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Interactions between woody plants, elephants and other browsers in the Chobe Riverfront, Botswana

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Preface

The work in this thesis was done as part of the Botswana Norway Institutional Cooperation and Capacity Building Project (BONIC), jointly funded by the Botswana Government and Norwegian Agency for Development Co-operation (NORAD). The aims of the BONIC project included training of the staff of the Botswana Department of Wildlife and National Parks (DWNP) and also to undertake research that should improve the understanding of the ecosystems in northern Botswana and the systematic changes that are taking place there. As an employee of DWNP I benefited immensely from the project. I would like to thank the Directorate of DWNP particularly Mrs Mojaphoko for giving me the opportunity to study for a PhD degree sponsored by the BONIC project.

I am grateful to my supervisors Prof. Håkan Hytteborn at the Department of Biology, NTNU and Associate Prof. Christina Skarpe at NINA, Trondheim for all their help and support. They helped me to be accepted as a student by NTNU and also helped me in the field and as co-authors of most of the papers in this thesis. Bård Pedersen advised me on statistical procedures. Thanks also to my colleagues in the Department of Biology, NTNU for valuable comments on my work during informal lunch seminars.

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I appreciate my mother, father, sisters, sons, nieces, nephews, dear wife and my late brother Keithokometse for the love and understanding they had for me all this time of my absence from them. My son Bhatsho always made sure he answered the phone whenever I called home.

Finally I would like to thank the Almighty God for all the blessings he gave me and for giving me loving Christian brothers and sisters both in Botswana and in Norway.

Contents

List of papers

This thesis is based on the following papers, which will be referred to by their roman numerals:

I. Makhabu, S. W., Skarpe, C., Hytteborn, H. and Mpofu, Z. D. The plant vigour hypothesis revisited - how is browsing by ungulates and elephant related to woody species growth rate? *Plant Ecology* (in press).

II. Makhabu, S. W. 2005. Resource partitioning within a browsing guild in a key habitat, the Chobe Riverfront, Botswana. *Journal of Tropical Ecology* 21: 641-649.

III. Makhabu, S. W., Skarpe, C. and Hytteborn, H. Elephant impact on shoot distribution on trees and on rebrowsing by smaller browsers. *Acta Oecologica* (Conditionally accepted).

IV. Makhabu, S. W. and Skarpe, C. Rebrowsing by elephant three years after simulated browsing on five woody plant species in northern Botswana. *South African Journal of Wildlife Research* (Conditionally accepted).

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Abstract

This thesis examines the interaction between woody plants, elephants and other browsers in a semi-arid savanna in northern Botswana, southern Africa. Particularly I studied how woody plants respond to herbivory, how browsers respond to previously browsed trees, and how the browsers share food resources.

Browsing pressure by twig biting ungulates showed a unimodal relationship with shoot vigour (first PCA axis scores generated from four shoot variables) of 14 tree species, which may be caused by low quantity and quality of food on trees with low vigour, and too large shoot diameters on the most vigorously growing tree species. Browsing pressure by elephants showed no relation with shoot vigour of plant species. Elephants, giraffe, impala and kudu largely used different food resources in terms of browse species and height levels selected. There was little resource-use overlap (Schoener's index) between the herbivore species. Elephants (ca. 3000 kg) predominantly browsed other woody species than those browsed by giraffe (ca. 1000 kg), impala (ca. 50 kg) and kudu (ca. 200 kg). Differences in body size could not explain this difference in food choice, as giraffe, impala and kudu browse the same tree species independent of considerable difference in body size. The differences in food selectivity may instead be explained by difference in digestive systems. Elephants are hindgut fermenters whereas the others are foregut fermenters (ruminants).

Trees that were strongly affected by elephant browsing had more shoots at low height levels than individuals without elephant impact. Impala and kudu preferred to browse from trees previously browsed by elephant rather than from trees without any elephant impact. This indicates that elephants facilitate the foraging by these two species. Elephants themselves are known to rebrowse previously impacted trees, and were found to recognize and preferentially browse trees that had been subject to simulated browsing three years earlier and since then protected from large herbivores.

The study did not find evidence that elephants compete with and deplete food for other browsers. Results in this thesis do not justify manipulation of elephant population and distribution as a means to increase populations of the other animal species investigated in this thesis. Instead it seems that elephants may act to facilitate browsing by other investigated animal species.

Introduction

Forage selection by browsers

Herbivores make foraging decisions at different spatial scales, e.g., on the level of landscape, habitat type, feeding patch and the single plant or plant module (Senft *et al*. 1987; Skarpe *et al*. 2000). A feeding patch or a feeding station for a browser may be a stand, a tree or a part, e.g., a height section, of a tree (Senft *et al*. 1987; Danell *et al* 1991; Spencer *et al*.1995). Herbivores respond to variation in food abundance or biomass in different ways (Gordon 2003). Herbivores may forage resources distributed patchily in a pattern that match availability, i.e., linear response (Senft *et al*. 1987; Spencer *et al*. 1995; Gordon 2003). However, herbivores may also employ foraging patterns, which are nonlinearly related to forage abundance (Senft *et al*. 1987). The nonlinearly foraging responses have been described as “overmatching”, when resource use in a patch is disproportionately high or “undermatching”, when resource use in a patch is disproportionately low (Staddon 1983; Senft *et al*. 1987; Spencer *et al*. 1995)

Differential selection of food items by herbivores relates to plant and animal characteristics. Plant characteristics involved may comprise morphology (Campbell 1986; Cooper and Owen-Smith 1986; Cooper and Ginnett 1998), chemistry (Coley *et al*. 1985; Bryant *et al*. 1992a; Bryant 2003), spatial distribution (Senft *et al*. 1987; Vivås and Sæther 1987) and earlier herbivory (du Toit *et al*.1990; Bergström *et al*. 2000; Bergqvist *et al*. 2003). Herbivores select food items from a chemically and structurally heterogeneous source. The chemical and structural properties of food items vary with plant species, plant parts, plant vigour, plant phenology and habitat conditions (Feeny

1976; Coley *et al.* 1985; Campbell 1986; Cooper and Owen-Smith 1986; Coley 1988; Bryant *et al.* 1992a; Grubb 1992; Cooper and Ginnett 1998; Bryant 2003).

Several theories, models and hypotheses with widely different purpose and scope, have been put forward to explain selection of food items by herbivores (White 1974; Pyke *et al.* 1977; Owen-Smith and Novellie 1982; Price 1991). Most of them are based on one or more of the assumptions that herbivores should (1) maximise intake rate of nutrients and/or energy, (2) minimise the intake rate of harmful compounds, (3) use optimal time in a feeding patch, and (4) move in an optimal way between feeding patches. Two theories (White 1974; Price 1991) use plant characteristics, stress level and plant vigour, respectively, which are not in themselves relevant for herbivore foraging, as proxy variables in order to explain differences in herbivore attack on plants and plant parts. The plant vigour hypothesis (Price 1991) proposes that any plant module, individual or species, that grows rapidly and ultimately reaches a large size, relative to the mean growth rate and ultimate size of the population of modules, individual plants or plant species, suffers enhanced probability of herbivore attack. The plant vigour hypothesis has been developed and tested mainly for insect attack on plant modules within a plant or a plant species (Whitham 1980; Price *et al.* 1987; Faria and Fernandes 2001). It has, however, also successfully described differences between plants within a species or between closely related species in attack by large mammalian herbivores both in temperate and tropical regions (Fritz *et al.* 1987; du Toit *et al.* 1990; Danell *et al.* 1985; Bergström and Danell 1987; Bergström *et al.* 2000). Price (1991) stated that if the plant vigour hypothesis gains support from patterns of herbivore attack within plant species, equivalent patterns should be expected on the broader scale of among species variation in herbivore attack.

Animal characteristics that have been used to explain differences in food selection include body size (Bell 1971; Jarman 1974; Jarman and Sinclair 1979; Owen-Smith 1988) and digestive system (Hanley 1982; Owen-Smith 1988). Body size of an animal relates to gut volume and retention time of food and hence affects the extent of digestion of the diet. This, together with the relatively lower energy requirement for maintenance metabolism of a large animal compared to a small one, makes it possible for large-bodied species to sustain themselves on food of much lower quality than that required by a small-bodied species (Jarman and Sinclair 1979; Owen-Smith 1988). The body size hypothesis or Jarman-Bell principle based on body size has therefore been considered as a possible mechanism for interspecific differences in diet (Bell 1971; Jarman 1974; Demment and Van Soest 1985). The digestive system also influence retention and digestion of the diet, with hindgut fermenters (e. g., elephant, horses and pigs) having faster passage rate and lower digestibility of forage than foregut fermenters (ruminants) of comparable size, and has also been considered as a possible mechanism for interspecific differences in food selection (Clauss *et al*. 2003).

Interactions between herbivores and plants

Plants respond to herbivory both in evolutionary and ecological time. Generally, the strategy of plants evolved in resource poor environments is to minimise loss of resources, i.e., to develop resistance traits like mechanical or chemical defences while plants evolved in resource rich environments have instead developed tolerance traits and maximise resource acquisition and growth (Coley *et al*. 1985; Grubb 1982; Stamp 2003). In ecological time plants respond phenotypically to herbivory within the limits set by the genetic variation and physiological restrictions (Herms and Mattson 1992; Stamp 2003).

Studies on plant responses to real or simulated herbivory have generated different results depending on plant species characteristics (Haukioja and Niemelä 1979; du Toit *et al*. 1990; Duncan *et al*. 1998; Rooke *et al*. 2004b; Bryant 1981; Bryant *et al*. 1983, Karban and Myers 1989; McNaughton 1979; Bowyer and Bowyer 1997; Bergström *et al*. 2000) timing, intensity and frequency of herbivore damage (Canham *et al*. 1994; Danell *et al*. 1994; Bergström *et al*. 2000; Rooke *et al*. 2004b), type of plant tissue removed and nutrient availability in the environment (Maschinski and Whitham 1989; Hjältén *et al*. 1993). In a number of studies plants have been found to respond with increased biomass production (McNaughton 1976, 1984; Dangerfield and Madukanele 1996). Some studies of browsing effects on woody plants have found browsed trees to produce larger, although fewer shoots (Bergström and Danell 1987; Molvar *et al*. 1993, Bergström *et al*. 2000) compared to unbrowsed individuals. In most of these cases, however, the total biomass of current season's shoots is lower on the browsed than on the unbrowsed individuals (Bergström and Danell 1987; Molvar *et al*. 1993; Bergström *et al*. 2000). The shoots developed following browsing may also have increased nitrogen concentration and decreased concentration of secondary compounds like condensed tannins (du Toit *et al*. 1990) compared with undamaged individuals. Plants that respond to herbivory with increased production (totally or of single modules) and chemical quality suffer enhanced risk for repeated grazing/browsing compared with previously not eaten individuals. Such responses of plants and animals may result in a 'feeding loop', leading to the creation of ‘grazing lawns’ or ‘browsing lawns’ (McNaughton 1976, 1984; du Toit *et al*. 1990; Bowyer and Bowyer 1997; Bergström *et al*. 2000; Bergqvist *et al*. 2003).

Food mediated interactions between herbivores

Interaction among species with similar food requirements has been a subject of investigation in ecology for decades (Schoener 1974; McNaughton 1976; Hanley and Hanley 1982; Sinclair and Norton-Griffiths 1982; Owen-Smith 1988; Gordon and Illius 1989; du Toit 1990; Putman 1996; Van der Wal *et al*. 1998; Voeten and Prins 1999; Mysterud 2000; Hulbert and Andersen 2001; McDonald 2002). The results of most of these studies show that species with similar food requirements coexist despite overlaps in fundamental niches provided the overlap in potential resource use is incomplete (Putman 1996). Interspecific competition and facilitation have both been proposed to promote niche separation and co-existence of species (Zaret and Rand 1971; Schoener 1974; Sinclair and Norton-Griffiths 1982).

Competition for limited food is a major driving force of evolution within assemblages of related and morphologically similar species (MacArthur and Levins 1967). Natural selection should therefore favour a separation in food niches among competing species (Levin 1970; Abrams 1983). Interspecific exploitation competition is likely to happen when there is overlap in habitat use, in diet consumed and the shared resources are limited (De Boer and Prins 1990; Mysterud 2000). Facilitation becomes possible when, first, consumption by a consumer produces a flow of resources into another consumer and, second, the latter consumer specialises on consuming the produced resource (Farnsworth *et al*. 2002). In facilitation, often one consumer increases the accessibility to food for another (Guy 1981; van de Koppel and Prins 1998), but facilitation may also be in the terms of enhanced quality of food (McNaughton 1976, 1984). Competition and facilitation are not mutually exclusive, but may take place at the same time concerning different species or vary over time (van de Koppel and Prins 1998; Taolo 2003).

Differences in body size and the associated differences in quantitative and qualitative food requirements, as discussed above, is often important in interactions between large herbivores. In many of the interacting systems described in literature a relatively large bulk feeder (e. g., wildebeest and/or zebra) facilitates subsequent foraging by a smaller more selective species (e. g., Thompson's gazelle) (Vesey-Fitzgerald 1960; Bell 1971; McNaughton 1976; Sinclair and Norton-Griffiths 1982; Sinclair *et al.*1985). The smaller species may at the same time compete with the larger species, by pre-empting the high nutrient component of the forage (van de Koppel and Prins 1998; Woolnough and du Toit 2001).

Food mediated interactions involving megaherbivores

Megaherbivores (herbivore species whose adult individuals attain a body mass over 10^3 kg) (Owen-Smith 1988) such as the African elephant *(Loxodonta africana* Blumenbach) are bulk feeders and are capable of transforming woodlands into shrublands (Owen-Smith 1988; Ben-Shahar 1993; Mosugelo *et al*. 2002) and grasslands (Laws 1970; Caughley 1976; Pellew 1983: Cumming *et al*. 1997). Many studies have suggested that such changes show a cyclic pattern (Laws 1970; Caughley 1976; Pellew 1983: Dublin *et al*. 1990). Caughley (1976) proposed that elephant and trees coexist in a stable limit cycle. However, Duffy *et al*. (1999) showed with realistic data that limit cycles are highly unlikely. It has been proposed that savanna-woodland ecosystems may switch between multiple stable states, as triggered by herbivores or fire (Dublin *et al* 1990).

Basically, these models assume that high populations of elephants lead to a change from woodland to grassland, which causes elephant populations to decline because of shortage of food until populations are low enough for the woodlands to re-establish and the elephant population to increase again. There is increasing evidence that small herbivores or the interactions between large and small herbivores strongly influence the shifts in savanna vegetation. While the destruction of mature trees by elephants is undeniable, their influence on savanna dynamics may be limited, as the regeneration and establishment of trees is governed by smaller browsers, primarily impala (Belsky 1984; Prins and van der Jeugd 1993; Rutina 2004). Van de Koppel and Prins (1998) hypothesise that in a situation with low plant biomass (grassland) there is competition between large and small herbivores for food, and small herbivores are generally the superior competitor. With increasing plant biomass, (larger proportion of woody vegetation) facilitation becomes more important, as reduction in the plant biomass from foraging increases the proportion of plant matter within reach for the small herbivore and makes access easier also for the larger species. The model by van de Koppel and Prins (1998) does only under specific conditions lead to a cyclic behaviour of the system. Fritz *et al*. (2002) analysed wildlife censuses from 31 conserved African ecosystems and concluded that elephants negatively affected populations of browsers and mixed feeders, but had no influence on grazers. However, facilitation of smaller browsers by elephant foraging, as suggested by the model by van de Koppel and Prins (1998), has also been found (Guy 1981).

Aims of the thesis

The main aim of this thesis is to examine the interactions between woody plants, elephants and other browsers, with a purpose to increase the predictive understanding of the dynamics of the Chobe Riverfront ecosystem. Emphasis is on food mediated interactions, including responses of woody plants to herbivory, the subsequent responses by herbivores to the changes in plant properties, and the sharing of food resources between mammalian herbivore species.

Specifically I examine:

1. The influence of browse quality and quantity on forage selection (Paper I, II, III)
2. The food resource partitioning between elephant, giraffe, impala and kudu (Paper II)
3. The significance of previous browsing on trees for subsequent foraging by browsers (Paper II, III, IV).

The study area

Location and Climate

The study was done in the northern most section of Chobe National Park, ca. 17°49' - 17°55' S, 24°50' - 24°59' E, in northern Botswana. The Chobe River forms the northern boundary of the study area, which stretches ca. 50 km E-W along the river and ca. 10 km S from it. There are a number of roads or tracks running almost perpendicular from the river southwards ca. 10 km to a major road and some roads along the river. The climate is semi-arid with summer rainfalls, mainly between November and April. The average annual rainfall is about 640 mm. Mean maximum and mean minimum monthly temperatures in October (hottest month) are 39º and 14ºC, respectively and in July (coldest month) are 30º and 4ºC, respectively (Botswana Meteorological Service Department, unpublished). The soils are mainly deep, well-drained, nutrient-poor Kalahari sands with some alluvial clay soils along the Chobe River.

Past and present woody vegetation

Over the last, past two centuries the structure and composition of vegetation not least the woody component has been dynamic (Simpson 1974, 1975; Moroka 1984; Walker 1986; Spinage 1990; Gibson *et al*. 1998; Mosugelo *et al*. 2002; Skarpe *et al*. 2004). The area on the alluvial soil that is now shrublands along the Chobe River was in the 1870s open flats (Selous 1881). At the beginning of the 1900s, a woodland with large *Acacia* and *Combretum* trees established (Fig. 1) possibly due to the decline of elephant and other herbivores caused by ivory hunting and of the 1890s rinderpest outbreak (Simpson 1975; Walker 1986; Skarpe *et al*. 2004). Since the 1960s the woodland on the alluvial soil has been declining (Mosugelo *et al*. 2002). A comparison of vegetation descriptions from the riverfront by Simpson (1974) and Addy (1993) with the present situation shows a succession of small woody species after the decline of the tall woodland. Many of the species most common today were not mentioned among the 15 most common species by Simpson (1974). Some of the species increasing on the alluvial soil, e. g., *Capparis tomentosa* and *Combretum mossambicense* are species that are not much eaten by elephants, but preferred by many ruminant browsers. The vegetation dynamics before the 1960s on Kalahari sands further away from Chobe River is less known. The available literature shows that vegetation next to the alluvial soil from the Chobe River was a strip of mixed woodland followed by a woodland (Mosugelo *et al*. 2002). The same zones exist today, but may have retreated further away from the river (Mosugelo *et al*. 2002; Skarpe *et al*. 2004).

