Will tree euphorbias (*Euphorbia tetragona* and *Euphorbia triangularis*) survive under the impact of black rhinoceros (*Bicornis diceros minor*) browsing in the Great Fish River Reserve, South Africa?

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Abstract

The impact of black rhinoceros (*Bicornis diceros minor*) on the tree euphorbias *Euphorbia tetragona* and *Euphorbia triangularis* was studied in the Great Fish River Reserve, South Africa. Black rhinoceros pushed over about 5–7% of the trees in a 2-month period. There was a preference of rhinos for smaller trees, however this preference did not guarantee euphorbia survival in the larger size classes. This means that tree euphorbias could very well disappear from all areas accessible to rhinos. Rhino feeding choices were correlated with higher plant moisture content, higher nitrogen content, and a higher digestibility.

Key words: damage, diet choice, food quality, moisture content, size preference, survival

Résumé

L'impacte du rhinocéros noir (*Bicornis diceros minor*) sur les euphorbias *Euphorbia tetragona* et *E. triangularis* fut étudié dans la Réserve de la Great Fish River, en Afrique du Sud. Les rhinocéros noirs défoncèrent 5 à 7% des arbres environ pendant une période de deux mois. Malgré la préférence des rhinocéros pour les plus petits arbres, la survie des euphorbias plus grands ne fut pas garantie. Ceci veut dire que les euphorbias pourraient bien disparaître de tous les endroits accessibles aux rhinocéros. Les choix alimentaires furent liés au contenu d'eau et de nitrogène chez les plantes, et la digestibilité.

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Introduction

Black rhinoceros (*Bicornis diceros minor* L.) and the tree euphorbias *Euphorbia tetragona* (Haw.) and *Euphorbia triangularis* (Desf.) are on the CITES-list of endangered species (Inskipp & Gillett, 2003). Black rhinos are in appendix I and both tree euphorbias in appendix II of this list. However, it is not known if the two species can co-exist. The Great Fish River Reserve (GFRR) in South Africa contains a rapidly growing population of about 70 black rhinos, established after their first re-introduction in 1986 (Ausland *et al.*, 2002). Black rhinos push over *E. tetragona* and *E. triangularis*, which usually results in the uprooting and death of the trees, even if *B. diceros* only takes a small bite (L.C. Heilmann & K. De Jong, Pers. obs.). This study was initiated because of concern by reserve management about declining densities of *E. tetragona* and *E. triangularis*.

Megaherbivores often have dramatic influences on their environment, not only because they have a large biomass intake, but also because of mechanical destruction (Owen-Smith, 1988). Penzhorn, Robbertse & Olivier (1974) showed that the average total biomass outside an elephant (*Loxodonta africana* Blum.) exclosure was only 45% of the biomass inside this exclosure. Especially *Portulacaria afra* (Jacq.) and *Aloe africana* (Mill.) suffered from the elephant damage. In the Rwenzori National Park, elephants were responsible for a tree mortality rate of 5.7% per annum with *Euphorbia candelabrum* (Trém.) as the dominant species (Eltringham, 1980). Other studies showed mortality rates for *Acacia tortilis* (Fors.), which ranged from 6% to 8% per annum (Lamprey *et al.*, 1967; Pellew, 1983; Mwalyosi,

1987). Also baobabs (*Adansonia digitata* L.) are highly in demand by elephants: Barnes (1980) reported an annual mortality rate of baobab, in Ruaha National Park in Tanzania of 2.7%, while Swanepoel & Swanepoel (1986) found an annual mortality rate of 4.9% for baobab in the Zambezi Valley in Zimbabwe. Although the damage was quite large in some of these studies, none of them reported complete plant extinction. Black rhinoceros have also a large influence on the vegetation. In Kenya black rhinos pushed over *Euphorbia tirucalli* trees (Goddard, 1968), and Mukinya (1977) reported considerable destruction by black rhinos in a game reserve in Kenya. In this study we aim to quantify the damage inflicted to the population of *Euphorbia* trees in the GFRR.

