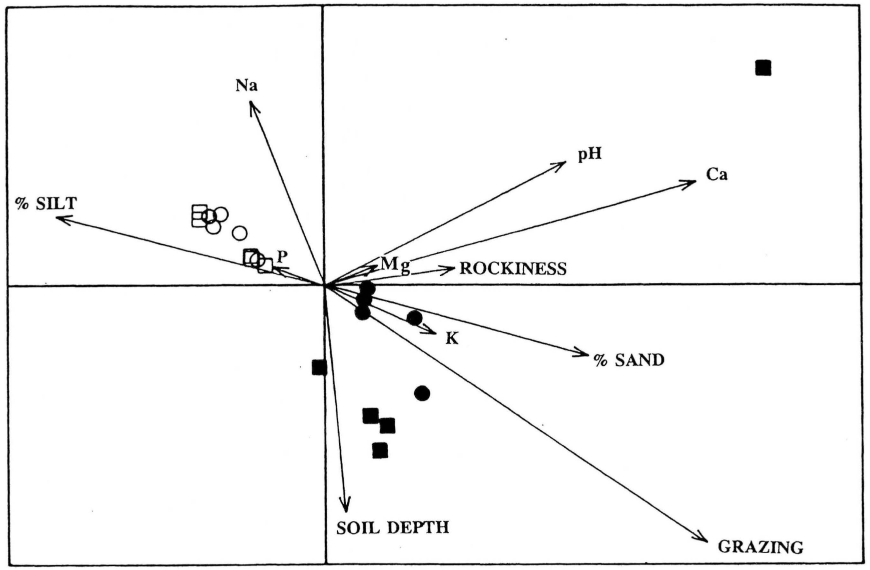

Figure 4. Canonical correspondence analysis (CCA) biplot of stands for axis 1 and 2 (○ not grazed 1994, ● grazed 1994, □ not grazed 1995, ■ grazed 1995). Arrows indicate individual gradients of soil and environmental parameters.

Table 4. Mean cover and standard deviation per height class from five 100 m^2 stands at sites with and without grazing pressure

	height class (cm)		
	0–25	26–50	51–100
1994			
grazed	35.4 ± 22.6	50.7 ± 27.1	13.5 ± 15.4
exclosure	21.8 ± 15.2	53.1 ± 20.7	1.0 ± 2.2
1995			
grazed	44.3 ± 19.5	41.7 ± 19.7	0
exclosure	20.6 ± 14.9	62.1 ± 26.8	24.0 ± 18.6

Table 5. Two-way analysis of variance from 10 stands at Kapokvlakte with respect to height class or growth form and effect of fencing

	F-ratio test statistics	
	1994	1995
Height class	13.90***	11.61**
Effect of fencing	1.31NS	1.03NS
Interaction	0.56NS	5.15*
Growth form	11.35***	8.62***
Effect of fencing	1.54NS	1.95NS
Interaction	3.95**	8.09***

NS not significant; $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$.

Discussion

Since game populations have been fairly stable during the last two decades (Ministry of Environment and Tourism, 1983–1988), the investigations in the fenced areas which excluded grazing pressure and comparable sites subjected to grazing suggest that the vegetation at this site on the Naukluft Mountain plateau has been changed by large herbivores. The data also show that the nature of the rainy season does affect vegetation recovery to a certain extent, since plants within the exclosure were on average higher in 1995 than in 1994. Impacts on floristic composition and vegetation structure have been analysed in detail and are discussed below.

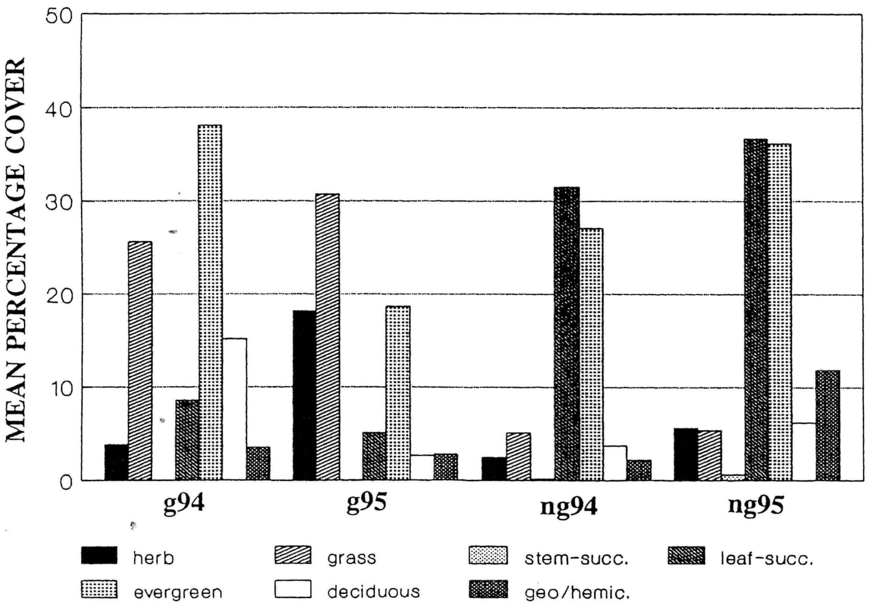

Figure 5. Mean percentage cover per 10 × 10 m stand per growth form group from five stands at sites with (g) and without (ng) grazing pressure (94 = rainy season 1994; 95 = rainy season 1995).

