# Impact of the black rhinoceros (*Diceros bicornis minor*) on a local population of *Euphorbia bothae* in the Great Fish River Reserve, South Africa

Bodina L. Luske[1], Tonja Mertens[1†], Peter C. Lent[2], Willem F. de Boer[1]* and Herbert H. T. Prins[1]

[1]*Resource Ecology Group, Wageningen University, Droevendaalsesteeg 3a, 6708 PB Wageningen, The Netherlands and* [2]*Faculty of Science and Agriculture, University of Fort Hare, Alice 5700, South Africa*

## Abstract

In the Great Fish River Reserve, South Africa, black rhinoceros (*Diceros bicornis minor*) feed extensively on a local population of *Euphorbia bothae.* Maintaining the endangered black rhinoceros and the protected *E. bothae* population are both conservation priorities of the reserve. Therefore, the sustainability of this plant–animal interaction was investigated by comparing population characteristics, browsing incidence and intensity within the reserve and in an adjacent exclosure without access to rhino. Fixed-point photographs showed that over a 2-month period 36.6% of 213 monitored plants were browsed, with an average biomass loss of 13%, and 1% were destroyed. Of 26 plants re-photographed after approximately 3 years, 70% showed a decrease in biomass, averaging 37.8% over this period. In this time span, 19% of the monitored plants died. Small plants (<45 cm) were over-represented in the rhino-browsed area, whereas the fraction of reproductively active plants and overall plant density were found to be lower than in the adjacent exclosure. No evidence of short-term compensatory growth in response to browsing was found for *E. bothae*. This study indicates that, with the current population size, rhinos are overexploiting the *E. bothae* population and special measures should be taken to prevent local extinction.

*Key words:* browsing, compensation, megaherbivores, population structure, thicket, reproduction

## Résumé

Dans la *Great Fish River Reserve*, en Afrique du Sud, le rhinocéros noir (*Diceros bicornis minor*) se nourrit en très grande partie d'une population locale d'*Euphorbia bothae*. Le maintien du rhino noir en danger et de la population protégée d'*E. bothae* sont deux priorités de la réserve en matière de conservation. C'est pourquoi on a investigué la durabilité de cette interaction plante-animal en comparant les caractéristiques des populations, l'incidence et l'intensité de la consommation du rhino dans la réserve et dans un enclos adjacent d'où les rhinos sont exclus. Des photographies prises d'un point fixe ont montré que, sur une période de deux mois, 36.6% des 213 plantes suivies avaient été broutées, avec une perte moyenne de biomasse de 13%, et un pour cent avait été détruit. Des 26 plantes qui avaient été rephotographiées après environ trois ans, 70% montraient une diminution de la biomasse, qui était de 37.8% en moyenne pour cette période. Pendant ce laps de temps, 19% des plantes suivies sont mortes. Les petites plantes (<45 cm) étaient surreprésentées dans la zone broutée par les rhinos, alors que la fraction des plantes actives au point de vue reproduction et la densité générale des plantes se sont avérées plus faibles que dans l'enclos adjacent. On n'a pu mettre en évidence aucune croissance compensatoire d'*E. bothae*à court terme en réponse au broutage des rhinos. Cette étude indique que, vu la taille actuelle de leur population, les rhinos surexploitent la population d'*E. bothae* et qu'il faut prendre des mesures spéciales pour empêcher l'extinction locale de cette dernière.

## Introduction

Megaherbivores such as black rhinoceros (*Diceros bicornis* Linnaeus) or African elephant (*Loxodonta africana* Blumenbach) were abundant in precolonial times in the Eastern Cape Province of South Africa (Boshoff *et al.*, 2002) but were extirpated or, in the case of the elephant,

nearly extirpated, in the 19th century. Because of their considerable biomass, they played an important role in ecosystem structure (Cowling, Proches & Vlok, 2005). To restore the original biome and its functioning, black rhinos (*Diceros bicornis minor* Drummond) were reintroduced into the Great Fish River Reserve (GFRR, Eastern Cape Province, South Africa), starting in 1986. The reserve (450 km$^2$) now hosts a population of over 100 black rhinoceros and a few individuals have been translocated already to other reserves. This successful reintroduction may have a negative impact on plant biodiversity, which poses dilemmas to nature reserve management (Johnson, Cowling & Phillipson, 1999). The rhinos feed extensively on a local population of *Euphorbia bothae* Lotsy and Goddijn. This succulent plant is included in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) list, while the black rhino is included in Appendix I. Maintaining both the critically endangered black rhinoceros and the *E. bothae* population are the conservation priorities of the reserve.