In most plant-herbivores interactions plants will modify their growth form in response to grazing or browsing (Pfab & Witkowski, 1999; Styles & Skinner, 2000). In this case, however, *B. diceros* kill the trees, making this interaction similar to a predator–prey interaction. Whether a prey population can sustain a certain predation pressure depends on the predation driven mortality rate, prey characteristics (e.g. growth, recruitment, natural mortality), and environmental parameters influencing the prey's vulnerability to predation (Errington, 1946). Predation is often expected to be size-dependent, depending on prey and predator size (Aljetlawi, Sparrevik & Leonardsson, 2004). This expectation is based on the assumption that foraging should maximize net energy or nutrient gain and minimizing the time and energy spent (Pyke, 1984; Stephens & Krebs, 1986). In this case larger *Euphorbia* trees do not offer larger nutrient or energy gains, because rhinos only take a few bites, so minimizing time and energy might be more important. This could result in a preference for smaller trees that are presumably easier to push over.

Predation pressure can also be dependent on accessibility (Taylor, Littler & Littler, 1986; Schmidt, 2004), which leads to the idea that Euphorbia trees co-existed with black rhinos before this megaherbivore was extirpated in the Eastern Cape, but in lower densities and principally in refugia (Kamineth, 2004). We therefore tested whether black rhinoceros avoid steeper areas, which would lead to a negative correlation between slope and tree mortality.

One would expect that large browsers select for highest biomass intake and to a lesser extent for food quality (Wieren, 1996; Alm, Birgersson & Leimar, 2002). In this case black rhinos only eat a small part, and so do not seem to select for biomass. Because of the relatively small off-take, it was hypothesized that the food quality rapidly declines with increasing distance from the tip, which would imply that black rhinos select for food quality. An additional factor promoting consumption of the tip only could be relatively high moisture content of the tip. Dudley (1997) has found that *Euphorbia ingens* (E. Meyer) can be a source of water for *B. diceros* and Goddard (1968) suggested the same for *E. tirucalli* (L.). Therefore we also tested the hypothesis that the tip has higher moisture content than the lower parts of the branches.

Material and methods

Study area

The GFRR is situated in the Eastern Cape Province of South Africa between 32°55′ S, 26°37′ E and 33°08′ S, 26°58′ E and totals approximately 45,000 ha. It was formed by the unification of three adjoining reserves (Fig. 1; Fabricius, Palmer & Burger, 2002). The GFFR lies within the thicket biome and is dominated by xeric succulent thicket (Evans, Avis & Palmer, 1997). The relatively homogenous tall euphorbia thicket vegetation type, in which *E. triangularis* and *E. tetragona* dominate, comprises roughly 12% of the GFRR (Lent, unpubl. data), occurring mainly on rocky slopes. Steep slopes are common, as a result of the large range in elevation, from 170 m at the banks of the Great Fish River to 800 m at the ridges. Rainfall varies from 250 mm to over 650 mm (Birch, Avis & Palmer, 1999). South facing slopes and sites on higher elevation generally
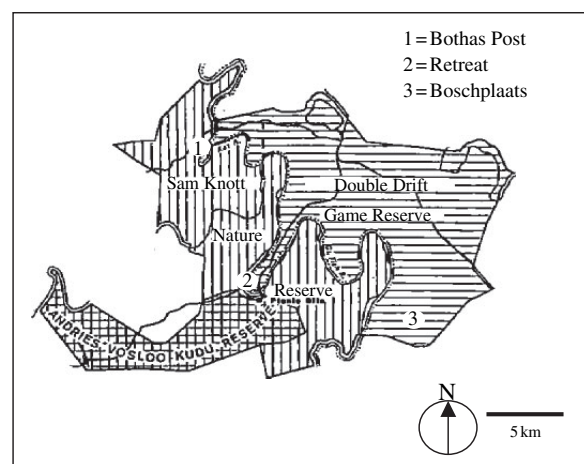

Fig 1 Map of the Great Fish River Reserve

have a higher mean annual rainfall and a lower mean temperature (Evans *et al.*, 1997).

Field analysis

Three study sites were chosen based on rhino occurrence, Retreat, Bothas Post and Boschplaats (Fig. 1). The hillside at Retreat was known by reserve staff to be an area of high rhino density with much visual evidence of damage. Bothas Post had intermediate rhino densities and Boschplaats was considered a reference site, because no tracks of *B. diceros* have been found there ever since the re-introduction of black rhinoceros in the reserve. Within each site one eastern slope with a high density of tree euphorbias was selected. Transects of 100 by 8 m were laid out along the contours (50 by 8 m at Boschplaats) with intervals of 17 m. Seven transects were laid at Retreat and at Bothas Post, five at Boschplaats.