Floristic composition and environmental variables

As indicated by the ordination analyses (DCA and CCA) the general habitat, represented by altitude, exposure, slope angle and aspect showed so little variation between stands, that it prompted removal from the analyses (Fig. 4). Although the same geological strata underlie all stands, soil physical and chemical parameters, in turn, varied sufficiently between stands to be included in the ordination analyses. However, soil parameters showed no significant differences between inside and outside the exclosure (Table 1), which eliminated the effect of possible pseudoreplication. Thus habitat parameters can be excluded as variables determining differences in species composition between inside and outside the exclosure, while climatic conditions are unlikely to vary significantly within an area of 200 × 200 m. The groupings in the classification and ordination analyses are thus largely attributed to differences in grazing pressure and season.

As suggested by Ter Braak (1986), a comparison of eigenvalues, inter-set correlations and cumulative variances between DCA and CCA revealed extremely low differences between values of axes 1 and 2 (Table 2). This indicated that the measured environmental data in this analysis reflected well the real situation in the field.

The classification (TWINSPAN) and ordination (DCA) showed that six of the stands from the grazed area (species groups D and E) were clearly different from the remaining 14 stands (Figs 2 and 3). Soil chemistry, particularly calcium concentrations and subsequently differences in pH may be responsible for this pattern (Fig. 4), since there were no obvious differences in general habitat or rainy season of these six stands. Three grazed stands of 1995 also marked a distinct group (species group A) (Figs 2 and 3), which besides grazing impact, may be attributed to soil depth (Fig. 4). The stands within the exclosure from different seasons are not clearly separated in the ordination (species groups B and C), although the separation between seasons emerged in the TWINSPAN classification (Fig. 2). This means that differences between seasons exist, but that they are not as important as for stands outside the exclosure. Seasonal effects thus had a greater impact on floristic composition under grazing pressure than when grazing was excluded. Floristic diversity in this study was higher when grazing was excluded, irrespective of season, while selective grazing by herbivores reduced floristic diversity more in a less favourable season than in a favourable season. This may explain the larger difference between seasons in grazed stands than in stands within the exclosure.

The CCA ordination diagram presents species distributions and their relationship with environmental variables. In this analysis axis 1 of the CCA analysis showed a high positive correlation with grazing impact, while axis 2 showed a negative correlation, thus both clearly represent a grazing gradient (Table 3). Accordingly, grazed and not grazed stands were organized diagonally between axis 1 and 2 (Fig. 4). The third axis was mainly determined by year, indicating climatic differences between the season of 1994 and 1995. Other environmental variables showed lower correlations with the canonical axes and were therefore of secondary importance in determining species compositions and stand groupings (Table 3). However, soil depth appeared to influence the grazed stands of 1995 (stand 82–85), while calcium concentrations and pH may be responsible for the isolated position of stand 81.

Floristic composition and herbivores

Although the total rainfall was only slightly higher in 1995, species richness was remarkably higher, which may indicate more favourable conditions for plant growth in this comparatively late rainy season. A similar pattern had been found in a study of population dynamics of desert plants in the Namib, which indicated that the timing of the rainy season was more important than the total amount of rainfall (Günster, 1993).

The classification (TWINSPAN) and ordination (DCA) of the floristic data resulted in four clearly distinct groups of stands, which are primarily determined by the position inside or outside the exclosure and secondarily by the effect of different rainy seasons (see also above) (Figs 2 and 3). Some species were only found in the exclosure in both seasons, indicating high susceptibility to grazing. These were the geophytes *Dipcadi longiflora* and *Oxalis purparescens*, the succulents *Ebracteola candida* and *Othonna protecta* and the grass *Fingerhutia africana*. The differences in floristic composition between grazed and not grazed stands are attributed to selective grazing and browsing by herbivores, which greatly reduce or even eliminate palatable species thus increasing the competitive advantage of less preferred plant species. Palatable shrubs in sheep grazed areas in the Karoo, for example, have shown noticeable reduction in canopy cover and reproductive parameters over a period of only three years (Milton, 1994, 1995). The most prominent browsers, kudu, springbok and klipspringer and the grazing mountain zebras, could have a similar impact on the vegetation in the Naukluft Mountains (Skinner and Smithers, 1990).

Vegetation structure

Evergreen dwarf shrubs, such as *Eriocephalus* species, *Pentzia calva* and *Pteronia glauca*, are the most prominent plant species on the Naukluft Mountain plateau, almost resembling what has been described by Acocks (1988) as Western Mountain Karoo.