*Euphorbia bothae* occurs in the xeric succulent thicket, which contains a high plant diversity and endemism especially among succulents and geophytes (Cowling & Hilton-Taylor, 1994). According to Low & Rebelo (1996), large browsers historically played a part in limiting the geographic distribution of this vegetation type. Since the early 1900s, the xeric succulent thicket was mainly used for farming goats (Mills & Martin, 2004). The removal of large indigenous browsers from the system may well have led to the expansion of *E. bothae* in the Eastern Cape (B. Fike pers. comm.; Low & Rebelo, 1996).

Previous studies have shown the importance of *E. bothae* in the diet of rhinos in the GFRR and its status as a preferred browse species, with estimates of the contribution of *E. botha* in the rhino's diet varying between 4% and 41% (Ausland *et al.*, 2002; Brown *et al.*, 2003; Ganqa, Scogings & Raats, 2005). As has been suggested for other species of *Euphorbia*, *E. bothae* may also be a seasonally important source of water for the rhinos (Dudley, 1997; Heilmann *et al.*, 2006). As has been reported for African elephant feeding on rare plant species in the Eastern Cape (Johnson *et al.*, 1999), the high density of rhinos may lead to unsustainable consumption of the local *E. bothae* population.

Several scenarios for plant–herbivore interactions are known from the literature. The worst-case scenario is a predator–prey interaction where the animals kill plants during one feeding event (Heilmann *et al.*, 2006). The second scenario is the one in which regrowth and recruitment of plants are not fast enough to compensate for the biomass removed by browsing, illustrated by a lowered recruitment rate or a decreased generative activity of the plants (Pfab & Witkowski, 1999; Russell & Fowler, 2004). Incessant browsing may also cause a shift in size distribution of the plants (scenario three), as has been recorded for similar interactions (Motta, 2003; Siipilehto & Heikkilä, 2005). The fourth scenario is that plants overcompensate browsing, so that browsing promotes rapid shoot regrowth (Paige & Whitham, 1987; Du Toit, Bryant & Frisby, 1990). It has been suggested that *E. bothae* may respond to browsing by an over-compensatory growth mechanism resulting in more side-shoots and stems (D. Brown, pers. comm.).

In other words, the impact of browsing by the population of black rhino on this species of *Euphorbia* in the GFRR may be either negative or positive. During this study, we focused on measuring specific population characteristics of *E. bothae* in the reserve such as size distribution, plant growth and browsing incidence and intensity to determine the impact of black rhino on the *E. bothae* population.

## Methods

### Study site and species

The research was conducted in the Great Fish River Reserve (33°07′S; 26°38′E) in the Eastern Cape Province of South Africa (45.000 ha). The area receives an average annual rainfall of 420 mm (Fabricius, Palmer & Burger, 2002).

Only a few studies are available on *E. bothae* (Fig. 1). Although in most literature this species is considered as an independent species, it was described by Rodriguez (1993) as a naturally occurring hybrid of *Euphorbia coerulescens* Haw and *Euphorbia tetragona* Haw. Similar to most Euphorbia species, *E. bothae* produces a potentially toxic latex, which apparently does not harm the rhinos. The plants bear distinctive inflorescences, called cyathia, and pairwise thorns, which protect them from herbivores. The colour of the individual stems varies from green to grey. Measurements were made in the 'short *Euphorbia* thicket' (SET), a vegetation type dominated by *E. bothae*, which only occurs in the south-western part of the reserve. SET is part of the xeric succulent thicket vegetation type, which contains mainly evergreen, drought-resistant woody

**Fig 1** Specimen of *Euphorbia bothae*

shrubs and succulents (Everard, 1987; Cowling *et al.*, 2005). A comparison was made between two contiguous areas of SET, one within the reserve that was used intensively by black rhino (browsed area) and the other in an exclosure without rhinos, just outside the fenced reserve (reference area). The vegetation type in the reference area is also dominated by SET. *Portulacaria afra* Jacq. is largely missing from the reference area, probably because of heavy grazing by livestock in the past.

Black rhinos, with a body mass of 850–1000 kg (Wilson & Kerley, 2003), are one of Africa's largest browsing herbivores. Black rhinos have a broad-spectrum diet and are not very selective feeders in the GFRR (Brown *et al.*, 2003; Ganqa *et al.*, 2005). They mainly occur in the Andries Vosloo Kudu Reserve and the Sam Knott Nature Reserve sectors on the southern side of the Great Fish River, an area of approximately 22 000 ha (Lent & Fike, 2003). The SET is heavily used by rhinos, as Lent & Fike (2003) reported especially large clusters of female rhinos with offspring, and also recorded the largest number of overlapping home ranges of rhinos within the SET. Kudu (*Tragelaphus strepsiceros* Blainville) is another important browser of the GFRR and occurs in both areas. We assumed that kudu browsing was equal in both areas, because kudu are known to be capable of jumping over the fences between the two areas, although a more recent study suggests that kudu densities may be slightly higher in the reference area (De Boer & Ijdema, 2008).