Woody species recruitment is low along the Chobe Riverfront particularly in the riparian woodland (Mathumo 2003; Rutina 2004). Rutina (2004) showed that woody seedling survival was negatively correlated with impala density, but neither with kudu nor elephant density (Rutina 2004), similar to the situation recorded in Lake Manyara National Park, Tanzania, by Prins and van der Jeugd (1993).

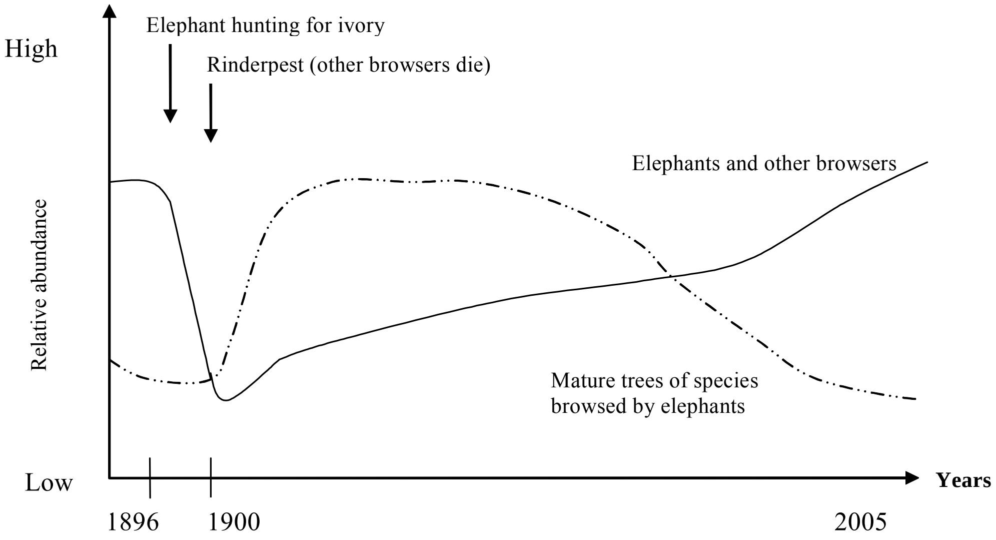

Fig. 1. Dynamics of herbivores and trees in the Chobe Riverfront (modified from Walker 1986)

Mammalian herbivore species - past and present population status

The Chobe Riverfront has a high diversity of mammal species. As Chobe River is the only permanent water source in northern-east Botswana, many species during the dry season gather along the river and disperse southwards during the wet season (Ben-Shahar

1993, Gibson *et al.* 1998; Verlinden and Gavor 1998; Omphile and Powell 2002; Stokke and du Toit 2002; Skarpe *et al.* 2004). Such migratory species include African elephant *(Loxodonta africana)*, buffalo (*Syncerus caffer)*, giraffe (*Giraffa camelopardalis)*, greater kudu *(Tragelaphus strepsiceros*), roan antelope (*Hippotragus equinus)* and sable (*Hippotragus niger*). Resident species at the Chobe Riverfront include impala *(Aepyceros melampus*), puku (*Kobus vardonii)*, bushbuck (*Tragelaphus scriptus)*, waterbuck (*Kobus ellipsiprymnus)* and hippopotamus (*Hippopotamus amphibious)*. Animal nomenclature accords to Skinner and Smithers (1990).

The population status of animals before 1973 is not well known since no formal population estimates were done (Vandewalle 2003). However, at the beginning of the 1800s, elephants were probably distributed almost throughout Botswana and there may have been as many as 400 000 animals (Campbell 1990; Gibson *et al*. 1998). Drought around 1870s, and before that, uncontrolled hunting reduced elephant numbers and by the beginning of the 1900s elephants were rare even in Chobe National Park (Walker 1986; Gibson *et al*. 1998) (Fig. 1). Also the population of browsing ungulates declined due to rinderpest that swept through Botswana during the 1890s and due to drought (Walker 1986; Vandewalle 2003) (Fig. 1). The populations of elephants and other browsing herbivores have now increased (Fig. 1). In 1987 the elephant population was estimated at 50 000 (Gibson *et al.* 1998) but in 2003 it was estimated at 130 000 in northern Botswana (DWNP 2003). The annual rate of increase of the elephant population is about 6 % (Gibson *et al.* 1998). Along the Chobe Riverfront the elephant density can be as high as 4/km^2 (Gibson *et al*., 1998) or 8.5/km^2 (DWNP 2003) during the dry season but during the wet season can be reduced to 0.5/km^2 (Gibson *et al*. 1998). Elephant densities above

$0.6/km^2$ have been shown in some ecosystems to cause major vegetation changes (Jachmann and Croes 1991). The populations of impala and buffalo have been shown to increase with that of elephant (Taolo 2003; Rutina 2004). For bushbuck, comparison of average monthly counts (Child 1968; Simpson 1974; Addy 1993; Dipotso *et al*. unpublished) from the Chobe suggests a pronounced decline in density between the 1970s and 1990s followed by a stabilisation or slight increase (Dipotso *et al*. unpublished).

Elephant population increase a concern

Unlike in some countries, elephants in Botswana are not culled and poaching is not prevalent. Concerns have been raised that the Chobe Riverfront is over-utilised by elephants and therefore, unattractive to tourists (Walker 1986; Omphile and Powell 2002). Concerns have also been raised that elephants compete with and deplete food available for other herbivores raising concerns that other species might be adversely affected (Owen-Smith 1989; Herremans 1995; Cumming *et al.* 1997; Fritz *et al.* 2002). The elephant, however, has also been identified as a 'keystone species' that play a disproportionately large role in the community structure (Owen-Smith 1987; Owen-Smith 1989). Owen-Smith (1987; 1989) argues that elimination of megaherbivores might negatively affect the population of some species. The importance of megaherbivores for ecosystem processes like nutrient dynamics and species diversity has also been hypothesised by e.g., Zimov *et al*. (1995). However, knowledge about interspecific competition, facilitation resource sharing and forage selection among species with similar food requirements in the Chobe system is just beginning to accumulate, but is still largely unknown.

Although the African elephant is unique in its size, the kind of concern alluded to above is not unique for elephant dominated ecosystems. Increasing populations of ungulates raise similar concerns in much of Europe and North America (Kay 1997; Weisberg and Bugmann 2003). A difference between the systems may be that while the ungulate populations historically to greater or smaller extent have been controlled by large predators until these recently were reduced or eradicated by man (Ripple *et al.* 2001), there is not in the modern fauna a predator that could more than marginally affect the elephant population.

The interactions of woody plants and browsing megaherbivores and mesoherbivores along the Chobe Riverfront are thought to be as shown on the conceptual model in Figure 2. The browsers share some food species but not others. Herbivory results in woody species responding to the damage and the response might or might not attract rebrowsing (feeding loop) by the same herbivore species or others.

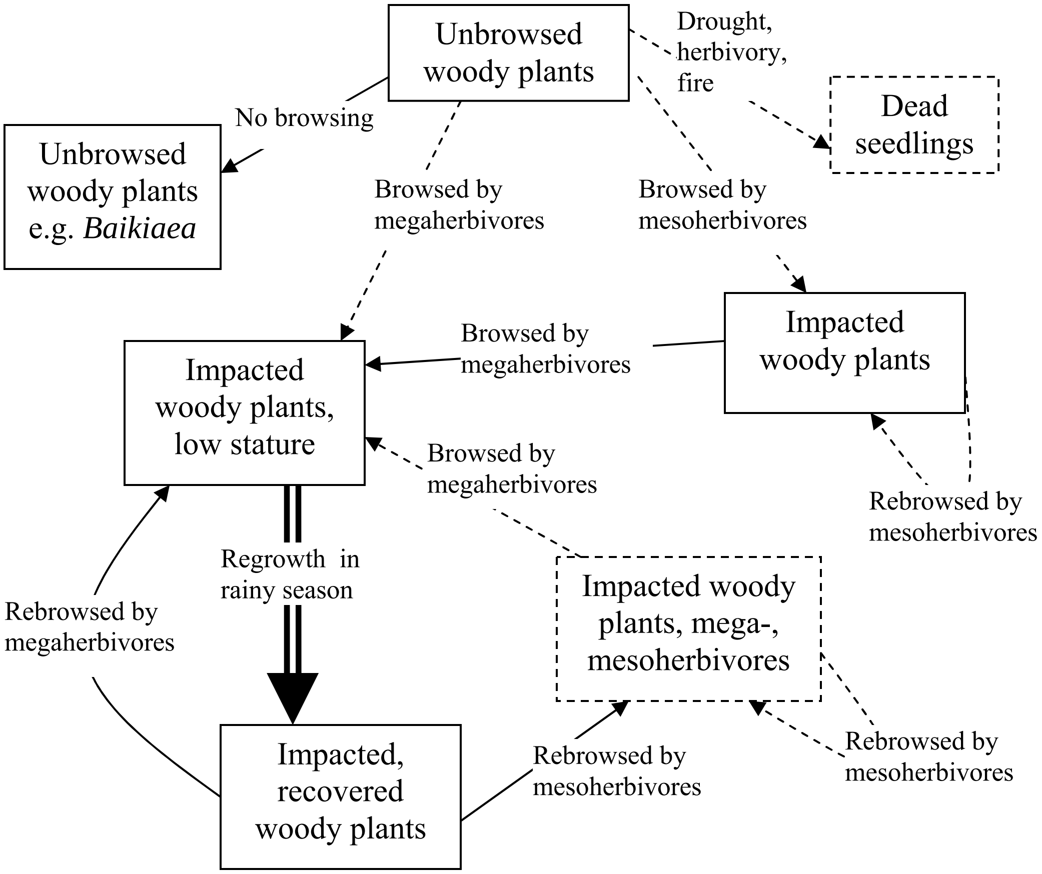

Fig. 2. Conceptual model demonstrating interactions between megaherbivores, mesoherbivores and woody species as examined in this thesis. Dashed boxes and arrows indicate parts of the model not assessed. Several processes are not shown, e.g. mortality of established plants in connection with browsing, drought or fire. Also shift in species composition caused by browsing is not shown.

Study species

Plant species

The study concentrated on woody species including both shrubs and trees (henceforth called ‘trees’). The species differed in many characteristics (Table 1). Plant nomenclature is according to Coates Palgrave (2002).

Table 1. Woody species characteristics according to Coates Palgrave (2002) and van Wyk and van Wyk (1997). + and – in the spinescence column refers to having spines and having no spines respectively. Height is common height of mature individuals.

Species	Family/subfamily	Life Form	Height (m)	Leaf type	Spinescence	Leaf fall	Paper
Baikiaea plurijuga	Caesalpinioideae	Tree	8 - 16	Pinnate	-	Deciduous	I, IV
Baphia massaiensis	Papilionoideae	Shrub	2 – 4	Simple	-	Deciduous	I, IV
Bauhinia petersiana	Caesalpinioideae	Shrub	3 - 4	Lobed	-	Deciduous	IV
Boscia albitrunca	Capparaceae	Tree	7	Simple	-	Evergreen	II
Canthium glaucum[1]	Rubiaceae	Shrub	5	Simple	+	Deciduous	I, II
Capparis tomentosa	Capparaceae	Shrub/tree	10	Simple	+	Evergreen	I, II, III
Combretum apiculatum	Combretaceae	Tree/shrub	3 - 10	Simple	-	Deciduous	I, II, III, IV
Combretum elaeagnoides	Combretaceae	Tree/shrub	6	Simple	-	Deciduous	I, II, III
Combretum mossambicense	Combretaceae	Tree/shrub	5	Simple	+	Deciduous	I, II, III
Croton megalobotrys	Euphorbiaceae	Tree/shrub	15	Simple	-	Deciduous	I, II
Dichrostachys cinerea	Mimosoideae	Shrub	5-6	Bipinnate	+	Deciduous	II
Erythrophleum africanum	Caesalpinioideae	Tree	4 - 12	Bipinnate	-	Deciduous	I
Erythroxylum zambesiacum	Erythroxylaceae	Tree/shrub	3 - 7	Simple	-	Deciduous	I, III
Flueggea virosa[2]	Euphorbiaceae	Shrub	2 - 3	Simple	-	Deciduous	I, II, III
Friesodielsia obovata	Annonaceae	Shrub	7	Simple	-	Deciduous	I, II
Markhamia zanzibarica	Bignoniaceae	Tree	7	Pinnate	-	Deciduous	II, III, IV
Ochna pulcra	Ochnaceae	Tree	3 - 7	Simple	-	Deciduous	I
Philenoptera nelsii[3]	Papilionoideae	Tree	4	Simple	-	Deciduous	I, II
Strychnos potatorum	Strychnaceae	Tree	5 - 15	Simple	-	Deciduous	II

[1] Synonym is *Canthium frangula.* [2] Synonym is *Securinega virosa.* [3] Synonym is *Lonchocarpus nelsii.*

Animal species

Four mammalian browsing species, the African elephant *(Loxodonta africana*), giraffe (*Giraffa camelopardalis)*, impala *(Aepyceros melampus*) and greater kudu *(Tragelaphus strepsiceros*) were considered in this thesis (Table 2). They differ in body sizes and digestive systems (Table 2).

Table 2. Description of the studied animal species. Feeding and digestion types for all species and measurements for giraffe and kudu are according to Skinner and Smithers (1990). Elephant measurements are according to Haltenorth and Diller (1980) while impala measurements are according to Smithers (1992)

Species	Shoulder height (m)		Weight (kg)		Feeding type	Digestion type
	male	female	male	female		
Elephant	3.5	2.7	4 550	2350	mixed feeder	hindgut fermenter
Giraffe	3.0	2.7	1192	828	browser	foregut fermenter
Impala	0.9	0.85	55	40	mixed feeder	foregut fermenter
Kudu	1.4	1.3	228	157	browser	foregut fermenter

Methods

Growth measurements of plant species

Shoot growth rate of 14 woody species was determined from monthly shoot measurements. Ten new shoots on 10 individual trees per species were randomly selected and marked in October and November 2002, when trees sprouted. The lengths of the shoots were measured to the nearest mm, each month over the complete growing season until April 2003. In February or in April 2003, when growth had terminated, basal shoot diameters were measured in order to determine annual shoot volumes. Growth rates of shoots, shoot lengths, basal shoot diameters and annual shoot volumes were used in a principal components analysis (PCA) (CANOCO software, ter Braak and Šmilauer 1998) to generate samples scores. In the further statistical analyses, the scores of the first PCA axis were used to represent the shoot vigour of the plant species.

Chemical analysis of plant samples

Leaves from trees monitored for growth rates were sampled in January 2003. The leaves were first air dried in paper bags indoors and later taken to the laboratory where they were dried for 24 hours at 80˚C, and then ground to pass through a 2 mm sieve prior to the analyses. The leaves were analysed for contents of nitrogen, potassium, sodium, magnesium, calcium, phosphorus, acid detergent fibre and neutral detergent fibre. Nitrogen was determined using Kjeldahl procedures (AOAC 1995). Potassium and sodium concentrations were determined using flame photometer (Corning Flame Photometer 410). Magnesium and calcium concentrations were determined by measuring the absorption with an atomic absorption spectrophotometer (manufactured by Varian Techron, Australia) at 285.2 nm and 422.7 nm wavelengths, respectively (AOAC 1995). Phosphorus was determined by measuring the absorption at 670.0 nm wavelengths on an UV Visible recording spectrometer (manufactured by Shimadzu Corporation, Japan) (AOAC 1995). Acid detergent fibre and neutral detergent fibre were determined using Ankom technology procedures (Ankom Technology Corporation 1997). Tuulikki Rooke (Swedish University of Agricultural Sciences, Umeå) kindly let us use data on tannin activity assessed through protein precipitation, using Hagerman (1987) radial diffusion procedure (Rooke *et al*. 2004a).

Browsing pressure

Data on ungulate and elephant browsing pressure were sampled in 58 plots of 20 m x 20 m including all vegetation types in a stratified design, 28 plots in the shrubland, 15 plots in the mixed woodland and 15 plots in the *Baikiaea* woodland**.** For all woody plant individuals > 0.5 m in height, numbers of current season's shoots, separated between shoots with and without bites, were counted up to the height of 2.5 m above ground. This height includes the browsing heights of most ungulates and also the preferred browsing height for elephant (Stokke and du Toit 2000). Bites included twig bites and removal of shoot tips during leaf stripping (Skarpe *et al*. unpublished). Browsing pressure of ungulates was calculated as the percentage of current season's shoots below 2.5 m of each tree species that was browsed within a plot. Browsing pressure of elephant was calculated as the percentage of individual trees of each species within a plot that had been browsed by elephants during the current season.

Browsing observations

From a vehicle driven at 20 km h^{-1} along the tracks in the study area, browsing animals were sighted and then observed. Whenever an animal or a group of animals of the four studied species, elephant, giraffe, impala and kudu, was seen, the vehicle was stopped and the animal or any animal in the group seen browsing was observed as it browsed. With the aid of a pair of binoculars, the tree species and the browsed plant parts were identified and recorded. After records were made, the plant was visited to measure the browsing height and to verify the species and the browsed plant parts. Accumulated elephant impact was visually determined and categorized into three levels according to the degree of change in tree growth form compared to “normal” growth of unaffected specimens of the species in question. Levels were: (0) no accumulated elephant impact, i. e., no obvious change in the growth form of the tree (generally the main stem and main branches with no signs of old breaking and/or biting by elephant), (1) low accumulated elephant impact, i. e., growth form of the tree obviously changed (generally signs of old breaking and/or biting by elephant being present on less than half of the total number of main branches and stems) and (2) high accumulated elephant impact, i. e., growth form of tree strongly changed (generally tree broken down or more than half of the total number of main branches and stems with old signs of breaking and/or biting by elephant).

On trees browsed by kudu and impala, the vertical distribution of shoots was determined. This was done by placing on the side where the animal had browsed, a frame 3 m x 1 m, marked with horizontal fish lines at every 20 cm along the vertical 3 m side. In each 20 cm by 1 m section from ground level to a height of 2.6 m, the number of shoots (defined as twig ends < 6 mm in diameter) was counted. A calliper was used to check the diameter of the shoots.

Browse availability on trees differentially impacted by elephant

Twenty plots, 25 m x 25 m, were used. The plots were distributed along four tracks perpendicular to the Chobe River. There were five plots along each track, the first was 200 m from the river and they were 400 m apart. All these plots were within 2 km from the river. In the plots all trees more than 0.5 m high were assessed and classified in three different classes for accumulated elephant impact as described above. Also the number of shoots in 20 cm height sections up to 2.6 m high on these trees was counted as described above. The frame was placed on a randomly selected side of the tree.

