Short communication

Rebrowsing by elephants three years after simulated browsing on five woody plant species in northern Botswana

Shimane W. Makhabu[1,3]* & Christina Skarpe[2]

[1]*Department of Biology, Norwegian University of Science and Technology, NO-7491, Trondheim, Norway*

[2]*Norwegian Institute for Nature Research, Tungasletta 2, NO-7485, Trondheim, Norway*

[3]*Department of Wildlife and National Parks, P.O. Box 11, Maun, Botswana*

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Utilization by the African elephant (*Loxodonta africana*) of five tree species of different acceptability was assessed on trees used three years earlier in a simulated browsing experiment. The experiment included two levels of treatment, twig cutting and stem cutting, and untreated controls. The experiment was done in northern Botswana in a fenced area, and there was no natural browsing by large herbivores. After three years, elephants broke into the area and their browsing of the experimental trees was assessed one month later. Four of the five species were browsed by the elephants, and for three of the species percentage utilization was higher on individuals subjected to simulated browsing three years before than on control trees. Treatment effects were strongest on the species intermediately used by the elephants. There was no difference in percentage utilization between trees with cut twigs and with cut stems. The results show that some aspect of the tree's response to a single browsing event is still discernible for the elephants after three years with protection from browsing.

Key words: browsing lawn, Chobe, percentage utilization, simulated browsing.

INTRODUCTION

Trees that have been subjected to real or simulated browsing often suffer higher probability to be browsed than do previously unbrowsed individuals (Danell *et al.* 1985; du Toit *et al.* 1990; Bergström *et al.* 2000; Bergqvist *et al.* 2001). This is a result of plant responses to the pruning, and involves both morphological and chemical changes in the plant. Twig biting by large herbivores reduces the number of meristems – often resulting in fewer and larger shoots, sometimes with higher concentration of nutrients and lower concentration of carbon-based defence compounds (Bergström & Danell 1987; Edenius 1993). Price (1991) argued that many herbivores prefer to feed on such large, vigorously growing shoots. The reasons may include larger bite size (Vivås *et al.* 1991) and improved nutritive quality (Danell & Bergström 1989; du Toit *et al.* 1990; Edenius 1993). If leading shoots are consumed or the stem is broken, the apical dominance is reduced, leading to reduced plant height and more shoots at lower level in the canopy, within browsing height for ground based mammalian herbivores (Stokke & du Toit 2000; Makhabu 2005). Rebrowsing is a common phenomenon, implying that a smaller proportion of trees are browsed than would be expected from random attack (Bergqvist *et al.* 2003), and repeated browsing of certain individual trees may lead to the development of a feeding loop (du Toit *et al.* 1990) and possibly to a 'browsing lawn' when the tree or tree stand is kept short and coppicing, producing high-quality browse (Owen-Smith 2003). Jachmann & Bell (1985) described elephants in the Kasungu National Park, Malawi, pushing over and repeatedly browsing selected trees, maintaining highly productive coppicing 'browsing lawns', seemingly selecting trees with high concentration of protein and sodium and low concentration of fibre.

Our aim was to assess whether treatment effects on trees were discernible by elephants after three years, and, if so, which species should give the strongest responses. We expected the effect of previous (simulated) browsing on rebrowsing patterns by the elephants to be most pronounced for intermediately preferred species, presuming those most preferred to be heavily browsed independent of previous treatment, and those most avoided hardly to be accepted even after treatment.

MATERIALS AND METHODS

Study area

The study was carried out in Kasane in northern Botswana. Annual average rainfall is about 640 mm with the wet season in summer mainly between November and April (Botswana Meteoro-

*To whom correspondence should be addressed.
E-mail: shimane.makhabu@bio.ntnu.no. and smakhabu@yahoo.co.uk

logical Service Department, unpublished records).

The specific location in Kasane was a fenced camp of 19 hectares belonging to the Department of Wildlife and National Parks. It was fenced in 1996 and since then, had been protected from large herbivores. The vegetation is mixed woodland with *Baikiaea plurijuga* and many smaller tree and shrub species (Skarpe *et al.* 2004). Plant nomenclature follows Coates Palgrave (2002).