*Data collection*

Twenty-five line transects of 100 m each were selected in a stratified random manner in both the browsed area and the reference area. Every 10 m, several characteristics (distance to the transect, height, crown diameter, percentage dead plant material, presence of cyathia or fruits, number of stem tips, number of browsed stem tips) of the plant nearest to the transect line were recorded. Plant cover was calculated as a projection of the crown area, and plant density by using the plotless distance method (Bonham, 1989).

To estimate browsing pressure, a stratified random method was used to select 40 sites in the browsed area and 20 in the reference area. From 16 November 2005 to 2 December 2005, a total of 332 plants, 213 in the browsed area and 112 in the reference area, were photographed from fixed points using a digital camera and tripod (see Fig. 1). A measuring rod was always present in the picture and, when possible, a white canvas was placed behind the plant to increase the visibility of the plant in the image. The plants were revisited and photographed again between 18 and 24 January 2006. Additionally, 26 plants distributed over seven sites in the browsed area that had been photographed in April 2003, were revisited and photographed from existing fixed points in January 2006. The successive pictures were compared for evidence of browsing during the time span by two researchers independently. Browsing incidence was recorded and if browsing had occurred, proportion of the volume of the original plant that was removed was estimated.

Browsing simulations on 31 different sized plants were used to calibrate the browsing intensity estimates on the basis of photographs. Browsing was simulated by randomly cutting different lengths of the stem. The length and diameter of the removed stem parts and the remaining stems were recorded to calculate the percentage biomass removed per plant. These percentages were compared with the estimated removed percentages on the basis of the fixed-point photographs. On average, the researchers overestimated the removed biomass only (0.56%; ±8 SD), as positive and negative deviations cancelled each other out. Because of the relatively small magnitude of this error, no corrections were made for these estimates.

The artificially browsed plants were also used to investigate the effects of browsing on the growth rates of green, grey and intermediate coloured stems. The lengths of 70 browsed and 39 undamaged stems distributed over

eighteen plants were measured 30 and 78 days after the simulated browsing events. The browsed stems were also monitored for the growth of side-shoots. Additionally, the presence of side-shoots was recorded on individual stems of randomly chosen plants in the browsed area and in the reference area.

### Statistical analyses

Mann–Whitney $U$-tests were performed to test for differences between the two areas in plant height, plant density, fraction of browsed stem tips, fraction of dead plant biomass, plant cover and fraction of dead plants. Moreover, plant height was compared between plants with cyathia or fruit (reproductively active) and those without (reproductively inactive). After allotting classes to plant height and plant cover (classes spanning 10 cm and 0.4 m$^2$ respectively), the distributions of these parameters were compared using a $\chi^2$-test. The distribution of plants over the height classes in the reference area yielded the expected values and those in the browsed area the observed values; 95% confidence intervals were calculated per height class to investigate the differences. A $\chi^2$-test was performed to test whether the fraction of browsed *E. bothae* in the browsed area differed from that in the reference area, assuming that identical proportions of browsed stems were expected in the two areas. A Kruskal–Wallis and *post hoc* Scheffé test were performed to test for differences in growth rates between green, intermediate and grey stems. $z$-Tests were performed for all stems together and for the browsed area and the reference area separately to test for differences in the proportion of stems with side-shoots between browsed and unbrowsed stems. The number of side-shoots encountered on browsed and unbrowsed stems was compared by using Mann–Whitney $U$-tests.

## Results

### Effects on population structure

Plant density and plant height were found to be significantly lower in the rhino-browsed area when compared with those in the reference area. The percentage browsed stem tips, percentage dead plant biomass and the fraction of dead plants were found to be significantly higher in the rhino-browsed area. No difference was observed in average plant cover (Table 1).

Considering all height classes together, the plants in the browsed area and those in the reference area had a significantly different height class distribution ($\chi^2 = 91.6$, df = 9, $P < 0.001$). Considering the height classes individually, there was a significant difference in the number of plants between the two areas for each of the height classes. Compared to the reference area, the four lowest height classes (5–44 cm high) were over-represented in the browsed area, whereas there were relatively few trees found in the browsed area in the height classes of 45–84 cm (Fig. 2a). The number of plants in different plant cover classes followed a negative exponential curve, described as $y_{ref} = 178.64x^{-1.86}$ and $y_{browsed} = 136.40x^{-1.64}$ (where $y$ represents the number of plants in plant cover class $x$), without a significant difference in the parameters between the two areas (Fig. 2b).