At the first visit all fallen and standing *E. triangularis* and *E. tetragona* within the transects were tagged with a unique number. Trees were identified to species, and height and circumference of the main stem were measured. Circumference was measured at 1 m. The slope of the hill was measured with a clinometer at 20 cm from the tree. About 2 months later a second visit was made to Retreat and Bothas Post and newly fallen trees in transects were recorded. No second visit was made to Boschplaats, which means that this site cannot be used as a control site for the number of newly fallen trees; it will be referred to as a 'reference site' throughout this paper.

Chemical analysis

At Retreat five top branches were cut off from each of 25 randomly selected *E. tetragona*, within those of <6 m height, because of accessibility. From each branch the top 5 cm was collected (top section), as well as the 5 cm portion directly below this (the penultimate section), and the top 5 cm of the lower grey part (the grey section). Samples consisted of five corresponding parts of a single tree.

Samples were weighed (wet weight, WW). Then they were dried for 5 days at 65°C and weighed again to obtain dry weight (DW). All weighing was carried out with an accuracy of 0.05 g. Thereafter the samples were ground in an AEG (AEG, Frankfurt, Germany) lbi 07-ip54 grinder with a 1 mm sieve. Digestibility was analysed following Tilley & Terry (1963); R^2-values for the digestibility cor-

rection lines had values of 0.88, 0.96 and 0.97. Total nitrogen and phosphorus were analysed with an auto-analyser (Temmingho *et al.*, 2000). Moisture content was calculated as $[(WW - DW)/WW] \times 100$.

Statistical analysis

The preferences for circumference, height and slope were analysed with a forward logistic regression, with fallen or standing as the dependent variable and height, d.b.h. and slope as covariates. To test for a unimodal distribution we also included the square of the covariates in the regression. The statistical analysis of these factors influencing rhino preference includes some level of pseudoreplication, as conditions at the site might not be independent. Therefore an additional analysis was carried out using the average values per transect, in a randomized block design, using a stepwise General Linear Model (GLM) on (arcsin-transformed) percentages of fallen trees, with site, slope, height, and d.b.h. as independent factors.

To test for differences in digestibility, total nitrogen, total phosphorus and water content between the different parts of the branches, ANOVAs were performed on arcsin transformed data, which followed a normal distribution, followed by a Tukey test. All analyses were carried out in SPSS (v. 10.0). All statistics were done with confidence intervals of 95%.

Results

Tree euphorbia numbers

In Retreat 195 standing trees >2 m height and 37 fallen trees >2 m were recorded within the transects with a mean density of 300 standing trees ha^{-1}, in Bothas Post there were 95 standing trees >2 m (100 trees ha^{-1}) and 41 fallen >2 m, and in Boschplaats, the reference site, 188 trees >2 m (900 trees ha^{-1}) and two fallen >2 m. In Retreat *E. tetragona* and *E. triangularis* grew together in similar numbers with respectively 92 and 93 trees >2 m, although *E. triangularis* seemed to occur more in the upper and lower transects. In Bothas Post only two trees >2 m of *E. triangularis* were found, and therefore only *E. tetragona* was analysed. In Boschplaats far more *E. tetragona* than *E. triangularis* were found with respectively 159 and 29 trees >2 m. In Retreat 22 and twenty trees <2 m were found of respectively *E. triangularis* and *E. tetragona*. In Bothas Post four small trees <2 m were found, all

Table 1 Forward logistic regressions for the probability of mortality (1 = fallen; 0 = standing) for *E. tetragona* in Retreat and Bothas Post, against height, circumference, and slope

Site	n	χ^2	R^2	P-model
Retreat	114	13.947	0.177	<0.001
Bothas Post	134	41.216	0.366	<0.001
		Coefficients of variables		
	Significant variables	B	Wald	P-value
Retreat	Height	−1.127	11.194	0.001
Bothas Post	Height	−3.846	8.534	0.003
	Height^2	0.224	5.568	0.018

E. tetragona, and in Boschplaats nineteen small *E. triangularis* were found and 42 *E. tetragona*.

Tree euphorbia mortality rate

At the second visit in Retreat thirteen trees >2 m were newly fallen in 2 months, two *E. tetragona* and eleven *E. triangularis*, equivalent to 6.7% of the total of euphorbia trees, or one tree pushed over every 4 days. In Bothas Post the damage was less with five trees pushed over in 2 months, corresponding to a mortality rate of 5.2% of the total number of tree euphorbias over 2 months. The mortality rate for Boschplaats could not be calculated, but because only two of 188 trees were found fallen during the first visit, we expect this rate to be very low.