Data collection

Twenty-six experimental sites spread over the fenced camp were chosen and marked in November 1999. At each site three individual plants each of *Baphia massaiensis, Baikiaea plurijuga, Bauhinia petersiana, Combretum apiculatum* and *Markhamia zanzibarica* were selected. The species were of different acceptability to elephants, from preferred species like *C. apiculatum* and *B. massaiensis* to strongly avoided ones like *B. plurijuga* (based on previous research in the same area by Stokke 1999; Stokke & du Toit 2000). The heights of the individual plants in our study ranged from 2.15 m (*B. petersiana*) to 3.5 m (*B. plurijuga*) but were as similar as possible within species. Each individual of a species at a site was randomly assigned to a different treatment. One had all stems cut at 50 cm height implying the removal of all the leaf area ('stumping'), the second had all twigs cut at the 8 mm diameter implying the removal of between 50 and 75% of the leaf area ('cutting'), and the third plant was left intact as a control. The selected individuals were marked and their positions recorded. There was no difference in initial height between treatment groups in any species. At the evaluation of the experiment in May 2000 the treated trees of all species had heavier and/or longer shoots than control trees. The study is not published.

Three years after the experiment was initiated, in October 2002, elephants broke into the fenced camp and browsed trees in the area. That gave us an opportunity to investigate how the elephants utilized trees of each species with different treatments. In November 2002 we revisited the marked trees. Of the initial 26 replicate sites, 12 had been cleared by humans and some of the remaining plants had lost their tags. The average number of replicates remaining for species and treatments was 10; the lowest was 5. On each tree the number of twigs <10 mm in diameter, browsed and unbrowsed, were counted.

Statistical analyses

The percentage of shoots browsed by elephant was calculated for each tree. The data were arcsine transformed and a two-way ANOVA applied to test for overall effects of treatments across species, of species across treatments and for interactions. Both species and treatment were treated as fixed factors in the two-way ANOVA. To test for differences in utilization by elephants of trees with different treatments within species, a one-way ANOVA was used, and for those that were different, multiple comparisons using a Tukey test was applied. Equality of variances was tested using the Levene's test of equality of group variances to make sure that the data met assumptions of one-way ANOVA. All tests were considered statistically significant at the $P < 0.05$. All statistical analyses were performed in SPSS for Windows (version 12.0.1) statistical package.

RESULTS AND DISCUSSION

At the analysis in November 2002, the number of twigs with a diameter of 10 mm did not differ within species between treatments except in *Combretum apiculatum,* where the 'stumped' trees had fewer such twigs than 'cut' and control trees ($n = 11$, $F = 13.397$, $P < 0.001$).

Elephant heavily browsed (in decreasing order) *Baphia massaiensis, Bauhinia petersiana* and *Combretum apiculatum.* They utilized *Markhamia zanzibarica* a little and *Baikiaea plurijuga* hardly at all (Fig. 1). The percentage utilization of trees by elephant was different between species ($F_{4,129} = 133$, $P < 0.001$) and between treatments ($F_{2,129} = 13.73$, $P < 0.001$). There was a significant interaction between species and treatment ($F_{8,129} = 5.15$, $P < 0.001$). The rank order of browsing by elephants differed from that found by Omphile (1997) and Stokke (1999), who found *C. apiculatum* to be most browsed of the species included in our study, followed (in decreasing order) by *B. massaiensis, B. petersiana* and *M. zanzibarica/B. plurijuga*. Concentration of fibre is relatively low in *Combretum apiculatum* and *B. massaiensis* (<40%) and high in *B. petersiana, B. plurijuga* and *M. zanzibarica* (>50%) (Makhabu *et al*., in press; Marokane & Skarpe, unpubl.). Nitrogen concentration is highest in *B. massaiensis* (*c.* 4%), followed by *B. plurijuga, B. petersiana* and *M. zanzibarica* (*c.* 3%) and *C. apiculatum* (*c.* 2%) (Makhabu *et al.,* in press; Marokane & Skarpe, unpubl.). The data suggest that it was more important for elephants to avoid intake of fibre than to maximize intake of