The fraction of flowering plants was equal in both areas (both 0.024). However, in the browsed area, a significantly smaller percentage of plants (7%) had fruit compared with 20% in the reference area ($\chi^2 = 17.52$, df = 1, $P < 0.001$). Considering both flowering and fruiting simultaneously, the difference was also significant, with fewer reproductively active plants in the rhino-browsed area ($\chi^2 = 20.2$, df = 1, $P < 0.001$). The plant height differed between reproductively active and inactive plants (Mann–Whitney $U = 7376$, $n_{inact} = 425$, $n_{act} = 75$, $P < 0.001$). Reproductively active plants were on average 64.9 ($\pm 2.0$ SD) cm tall, whereas reproductively inactive plants were on average 44.6 ($\pm 1.0$ SD) cm. To investigate whether or not the observed differences in generative activity between the two areas were in fact caused by differences in size distribution, the analysis was repeated using only the 'mature' (height $\geq 27$ cm) plants in the comparison. Again, a significant difference was found with a lower fraction of reproductively active plants in the browsed area ($Z = 1.916$, $n_{rhi} = 216$, $n_{ref} = 187$, $P = 0.028$) (Table 2).

### Browsing incidence and intensity

In the rhino-browsed area, 78 of the 213 monitored plants (36.6%) were browsed within the 2-month study period, whereas in the reference area only ten of 112 plants (8%) were browsed. A Chi-squared test showed a significant difference in the fraction of browsed plants between the areas ($\chi^2 = 20.787$, df = 1, $P < 0.001$). Assuming an equal level of browsing by animals other than rhinos for both areas, the percentage of plants affected by rhino browsing can be estimated by subtracting the frequency of

**Table 1** Sample size, minimum, median and maximum measured values and Mann–Whitney *U*-test results (*U* statistics and *P* value) comparing *E. bothae* plant density, plant height, percentage of browsed stem tips, percentage of dead plant biomass and plant cover in the reference and the browsed area, and comparing the number of side-shoots on browsed and unbrowsed stems in both areas, and in the reference and browsed area separately

| Sample area | Variable of interest | min/median/max value group 1 (reference area or unbrowsed stems) | min/median/max value for group 2 (browsed area or browsed stems) | n reference area/browsed area, or unbrowsed/ browsed stems | U | P |
|---|---|---|---|---|---|---|
| Both | Density (plants m$^{-2}$) | 0.1/0.25/0.51 | 0.07/0.16/0.43 | 248/248 | 26,483 | 0.007 |
| Both | Plant height (cm) | 7.0/54.0/100.0 | 5.0/40.5/110.0 | 250/250 | 23,726.5 | 0.000 |
| Both | Browsed stem tips (%) | 0.0/20.0/100.0 | 0.0/55.0/100 | 250/250 | 15,446 | 0.000 |
| Both | Percentage dead plant biomass (%) | 0.0/10.0/90.0 | 0.0/25.0/95.0 | 250/250 | 19,832.5 | 0.000 |
| Both | Plant cover (dm$^2$) | 0.03/44.2/829.6 | 0.02/42.7/604.8 | 250/250 | 21,203.5 | 0.977 |
| Both | N side-shoots (all stems) | 0/0/7 | 0/0/9 | 660/779 | 245,548 | 0.054 |
| Reference area | N side-shoots (all stems) | 0/0/7 | 0/0/6 | 410/293 | 57,507 | 0.225 |
| Browsed area | N side-shoots (all stems) | 0/0/6 | 0/0/9 | 293/486 | 67,536 | 0.125 |
| Both | N side-shoots (stems with side-shoots) | 1/2/7 | 1/2/9 | 150/213 | 15,632 | 0.72 |
| Reference area | N side-shoots (stems with side-shoots) | 1/2/7 | 1/2/6 | 109/91 | 4831 | 0.74 |
| Browsed area | N side-shoots (stems with side-shoots) | 1/3/6 | 1/2/9 | 41/122 | 2189.5 | 0.22 |
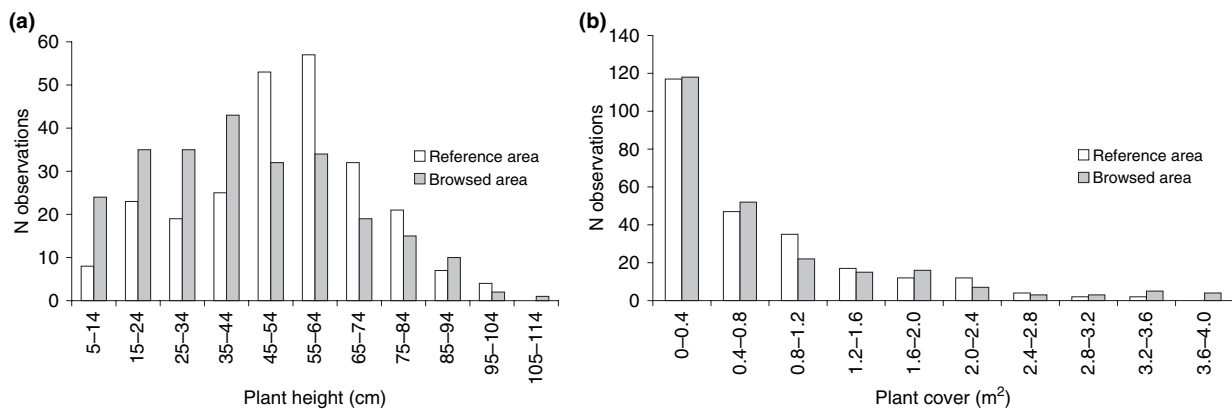