Preferences

The shortest tree pushed over was 2.03 m, therefore only trees >2 m height were taken into account. No preferences for height, d.b.h. or slope of *E. triangularis* were found. In the forward logistic regression of *E. tetragona*, the height was the only significant variable in the model of Retreat, and in the model of Bothas Post height and height^2 were significant (Table 1). Smaller trees of *E. tetragona* were pushed over more often in both Retreat and Bothas Post (Fig. 2a–d).

A stepwise GLM on the percentage of fallen *E. tetragona* trees showed that site ($F_{2,17} = 40.405$; $P < 0.001$), height ($F_{1,17} = 18.210$; $P < 0.001$), and d.b.h. were significant factors ($F_{1,17} = 11.098$; $P < 0.01$). Slope was not significant in the model. Both height and d.b.h. had significant negative regression coefficients, indicating a preference for smaller trees. All sites were significantly different (Tukey

multiple comparison, $P < 0.02$), with an increase from Boschplaats (the reference site) to Retreat, and with highest values recorded in Bothas post. The $R^2_{adjusted}$ was 0.82, indicating a very good fit between model predictions and observed percentages.

Chemical analysis

The digestibility of the grey section was significantly lower than that of the top and the penultimate sections ($P < 0.001$, $F = 18.030$, d.f. = 2, n = 47; Fig. 3a). The same was found for total nitrogen ($P = 0.004$, d.f. = 2, $F = 5.901$, n = 74; Fig. 3b). The percentage of total phosphorus showed the opposite of what was expected ($P = 0.014$, d.f. = 2, $F = 4.516$, n = 74; Fig. 3c). Phosphorus was highest in the grey part and lowest in the top. The moisture content in the top section was found to be significantly higher than that of the penultimate and the grey sections; the latter two did not differ significantly in their moisture content ($P < 0.001$, d.f. = 2, $F = 19.144$, n = 75; Fig 3d).

Discussion

The mortality rates of both *E. tetragona* and *E. triangularis* in the GFRR are substantial, between 5.2% and 6.7% of the tree euphorbias were killed in 2 months. If the mortality rate in the rest of the year is similar, and there is no recruitment during this period, all trees of *E. tetragona* and *E. triangularis* might disappear from Retreat in <8 and 1.5 years, respectively. At Bothas Post *E. tetragona* may then disappear in <2 years.

However, to attribute all damage to rhino destruction, other causes (e.g. abiotic factors or other animals) have to
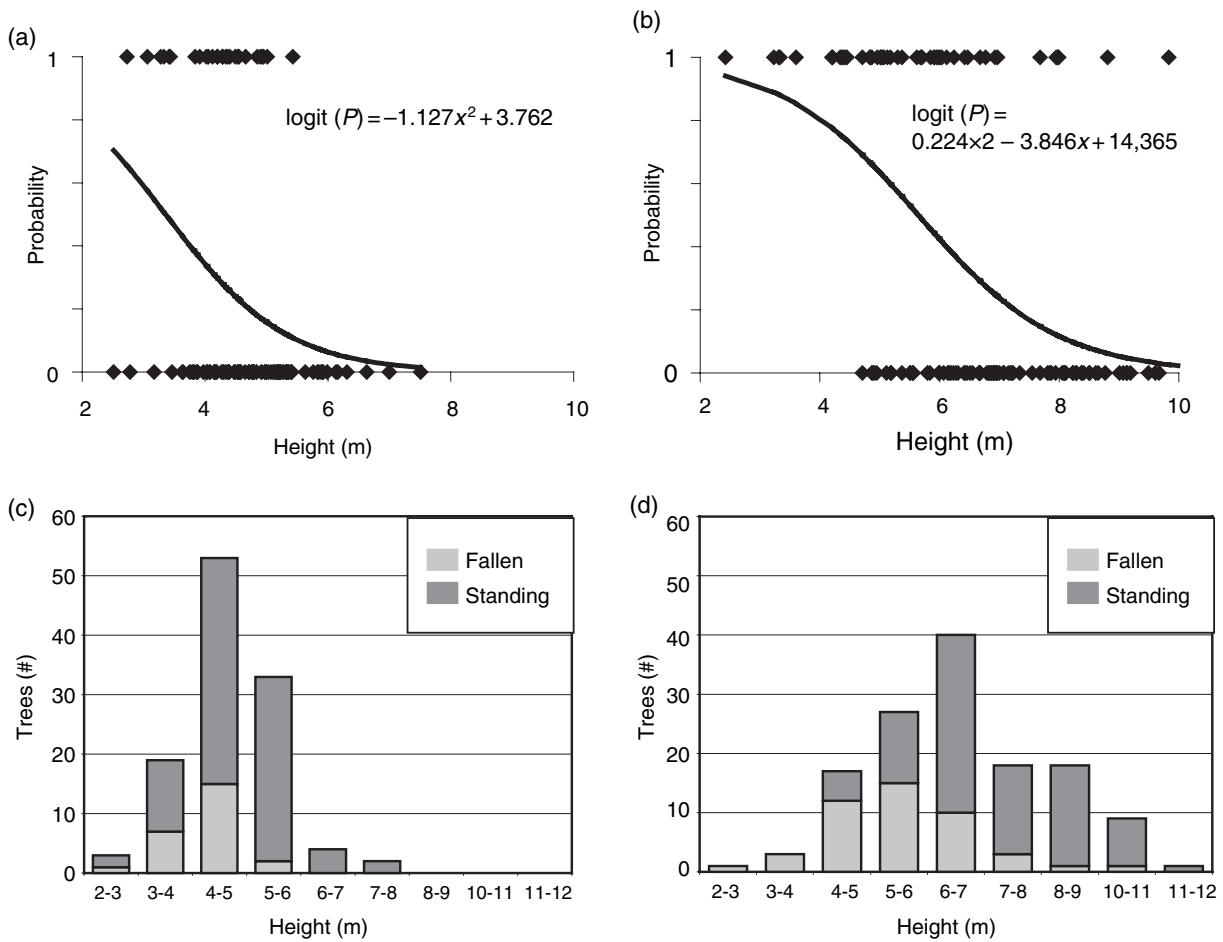
Fig 2 The probability of mortality (1 = fallen; 0 = standing) for trees with a certain height in (a) Retreat, (b) Bothas Post and histograms showing the size structure of trees damaged versus all trees in (c) Retreat and (d) Bothas Post