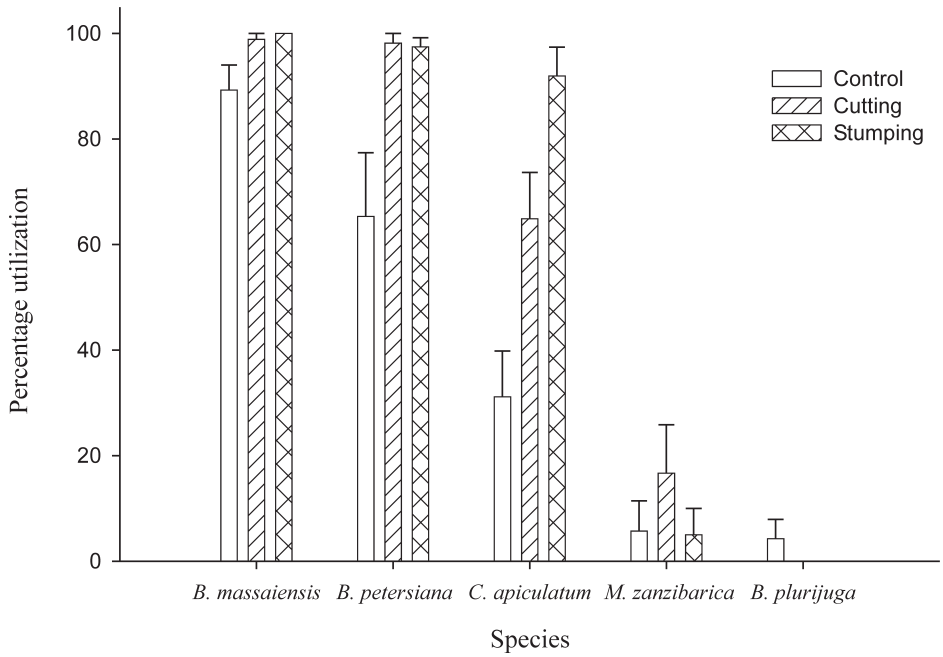

Fig. 1. Mean (±S.E.) browsing pressure by elephant on *Baphia massaiensis, Bauhinia petersiana, Combretum apiculatum, Markhamia zanzibarica* and *Baikiaea plurijuga* trees with different previous intensities of simulated browsing (control, cutting and stumping).

nitrogen. Elephant food selection against fibre is also recorded by Jachmann & Bell (1985).

Analysing the species separately showed that for the three heavily browsed species, *Combretum apiculatum, Baphia massaiensis* and *Bauhinia petersiana,* the percentage utilization differed between treatments (Table 1). Multiple comparisons showed that elephant browsed more on trees that had been subjected to simulated browsing than on controls (Table 1). There was no difference in browsing between the cut and stump treatments, and no difference between treatments in *Markhamia zanzibarica* or *Baikiaea plurijuga.* We expected intermediately preferred species to show the strongest effect of previous treatment on rebrowsing by elephant. Following the ranking observed in our study this was true, with the strongest treatment effect in *C. apiculatum* and intermediate effect in the most-browsed species, *B. petersiana* and *B. massaiensis,* of which most shoots had been browsed both on treated trees and controls, and no effect in the little browsed *M. zanzibarica* and *B. plurijuga.* However, with the ranking by Omphile (1997) and Stokke (1999) the most preferred species, *C. apiculatum,* showed the strongest treatment effect.

Most studies of rebrowsing following real or simulated browsing treatments have been evaluated within a year of the treatment [Bergström & Danell 1987 (12 months), Bowyer & Bowyer 1997

Table 1. Comparison of percentage utilization means for species and treatments. 0 = control, 1 ='cut', 2 ='stump'. Species ranked from highest (top) to lowest (bottom) acceptability by elephants in our study.

Species	ANOVA between treatments			*P* of Tukey's comparisons		
	d.f.	*F*	*P*	0 *vs* 1	0 *vs* 2	1 vs 2
Baphia massaiensis	2, 29	4.98	0.014	0.037	0.023	0.917
Bauhinia petersiana	2, 30	7.207	0.003	0.006	0.009	0.983
Combretum apiculatum	2, 32	15.57	<0.001	0.016	<0.001	0.019
Markhamia zanzibarica	2, 15	0.923	0.419	–	–	–
Baikiaea plurijuga	2, 23	1.683	0.208	–	–	–

(~12 months), Bergström *et al.* 2000 (eight months), Cooper *et al.* 2003 (12 months), Rooke & Bergström 2003 (three months)]. We found treatment effects to remain after three years in the plants browsed by elephants. It is, however, likely that the dynamics and pattern of decline in the induced response traits differ between plant species, and the ranking of the three species according to elephant response to treatment effects might have varied over time.

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