Rebrowsing by elephant

Rebrowsing by elephants of trees with previous different intensities of (simulated) browsing was assessed in an experiment. A simulated browsing trial had been performed in a fenced area which excluded large herbivores. The treatments, applied in November 1999, were, severe browsing, meaning that all stems were cut at 50 cm height, and that 100 % of the leaves were removed, light browsing, meaning that all twigs were cut at the 8 mm diameter and that 50 - 75 % of all leaves were removed and finally no browsing, meaning that the trees were left intact as controls. Three years after the treatment, in October 2002 elephants broke into the fenced camp and browsed trees in the area. In November 2002 the trees used in the experiment were revisited and the number of browsed and unbrowsed twigs < 10 mm in diameter was counted.

Results and discussion

Forage selection and resource partitioning between browsers

Elephant, giraffe, impala and kudu selectively browsed woody species (Paper I, II and IV). Elephants predominantly browsed woody plant species different from those browsed by giraffe, impala and kudu. Giraffe, impala and kudu browsed the same woody species but at different heights (Paper II). Impala and kudu seemed to treat height levels of trees as feeding patches, and used them differently depending on density of shoots available.

Both species showed a pattern of overmatching (sensu Senft *et al.* 1987) in relation to relative shoot availability in the different height levels (Paper III). There was little overlap, measured as Schoener's index (Schoener 1970), in resource use (plant species, plant parts and height levels) between the four species. Browsing height stratification between the three ruminants was dependent on the size of the animals and on interspecific scramble competition (Illius and Gordon 1987; Stokke and du Toit 2000; Paper II). Overlap in resource-use was not larger in the wet season, when food was relatively abundant, than in the dry season, when food was scarce, as might have been expected if there were strong interspecific competition for food (Gordon and Illius 1989; Mysterud 2000). Elephant, impala and kudu browsed more on trees that had previously been browsed by elephants or subjected to simulated browsing than from previously unbrowsed trees (Papers III and IV). Shoot vigour among tree species (first PCA axis scores generated from 4 measured shoot growth variables) was positively correlated with nutrient concentrations and negatively correlated with concentrations of fibre in the leaves (Paper 1). The relationship between plant species' shoot vigour and browsing pressure by twig biting ungulates showed a unimodal pattern, instead of positive monotonic as predicted by the plant vigour hypothesis (Price 1991). There was no relationship between shoot vigour of woody species and elephant browsing pressure (Paper I).

Mammalian herbivores are selective feeders that choose among alternative foods on the basis of their nutritional value, structural and chemical defences, spatial distribution and growth architecture as related to intake rate of food (Owen-Smith 1982; Owen-Smith and Novellie 1982; Danell *et al.* 1985; Cooper and Owen-Smith 1986; Vivås and Sæther

1987; Jachmann 1989; Coley and Aide 1991; Price 1991; Bryant *et al*. 1992b, Holdo 2003; Wilson and Kerley 2003). It was expected that the difference in woody species browsed by the different herbivore species would be explained by a combination of the body size hypothesis or Jarman-Bell principle (Bell 1971; Jarman 1974) and the difference in animal species digestive systems (Demment and van Soest 1985; Clauss 2003). These theories predict that a large animal or a hindgut fermenter requires large amounts of food and can use forage of low quality, which is usually abundant, while a small animal or a foregut fermenter (a ruminant) needs small quantities of high quality food, which is usually rare. The giraffe, impala and kudu are all foregut fermenters and this might explain why they browse different plants from the elephant. However, we do not know explicitly what traits of the respective tree species that govern the selectivity. The difference in body size between the giraffe (ca. 1000 kg) and the impala (ca. 50 kg) does, however, not seem to influence choice of food species or items (Paper II). While large-bodied animals have the capacity to persist on poor quality food, they will select food of high quality if the availability is adequate. We still know little about the quality and quantity of the browse resource for ungulates along the Chobe Riverfront.

Large herbivores interact with food resources in different spatial scales, often described as a hierarchy of decisions taken by the herbivore (Senft *et al*. 1987). Hebivores may forage selectively in scales from regional systems to landscapes, plant communities and micropatches (or feeding stations or plants) (Senft *et al*. 1987). We found the foraging response by impala and kudu to change with vertical variation in shoot abundance within a tree and to show an overmatching pattern (Paper III). This agrees with some findings that have shown a nonlinear relationship between relative food abundance and intake rate (Allen and Clarke 1968; Cook and Miller 1977; Fullick and Greenwood 1979; Lundberg and Danell 1990; Fritz and de Garine-Wichatitsky 1996). However, our result may differ from those suggesting that the consumption of browse by browsers give a linear relationship between the biomass available and the intake rate (Renecker and Hudson 1986; Spalinger *et al*. 1988; Spalinger and Hobbs 1992). It is, however, possible that different functional responses describe food selection by the same animal in different spatial scales. Further, we did not measure intake rate, only the relative frequency of browsing observed in the different height levels. The likely explanation to the overmatching observed may be that animals select patches with high density of food in order to optimize intake and reduce searching time (Schoener 1971). This is important for animals browsing in a group, like impala, because other profitable sites might be occupied by other members of the group (Fritz and de Garine-Wichatitsky 1996).

The separation in browsing height between the three ungulate species appears to depend on the height of the animal and on interspecific scramble competition (Paper II). For animals of different size, the hypothesis on scramble competition (Hughes 1980; Illius and Gordon 1987; Woolnough and du Toit 2001) would predict that the smaller species pre-empt the high quality food at low heights in the tree canopy, displacing animal species of intermediate height, which in turn force large animal species to browse high in the tree canopy (Paper II). There was no decrease in resource-use overlap during the period of food scarcity (dry season), which could have indicated increased interspecific competition (Gordon and Illius 1989, Mysterud 2000), on the other hand, overlap was very small during both seasons. As the elephant browse different woody species than the ruminants, it is unlikely that elephant influence the competition between the ruminant species.

The preference by browsers for previously browsed trees compared to previously unbrowsed ones is a common response (Danell *et al*. 1985; Owen-Smith 1988; du Toit *et al*. 1990; Bergström *et al* 2000; Bergqvist *et al*. 2003), although the opposite response, where induced defences reduce the palatability of browsed trees, also is reported (Bryant 1981; Hulbert and Andersen 2001). Regrowth shoots after browsing may differ from shoots on unbrowsed trees in morphological and chemical characteristics as well as in position on the tree, thus affecting both quality and availability of browse.

The plant vigour hypothesis predicts a positive monotonic relationship between plant vigour and herbivore attack (Price 1991). Studies supporting the plant vigour hypothesis have mostly concerned selection of modules within plants (Whitham 1980; Price *et al*. 1987; Faria and Fernandes 2001) and of plants within a species (Fritz *et al*. 1987; du Toit *et al*. 1990; Danell *et al*. 1991; Bergström *et al*. 2000). Broadening the scale in variation of herbivore attack from variation between modules within a plant to intraspecific variation among individual plants and to interspecific variation among plant species logically implies increasing variation in other herbivory related plant traits without relation to plant vigour, possibly reducing the predictive power of the hypothesis. Price (1991) also states that regrowth shoots after herbivory often show enhanced vigour compared with shoots from unbrowsed plants, which may contribute to the high probability for herbivory on such shoots. Also the size of the herbivore in relation to the attacked unit plant may be of significance. An insect, typically consuming a portion of a leaf or a shoot, is likely to respond to chemical and structural properties of the module

(Haukioja and Niemelä 1979) but not to the size as such. However, a mammal, typically consuming whole modules, is likely to respond to chemical and structural quality (Bryant 1981; Palo 1984; Cooper and Owen-Smith 1986) but also to the size and shape of the module (Vivås *et al*. 1991; Wilson and Kerley 2003).

Instead of the positive monotonic relationship between woody species' shoot vigour and browsing pressure by twig biting ungulates, we found a unimodal relationship (Paper I). The preference by browsers for tree species with intermediate shoot vigour was supported by the observation that these species contributed substantially to the diets of browsing ungulates (Paper II). The unimodal response by browsers to shoot vigour may be explained by shoots with low vigour having poor nutritive value and offering small bite size while the most vigorous shoots had high nutritive value but a shoot diameter exceeding the bite diameter for most ungulates. Thus, the plant vigour hypothesis was not supported by browsing pressure exerted by twig biting ungulates on plants across woody species (Paper I). Shoots of some woody species, particularly following browsing, may grow fast and reach larger diameters than the bite diameters of most ungulates (du Toit *et al*. 1990; Paper I). This might be an evolutionary strategy by such woody species to escape predation by twig biting ungulates. Elephants are fairly independent of shoot diameters, being able to break branches as thick as 333 mm (Stokke and du Toit 2000). Hence, they could be expected to respond to the nutritive properties of the shoots and show the predicted monotonic response to shoot vigour. However, we found no relationship between shoot vigour of plant species and elephant browsing pressure.

Effect of browsing on shoot distribution on trees and on rebrowsing

The accumulated elephant impact on woody plants varied between species (Paper III).

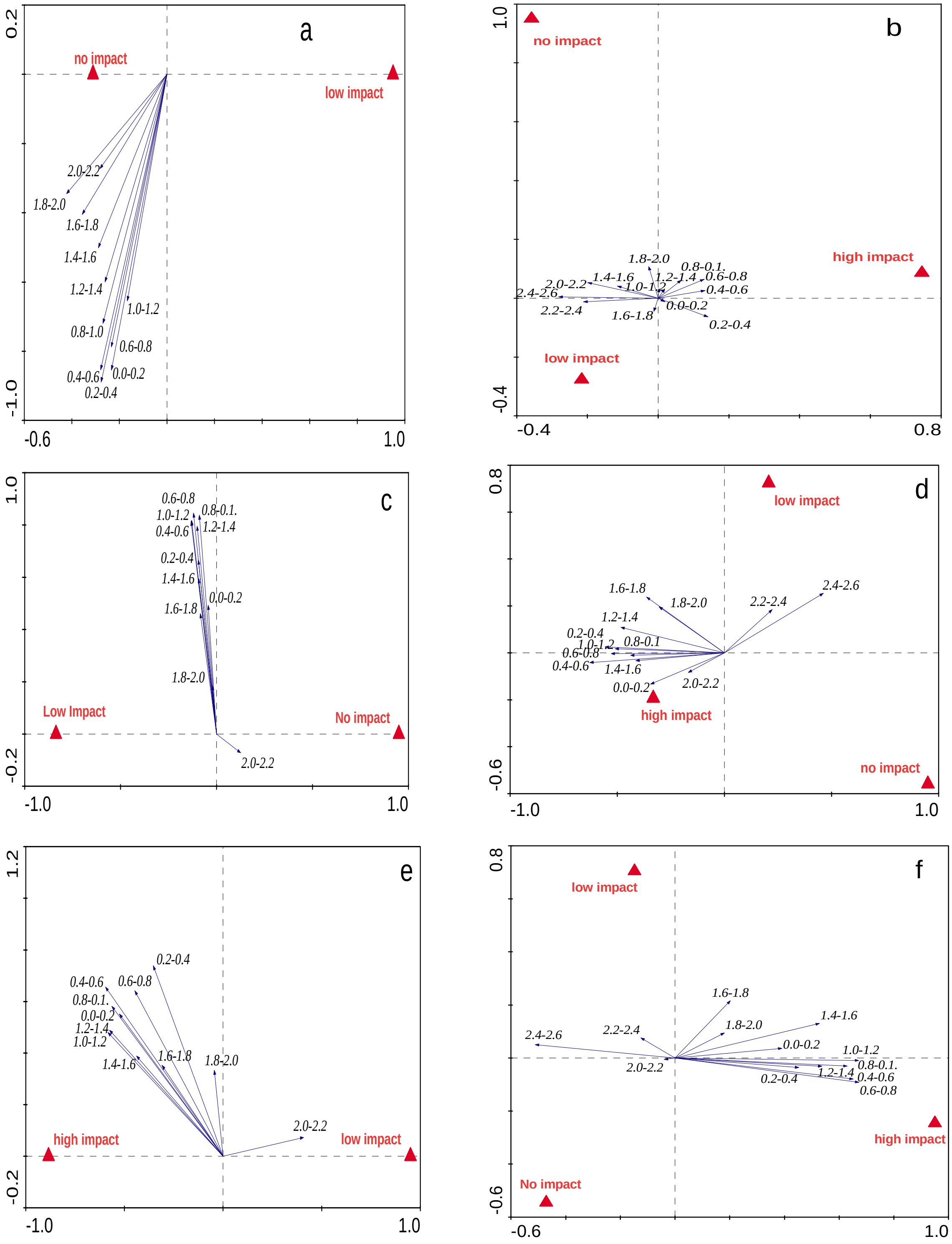

Fig. 3. RDA ordination of shoot numbers in different height sections with accumulated elephant impact being the environmental variable. (a) *Capparis tomentosa* (b) *Combretum apiculatum*, (c) *Combretum mossambicense*, (d) *Erythroxylum zambesiacum*, (e) *Flueggea virosa* and (f) *Markhamia zanzibarica*.

Elephant impacted trees were shorter than those not impacted. Trees with accumulated elephant impact had more shoots (diameter < 6 mm) on low levels in the canopy than trees with no accumulated elephant impact (Paper III). The pattern of vertical distribution of shoots was statistically tested using nonparametric multivariate analysis (Paper III) and also confirmed graphically by the use a redundancy analysis (RDA) (Fig. 3). Impala and kudu browsed more on trees with either high or low accumulated elephant impact than on trees with no accumulated elephant impact (Paper III). Both herbivores treated the height levels of trees as foraging patches, as described above. Three years after a trial with simulated browsing, elephants distinguished between treated and untreated trees and browsed more on previously cut or clipped trees than on control trees of preferentially browsed species, whereas there was no difference in browsing pressure with treatment on little used browse plants (Paper IV).

The large absolute number of shoots at low levels on trees with high accumulated elephant impact could be explained by the activation of dormant lateral buds after weakening of the apical dominance by removal of leading shoots (Järemo *et al*. 1996; Smit and Bolton 1999) as described above (Introduction). A common result of this is the development of fewer but larger shoots on browsed trees, as discussed above (Introduction) (Danell *et al*. 1985, 1994; Bergström 1992). Such responses have also been recorded in studies in Botswana (Bergström *et al*. 2000; Rooke *et al*. 2004). The high densities of resprouting shoots on trees in our study area may represent an adaptation to severe impact by browsing animals and/or fires (Bond and Midgley 2001). As canopy architecture varies between tree species, all comparisons of shoot numbers were within species. Resprout shoots on trees after browsing are often larger (but fewer) than on unbrowsed trees and differ in chemical characteristics (Danell *et al*. 1985; du Toit *et al*. 1990; Duncan *et al*. 1998; Bergström *et al*. 2000), and enhanced shoot size and vigour following browsing is one explanation for rebrowsing (Danell *et al*. 1985; Price 1991). In those cases high quality of shoots attract rebrowsing, in spite of fewer shoots and often lower total shoot biomass than on unbrowsed trees (Bergström *et al* 2000). In this study we did not assess size or chemistry of shoots, and except the number of shoots, we do not know whether other shoot properties, differed within plant species between trees with different levels of accumulated elephant impact (Paper III). Further, we defined shoots as any twig end less than 1 year old with a diameter < 6 mm. Thus, we cannot exclude that some of our "shoots" are in fact branches on large annual shoots.

The fact that impala and kudu preferred to browse tree individuals impacted by elephant, is an indication that elephants facilitates browsing by these species, as described from other ecosystems by Jachmann and Croes (1991), Prins and Olff (1998), van de Koppel and Prins (1998) (Paper III). The relationship is analogous to the situation in Serengeti where grazing by wildebeest facilitates grazing by Thompson's gazelle (Bell 1971; McNaughton 1976). Elephants facilitate browsing by impala and kudu by conversion of tall trees to 'browsing lawns' that lead to more and possibly higher quality shoots within reach for ungulates in some plant species. On the Chobe Riverfront browsing pressure is intense during the dry season, when animals gather along the river and when plants are largely dormant. During the wet season trees grow with comparatively little browsing, as elephant and other migratory browsers have dispersed to their wet season ranges and the resident impala predominantly graze during the wet season (Omphile 1997).

We expected the response by browsing elephants on previous (simulated) browsing treatment to be most pronounced for intermediately preferred tree species, presuming the most preferred ones to be heavily browsed independent of previous treatment, and those most avoided not to be accepted even after treatment. Elephant browsing pressure (% of shoots browsed) was high on three of the five species in the trial, low on one species and there was virtually no browsing on the fifth species (Paper IV). For the three much browsed species previously treated trees had significantly higher browsing pressure than the control trees, $p = 0.014$, $p = 0.003$ and $p < 0.001$ (in declining order of browsing pressure). Thus the expectation of strongest treatment effect on intermediately browsed species may be true for the ranking of species in the current study, it does, however, not fully agree with the ranking of elephant food species in the region by Omphile (1997) and Stokke and du Toit (2000) (Paper IV). The expectation that the treatment effect would not make any difference for the species with lowest acceptability was confirmed.

Rebrowsing by elephant creating highly productive coppice stands, 'browsing lawns' has been described by e. g., Jachmann and Bell (1985) and Owen-Smith (1988, 2003), and rebrowsing of previously affected trees is common in different ecosystems and with different animal and tree species (Danell and Bergström 1989; Duncan *et al.* 1998; Bergström *et al.* 2000) as discussed in the Introduction. The treatment response by the three preferred species was obviously one of increased palatability. At the evaluation of the initial experience, treated trees of all five species had longer and heavier shoots than control trees of the same species (Skarpe *et al.* unpublished). No measurements on trees or shoots were made at the analysis of rebrowsing two years later. The duration and long term dynamics of tree responses following real or simulated browsing is little known. Most studies recording increased palatability following browse treatment have used a year or shorter response time (Paper III). Fox and Bryant (1984) showed that reduced palatability and biomass of regrowth in North American species responding to browsing with induced defences lasted between 2 and 10 years. In at least 3 of our 5 species treatment effect obviously remained after 3 years, but we do not know whether duration and dynamics of the effects on elephant foraging differ between plant species, and how ranking of tree species according to elephant responses to treatment may vary over time.