be ruled out. It is unlikely that abiotic factors, like storms or natural death, were responsible for significant numbers of fallen trees, while in Boschplaats, the reference site, only two fallen trees (1.2%) were found in total. Of the other species occurring in the study area, baboons (*Papio ursinus* Kerr.) and porcupine (*Hystrix africaeaustralis* Peters) are known to damage tree euphorbias. Baboons eat the growth meristem out of trees (Midgley *et al.*, 1997), but it is not plausible that they kill many trees this way (Midgley, 1993). Porcupines eat the bark from the trunk of living trees, which can lead to rotting of the stem (Sharma & Prasad, 1992; Midgley *et al.*, 1997), but almost no traces of *H. africaeaustralis* were found during the study.

The mortality rate was calculated without taking rhino preferences into account. This study showed that

black rhinoceros prefer smaller tree size-classes. The GLM model showed that the average percentage of fallen trees could be predicted quite well ($R^2 = 0.82$) from local differences in height, circumference and site effects. Rhino preference, going for the smaller trees in the population, could form an additional problem for the tree euphorbias. The population structures could become unbalanced, as the intermediate size-classes that should develop into the cohort responsible for reproduction, suffer most from rhino damage.

In this study we have not been able to assess recruitment rate, but under the observed damage rate, Euphorbia trees could only survive if their reproduction rate is high. While the recruitment of *E. tetragona* and *E. triangularis* is poorly documented, an indication of recruitment was
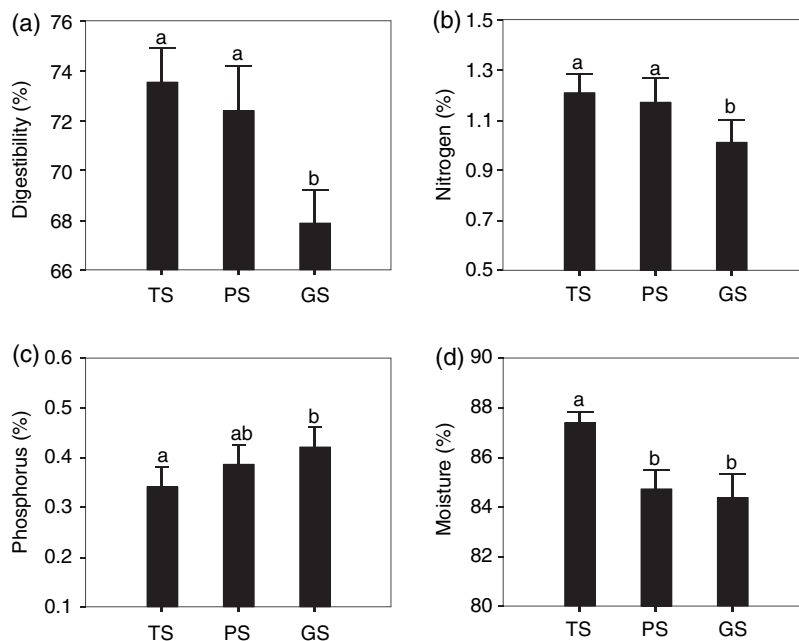
Fig 3 The differences between the different plant samples (TS, top section; PS, penultimate section; GS, grey section) in (a) digestibility, (b) nitrogen content, (c) phosphorus content and (d) moisture content