**Fig 2** (a) Plant height distributions of *E. bothae* in the reference and the browsed area. (b) Plant cover distributions of *E. bothae* in the reference and the rhino-browsed area

browsing in the reference area from that in the browsed area. For the 2-month monitoring period, this amounted to 28.6% of the plants being browsed by rhino.

In the browsed area, browsing removed on average 4.8% of the original plant biomass (browsed and un-browsed plants lumped in the analysis). Only those plants

**Table 2** Z-test results of the comparisons between the proportion of reproductively active plants in the reference and browsed area

| Variable of interest | Plants considered | Proportion in reference area | Proportion in rhino-browsed area | n reference/rhino-browsed area | Value test statistic (z) | P |
|---|---|---|---|---|---|---|
| Flowering | All | 0.024 | 0.024 | 250/250 | 0 | 0.500 |
| Flowering | ≥27 cm | 0.027 | 0.032 | 216/187 | −0.062 | 0.485 |
| Fruit bearing | All | 0.196 | 0.196 | 250/250 | 1.898 | 0.028 |
| Fruit bearing | ≥27 cm | 0.227 | 0.096 | 216/187 | 1.830 | 0.034 |
| Flowering or bearing fruit | All | 0.216 | 0.084 | 250/250 | 2.011 | 0.022 |
| Flowering or bearing fruit | ≥27 cm | 0.250 | 0.112 | 216/187 | 1.916 | 0.028 |

(two of 213 monitored plants, 0.9%) with more than 60% browsing damage were in fact killed. In the reference area, plants lost on average 1.4% of their biomass and no plant lost more than 60% of its total biomass (Fig. 3a). The browsed plants lost on average 13.0% (browsed area) and 15.2% (reference area) of their total biomass.

The analysis of photographs taken over the 3-year time span showed that 20 of 26 plants (76.9%) in the browsed area decreased in total biomass. Five of these (19.2%) were totally destroyed during this period and fourteen plants showed a biomass decrease under 50% (Fig. 3b). Only one of these 26 plants increased in biomass; five plants showed no change. When considering all (browsed and unbrowsed) plants, there was a mean biomass loss of 18.4%. Among the browsed plants only, the mean decrease was 37.8%.

*Plant response to browsing*

In contrast to the unbrowsed stems, all artificially browsed stems ceased to grow in the monitoring period. Furthermore, 60% of the artificially browsed grey stems died after approximately 2 months, with a typically shrivelled appearance. None of the artificially browsed green or intermediate stems died during this period and neither did any of the unbrowsed stems. The growth rates of stems of different colour that were not browsed showed significant differences (Kruskal–Wallis = 12.787, $n_{green} = 19$, $n_{int} = 40$, $n_{grey} = 11$, $P = 0.002$, followed by a Scheffé *post hoc* test at $P = 0.05$). Among these unbrowsed stems, green stems grew significantly faster than the intermediate or grey stems (median growth rate: 0.05, 0.01 and 0.00 cm day$^{-1}$, respectively).
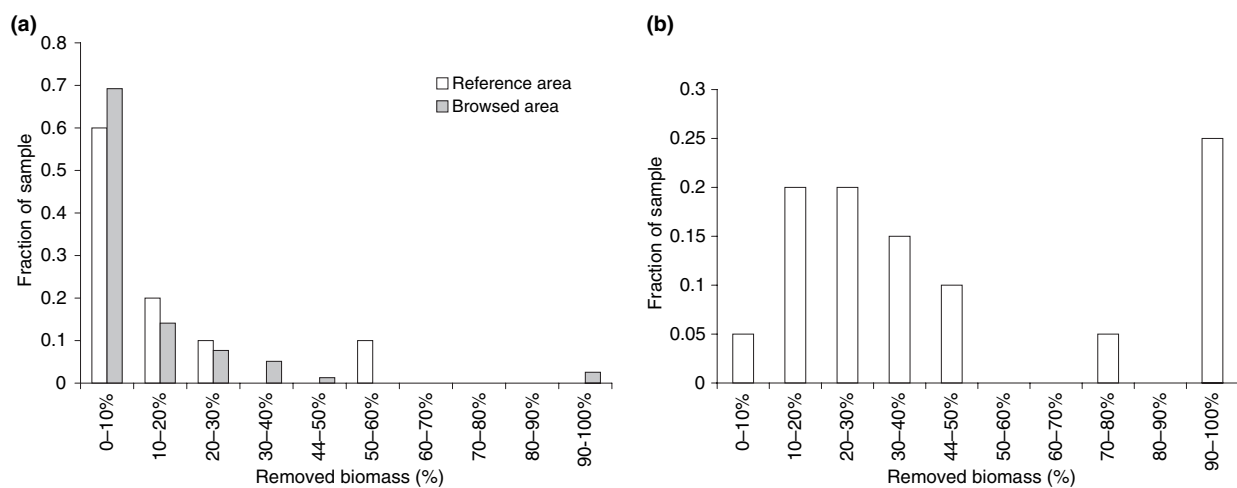