Likely consequences of continued elephant population increase

There is no doubt that elephant impact result in a decline in the number of mature trees of some species like the *Acacia* (Walker 1986; Barnes 2001). In the past, the woodland along the Chobe River was replaced by a shrubland (Mosugelo 2002; Skarpe *et al*. 2004). It is likely that with the increase in elephant population, the shrubland might extend into the mixed woodland and the result might be a more open and patchy mosaic shrubland, as also predicted by Owen-Smith (1987, 1989). The species composition of the shrubland might be devoid of species like which we show in this thesis to be heavily impacted by elephant (Paper III) but this will depend on other factors such as fire, predation by other herbivores and how the plant species respond to herbivory. How far into the woodlands the change will proceed will depend on the future development of the elephant population and the herbivore community as a whole.

Whether the increase in elephant population might drive the vegetation on the raised alluvial soils close to the river into an open flat as it was in the 1870s (Selous 1881) is difficult to predict as various factors like fire, climate conditions and other herbivores play a role in vegetation change. Not only will the density of elephants be important for the future development of the Chobe Riverfront ecosystem, but also their dynamics. Van de Koppel and Prins 1998 and Duffy *et al* (1999) suggest that elephant dominated ecosystems could not behave cyclic. A cyclic behaviour means that large numbers of elephants would either migrate out of the area or die in the decline phase. A major die-off may be unproblematic from an ecological point of view, but may raise major concern among the public, unless proper information is given.

The elephant increase appears to be associated with an increase of other herbivore species like buffalo and impala (Taolo 2003; Rutina 2004); hence these other herbivore species might retard regeneration of species they favour by seedling predation (Barnes 2001; Rutina 2004). In this thesis we report that impala browse *Capparis tomentosa* and *Combretum mossambicense* the most (Paper I and II), the species that have been reported to increase along the Chobe Riverfront, hence the increase of these species is likely to be retarded. However, in the absence of fire the Chobe Riverfront might still not be modified into grassland because some of the woody species, preferred by elephant, although not *Acacia* spp., show profuse seasonal regrowth (coppicing) following elephant use (Jachmann and Bell 1985; Makhabu 1994; Ben-Shahar 1993). The results in this thesis support this profuse seasonal regrowth of some species in that we found that the shoot vigour of plant species heavily browsed by elephant was higher than those elephants avoided (Paper I and II). A new stable state might exist as proposed in the multiple stable states scenario (Dublin *et al*. 1990). Therefore, the vegetation of the Chobe Riverfront should be expected to be dynamic and not to remain as a woodland as it was in the 1950s as some people wish.

How long the elephant population of Chobe Riverfront will continue to increase is not known, but in the past there has been a population crash due to poaching and natural factors like diseases and drought (Walker 1986). Apart from the occasional outbreaks of diseases like anthrax, the area has predators and frequent drought years. No populations can grow infinitely, and the Chobe elephant population is likely to level out as a result of density-dependent dry season mortality caused by inadequate nutrition.

This study did not find evidence to support the concern that elephants compete for food with other browsing animals. This conclusion is based on that elephants and the other browsers do not predominantly browse the same woody species and that their wet and dry seasons woody species use overlaps do not differ. Contrary, it appears that elephants facilitate browsing by some of these other browsing herbivores. It therefore, seems unlikely that the increase in elephant population might negatively affect browse available for giraffe, impala and kudu. Thus the population of each of these herbivore species is unlikely to be negatively affected by food depletion caused by elephant.

Management implications

The decisions on elephant management are usually based on ecological, economic, social, political, ethical and practical considerations (Waithaka 1997). This thesis addresses some ecological aspects only. The findings call for a careful balanced assessment of the ecological role of major species in the ecosystem before decisions to manipulate population and distribution of any of them can be done. In the case of elephants, rather than mostly considering them as bad for other herbivores they could also be considered as a ‘keystone herbivore’ that benefit other species such as the example of facilitation of browsing of impala and kudu reported in this thesis. In the management of elephant populations it is sometimes debated which policy to adopt among various options comprising “cropping” (maintaining a stable elephant population by culling or harvesting), “laissez faire” (letting elephant populations rise and/or fall naturally) and translocation (Chafota and Owen-Smith 1996; Waithaka 1997). The findings in this thesis appear not to support the concern that elephant deplete food available for other browsers, hence it may not be valid to adopt the “cropping” policy on the management of elephant populations along the Chobe Riverfront based on this concern. Probably adopting the “laissez faire” policy as currently done in National Parks of Botswana is not a bad option. In 1966 the “laissez faire” policy was adopted in Tsavo National Park, Kenya and the elephant population was in the 1970s reduced by mortalities caused by drought. Unlike the Tsavo elephants, the Chobe elephants have some flood plain grasses available to them during the dry season (Spinage 1990) and also have the possibility to migrate to other areas. The Chobe elephant range is fairly large, hence elephants can move in search of food in their wet and dry season ranges which extend beyond the borders of Botswana into Zimbabwe and Caprivi Strip in Namibia (Verlinden and Gavor 1998). In Chobe National Park, some artificial watering points have been developed in areas where there is no perennial surface water. This has some benefits but might allow elephant population to increase and the impact of elephant on woodland to spread to larger areas (Owen-

Smith 2003). Provision of artificial watering points possibly should be restricted to the now dry rivers that used to be perennials like Savuti River, and with the understanding that it is likely to further increase the elephant population. Adoption of the “laissez faire” policy might result in an increase of elephant that might be forced to forage in areas that they might conflict with people. Probably the cropping and translocation elephant management policies might be justifiable in such areas where elephants are in conflict with people.

Future studies

The Botswana Norway Institutional Cooperation and Capacity Building Project (BONIC), of which these studies form part, has initiated research to understand the main processes governing the dynamics of the Chobe Riverfront ecosystem, and has created a base for future research to build on. The studies done up to now are all of relatively short duration, ca 5 years. As the rainfall is one of the main external drivers of the ecosystem and is highly variable between years with a tendency to 20 years cycles, a much longer period of research is necessary for understanding more of the dynamics and increase reliability of results and conclusions. The new GPS telemetry has been little used in Chobe, but the technique offers immensely improved possibilities for data collection on animal movements and utilisation of different habitat types. It could, for example, be applied for understanding more of the bushbuck habitat preferences and use in the park which is not covered in this thesis. We may even need to learn more about the detailed movements and habitat utilisation of the Chobe elephants. Among the most important determinants of the Riverfront ecosystem is the interactions between vegetation and large and small herbivores, e. g. elephants and impala. To solve such questions and test the existing hypotheses an experimental approach is needed, and in the future much more experimental studies should be carried out, targeting the facilitation-competition relations between small and large herbivores, as well as the significance of different herbivores or herbivore assemblages for the vegetation dynamics

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Paper I

Twig biting ungulates - Impala

Growth of shoots on *Combretum elaeagnoides*

The plant vigour hypothesis revisited - how is browsing by ungulates and elephant related to woody species growth rate?

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Abstract

The way herbivores select what to eat is of considerable practical and theoretical interest, and has given rise to different theories and hypotheses. The plant vigour hypothesis predicts that herbivores feed preferentially on vigorous, i. e., large and/or fast-growing plants or plant parts. These predictions have previously primarily been tested on variation within plant species. Here we test whether differences in vigour among plant species in the same environment can explain differences in herbivore attack. We studied variation in browsing pressure by a guild of large herbivores on different woody species in an African savanna ecosystem. Shoot growth rate, annual shoot length, basal shoot diameter and annual shoot volume of fourteen woody plant species were measured in the field. Plant species' shoot vigour represented by the first PCA axis scores generated from the four shoot variables were then related to browsing pressure (% utilisation) on each of the species by native ungulates and elephant. Nutrient and fibre concentrations and tannin activity were also determined for the fourteen woody plant species. We found ungulate browsing pressure to show a unimodal relationship with plant species' shoot vigour. The heaviest browsing pressure was on plant species with shoots of intermediate vigour. We suggest that species with less vigorous shoots had low nutrient and high fibre concentrations and offered small bite sizes, whereas species with vigorous shoots had high nutrient concentrations but larger shoot diameters than the bite diameters of browsing ungulates. Elephant browsing pressure was not related to plant species' shoot vigour.

Key words: Botswana, plant nutrients, tannin activity, unimodal relationship, fibre content

Introduction

Studies on herbivore feeding have generated a number of hypotheses to explain why herbivores preferentially feed on certain plants or plant parts (Greenbank 1956; White 1974; Mattson and Haack 1987; Price 1991). The plant vigour hypothesis (Price 1991) proposes that any plant module, individual or species, that grows rapidly and ultimately reaches a large size, relative to the mean growth rate and ultimate size of the population of modules, individual plants or plant species, suffers enhanced probability of herbivore attack. Studies supporting this hypothesis have mostly concerned selection of modules within plants and of plants within a species. Whitham (1980), Price et al. (1987) and Faria and Fernandes (2001) found a strong preference in galling insects for large young leaves and rapidly growing shoots. Both insect and mammalian herbivores have been shown to prefer vigorously growing plant modules and individual plants within a species (Fritz et al. 1987; du Toit et al. 1990; Danell *et al*. 1991, Bergström et al. 2000). If the plant vigour hypothesis is supported by patterns of herbivore attack within plant species, equivalent patterns may be expected to apply on the broader scale of differences in herbivory among plant species (Price 1991).

Broadening the scale of variation in herbivore attack from differences between modules within a plant to intraspecific differences among individual plants and to interspecific variation among plant species logically implies increasing the range of variation in other herbivory related traits besides plant vigour, possibly reducing the predictive power of the hypothesis. On the other hand, the size of the herbivore in relation to the plant unit being attacked may be of significance in testing the plant vigour hypothesis. An insect herbivore, typically consuming a portion of a leaf or a shoot, is likely to respond to chemical and structural properties of the module but not to the size as such. However, a mammalian herbivore, typically consuming whole modules, is likely to respond not only to the chemical and structural quality (Palo 1984; Cooper & Owen-Smith 1986) but also to the size and shape of the module (Vivås et al. 1991; Wilson and Kerley 2003). The mechanistic basis for the plant vigour hypothesis (Price 1991) suggests that there should be a positive correlation of nutrient concentration and/or a negative correlation of plant defences with plant vigour. Such a correlation is also predicted for phenotypic variation between plants and, possibly, for variation within plants by the growth differentiation balance hypothesis (Herms and Mattson 1992; Stamp 2003), as well as for genotypic variation between or within plant species by the resource availability hypothesis (Coley et al. 1985).

We tested predictions from the plant vigour hypothesis (Price 1991) on the relationship between browsing pressure by large mammals and variation in shoot vigour among a suite of woody plant species in a southern African savanna ecosystem. African savanna ecosystems are suitable for studying plant-herbivore interactions due to their long evolutionary history and the high species richness of large herbivores. We investigated patterns of shoot growth rate, final shoot length and basal diameter, leaf nutrient and fibre concentrations, tannin activity, and browsing pressure by a guild of ungulate browsers and elephant on 14 co-occurring woody species in order to test the following hypotheses:

1. Vigorously growing species have higher nutrient concentrations, lower tannin activity and lower fibre concentrations than less vigorously growing species.
2. Browsing ungulates and elephant browse more on vigorously growing species than on less vigorously growing species (the plant vigour hypothesis).

Methods

The study area

The study area was the northern-most section of the Chobe National Park, ca. 17°49' - 17°55' S, 24°50' - 24°59' E, in northern Botswana. The Chobe River forms the northern boundary of the study area, which stretches ca. 50 km E-W along the river and ca. 10 km S from it. The climate is semi-arid with summer rain falling mainly between November and April. The average annual rainfall at Kasane, 1 km east of the study area, is about 640 mm. Average monthly maximum and minimum temperatures in October (hottest month) are 39° and 14° C, respectively and in July (coldest month) are 30° and 4°C respectively (Botswana Meteorological Service Departmental records). The soils are mainly deep, well-drained, nutrient-poor Kalahari sands with some alluvial clay soils along the Chobe River.

The vegetation forms zones running more or less parallel to the Chobe River (Skarpe et al. 2004). Shrub vegetation with *Capparis tomentosa* and *Combretum* spp. dominates near the river on alluvial soils and in the transition between alluvial soils and Kalahari sands. Mixed woodlands with scattered large *Baikiaea plurijuga* and many smaller species like *Combretum* spp. and *Philenoptera nelsii* grow on Kalahari sands. Further inland also on Kalahari sands, *Baikiaea plurijuga* woodlands dominate (Skarpe et al. 2004).

Large mammal browsers in the area include African elephant (*Loxodonta africana*), giraffe (*Giraffa camelopardalis*), greater kudu (*Tragelaphus strepsiceros*), impala (*Aepyceros melampus*), steenbok (*Raphicerus campestris*) and bushbuck (*Tragelaphus scriptus*). All species except giraffe browse mainly below 2.5 m (du Toit 1990; Stokke and du Toit 2000). Kudu and impala are the most common large browsing ungulate species. Animal species nomenclature follows Skinner and Smithers (1990).

Data collection

The study was conducted in 2002 and 2003. Fourteen common woody plant species with different characteristics (Table 1) were studied in the shrub and mixed woodland vegetation types. Growth measurements of each species were done in the vegetation type where it was most common. Plant species nomenclature is according to Coates Palgrave (2002).

Shoot growth rates were determined by measuring the length of individually marked new shoots over the growing season. During October and November 2002, when new shoots started to sprout, we randomly selected 10 individual, medium sized, actively growing woody plants (henceforth called ‘trees’) of each of the 14 study species, for a total of 140 trees. Selected trees showed insignificant or no signs of prior browsing. Ten new shoots per tree distributed throughout the canopy were randomly chosen for measurement, excluding the leading shoots and regrowth from the base. The total number of shoots measured was then 1400, with 100 shoots per species. A numbered metallic tag was fastened to the main branch next to the new shoot to mark it. Measurements included monthly records of shoot length (mm) and two measures of shoot basal diameter (diameter of the shoot just above the point where it emerges from the main branch; 0.1 mm) conducted in February and April 2003, when the shoots were fully-grown. In January 2003, when most leaves were fully grown and wilting had not started, about 5 g (wet weight) of leaves were collected for chemical analyses from unmarked branches of selected individual trees. The leaves were placed in paper bags and air-dried at room temperature (27° C).

Data on ungulate and elephant browsing pressure were collected late in the rainy season, mainly in March and April. Sampling during these months (the end of the growing season) allowed us to include all browsing on that shoot generation before leaf fall. Sampling was conducted in 58 plots of 20 m x 20 m, including all vegetation types in a stratified design (28 plots in the shrubland, 15 plots in mixed woodland and 15 plots in *Baikiaea* woodland)**.** For each species, only data from the vegetation type(s) where it occurred in at least three plots were used. For all woody plants > 0.5 m in height, current season's shoots with and without bites, separating between ungulate bites and elephant bites and "breaks" (Stokke and du Toit 2000), were counted within browsing height (< 2.5 m above ground). All bites on current season’s shoots were recorded, including twig bites and removal of shoot tips during leaf stripping.

Laboratory methods

All analyses except that for tannin activity were done at the Plant Laboratory of the Department of Agricultural Research at Sebele in Botswana. The sampled leaves were dried for 24 hours at 80^{o} C and then ground to pass through a 2 mm sieve. Nitrogen was determined using Kjeldahl procedures (AOAC 1995). Potassium (K) and sodium (Na) concentrations were determined using a flame photometer (Corning Flame Photometer 410). Magnesium (Mg) and calcium (Ca) concentrations were determined using an atomic absorption spectrophotometer (Varian Techron, Australia) at 285.2 nm and 422.7 nm wavelengths, respectively (AOAC 1995). Phosphorus (P) was determined by measuring the absorption at 670.0 nm wavelengths on an UV Visible recording spectrometer (Shimadzu Corporation, Japan) (AOAC 1995). Acid detergent fibre (ADF) and neutral detergent fibre (NDF) were determined using Ankom technology procedures (Ankom Technology Corporation 1997). Tannin activity data, including all our species and sampled in the same study area as we used, were kindly provided by Dr. Tuulikki Rooke, (Swedish University of Agricultural Sciences). She assessed tannin activity through protein precipitation using the Hagerman (1987) radial diffusion procedure. Sampling and laboratory procedures for tannin activity determinations are described in Rooke et al. (2004).

Data Analysis

For each shoot, the maximum shoot growth rate was determined by plotting changes in shoot length (mm) against time (days) and then calculating the slope of the steepest section of the graph. The formula used was:

Shoot growth rate = $(L_n-L_{n-1})/\ (t_n-t_{n-1})$,

where L_n and L_{n-1} are shoot lengths at time t_n and t_{n-1} respectively of the steepest section of the graph (modified from Hunt 1990). The maximum shoot growth rate for each species was calculated from the average of the individual shoots on each tree (n = 10).

Annual shoot length is the average shoot length for each species (n = 10) in April, when shoot growth had flattened out and sampling was terminated. Shoot growth rate is usually measured as length increment over time. However, plant resource allocation to growth is probably best measured as increment in biomass (Hunt 1990). If biomass cannot be measured, a function including shoot basal diameter as well as shoot length may correspond better to resource allocation than does only shoot length or diameter separately (Bilbrough and Richards 1993).

Annual shoot volume was calculated using the formula for the volume of a cone.

Annual shoot volume = (shoot basal area x annual shoot length)/3

= $(\pi r^2 L)/3$, where r is the basal radius and L the annual shoot length.

The annual shoot length, annual shoot volume, annual basal shoot diameter and maximum shoot growth rate were included in a principal components analysis (PCA) performed using CANOCO software (ter Braak and Šmilauer 1998) to generate sample scores for shoot ‘vigour’ summarising the four growth measures taken on the shoots of each species. This was done after the values of the four shoot growth variables were standardised ($Y_i^1 = \frac{Y^i - \overline{Y}}{SD(Y)}$) to stabilise the variance. The eigenvalue of the first PCA axis was high (0.861) and hence the sample scores of the first axis were used to represent shoot vigour in further calculations. Vigour, as used in the plant vigour hypothesis includes both growth rate and final size of the plant module.

Ungulate browsing pressure was calculated as the percentage of current season's shoots below 2.5 m of each tree species that was browsed within a plot. Elephant browsing pressure was calculated as the percentage of individual trees of each species within a plot that had been browsed by elephants during the current season. There were no significant differences in browsing pressure within species among the vegetation types sampled ($P > 0.05$, ANOVA). The mean browsing pressure for each species was then calculated from the plot means and used in the analysis (n was the number of plots taken for each species, ranging from 9-37).