Exclusion of grazing had no significant effect on the height of the vegetation which was equally variable inside and outside the fenced areas in both seasons (Tables 2 and 3). Only in the more favourable rainy season of 1995, was the proportion of plants above 50 cm height greater inside the fenced area, which indicates that under favourable climatic conditions recovery is higher if grazing pressure is excluded. Observations of perennial rangeland shrubs in Australia support this finding in showing that while grazing had no effect on population dynamics, shrub size was affected (Eldridge *et al.*, 1990).

Despite greater grass cover outside the fenced area and leaf-succulents within the exclosure in both seasons (Fig. 5), these differences were not supported statistically (Table 5). This is probably due to the high variability of the growth form mix in the different seasons and under different grazing pressures (Table 4), a phenomenon which has been observed in many arid regions (Westoby, 1980). Nevertheless, it is obvious that some leaf-succulents such as *Ebracteola candida* and *Othonna protecta* occurred only when large herbivores were excluded, while others such as *Mestoklema arboriforme*, *Ruschia muricata* and *Zygophyllum pubescens* were greatly reduced under grazing pressure (Fig. 5). This suggests that these shrubs, all with comparatively high water content, are probably important fodder species for herbivores in the Naukluft Mountains. Observations of severely grazed *Ruschia muricata* plants outside the fenced area partially support this statement.

The changes in floristic composition and in vegetation structure found in this study are in line with what has been reported in arid and semi-arid rangelands elsewhere. Protection from grazing in North Africa, for example, induced vegetation changes even over relatively short time spans of three and seven years (Ayyad and El-Kadi, 1982; Floret, 1981; Veetas, 1993). Whether these changes are beneficial or detrimental depends on the type of vegetation, the nature and intensity of grazing pressure and the viewpoint of the land user (Noy-Meir, 1993). Certain plant communities, such as Tunisian steppe vegetation, which support large herds of livestock, can only be maintained under heavy grazing pressure (van Duivenbooden, 1993). In many conservation areas, in turn, herbivores are inherent components of the ecosystem. Long-term observations of vegetation under grazing have shown that vegetation has a remarkable recovery potential, and only when a certain degree of degradation is reached, do vegetation changes become irreversible (Westoby *et al.*, 1989). In semi-arid and arid rangelands these processes 'beyond the state of repair' are unfortunately taking place rapidly (Darkoh, 1991; Omar, 1991). Literature on this topic is abundant, but beyond the scope of this paper (for review compare Darkoh, 1989; Schlesinger *et al.*, 1990; Dean *et al.*, 1995). The high variability of climate in arid and semi-arid regions must be taken into account when the carrying capacity of a conservation area or rangeland is determined, to avoid overstocking and subsequent degradation, especially during drought periods.

Implications for management

How many herbivores the Naukluft Mountains, an eastern outpost of the Namib-Naukluft Park, can support, has been a long-standing debate. Several culling operations of mountain zebra have taken place in the past on the basis of game counts, which suggested that numbers were too high for the park area (Bridgeford, pers. comm.). Although the vegetation data show that herbivores have changed the floristic composition at this particular site, seasonal effects also play an important role. The fact that the vegetation structure and growth form spectrum were not changed sufficiently to show a statistically significant difference between grazed and not grazed areas supports the statement that impacts exist, but they are not severe and might be part of the natural 'semi desert and savanna transition' ecosystem. However, although the data suggest that the general physiognomy of the vegetation may not be affected too severely, particular species which are of conservation interest (*Ebracteola candida* and *Othonna protecta*) (Nature Conservation Ordinance No. 4 of 1975) only occur when grazing pressure is excluded. During an extensive vegetation survey over the entire Naukluft Mountain range, it became evident that this study site is a special habitat, since many of the species recorded here did not occur at any other site (pers. obs.). To provide more accurate figures on carrying capacity of this section of the Namib-Naukluft Park, it is imperative that similar observations should be made at other sites to cover the variety of different habitats within the park.

Conclusion

The three parameters selected to study the effect of large herbivores on desert mountain vegetation did not show uniform trends in response to grazing pressure. The floristic composition was clearly affected by grazing herbivores, while slight differences in vegetation structure and growth form spectrum occurred, but were not supported statistically. This is evidence that herbivores are changing the vegetation at the study site in the Naukluft Mountains on a long-term basis, but that their impact is not severe. Whether these trends are also maintained in other vegetation types of the Naukluft Mountains remains to be investigated.

Acknowledgements

I am indebted to Peter Bridgeford and my husband for initial encouragement and invaluable logistic support during the field work. Many thanks to the staff of the National Herbarium for help with plant identifications and to the soil laboratory at the Ministry of Agriculture and Rural Development for soil analysis. Valuable comments from P. Bridgeford and two anonymous referees greatly improved the manuscript. The Ministry of Environment and Tourism gave permission to work in the Namib-Naukluft Park.

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