**Fig 3** (a) Browsing incidence and intensity in both areas over 2 months ($n_{ref} = 10$, $n_{br} = 78$). (b) Percentage of biomass loss after 3 years of exposure to rhino browsing. Only plants which showed a decrease in biomass are included ($n = 20$)

Formation of side-shoots was not observed for any of the artificially browsed plants. When comparing all described stems from both areas, both browsed and unbrowsed, a significantly larger proportion of browsed stems had side-shoots (z-test, $z = -3.74$, $n_{unbr} = 660$, $n_{br} = 779$, $P < 0.001$). In total, 33% of the browsed stems had side-shoots compared to 17% for unbrowsed stems. Analysing the stems per area separately, side-shoots were also encountered significantly more often on browsed stems than on unbrowsed stems in both the reference area (Z-test, $z = -4.98$, $n_{unbr} = 410$, $n_{br} = 293$, $P < 0.001$) and the browsed area (Z-test, $z = -2.64$, $n_{unbr} = 250$, $n_{br} = 486$, $P < 0.01$). However, no significant difference was found in the number of side-shoots on browsed and unbrowsed stems (Table 1).

## Discussion

Megaherbivores such as black rhino and African elephant play an important role in ecosystem structure and functioning (Cowling *et al.*, 2005) and can have a large impact on the vegetation (Moolman & Cowling, 1994; Birkett, 2002). High elephant densities, for example, have been associated with a decline in plant species richness (Johnson *et al.*, 1999) and can lead to opening up of woodlands and changing plant species composition (Cumming *et al.*, 1997). Black rhinos destroy *Euphorbia tetragona* and *Euphorbia triangularis* Desf. trees by pushing them over to feed upon the tips of the branches (Heilmann *et al.*, 2006). In this study, the impact of the black rhino on a local *E. bothae* population was analysed to determine the sustainability of this plant–herbivore interaction. The results demonstrate that black rhinos can have a significant impact on the survival of a population of a selected browse species, *E. bothae*.

The fixed-point photographs showed that 0.9% of the monitored plants were destroyed within 2 months amounting to 19.0% within 3 years, which is similar to what was found when comparing photographs taken 3 years apart. As for the population structure, rhino browsing lowers *E. bothae* density and plant height. It also causes a shift in the height distribution of *E. bothae* towards relatively smaller plants (those <45 cm). Similar results were obtained for the tree height of pines browsed by moose (Siipilehto & Heikkilä, 2005) or *Quercus buckleyi* Dorr & Nixon browsed by deer (Russell & Fowler, 2004). Modelling studies of the impact of megaherbivore browsing on woodland dynamics, termed this phenomenon 'inhibi-

tion', because browsing inhibits plants from moving to the next height class (Ben-Shahar, 1996). Eventually, this reaction may result in a division of the browse species population, where one part can establish itself above browsing height while another part of the population is kept under maximum browsing height through browsing (Motta, 2003). This, of course, is only possible if a sufficient large proportion of the population can grow out of the browse trap zone. The maximum height of *E. bothae* is, however, only 120 cm (B.L. Luske pers. obs.), so no plants seem to be able to escape into a nonbrowse height class. The taller height class (45–84 cm high), which was under-represented in the browsed area (Fig. 2a), lies at and just above the height of 50–60 cm at which rhinos prefer to browse (Ausland *et al.*, 2002; Winkel, 2004). In contrast to the height distribution, plant cover of *E. bothae* was not affected by rhino browsing (Fig. 2b). A possible explanation for this is the fact that individual stems are roughly in an upright position and not widely spreading (Fig. 1). Partial removal of stems will therefore generally have a larger effect on plant height than on plant cover.