Spearman rank (bivariate) correlations between plant species' shoot vigour (represented by the first PCA axis scores) and nitrogen, phosphorus, calcium, potassium and magnesium (“nutrients¨) and acid and neutral detergent fibre and tannin activity (“defence”) and browsing pressure were calculated in SPSS 12.0.1 for Windows (2003). The non-parametric Spearman rank (bivariate) correlation was done after the values of nutrients, defence and browsing pressure were graphically checked for normality and were found not to comply with the requirements for parametric analyses. All tests were regarded significant at $P < 0.05$ and to be marginally significant when P-values were between 0.05 and 0.10.

Results

Shoot vigour of plant species in relation to nutrients, fibres and tannin activity

Plant species with less vigourous shoots had higher content of both ADF and NDF than plant species with vigourous shoots (Table 2). Plant species' shoot vigour was positively correlated with the concentration of nitrogen, phosphorus, calcium and potassium but not with magnesium and sodium (Table 3). Fibre concentration was negatively correlated with plant species' shoot vigour. Tannin activity did not significantly correlate with shoot vigour across plant species (Table 3).

Shoot vigour of plant species and browsing pressure

Browsing pressure by ungulates had no monotonic correlation with plant species' shoot vigour. The best fit was a quadratic polynomial curve describing a unimodal relationship (Fig. 1). The fitted curve ($y = -4.128 x^2 + 0.599 x + 9.233$) comprised a significant quadratic term ($P = 0.038$) but the overall model was only marginally significant ($F_{(2,11)} = 3.22$ and $P = 0.08$).

The PCA-ordination diagram (first and second axes scores) based on shoot growth variables placed the species in a pattern similar to the extent they were browsed by ungulates (Fig. 2). Only the position of *Baphia massaiensis* was different in that it was grouped with species heavily utilised by ungulates whereas it was not (Fig. 2). *Combretum elaeagnoides*, *Croton megalobotrys* and *Philenoptera nelsii*, which were separated from the other species in the ordination space, were less browsed and had a large basal shoot diameter (Fig. 3). Plant species showing the highest browsing pressures were those with an intermediate basal shoot diameter (Figs. 2 and 3). *Flueggea virosa,* which had a vigorous growth (high score on the first PCA axis) but slender shoots with intermediate basal shoot diameter, was browsed more heavily than *Combretum elaeagnoides, Croton megalobotrys* and *Philenoptera nelsii,* which also had vigorous shoots but were shorter and had larger shoot diameter. Browsing pressure by elephant showed no significant correlation with plant species' shoot vigour.

Discussion

Shoot vigour of plant species in relation to nutrients and defences

We have tested whether variation in plant vigour among woody species growing under the same habitat conditions could account for differences in browsing pressure by a guild of browsing mammals. Price (1991) states that the plant vigour hypothesis can be expected to relate to patterns across plant species as well as to patterns within plant populations. However, to our knowledge, this extension of the original hypothesis has rarely been tested.

Our first hypothesis, predicting that vigorously growing woody species should have higher nutrient concentrations, lower tannin activity and lower fibre concentrations than less vigorously growing species was partly supported. The positive relationship observed between some of the plant nutrients analysed and shoot vigour (Table 3) can be explained by the close relationship between leaf nutrients, particularly nitrogen, and photosynthetic rate (Hirose and Werger 1987). We found species with less vigorous shoots to invest in tissues with high fibre content, as predicted by Coley et al. (1985). However, we did not find evidence that species with more vigorous shoots had lower tannin activity than species with less vigorous ones, as would have been predicted from the resource availability hypothesis (Coley et al. 1985), provided that interspecific differences in growth rate were due to the species having evolved under different resource availabilities. The lack of correlation between shoot vigour of plant species and tannin activity was not caused by some species having morphological defence (spines) instead of chemical defences. If the three spiny species were not included in the analysis, there would still be no linear correlation. The lack of an inverse correlation between shoot vigour and tannin activity across species could also reflect the fact that we analysed chemical components of leaves and not of twigs with their leaves. The relative concentrations of both secondary metabolites and nitrogen often differs between leaves and twigs (Palo 1984; Skarpe and Bergström 1986) and, therefore, foliar concentrations might not adequately represent levels of nutrients and chemical defences in the corresponding shoots.

The plant vigour hypothesis revisited

The plant vigour hypothesis has previously been tested using selection of plants or plant parts within a species by insect herbivores or mammalian browsers (Whitham 1980; Danell et al. 1985; Price et al. 1987; Danell and Bergström 1989; Bergström et al. 2000; Faria and Fernandes 2001). Here we tested the hypothesis for differences in herbivory across plant species, the herbivores being browsing ungulates and elephant. The weak unimodal relationship we found between shoot vigour and ungulate browsing pressure differs from the positive monotonic relationship predicted by the plant vigour hypothesis (Price 1991). The apparent contradiction between the significance of the quadratic term of the model and the marginal significance of the overall model that best fitted the relationship between shoot vigour and browsing pressure might have reflected the relative small number of plant species (14) sampled in this study.

Tree species with intermediate shoot vigour tended to show the highest ungulate browsing pressure. The top two and the fifth species with the highest browsing pressures do not only have intermediate shoot vigour but also possess spines. African tree species palatable to ungulates have often been found to be spinescent (Owen-Smith and Cooper 1987), although spines have been found to decrease the feeding rate, particularly by reducing bite size (Cooper and Owen-Smith 1986).

We suggest that species with less vigorous shoots experienced low ungulate browsing pressure both as a result of their chemical properties and because their shoots offer a small bite size, thereby decreasing the animal's food intake rate (Vivås et al. 1991). We further suggest that highly vigorous woody species experienced lower ungulate browsing pressure than those with intermediate vigour because their shoot diameters exceeded the common bite diameters of the browsing ungulates (Vivås et al. 1991). Herbivores have certain ranges of bite diameters they are capable of biting depending mainly on mouth size, which is known to scale with body size (Jia et al. 1995; Wilson and Kerley 2003). In our study area, the maximum bite diameters of the two most common browsers, impala and kudu, are 4 mm and 4.8 mm respectively. Plant species with shoot basal diameters greater than 4 mm experienced lower ungulate browsing pressure. There is in many cases a close correlation between shoot diameter and bite diameter (Danell et al. 1985; Shipley et al. 1999), but not for very large shoots. With increasing shoot size the food quality decreases, as the proportion of wood in relation to leaf, buds and bark increases (Hjeljord et al. 1982; Owen-Smith and Novellie 1982; Vivås and Sæther 1987). Browsing ungulates have been found to make decisions about where to bite a shoot out from the trade-off between maximizing the bite size and intake rate or maximizing the nutrient gain (Vivås et al.1991; Shipley et al. 1999). If the low browsing pressure on the more vigorously growing species is mainly caused by too large a shoot diameter, one might expect animals to bite the tip of large conical shoots where the diameter suits them, unless shoots are even in diameter rather than cone-shaped. However, *Flueggea virosa*, a species with very long but slender shoots, had a high browsing pressure even though its shoots grew rather vigorously. Species with vigourously growing shoots might also have qualitative defences (Coley et al. 1985), for which we did not analyse in the present study.

The shoots of vigorously growing woody species may ultimately reach a large basal diameter that exceeds the bite diameter of twig biting ungulates, thus escaping from being browsed. In our study area, during the wet season when plant growth is very active, the resident mixed feeder impala tend to be predominantly grazers (Omphile 1997). Other herbivores migrate from the study area to their wet season ranges and only come back at the beginning of the dry period (Omphile 1997) when most shoots are fully grown and thicker than the twig bite diameter by ungulates.

Foraging elephants may bite twigs or break branches of up to 333 mm diameter with their trunk while feeding (Stokke and du Toit 2000), and are, hence, independent of shoot diameters. Thus they would be expected to respond to shoot chemical properties and to show the monotonic relationship predicted by the plant vigour hypothesis (Price 1991). However, we found no evidence of such a relationship. In most foraging situations, the current season's shoots form a minor part of the bite by elephants, and they may respond to the combined food quality of larger branches with wood, bark and leaves, that may not be closely correlated with the quality of current season's shoots. Additional studies that will not only include fibres and tannin activity as defences but also toxic substances (qualitative defences) are needed, and might help us understand why herbivory pressure by elephants differ among plant species.

Acknowledgements

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Legend to figures

Figure 1**.** Relationship between plant species' shoot vigour (PCA first axis scores of shoot growth variables) and browsing pressure by ungulates fitted with a quadratic polynomial curve, $r^2 = 0.369$, $P = 0.038$ for the quadratic term of the model ($n = 14$ species). Plant species abbreviations are as in Table 1. Error bars indicate ± SE.

Figure 2. Principal component analysis of basal shoot diameter (*BSD*), annual shoot length (*ASL*), annual shoot volume (*ASV*) and maximum shoot growth rate (*MSGR*). Plant species abbreviations are as in Table 1.

Figure 3. Relationship between annual shoot length and basal shoot diameter across 14 woody plant species from the Chobe Riverfront, Botswana. Plant species abbreviations are as in Table 1. Error bars indicate ± SE ($n = 10$ plants per species).

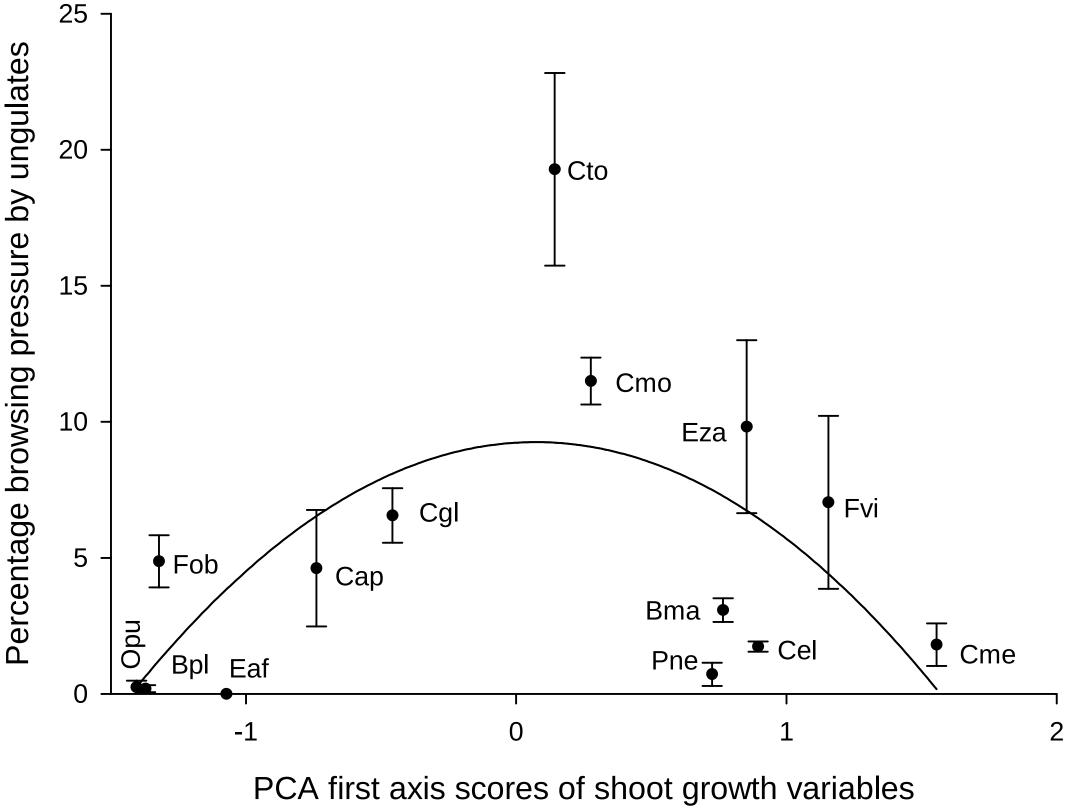

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Fig.1

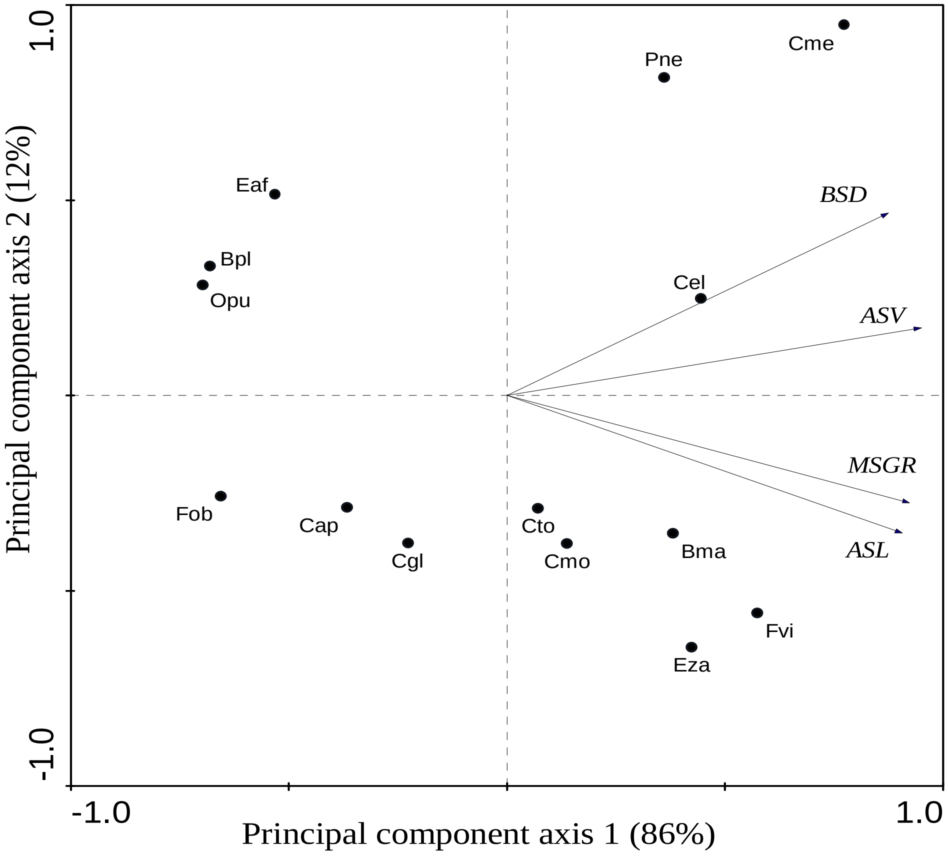
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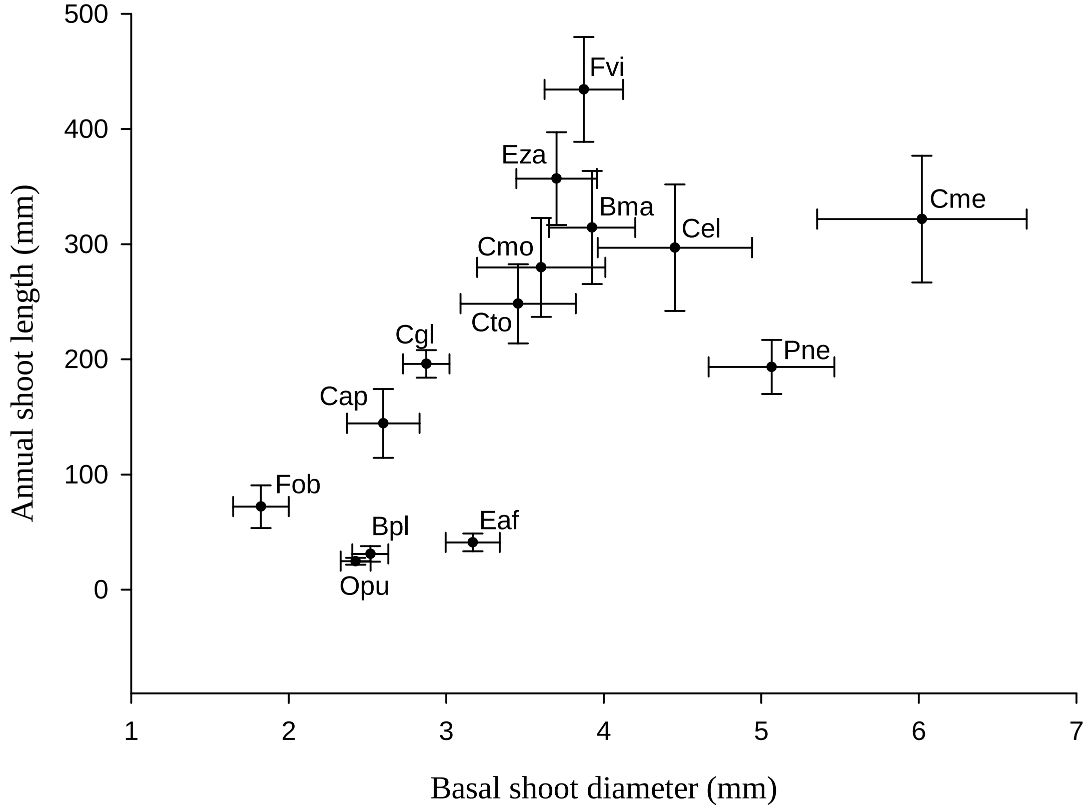
Fig. 2.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Cap
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Bpl
Eaf
Opu

Fig. 3.

Table 1. Characteristics of the studied woody plant species according to Coates Palgrave (2002). + and – in the spinescence column refer to the presence and absence of spines, respectively.

Species	Family/sub family	Life form	Height (m)	Leaf type	Spinescence	Abbreviations
Baikiaea plurijuga	Caesalpinioideae	Tree	8 - 16	Paripinnate	-	Bpl
Baphia massaiensis	Papilionoideae	Shrub	2 – 4	Simple	-	Bma
Canthium glaucum[1]	Rubiaceae	Shrub	5	Simple	+	Cgl
Capparis tomentosa	Capparaceae	Shrub/tree	10	Simple	+	Cto
Combretum apiculatum	Combretaceae	Tree/shrub	3 - 10	Simple	-	Cap
Combretum elaeagnoides	Combretaceae	Tree/shrub	6	Simple	-	Cel
Combretum mossambicense	Combretaceae	Tree/shrub	5	Simple	+	Cmo
Croton megalobotrys	Euphorbiaceae	Tree/shrub	15	Simple	-	Cme
Erythrophleum africanum	Caesalpinioideae	Tree	4 - 12	Bipinnate	-	Eaf
Erythroxylum zambesiacum	Erythroxylaceae	Tree/shrub	3 - 7	Simple	-	Eza
Flueggea virosa[2]	Euphorbiaceae	Shrub	2 - 3	Simple	-	Fvi
Friesodielsia obovata	Annonaceae	Shrub	7	Simple	-	Fob
Ochna pulcra	Ochnaceae	Tree	3 - 7	Simple	-	Opu
Philenoptera nelsii[3]	Papilionoideae	Tree	4	Simple	-	Pne

[1] Synonym is *Canthium frangula;* [2] Synonym is *Securinega virosa;* [3] Synonym is *Lonchocarpus nelsii*.