made based on the percentages of small trees. In Retreat about 18% of both the *E. tetragona* and the *E. triangularis* population consisted of small trees (<2 m), in Bothas Post this was only 4% for *E. tetragona*. In Boschplaats, the reference site, 39% of the population of *E. triangularis* and 20% of the population of *E. tetragona* consisted of trees <2 m. This recruitment seems to be sufficient to sustain the population, but when the trees between 1 and 2 m are examined, it becomes clear that only a small portion of the trees develop into this size-class. The percentage of trees between 1 and 2 m in Retreat was only 3% for *E. triangularis* and 2% for *E. tetragona*. In Bothas Post no trees between 1 and 2 m were found at all, while in Boschplaats, the site without rhinos, 18% and 6% of the trees were between 1 and 2 m for *E. triangularis* and *E. tetragona*, respectively. This could indicate that the browsing pressure on 1–2 m trees was relatively large, reducing natural recruitment, and threatening population persistence.

The tree euphorbias in the reserve might survive in refugia. Such a scenario was found for *Acacia davyi* (NE.Br.) eaten by giraffes (*Giraffa camelopardalis* L.); the Acacia mortality on steep slopes was very low, as giraffes preferred less steep slopes (Bond & Loell, 2001). Elephants were found to damage fewer baobab on steeper slopes at Lake Manyara National Park (Weyerhaeuser, 1985). In this study such an effect was not found, but refugia could exist on steeper hills than the ones studied.

There is also a possibility that rhinos will stop pushing over trees once the tree density drops below a certain threshold density or because the number of fallen trees on the ground makes it increasingly difficult for rhinos to negotiate the terrain. However, Goddard (1968) and Oloo, Brett & Young (1994) found that rhinos will cover great distances to find euphorbias. Both Goddard (1968) and Dudley (1997) thought that the water content of tree euphorbias was the main factor explaining rhino behaviour, based on their findings that *E. tirucalli* and *E. ingens* are mainly pushed over in the dry season. This theory is supported by the fact that *E. tetragona* is among the species with the highest water content in the GFFR (van Lieverloo & Schuiling, 2004), although there are more accessible plant species with a higher water content available in the GFRR. Moreover, rhinos can also drink from the river nearby. Our fieldwork was conducted in the dry season and it is possible that mortality rates of *E. triangularis* and *E. tetragona* will be less in other seasons. But even when there would be no damage in the rest of the year, the destruction in this dry season was sufficiently high that it could, if persistent, cause the death of all accessible euphorbia trees higher than two meters at the time of study. And we did not find any evidence for a recruitment rate that could balance this effect.

This study was also able to correlate rhino feeding choices to a higher plant moisture content, a higher

nitrogen content, and a higher digestibility. Apparently the water and quality hypothesis both explain differences in feeding choices of *B. diceros*. At first sight, food quality is the less likely hypothesis, because large browsers are expected to mainly select for food quantity. Owen-Smith (1988) stated that large herbivores could support their lower specific requirements by eating less food per day or by accepting food with lower nutrient concentrations or a combination of the two. If rhinos adopt a strategy of a decreased food intake, it is well possible that *E. triangularis* and *E. tetragona* were pushed over for their high nutrient content.

An aspect not addressed in this paper is the avoidance of secondary compounds, which Bozinovic, Novoa & Sabat (1997), and Bryant & Kuropat (1980) found to influence diet choice. *Euphorbia species* contain poisonous latex compounds (Betancur *et al.*, 2003), which are irritating to human skin and could cause blindness. *B. diceros* however seem to be very resistant to these poisonous compounds: some other euphorbia species, like *Euphorbia bothae* (Lotsy & Goddijn), are eaten in large quantities without any visible problems (Brown *et al.*, 2003).

Acknowledgements

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