The results of this study indicate that rhino browsing causes a decline in the number of *E. bothae* plants that bear cyathia or fruit, a measure for reproductive potential. The possibility that the observed differences in height distribution were responsible for the difference in generative activity was ruled out by excluding juvenile plants (plants <27 cm) from the analysis, indicating that rhino browsing had an effect on *E. bothae* reproduction potential. The effect of browsing on reproduction may even be stronger if the number of inflorescences or fruits per plant is taken into account. For *Euphorbia clivicola* R.A. Dyer, for example, it was found that herbivores cause a reduction in the number of flowers and fruits per plant (Pfab & Witkowski, 1999).

The hypothesis that browsing of rhinos on *E. bothae* induces a compensatory growth mechanism in the plants was not supported. Browsed stems seem to cease their apical growth or form side-shoots. No artificially browsed stems formed side-shoots during the 78-day monitoring period. This absence could be because of the time limitation of the study as growth rates were found to be very low. Compensatory growth can be important over a longer time period, because our analysis showed that side-shoot formation was encountered in a significantly higher proportion of browsed stems than unbrowsed stems, but browsed stems did not bear more side-shoots.

On the basis of this study, we conclude that the rhinos can cause a decline in the *E. bothae* population on the

GFRR in the long term. Evidence has been found that three different plant–herbivore interaction scenarios exist between the two species. To a small extent, plants were killed by rhinos (scenario one), more generally the reproductive potential was lowered (scenario two) and the height distribution was altered by rhino browsing (scenario three). It seems that the two species cannot coexist in high densities. These results corroborate the idea put forward by Low & Rebelo (1996) that large browsers limited the distribution of xeric succulent thicket in the eastern Cape and that this vegetation type (with its associated *E. bothae*) was able to expand in the Great Fish River valley because of the reduction of large herbivores by humans. *E. bothae* is now a protected species (CITES II). However, the great success of the black rhino population (CITES I) in the reserve threatens the viability of the *E. bothae* population and poses a dilemma to the reserve management, which needs to take measures to protect the *E. bothae* population from local extinction. Our study is thus a good example of the conflict between the management and protection of nature, for which the protection of black rhino is exemplary, and that of man-induced cultural landscapes with their associated flora and fauna, in this case typified by *Euphorbia bothae*. Such dilemmas are normal for conservationists in Europe and other areas where landscapes with ancient land-use practices received protection status labelled as 'nature', but are still often unrecognized in Africa.

## Acknowledgements

## References

Ausland, C., Sveipe, A., Ganqa, N.M., Raats, J.G. & Palmer, A.R. (2002) Foraging behaviour of black rhino in the Great Fish River Reserve, Eastern Cape Province, South Africa. In: *Proceedings of the Fifth International Wildlife Ranching Conference, Pretoria 2001*. (Eds H. Ebedes, B. Reilly, W. Van Hoven and B. Penzhorn, Pretoria University, Pretoria.

Ben-Shahar, R. (1996) Woodland dynamics under the influence of elephants and fire in Northern Botswana. *Vegetatio* **123**, 153–163.

Birkett, A. (2002) The impact of giraffes, rhino and elephant on the habitat of a black rhino sanctuary in Kenya. *Afr. J. Ecol.* **40**, 276–282.

Bonham, C.D. (1989) *Measurements for Terrestrial Vegetation*. Wiley, New York.

Boshoff, A.F., Kerley, G.I.H., Cowling, R.M. & Wilson, S.L. (2002) The potential distributions, and estimated spatial requirements and population sizes, of the medium to large-sized mammals in the planning domain of the Greater Addo Elephant National Park project. *Koedoe* **45**, 85–116.

Brown, D.H., Lent, P.C., Trollope, W.S.W. & Palmer, A.R. (2003) Browse selection of black rhinoceros (*Diceros bicornis*) in two vegetation types of the Eastern Cape Province, South Africa, with particular reference to Euphorbiaceae. In: *Proceedings of the VIIth International Rangelands Congress held in Durban 2003* (Eds N. Allsop, A.R. Palmer, S.J. Milton, K.P. Kirkman, G.I.H Kerley, C.R. Hurt and C.J. Brown). International Rangelands Congress, Durban.

Cowling, R.M. & Hilton-Taylor, C. (1994) Patterns of plant diversity and endemism in southern Africa: an overview. In: *Botanical Diversity in Southern Africa* (Ed. B.J. Huntley). Strelitzia 1, National Botanical Institute, Pretoria.

Cowling, R.M., Proches, Ş. & Vlok, J.H.J (2005) On the origin of southern African subtropical thicket vegetation. *S. Afr. J. Bot.* **71**, 1–23.