Table 2. Chemical properties, neutral detergent fibre (NDF) and acid detergent fibre (ADF) of leaves of each species (± SE). Sodium concentration for all species was lower than 0.001 %.

Species	N (%)	P (%)	Ca (%)	K (%)	Mg (%)	NDF (%)	ADF (%)
Baikiaea plurijuga	3.45 ± 0.09	0.15 ± 0.01	0.48 ± 0.02	1.27 ± 0.04	0.23 ± 0.01	52.37 ± 0.63	31.96 ± 0.54
Baphia massaiensis	4.24 ± 0.16	0.22 ± 0.01	1.12 ± 0.40	1.68 ± 0.08	0.23 ± 0.01	37.17 ± 1.70	24.61 ± 1.10
Canthium glaucum	4.17 ± 0.10	0.19 ± 0.01	1.59 ± 0.10	2.66 ± 0.07	0.32 ± 0.01	30.27 ± 0.81	23.14 ± 0.69
Capparis tomentosa	3.48 ± 0.06	0.10 ± 0.01	1.51 ± 0.08	2.56 ± 0.08	0.78 ± 0.05	30.07 ± 0.33	17.38 ± 0.16
Combretum apiculatum	2.73 ± 0.04	0.13 ± 0.01	1.19 ± 0.06	1.70 ± 0.07	0.42 ± 0.01	32.8 ± 0.89	18.95 ± 0.39
Combretum elaeagnoides	3.96 ± 0.12	0.17 ± 0.01	1.12 ± 0.08	1.37 ± 0.12	0.21 ± 0.01	38.46 ± 1.96	26.4 ± 1.70
Combretum mossambicense	3.05 ± 0.03	0.17 ± 0.01	2.71 ± 0.05	1.52 ± 0.03	0.25 ± 0.01	37.79 ± 0.30	23.86 ±0.27
Croton megalobotrys	4.31 ± 0.08	0.24 ± 0.01	2.56 ± 0.20	2.61 ± 0.13	0.62 ± 0.06	28.49 ± 0.6	19.17 ±0.67
Erythrophleum africanum	3.19 ± 0.09	0.11 ± 0.01	0.74 ± 0.08	0.65 ± 0.04	0.27 ± 0.02	55.46 ± 0.79	41.23 ± 1.24
Erythroxylum zambesiacum	2.30 ± 0.04	0.18 ± 0.01	1.07 ± 0.05	1.22 ± 0.07	0.31 ± 0.02	34.07 ± 0.48	19.86 ± 0.25
Flueggea virosa	4.03 ± 0.04	0.19 ± 0.01	2.53 ± 0.14	2.33 ± 0.06	0.33 ± 0.01	17.90 ± 0.29	11.98 ± 0.37
Friesodielsia obovata	3.46 ± 0.13	0.14 ± 0.03	0.97 ± 0.09	1.28 ± 0.23	0.33 ± 0.03	48.06 ± 1.92	25.18 ± 2.64
Ochna pulcra	2.62 ± 0.12	0.11 ± 0.01	0.38 ± 0.05	0.89 ± 0.04	0.20 ± 0.01	52.36 ± 0.64	36.74 ± 0.53
Philenoptera nelsii	4.52 ± 0.10	0.14 ± 0.01	1.11 ± 0.08	1.60 ± 0.05	0.35 ± 0.01	56.73 ± 0.67	33.45 ± 0.46

Table 3. Spearman bivariate correlations between plant species traits and plant species' shoot vigour, represented by the first PCA axis scores of shoot growth variables. P values are 2-tailed.

Plant traits	r	P
Nitrogen	0.569	0.034
Phosphorus	0.727	0.003
Calcium	0.582	0.029
Potassium	0.582	0.029
Magnesium	0.182	0.533
Sodium	0.216	0.459
Neutral detergent fibre	-0.538	0.047
Acid detergent fibre	-0.547	0.043
Tannin activity	-0.448	0.108

Paper II


Elephant


Impala


Giraffe


Kudu

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Resource partitioning within a browsing guild in a key habitat, the Chobe Riverfront, Botswana

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Abstract: Resource partitioning between elephant, giraffe, kudu and impala was assessed. This was to address concerns that elephant population increase adversely affects other species through depleting their food in key areas close to permanent water. Resources considered were woody species browsed, height browsed and plant parts browsed. Animals were observed as they browsed and the plant species, browsing heights and plant parts browsed were recorded. Observations were made over 1 y and the data were divided between wet and dry season. Schoener's index of resource use overlap was calculated for plant species, browsing heights and plant parts eaten and differences in overlap between wet and dry season were tested. Levin's measure of niche breadth in plant species utilized by the different browsers was calculated. Woody species identity was the main separator between food resources that elephant used and those giraffe, impala and kudu used. Giraffe, kudu and impala mainly browsed the same species and plant parts but browsed at different heights. There was no difference in resource use overlap between seasons with different resource availability. Since elephant browsed different woody species from those browsed by the others, it is unlikely that the increasing elephant population will deplete food resources for the other browsers.

Key Words: Botswana, browsing, elephant, giraffe, impala, kudu, niche breadth, overlaps

INTRODUCTION

Resource partitioning is the differential use of resources such as food and space by species in the same community (Schoener 1974, Voeten & Prins 1999). Resource partitioning between animal species has been described for many taxa in various ecosystems (Gordon & Illius 1989, Hansen & Reid 1975, Jarman & Sinclair 1979, Leuthold 1978, McDonald 2002, Mysterud 2000, Putman 1996, Voeten & Prins 1999). Species coexist despite overlaps in fundamental niches provided the overlap in potential resource use is incomplete (Putman 1996). Each species can occupy a distinct and non-overlapping 'realized' or 'post-interactive' niche in the presence of the other potentially competing species (Putman 1996).

The Jarman–Bell principle, that relates body size to diet quality, states that larger ungulates can tolerate a wider range of diet quality than smaller ungulates (Bell 1971, Jarman 1974, Stokke & du Toit 2000). This 'body size hypothesis' has been used to explain differences in resource use depending on different metabolic demands both within and between species (Jarman & Sinclair 1979, Stokke & du Toit 2000). The dilemma faced by animals is that high-quality forage is rare whereas low-quality forage is common (Demment & Van Soest 1985). Partition of resources by animal species could, however, also be explained by the scramble competition hypothesis (Hughes 1980, Illius & Gordon 1987, Stokke & du Toit 2000). The scramble competition involves exploitation and interference components whereby an animal species displaces other species from prime areas or diets forcing them to feed in lower quality areas or to accept poorer diets. Stokke & du Toit (2000) described scramble competition in detail for elephant. When dealing with animal species that differ in body size, it could be predicted that small animal species browse at lower heights of tree canopies displacing animal species of intermediate size which will in turn force large animal species to browse high in the tree canopy. Food availability might also be the reason behind browsing height stratification between animal species of different body sizes. It has been suggested that giraffe browse higher in the tree canopy to gain a bite-size advantage by browsing above the reach of smaller species (Woolnough & du Toit 2001).

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Table 1. Descriptions of the studied animal species. Feeding and digestion types for all species and measurements for giraffe and kudu are according to Skinner & Smithers (1990). Elephant measurements are according to Haltenorth & Diller (1980) while impala measurements are according to Smithers (1992).

Species	Shoulder height (m) Male	Shoulder height (m) Female	Weight (kg) Male	Weight (kg) Female	Feeding type	Digestion type
Elephant	3.5	2.7	4550	2350	mixed feeder	hindgut fermenter
Giraffe	3.0	2.7	1192	828	browser	foregut fermenter
Kudu	1.4	1.3	228	157	browser	foregut fermenter
Impala	0.90	0.85	55	40	mixed feeder	foregut fermenter

Resource use overlap between competing species is expected to be high during the periods of food abundance (wet season) and low during the periods of food scarcity (dry season). This is because during the periods of food abundance both species have enough food even if resource use overlaps (Gordon & Illius 1989, Mysterud 2000). However, when food becomes scarce one of the competing species turns to feed on less suitable food and reduce competition (Gordon & Illius 1989, Mysterud 2000).

The Chobe Riverfront in Chobe National Park, northern Botswana has high abundance and diversity of wild animals including the elephant population that is increasing at an annual rate of 6% (Gibson *et al.* 1998). The Chobe Riverfront is here referred to as a key habitat in reference to its high importance to the water-dependent animal species compared to other surrounding areas. The Chobe–Zambezi river system is the only dry-season water source in the ecosystem. This forces all water-dependent animals to use the Riverfront during the dry season (Ben-Shahar 1993, Gibson *et al.* 1998, Omphile & Powell 2002, Skarpe *et al.* 2004, Stokke & du Toit 2002, Verlinden & Gavor 1998). In this habitat, herbivores that mainly browse woody species during the dry season include elephant *(Loxodonta africana)*, giraffe (*Giraffa camelopardalis*), greater kudu (*Tragelaphus strepsiceros*), impala (*Aepyceros melampus*), steenbok (*Raphicerus campestris*) and bushbuck (*Tragelaphus scriptus*). However, little is known on resource partitioning between these coexisting species, and there is concern that the increasing elephant population may deplete food resources for other browsers. Information on resource partitioning between these species in this key habitat would therefore be an indicator of how they share resources when they use the same area and whether the elephants are likely to compete with other browsers for food. It should, however, be noted that elephant, giraffe and kudu do not entirely depend on food resources in the study area even during the dry season but also forage in the woodlands further away from the river (Omphile & Powell 2002, Stokke & du Toit 2002). Animal nomenclature accords to Skinner & Smithers (1990).

The study estimates resource partitioning between impala, kudu, giraffe and elephant. Steenbok and bushbuck are rare and they are not considered. Resource partitioning between the species was expected to be according to difference in body size and digestive system (Table 1). Particularly the study addressed the following questions: (1) Do impala, kudu, giraffe and elephant browse different woody species? (2) Do impala, kudu, giraffe and elephant browse at different heights? (3) When browsing the same species, do impala, kudu, giraffe and elephant browse different plant parts? (4) Is overlap in resource use within the browsing guild larger during the period of food abundance (wet season) than when food is scarce (dry season)?

METHODS

Study site

The research was conducted in the northern part of Chobe National Park (17°49′–17°55′S, 24°50′–24°59′E) in semi-arid northern Botswana. The northern boundary of the study area is the Chobe River. The rainfall is seasonal, with the wet season in summer between November and April. Annual average rainfall is about 640 mm (Botswana Meteorological Service Department, unpubl. data). The period from May to October, is the dry season. Mean maximum and mean minimum monthly temperatures during October (hottest month) are 39 °C and 14 °C, respectively and in July (coldest month) 30 °C and 4 °C, respectively (Botswana Meteorological Service Department, unpubl. data).

The vegetation in the study area tends to form zones from the river changing with soil type and herbivore impact. Along the river on the alluvial soils is a thin strip of riparian forest followed by shrublands dominated by *Capparis tomentosa* and *Combretum mossambicense* (Mosugelo *et al.* 2002, Skarpe *et al.* 2004). Over the past decades woodland has gradually retreated away from the Chobe Riverfront (Mosugelo *et al.* 2002). The area that is now shrubland on the alluvial soils earlier had large *Acacia* and *Combretum* trees, and before that it was open flats (Skarpe *et al.* 2004). Further away from the river, on Kalahari sand, woodlands with *Baikiaea plurijuga* occur (Mosugelo *et al.* 2002, Skarpe *et al.* 2004). Plant nomenclature accords to Coates Palgrave (2002).

Data collection

The study was done for 1 y from July 2002 to June 2003. Impala, kudu, giraffe and elephant were observed while browsing. A vehicle was driven at 20 km h^{-1} along the road network in the study area. Whenever a group or a single animal of the four species was sighted, the vehicle was stopped and the animal or any animal seen browsing in the group was observed as it browsed. With the aid of a pair of binoculars, woody species and plant parts browsed were identified. The plant parts were categorized as leafless shoots, shoot with leaves, leaves only and bark. After records were made, the plant was visited to measure the browsing height and to verify the plant species and part browsed. The point browsed was in most cases easy to locate because the fresh wet bites could be seen. Browsing height was measured with a measuring rod to the nearest 10 cm. If the animal had browsed several points on an individual tree, each point was recorded and height measured. In such a case the average height browsed was used in the calculations. Browsing heights of elephant were sometimes estimated when animals did not move away from the browsed plant.

A total of 2885 observations were made. They comprised 670 for elephant, 461 giraffe, 971 impala and 783 for kudu. More animals were observed browsing during the dry season than during the wet season because most of the elephants, giraffe and kudu move out of the study area during the wet season. Impala and elephant shift more to grazing than browsing during the wet season whereas they predominantly browse during the dry season. During the dry season the observations were distributed as 517 elephant, 352 giraffe, 595 impala and 669 kudu. The wet season observations were distributed as 153 elephant, 109 giraffe, 376 impala and 114 kudu.

Data analysis

The data were analysed both for the whole year across seasons and separated into wet and dry season. The proportion contributed by each plant species to the total observed browsing by each herbivore species, here referred to as 'diet composition' was calculated from the data of observed browsing. Spearman rank correlation based on these proportions was used to compare diet compositions of each pair of herbivore species. Overlap in resource use in terms of browsed species, browsing height and plant parts browsed were assessed using the Schoener's index (Schoener 1970). This measure has been recommended by Abrams (1980) because it meets all the criteria required in choosing an overlap measure. The Schoener's index used for browsed species overlap was:

$$O_{jk} = 1 - \frac{1}{2}\sum_{i=1}^{n} |P_{ij} - P_{ik}|$$

where O_{jk} is the overlap between herbivore species j and k. P_{ij} is the proportion of all browsing events on plant species i by the herbivore species j, while P_{ik} is the same proportion, but for the herbivore species k and n is the number of plant species. In calculating browsing height overlaps, the browsing height section replaced plant species in the above Schoener's index. Heights were categorized into classes of 20-cm intervals and each interval represented browsing height section (i) in the Schoener's index. To calculate browsed parts overlaps, the Schoener's index was:

$$O_{jk} = 1 - \frac{1}{2}\sum_{i=1}^{n} |P_{hij} - P_{hik}|$$

where O_{jk} is the overlap between herbivore species j and k. P_{hij} is the proportion of all browsing events on plant part i on plant species h by the herbivore species j, P_{hik} is the same proportion, but for the herbivore species k.

The Schoener's index ranges from zero to one. It is zero when species do not share any resources and one when they use identical resources (Wallace 1981). Overlap indices are generally considered significant when the value exceeds or equals 0.60 (Wallace 1981, Zaret & Rand 1971). The Mann–Whitney U-test was applied to test the difference between the wet and dry season overlaps in plant species and parts eaten by comparing the $|P_{ij} - P_{ik}|$ part of the overlap index equation.

The niche breadth of the use of plant species by herbivores was assessed using Levins' measure (Levins 1968),

$$B = 1 \Big/ \sum_{i=1}^{n} P_i^2$$

where B is the niche breadth, P_i is the proportion of all feeding observations on woody species i and n is number of woody species browsed (Menard *et al.* 2002, Mishra *et al.* 2004). It was then standardized to a scale of 0–1 using Hurlbert's (1978) procedure.

$$Bs = (B - 1)/(n - 1),$$

where Bs is the standardized niche breadth. B is the niche breadth and n is the number of species recorded eaten at least once by at least one of the herbivore species during that season. Zero on the standardized niche breadth scale refers to an ultimate specialist herbivore that browses only one species and ignores others, while 1 refers to a perfect generalist herbivore that browses all species without preferences (Hurlbert 1978).

The Welch's robust ANOVA test (Quinn & Keough 2002) that does not assume equal variances was applied to test the differences in browsing heights by different herbivore species. It was applied after the Levene's test of equality of group variances and the inspection of box plots revealed that variances were not equal. The Welch's robust ANOVA test was followed by multiple comparisons test using the robust Dunnett's T3 test that also does not assume equal variances (Quinn & Keough 2002). In comparing browsing heights it was assumed that browsing heights were independent of plant species. The above was done using data of browsing heights each herbivore species browsed on any woody species. Calculations were also done using only the data when giraffe, impala and kudu browsed *Capparis tomentosa*. All statistical procedures were undertaken in the SPSS for Windows (version 12.0.1) statistical package.

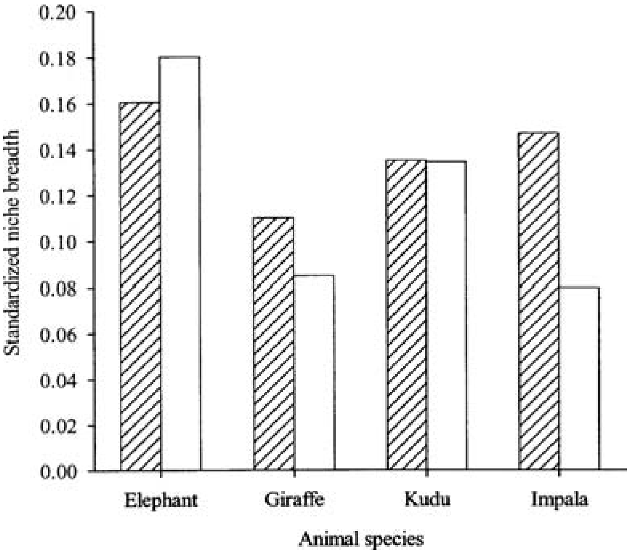

Figure 1. Seasonal standardized niche breadth of woody plant species browsed, represented by Levins' (1968) niche breadth index, standardized to a scale of 0–1 following Hurlbert (1978). Wet (hatched) and dry (open) seasons.

RESULTS

Woody plant species browsed

A total of 35 woody species were observed browsed by at least one of the four herbivore species during either the wet or the dry season. Few woody species, between three and six, contributed more than 5% to the diet composition of each herbivore species during the two seasons (Table 2). The top two or three most-browsed woody species contributed more to the diet composition of giraffe, kudu and impala than to that of the elephant (Table 2). Contribution of *Capparis tomentosa* to the diet compositions of giraffe, kudu and impala increased during the dry season while that of *Combretum mossambicense* decreased (Table 2). Levins' standardized niche breadth for plant species browsed was slightly broader for elephant than for the other herbivore species (Figure 1). The browsed species niche breadth for giraffe and impala were broader during the wet season than during the dry season (Figure 1).

Plant species browsed by elephant did not significantly overlap (Schoener's index < 0.6) with those browsed by the other herbivore species (Table 3). The overlap in woody species browsed by giraffe, kudu and impala was significant between impala and giraffe during the dry season and between impala and kudu during both seasons (Table 3). The overlap between giraffe and kudu during both seasons was not significant but still high (Schoener's

Table 2. Diet composition of each member of the browsing guild studied. The values are percentage contribution by each plant species to the observed browsing by each herbivore species. The table only shows plant species that contributed at least 5% to the observed browsing by at least one of the animal species. Plant species that contributed less than 5% are grouped as others. Plant names are according to Coates Palgrave (2002) while plant type and evergreenness are according to van Wyk & van Wyk (1997). Deciduousness of *Friesodielsia obovata* is from own observation.

			Elephant		Giraffe		Kudu		Impala	
Plant species	Leaf fall	Plant type	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry
Boscia albitrunca	E	ST	0.0	0.2	1.3	5.5	0.0	1.5	0.3	1.0
Canthium glaucum	D	Sh/ST	0.0	1.4	0.0	0.5	1.8	2.4	8.0	0.8
Capparis tomentosa	E	Sh/ST	5.7	0.8	45.6	50.3	20.2	23.9	11.2	50.4
Combretum apiculatum	D	ST/MT	0.0	9.1	0.0	0.5	0.0	0.0	0.0	0.2
Combretum elaeagnoides	D	Sh/ST	39.6	29.8	0.0	0.5	0.0	10.2	0.0	0.7
Combretum mossambicense	D	Sh/ST	1.9	1.4	20.3	15.7	42.1	35.7	42.0	19.2
Croton megalobotrys	D	ST/MT	9.4	22.1	1.3	0.8	1.8	0.7	0.8	0.3
Dichrostachys cinerea	D	Sh/ST	7.5	3.5	10.1	0.5	2.6	1.3	6.4	3.5
Friesodielsia obovata	D	Sh/ST	5.7	2.5	0.0	0.0	0.9	1.3	1.9	1.8
Philenoptera nelsii	D	ST/MT	3.8	7.7	0.0	3.1	5.3	1.8	1.3	1.2
Markhamia zanzibarica	D	ST	0.0	0.6	3.8	6.5	8.8	3.6	6.1	3.7
Flueggea virosa	D	Sh/ST	3.8	6.2	11.4	3.7	5.3	6.3	12.8	8.2
Strychnos potatorum	D	ST/MT	15.1	3.3	0.0	2.1	2.6	2.4	0.5	0.7
Others			7.5	11.6	6.3	10.2	8.8	8.8	8.8	8.2
Number of species that contributed with > 5%			6	5	4	4	5	4	6	3

D, deciduous; E, evergreen; Sh, shrub; ST, small tree; MT, medium tree.

Table 3. Schoener's indices of resource-use overlap during the dry and wet seasons for the studied browsing guild.

	Plant species overlap (S)		Height overlap (H)		Plant part overlap (P)		Species × height (H × S)		Combined overlap (S × H × P)	
Species pair	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry
Elephant/impala	0.24	0.22	0.46	0.44	0.12	0.07	0.11	0.10	0.01	0.01
Elephant/giraffe	0.23	0.20	0.35	0.40	0.10	0.10	0.08	0.08	0.01	0.01
Elephant/kudu	0.24	0.32	0.45	0.58	0.15	0.14	0.11	0.18	0.02	0.03
Impala/giraffe	0.58	0.82*	0.10	0.04	0.49	0.70*	0.06	0.03	0.03	0.02
Impala/kudu	0.76*	0.63*	0.35	0.32	0.72*	0.59	0.27	0.20	0.19	0.12
Giraffe/kudu	0.56	0.57	0.33	0.37	0.52	0.55	0.18	0.21	0.10	0.12

* Values above or equal to 0.6 are considered significant for single variables (species, height and plant parts).

Table 4. Spearman rank correlation coefficients between animal species' diet compositions (woody species that at least contributed with 5% and the rest grouped as others) during the wet season (bottom left section of the table) and during the dry season (upper right section of the table). n = 14 in all cases and is the number of pairs of woody species in the correlation test.

	Elephant	Giraffe	Kudu	Impala
Elephant	–	– 0.382	– 0.178	– 0.426
Giraffe	– 0.043	–	0.657	0.687
Kudu	– 0.027	0.714	–	0.663
Impala	– 0.148	0.754	0.815	–

index > 0.5). The Spearman rank correlation between diet compositions for the different browsers (Table 4) supported the diet overlaps shown by the Schoener's index. There was a positive correlation in diet composition between giraffe, kudu and impala but no correlation between the diet composition of elephant and the other species (Table 4). The rank correlation coefficients were slightly weaker in the dry season (Table 4).

There was no difference in overlap of plant species eaten by the herbivores between the wet and the dry season ($P > 0.05$, Mann–Whitney U-test).

Browsing height stratification

The browsing height ranges by elephant and giraffe during both wet and dry seasons were much wider than of impala and kudu (Figure 2). There was no difference in browsing heights between the wet and the dry season for elephant ($F_{1,65} = 2.39$, $P = 0.13$) or kudu ($F_{1,52} = 3.29$, $P = 0.07$). Browsing height was higher in the dry season than in the wet season for both giraffe ($F_{1,126} = 10.9$, $P = 0.001$) and impala ($F_{1,350} = 6.63$, $P = 0.01$). Browsing height differed between the herbivore species during both the wet season ($F_{3,106} = 123$, $P = 0.001$) and the dry season ($F_{3,995} = 602$, $P = 0.001$). Multiple comparisons showed that mean browsing heights by elephant and impala were not different.

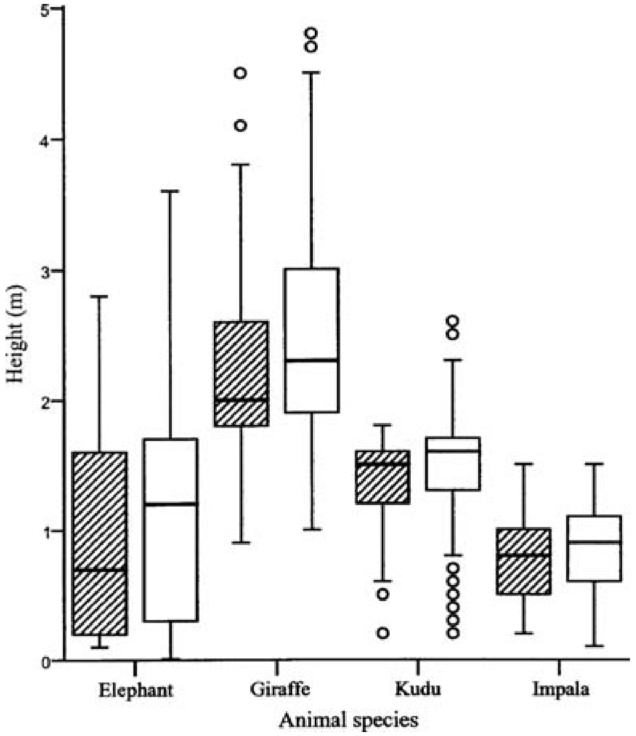

Figure 2. Box plots showing location and variation in heights browsed by animal species during the wet (hatched) and dry (open) seasons. The lines in the box are sample medians, the lower and upper box ends are 25th and 75th quartiles respectively, and the lines outside the box extend to the minimum and maximum values within the next 25th quartile from the box hinges while the symbols beyond the lines are outlying observations.

The overlaps in browsing heights between all pairs of species were not significant (Schoener's index < 0.6) during any of the seasons (Table 3). Even if not significant, the index was higher when elephant was included than when the other species were paired between themselves (Table 3). The overlap was lowest when giraffe was paired with impala. Browsing height stratification between giraffe, impala and kudu was even stronger when considering heights they browsed on *Capparis tomentosa*, a species they both heavily browse during the dry season. During the dry season the browsing height overlap between giraffe and impala when browsing on *Capparis tomentosa* was 0.03, while between impala and kudu was 0.23 and between kudu and giraffe was 0.29. The mean browsing heights on *Capparis tomentosa* by giraffe, impala and kudu were different ($F_{2,648} = 547$,

Table 5. Percentages each plant part was observed browsed by each animal species throughout the year.

	Animal species			
Plant part	Elephant	Giraffe	Kudu	Impala
Leafless shoots	34.1	2.2	1.9	0.2
Shoots + leaves	26.1	25.9	22.6	24.3
Leaves only	39.6	65.1	72.2	74.6
Bark	0.2	1.7	0	0.7
Flowers/fruits	0	5.2	3.3	0.2

$P < 0.001$). Multiple comparisons of mean browsing height on *Capparis tomentosa* between each pair of the three species were significantly different ($P < 0.001$).

Browsed plant parts

Elephant browsed fairly equal proportions of leaves, leafless shoots and shoots with leaves whereas giraffe, kudu and impala mostly browsed leaves (Table 5). When *Combretum elaeagnoides* had leaves, the elephant stripped off the leaves and ate the leafless shoots. Contrary to the elephant, the kudu was observed eating the leaves of *Combretum elaeagnoides* but not the shoots. The elephant, however, stripped the leaves of *Croton megalobotrys* to eat, leaving the shoots. Bark eating by giraffe was mainly on *Markhamia zanzibarica*.

There was no overlap in plant parts browsed between elephant and the other species (Table 3). Impala and giraffe overlapped in plant parts browsed during the dry season while impala and kudu overlapped in the wet season (Table 3). Overlap between plant parts browsed by giraffe and impala was lower during the wet season than during the dry season ($P < 0.05$). There was no difference between the dry- and wet-season overlaps in plant parts browsed by other species.

Woody species, browsing height and browsed plant parts combined overlaps

The products of browsed plant species and height overlaps were low for all species pairs, with those for impala and kudu and for giraffe and kudu being higher than for other species pairs (Table 3). The combined overlaps (plant species × height × plant parts) were also low, with that for impala and kudu, and giraffe and kudu pairs being higher than for other pairs (Table 3).

DISCUSSION

Woody plant species browsed

The elephant predominantly browses woody plant species different from those mostly browsed by impala, kudu and giraffe (Table 2). The choices of woody plant species browsed by each of the four herbivores agree with those reported in other studies conducted in the same area (Omphile 1997, Stokke & du Toit 1999). The difference in woody species browsed by elephant and those browsed by the other species could be explained by a combination of differences in body sizes and digestive systems (Table 1). Relative energy requirement decreases with increasing body size, whereas total energy requirements and retention times increase, while the gut capacity remains virtually constant in relation to body mass (Bell 1971, Clauss *et al.* 2003, Demment & Van Soest 1985). This allows the larger animal species to use forage of lower quality, which in most cases is available in large quantities while small animal species meet their high relative energy requirements by browsing rare high-quality foods (Clauss *et al.* 2003, Demment & Van Soest 1985, Jarman 1974). The elephant, a hindgut fermenter, however, has comparatively fast passage rate and achieves only low digestibility coefficients (Clauss *et al.* 2003) which allow it to use forage of even lower quality than other large herbivore species that are foregut fermenters like the giraffe. The body size hypothesis is not supported by the data in this study because the giraffe, a large foregut fermenter, browses largely the same woody species as browsed by the smaller foregut-fermenting kudu and impala.

Browsed plant parts

The difference in digestive system appears also to be the reason for the absence of overlaps between elephant and other species in plant parts browsed. The rate of passage of food in ruminants is low when the diet contains much cell wall material particularly if heavily lignified (Bell 1971). By feeding on plant parts with high lignin content or fibrous tissues, a ruminant fails to assimilate enough protein for its maintenance requirement. This forces a ruminant to select components of vegetation that have thin cell walls and high concentration of protein such as leaves and fruits (Bell 1971, Jarman 1974). The hindgut-fermenting elephant browses shoots more than the other species do (Table 5). This might be explained by the fact that shoots pass through the gut of an elephant relatively faster, even if less digested, than they will pass through the guts of the other ruminant species (Bell 1971, Clauss *et al.* 2003). The bark contribution to diet compositions of animals was low (Table 5). However, shoots were probably ingested more for the bark than for the woody material. Barks of some woody species have low lignin content hence they might improve the digestibility of ingested shoots (Malan & Van Wyk 1993).

The elephant eat shoots of *Combretum elaeagnoides* but not its leaves whereas the kudu eat the leaves but not its shoots, possibly because the two herbivore species have different tolerance for plant chemical defences. Types and quantity of secondary metabolites can differ between parts of an individual plant (Palo 1984). Hindgut fermenters like the elephant may be more sensitive to rapidly absorbed toxins like alkaloids whereas foregut fermenters like kudu may be more sensitive to digestibility-reducing compounds (Palo 1987).

Food quality changes with season (Senft *et al.* 1987), as does food availability. The increase of *Capparis tomentosa* and a decrease of *Combretum mossambicense* in diet composition of giraffe, kudu and impala during the dry season may be due to these herbivore species mostly browsing leaves (Table 2 and 5). *Capparis tomentosa* is evergreen whereas *Combretum mossambicense* is deciduous (Table 1). This might also explain why the browsed species niche breadth of giraffe and impala shrinks during the dry season whereas that of elephant expands (Figure 1). When deciduous species lose their leaves, animal species that mostly eat leaves have fewer woody species to choose from. The elephant, that mostly eats shoots, can instead distribute its browsing to more species during the dry season when food becomes scarce.

Browsing height stratification

Browsing height stratification reduces overlap in the use of browse resources among browsers (du Toit 1990, Leuthold 1978). Browsing height stratification considerably reduced the overlap in resources used by impala, kudu and giraffe but it more effectively reduced overlap between impala and giraffe (Table 3, Figure 2). This agrees with results found in Kruger National Park, South Africa (du Toit 1990). An elephant often uses its trunk to collect food (Owen-Smith 1988), and thus overlaps with other species in browse height. I suggest that browsing height stratification between impala, kudu and giraffe can, apart from body size differences (Leuthold 1978), be explained by the scramble competition hypothesis that relates to food availability (Hughes 1980, Illius & Gordon 1987, Stokke & du Toit 2000). At lower levels of the tree canopy, the smaller browsers like impala reduce food quality by taking small selective bites and removing individual leaves (Woolnough & du Toit 2001). Giraffe therefore profit from browsing at higher levels in the canopy than impala and kudu as predicted by the scramble competition hypothesis (Hughes 1980, Illius & Gordon 1987, Stokke & du Toit 2000). This might also be the reason why the mean heights browsed by giraffe and impala were higher during the period of food scarcity (dry season) than during the period of food abundance (wet season). When animals deplete the food lower in the canopy they search for food at higher reachable levels. The likely explanation for no difference in mean heights browsed by kudu between the two seasons might be that they do not profit from browsing higher up in the canopy during the dry season. The mean heights browsed by kudu during both seasons were above the reach of impala that selectively picks leaves.

Resource partitioning at the Chobe riverfront

I did not find support for the hypothesis that overlap in resource use within the browsing guild is higher during the period of food abundance (wet season) than when food is scarce (dry season) which could have indicated interspecific competition between species (Gordon & Illius 1989, Mysterud 2000). Overlap in resources did not increase during food scarcity as predicted for an optimally foraging ungulate (Owen-Smith & Novellie 1982). The species widened their foraging without increasing overlap in resource use between each other. The elephant achieved that by expanding its browsed species niche breadth without a change in browsing height. Giraffe and impala reduced their browsed species niche breadth but they browsed higher in the canopy during food scarcity. The kudu was the only exception because neither its browsed species niche breadth (Figure 1) nor its browsing height differed between the two seasons.

Since the elephant browse different woody species from those browsed by the other browsers the increase in elephant population is unlikely to cause an increase in interspecific competition between it and the other three species. It is likely to cause intraspecific competition within the elephant population, but Stokke & du Toit (1999) found no evidence of this in the same study area. The concerns that elephant population increase could result in them depleting food for impala, kudu and giraffe thus, negatively affecting their population is not supported by this study. It would therefore not be appropriate to manipulate the elephant population on the basis that it competes for food with impala, kudu and giraffe. However, there may be social and economic reasons to limit elephant numbers outside the Park, as suggested by Skarpe *et al.* (2004). It should also be noted that this study did not take into account other factors that elephant population increase can have on other species, such as behavioural intolerance, changing vegetation structure offering shelter and hiding, interference at water sources, disease and parasites shared. It also did not consider the benefits the effect of elephant has on other browsers such as opening dense thickets and keeping trees and shrubs down to a level reachable by smaller browsers.

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Paper III

Erythroxylum zambesiacum with no and with high accumulated elephant impact

Elephant impact on shoot distribution on trees and on rebrowsing by smaller browsers

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Abstract

In order to determine the effects of a megaherbivore, the African elephant *(Loxodonta africana* Blumenbach) on browse available for mesoherbivores, we assessed the vertical distribution of shoots (< 6 mm in diameter) on trees with different accumulated elephant impact. We also determined the foraging responses by a mixed feeder, impala *(Aepyceros melampus* Lichtenstein*)* and a browser, greater kudu *(Tragelaphus strepsiceros* Pallas) which are mesoherbivores. The foraging responses by impala and kudu were in terms of preferences of trees with different accumulated elephant impact levels and whether animals browsed in different height sections in proportion to availability of shoots. We counted shoots in each 20 cm height section up to 2.6 m on trees in 25 m by 25 m plots and on trees observed to be browsed by impala and kudu. In most tree species, individuals with high accumulated elephant impact were shorter and had more shoots at low levels than tree individuals with either low or no accumulated elephant impact. Impala and kudu preferred to browse tree individuals with accumulated elephant impact over those without such impact. Impala and kudu browsed more than expected at height sections with many shoots and less than expected at height sections with fewer shoots indicating a nonlinear overmatching foraging response. We suggest that increased shoot abundance at low levels in the canopy might explain part of the observed preferences. Elephants, therefore, seem to facilitate browsing by mesoherbivores by generating 'browsing lawns'. Such benefits need to be considered when making decisions on how to manage populations of megaherbivores like elephant.