Cumming, D.H., Fenton, M.B., Rautenbach, I.L., Taylor, R.D, Cumming, G.S., Cumming, M.S., Dunlop, J.M., Ford, G.A., Hovorka, M.D., Johnston, D.S., Kalcounis, M., Mahlanga, Z. & Portfors, C.V.R. (1997) Elephants, woodlands and biodiversity in southern Africa. *S. Afr. J. Sci.* **93**, 231–236.

De Boer, F & Ijdema, H. (2008) *Competition between Black Rhinoceros (Diceros bicornis) and Greater Kudu (Tragelaphus strepsiceros) in the Great Fish River Reserve, South Africa*. MSc thesis, Wageningen University, Wageningen.

Du Toit, J T., Bryant, J.P. & Frisby, K. (1990) Regrowth and palatability of acacia shoots following pruning by African savanna browsers. *Ecology* **71**, 149–154.

Dudley, C.O. (1997) The candelabra tree (*Euphorbia ingens*): a source of water for black rhinoceros in Liwonde National Park, Malawi. *Koedoe* **40**, 57–62.

Everard, D.A. (1987) A classification of the subtropical transitional thicket in the Eastern Cape, based on syntaxonomic and structural attributes. *S. Afr. J. Bot.* **53**, 329–338.

Fabricius, C., Palmer, A.R. & Burger, M. (2002) Landscape diversity in a conservation area and commercial and communal rangeland in xeric succulent thicket, South Africa. *Landscape Ecol.* **17**, 531–537.

Ganqa, N.M., Scogings, P.F. & Raats, J.G. (2005) Diet selection and forage quality factors affecting woody plant selection by black rhinoceros in the Great Fish River Reserve, South Africa. *S. Afr. J. Wildl. Res.* **35**, 77–83.

Heilmann, L.C., De Jong, K., Lent, P.C. & De Boer, W.F. (2006) Will tree euphorbias (*Euphorbia tetragona* and *Euphorbia triangularis*) survive under the impact of black rhinoceros (*Diceros bicornis minor*) browsing in the Great Fish River Reserve, South Africa? *Afr. J. Ecol.* **44**, 87–94.

JOHNSON, C.F., COWLING, R.M. & PHILLIPSON, P.B. (1999) The flora of the Addo Elephant National Park, South Africa: are threatened species vulnerable to elephant damage? *Biodivers. Conserv.* **8**, 1447–1456.

LENT, P.C. & FIKE, B. (2003) Home ranges, movements and spatial relationships in an expanding population of black rhinoceros in the Great Fish River Reserve, South Africa. *S. Afr. J. Wildl. Res.* **33**, 109–118.

LOW, A.B. & REBELO, A.G. (1996) *Vegetation of South Africa, Lesotho and Swaziland*. Department of Environmental Affairs and Tourism, Pretoria.

MILLS, A. & MARTIN, F.E.Y. (2004) Transformation of thicket to savannah reduces soil quality in the Eastern Cape, South Africa. *Plant Soil* **265**, 153–163.

MOOLMAN, H.J. & COWLING, R.M. (1994) The impact of elephant and goat grazing on the endemic flora of South African succulent thicket. *Biol. Conserv.* **68**, 53–61.

MOTTA, R. (2003) Ungulate impact on rowan (*Sorbus aucuaria* L.) and Norway spruce (*Picea abies* (L.) Karst.) height structure in mountain forests in the eastern Italian Alps. *For. Ecol. Manage.* **181**, 139–150.

PAIGE, K.N. & WHITHAM, T.G. (1987) Overcompensation in response to mammalian herbivory: the advantage of being eaten. *Am. Nat.* **129**, 407–416.

PFAB, M.F. & WITKOWSKI, E.T.F. (1999) Contrasting effects of herbivory on plant size and reproductive performance in two populations of the critically endangered species *Euphorbia clivicola* R. A. Dyer. *Plant Ecol.* **145**, 317–325.

RODRIGUEZ, A. (1993) A survey of succulent Euphorbias. *New Plantsman* **14**, 204–233.

RUSSELL, F.L. & FOWLER, N.L. (2004) Effects of white-tailed deer on the population dynamics of acorns, seedlings and small saplings of *Quercus buckleyi. Plant Ecol.* **173**, 59–72.

SIIPILEHTO, J. & HEIKKILÄ, R. (2005) The effect of moose browsing on the height structure of Scots pine saplings in a mixed stand. *For. Ecol. Manage.* **205**, 117–126.

WILSON, S.L. & KERLEY, G.I.H. (2003) Bite diameter selection by thicket browsers: the effect of body size and plant morphology on forage intake and quality. *For. Ecol. Manage.* **181**, 51–65.

WINKEL, F. (2004) *Diet choice of the black rhinoceros (Diceros bicornis) in the Double Drift Game Reserve, Eastern Cape Province, South Africa*. MSc thesis, Wageningen University, Wageningen.