Keywords: Accumulated elephant impact; Botswana; Chobe Riverfront; Impala; Kudu

1. Introduction

Ecologically similar mammal species may directly or indirectly interfere with the food resources for each other and could alter each others' foraging behaviour and population dynamics (Bell, 1971; McNaughton, 1976; Sinclair and Norton-Griffiths, 1982; Belovsky, 1984; de Boer and Prins, 1990; Western and Gichohi, 1993; Putman, 1996; Prins and Olff, 1998; Makhabu et al., 2002). Interspecific competition (Belovsky, 1984; Putman, 1996; Hulbert and Andersen, 2001) and facilitation (McNaughton, 1976; Guy, 1981; van de Koppel and Prins, 1998) has been reported, as well as indifference (de Boer and Prins, 1990). Competition and facilitation are not mutually exclusive, but may occur at the same time concerning different species or fluctuate over time (van de Koppel and Prins, 1998; Taolo, 2003). Facilitation becomes possible when, first, consumption by a consumer produces a flow of resources into another consumer and, second, the latter consumer specializes on consuming the produced resource (Farnsworth et al., 2002). In facilitation, often one consumer increases the accessibility to food for another (Guy, 1981; van de Koppel and Prins, 1998), but also the quality of food may be enhanced (McNaughton, 1976). Body size has often been found important for food mediated interactions between small and large herbivore species. Relatively small species consume highly nutritious plant parts and survive on low food biomass, and may, thus, pre-empt food resources for larger species and out compete them (van de Koppel and Prins, 1998; Woolnough and du Toit, 2001; Taolo, 2003). Relatively large-bodied herbivores may, on the other hand, by consuming large amounts of relatively nutrient poor plant material, increase the production and/or availability of young nutritious plant tissue for smaller herbivores, thus facilitating their foraging (Bell, 1971; McNaughton, 1976, 1984; Guy, 1981; van de Koppel and Prins, 1998; Taolo, 2003). For animals browsing on trees also the height distribution of nutritious regrowth is important for which herbivore species are able to use it.

Large herbivores have the potential to modify the architecture, physiology, biochemistry productivity and phenology of plants they feed on (Laws, 1970; Bryant, 1981, 2003; Bergström and Danell, 1987; du Toit et al., 1990; Ben-Shahar, 1993; Prins and Olff, 1998). Such modification of plants by herbivores may include the activation of resistance traits, reducing subsequent herbivory (Bryant, 1981; Karban and Meyers, 1989; Hulbert and Andersen, 2001). More often it leads to increased palatability and probability for repeated foraging (Bell, 1971; McNaughton, 1976, 1984; Danell et al., 1985; du Toit et al., 1990; Duncan et al., 1998; Bergström et al., 2000). Thus a "feeding loop" can develop, where animal induced changes in plant morphology and physiology lead to further herbivory and further changes in the plants (McNaughton, 1984; du Toit et al., 1990; Bergqvist et al., 2003). Such "feeding loops" are, by definition, advantageous for the herbivore creating them, but may also facilitate foraging by other species, which, if smaller than the herbivore initiating the loop, may be more efficient harvesters of the nutritious regrowth biomass. While much of the fundamental studies of herbivore competition/facilitation is related to one-layered herbaceous vegetation or a theoretical single compartment vegetation (McNaughton, 1976, 1984; Prins and Olff, 1998; van de Koppel and Prins, 1998; Farnsworth et al., 2002), the three-dimensional browsing system may be more complex (du Toit 1990; Makhabu 2005). In such systems not only quality and quantity of plant regrowth following (repeated) browsing, but also the height distribution of such regrowth in relation to possible foraging heights and foraging responses by members of the browsing guild, is essential. Browsing by megaherbivores, e. g., African elephant (*Loxodonta africana*) or giraffe (*Giraffa camelopardalis*) has been shown in savanna ecosystems to reduce the height of browsed trees (Pellew, 1983; Belovsky, 1984; Owen-Smith, 1988; Ben-Shahar, 1993) but the effect on shoot distribution within the canopy of these trees is little known. Foraging herbivores may respond differently to variation in food biomass or density, and linear (matching), asymptotic and exponential (overmatching) relationships between intake rate and food availability have been described (Stephens and Krebs, 1986; Senft et al., 1987; Spalinger and Hobbs, 1992; Ginnett and Demment, 1995; Gordon 2003). The response may be scale dependent as animals make foraging decisions at different scales, e. g., on the level of a tree stand, a tree or a height section of a tree (Senft et al., 1987; Danell et al., 1991; Spencer et al. 1995). Browsers have been shown to preferentially feed at about neck height (du Toit, 1990; Makhabu 2005; Rutina et al. 2005), but differences in browse availability between different height levels may modify this pattern.

We studied the effects of accumulated elephant impact on trees on distribution of shoots and on browse utilisation by the two most common smaller browsing, "mesoherbivore", species, the greater kudu (*Tragelaphus strepsiceros*) and impala (*Aepyceros melampus*) in order to assess competition/facilitation between elephant and the smaller herbivores. We predicted that:

(a) accumulated elephant impact has a negative effect on tree height

(b) accumulated elephant impact has a positive effect on shoot numbers in lower levels of the tree canopy

(c) feeding frequencies by mesoherbivores in different height sections is in proportion to the abundance of shoots present at those height sections (i. e., a linear response)

(d) browsing mesoherbivores prefer trees with accumulated elephant impact to such without.

2. Materials and methods

2.1. Study area

The research was conducted in the northern part of Chobe National Park (17º49' - 17º55' S, 24º50' - 24º59' E) in semi-arid northern Botswana. The study area stretches ca. 50 km along the south side of the Chobe River and being within 2 km of the river but excluding the riparian forest on the banks of the river. The rainfall is seasonal, with the wet season in summer mainly between November and April. Annual average rainfall is about 640 mm. Mean maximum and mean minimum monthly temperatures in October (the hottest month) are 39ºC and 14ºC, respectively and in July (the coldest month) 30ºC and 4ºC, respectively (Botswana Meteorological Service Department records).

The vegetation in the region of the study area is mainly a shrubland apart from floodplains and a narrow and in some places broken strip of riparian forest. The shrubland is dominated by *Capparis tomentosa* in some sections and by *Combretum mossambicense* in others (Mosugelo et al., 2002; Skarpe et al., 2004). The species composition in the shrubland further from the river becomes mixed with small and medium sized tree species. The soils are Kalahari sands with a strip of alluvial soil along the river (Mosugelo et al., 2002; Skarpe et al., 2004). The area that is now shrubland on alluvial soil was open flats in the 1870s (Selous, 1881). After the 1870s a woodland established, which with time was dominated by large *Acacia* and *Combretum* trees. Subsequently in the 1960s the woodland declined and was replaced by shrublands (Simpson, 1975; Skarpe et al., 2004). This change from open flats to woodland and then to shrublands has been attributed to the decline and later recovery of the populations of large herbivores, particularly elephant and impala (Rutina 2004; Skarpe et al. 2004). Bushfires have been absent for some years in the area largely as a result of a major road ca. 10 km south of the river acting as a firebreak (Mosugelo et al., 2002; Taolo, 2003).

In the study area, browsing megaherbivores comprise the African elephant *(Loxodonta africana*) and giraffe (*Giraffa camelopardalis)* while browsing mesoherbivores include greater kudu *(Tragelaphus strepsiceros*), impala *(Aepyceros melampus*), steenbok (*Raphicerus campestris*) and bushbuck *(Tragelaphus scriptus).* Animal nomenclature accords to Skinner and Smithers (1990). The elephant population is increasing at an annual rate of 6 % and its density along the Chobe Riverfront during the dry season can be as high as 4/km^2 (Gibson et al., 1998) or 8.5/km^2 (DWNP, 2003) but during the wet season it can be reduced to 0.5/km^2 (Gibson et al., 1998). Elephant densities above 0.6/km^2 have been shown in some ecosystems to cause major vegetation changes (Jachmann and Croes, 1991). The elephant population of northern Botswana, unlike in many other ecosystems, remain little affected by either management culling or illegal hunting (Owen-Smith, 1989). However, that elephants and other herbivores have transformed the woodland fringing the Chobe River to shrubland is of great concern among some conservationist and members of the public (Owen-Smith, 1989; Cumming et al., 1997). One of the concerns is that elephants deplete food resources for other herbivores. The elephant, however, has also been identified as a 'keystone species' that play a disproportionately large role in the community structure (Owen-Smith, 1987, 1989). Owen-Smith (1987, 1989) argues that elimination of megaherbivores might negatively affect the population of some species.

2.2. Data collection

Data were collected during June - August 2004 and consisted of three datasets. These were: (a) food selection by impala and kudu in relation to shoot distribution and level of accumulated elephant impact, (b) proportions in the environment of woody plants (henceforth called 'trees') with different levels of accumulated elephant impact ,and (c) shoot distributions on trees with different accumulated elephant impact levels.

To observe impala and kudu browsing, a car was driven on the dense net of tourist tracks taking care to cover different parts of the study area approximately evenly. The area is fairly open and during the months the data were collected, animals were visible at distances greater than 100 m. Whenever a kudu or impala was sighted browsing, the vehicle was stopped and the browsing animal was observed for five minutes. Afterwards the browsed tree was visited for identification and measurements. A frame, 3 m x 1 m, marked with horizontal fish lines at every 20 cm along the vertical 3 m side was placed on the side where the animal browsed. In each 20 cm by 1 m section from ground level to a height of 2.6 m, the number of shoots was counted. Shoots were defined as any current season twig-end < 6 mm in diameter. A calliper was used to check the diameter of shoots. The height browsed by the animal was measured with a measuring rod to the nearest cm. Accumulated elephant impact was visually determined and categorized into three levels according to the degree of change in tree growth form compared to "normal" growth of unaffected specimens of the species in question. Levels were: (0) no accumulated elephant impact, i. e., no obvious change in tree growth form (generally the main stem and main branches with no signs of old breaking and/or biting by elephant), (1) low accumulated elephant impact, i. e., growth form of tree obviously changed (generally signs of old breaking and/or biting by elephant on less than half of the total number of main branches and stems) and (2) high accumulated elephant impact, i. e., growth form of tree strongly changed (generally tree broken down or with old signs of breaking and/or biting by elephant on more than half the total number of main branches and stems).

In order to determine the overall proportions, within each tree species, with different accumulated elephant impact levels, sampling plots were distributed along four transects running ca. 5 km apart and perpendicular to the Chobe River. The plots were 25 m x 25 m. Five plots were placed within the study area 400 m apart along each transect, starting 200 m from the river making a total of 20 plots. In each plot, all individuals of the selected tree species (see below) higher than 0.5 m were assessed for accumulated elephant impact levels and shoot distributions. The shoot distribution was assessed in the same way as was done on trees observed browsed by kudu and impala. The frame was placed on a randomly selected side of the tree and shoots were counted in each 20 cm height section.

Two species, *Combretum elaeagnoides* and *Flueggea virosa* were heavily impacted in the park. To increase sample sizes of low impacted individuals of these species, additional individuals were assessed for shoot distribution in shrubland areas with low elephant activity, also within 2 km of the Chobe River, in a nearby village. The tree individuals of these species near the village were not heavily browsed by small browsers.

A total of 1749 trees of seven species were assessed of which 193 were *Capparis tomentosa*, 254 *Combretum apiculatum,* 313 *Combretum elaeagnoides,* 516 *Combretum mossambicense,* 57 *Erythroxylum zambesiacum,* 128 *Flueggea virosa* and 288 *Markhamia zanzibarica.* Plant names follow Coates Palgrave (2002).

2.3. Data analysis

Calculations were made separately for each tree species. We calculated the proportion of tree individuals within each accumulated elephant impact level based only on measurements in the plots. We also used measurements in the plots to calculate mean tree height of the three accumulated elephant impact levels. Differences in the mean tree heights in these three levels of accumulated elephant impact were tested using one-way ANOVA, after testing that the data met the required assumptions. Pair-wise contrasts with Tukey's HSD test were made when significant differences were found.

To estimate the vertical distribution of shoots on trees with different accumulated elephant impact level, we used both tree individuals in plots and those individuals observed browsed by impala and kudu. Also included in the calculations were the additional trees of *F. virosa* with low impact sampled near the village. In estimating the vertical distribution of shoots we used only the sampled portion of the tree (1 m wide and 2.6 m high) to represent the distribution on the tree. The number of shoots in each 20 cm height section was log transformed. The mean of log transformed number of shoots in each height section within an accumulated elephant impact level was calculated for each tree species. In calculating these means for *C. tomentosa, C. mossambicense* and *F. virosa,* which are shrubs to small trees, only individuals at least 2.2 m high were included. For *C. apiculatum, E. zambesiacum* and *M. zanzibarica,* which are small to medium sized trees, only individuals at least 2.6 m high, were included. To establish the relationship between height section and the mean number of shoots, a best fit regression curve was fitted.

To test whether accumulated elephant impact affects the number of shoots in each height section, a non-parametric multivariate analysis of variance (MANOVA) was done using DISTLM v.5 FORTRAN computer program (Anderson, 2004) which does the test by permutation (Anderson, 2001; McArdle and Anderson, 2001). XMATRIX FORTRAN computer program (Anderson, 2003) was used to generate design matrices corresponding to the factor in ANOVA design used in the DISTLM v.5 FORTRAN computer program. The non-parametric MANOVA was based on Bray-Curtis dissimilarities measured on $\log_{10}(x+1)$ transformed shoot counts data. In conducting the test, the number of shoots in each 20 cm height section was the variable and accumulated elephant impact level was the only factor. The test was of ANOVA design and in all cases the P-values were obtained with 999 permutations. Both permutation and Monte Carlo P-values were obtained from the analysis. The number of tree individuals (sample sizes) in the three levels of accumulated elephant impact within the species was not equal, hence our tests were of an unbalanced ANOVA design. For species with individuals in all the three accumulated elephant impact levels, pair-wise contrasts of specific levels of the unbalanced design were made by the use of the DISTLM v.5 FORTRAN computer program. The P-values were then adjusted using the sequential Bonferroni (Holm, 1979) procedure (Quinn and Keough, 2002).

To test whether impala and kudu browsed in the different height sections in proportion to the number of shoots in the same height sections, the Chi-square test was applied. The mean number of shoots in each height section was calculated only from trees observed browsed. The number of observations of recorded browsing by an animal species in a height section was used as observed values while the expected values were the mean number of shoots in the height section. The height sections used were pooled to 40 cm intervals within heights reachable by each species, 1.6 m for impala and 2.2 m for kudu (Makhabu 2005).

Preference index (P_{ijk}) for woody species i with accumulated elephant impact level j by herbivore species k was calculated as in Hunter (1962) and de Garine-Wichatitsky et al. (2004):

$$P_{ijk} = \frac{U_{ijk}}{A_{ij}}$$

where A_{ij} is the proportion of the woody species i with accumulated elephant impact j in the habitat and U_{ijk} is the proportion of the woody species i with accumulated impact j in the diet browsed by herbivore species k. Only trees assessed in the plots were used to calculate A_{ij}. U_{ijk} was calculated from trees observed browsed by the herbivores. The preference index ranges from 0 for species totally avoided to nearly infinity for highly preferred ones. Values > 1 are generally understood to indicate preference and values < 1 to indicate avoidance. The index is in this study used only for ranking, and the class of accumulated elephant impact with the highest preference index within a species was taken to be the most preferred.

All analyses except non-parametric MANOVA were carried out using SPSS for Windows (version 13.0) statistical package. Non-parametric MANOVA was done using DISTLM v.5 FORTRAN computer program (Anderson, 2004). All tests were considered significant at $P < 0.05$ level.

3. Results

3.1. Tree height and distribution of shoots on trees with different accumulated elephant impacts

A large percentage of the individuals of *C. apiculatum, C. elaeagnoides, E. zambesiacum* and *F. virosa* were affected by elephants either having low or high accumulated elephant impact (Fig. 1). *Capparis tomentosa* and *C. mossambicense* however, had most of their individuals not impacted by elephants. Almost half of the individuals of *M. zanzibarica* had no accumulated elephant impact (Fig. 1). *Capparis tomentosa* and *C. mossambicense* individuals with high accumulated elephant impact were very few hence this impact level is not used in further analysis for these species.

Trees with high accumulated elephant impact were significantly shorter than those with no accumulated elephant impact in all species (Fig. 2). The mean heights of trees with no accumulated elephant impact differed significantly from those with low accumulated elephant impact in *C. mossambicense* and *M. zanzibarica,* but in the other species (Fig. 2). *Markhamia zanzibarica* individuals with low accumulated elephant impact were significantly shorter than those with no accumulated elephant impact. *Combretum mossambicense* was the only species that showed individuals with low accumulated impact being significantly taller than those with no accumulated elephant impact (Fig. 2).

The interaction between accumulated elephant impact and tree species had an effect on the number of shoots in different height sections ($F_{2,593} = 50.23$; $P = 0.001$). Species were therefore analysed separately. The results of the non-parametric MANOVA test indicated that accumulated elephant impact level explained a significant proportion of the variation in the number of shoots in height sections of four of the six species (Table 1). This was indicated by a significant multivariate variation in number of shoots in different height sections in the overall comparison test for all species except for *C. apiculatum* and *C. mossambicense* (Table 1). The permutation and the Monte Carlo P-values were in all cases in agreement for overall and some pair-wise comparisons. The pair-wise contrasts of the variation in the number of shoots in different height sections of no and high accumulated elephant impact levels was significant for *E. zambesiacum* and for *M. zanzibarica* (Table 1). The pair-wise contrasts of no and low accumulated elephant impact levels for *E. zambesiacum* and *M. zanzibarica* indicated no significant variation in the number of shoots in different height sections (Table 1). The pair-wise contrasts of low and high accumulated elephant impact levels for *E. zambesiacum* also indicated no significant variation in the number of shoots in different height sections whereas that of *M. zanzibarica* indicated a significant variation (Table 1).

The relationships between height sections and number of shoots in each height section were best fitted (adjusted $R^2 > 0.9$) by second-order polynomial (quadratic) regression models (Fig. 3). Few *C. elaeagnoides* with either low or high accumulated elephant impact levels were at least 2 m high and hence no comparisons of shoot numbers in different height sections across impact levels were made for this species. The fitted second-order polynomial (quadratic) regression curves give a general picture of the distribution of shoots in the different height sections for trees with different accumulated elephant impact levels (Fig. 3). *Erythroxylum zambesiacum* and *M. zanzibarica* with high accumulated elephant impact had more shoots in lower height section than trees with no accumulated elephant impact level (Fig. 3d, f). *Flueggea virosa* individuals with high impact had more shoots in lower height sections than trees with low accumulated elephant impact level (Fig.3e). On *C. tomentosa* it was the reverse with more shoots at lower heights on trees with no accumulated elephant impact than on trees with low accumulated elephant impact (Fig. 3a). Number of shoots in different height sections of *C. apiculatum* (Fig. 3b) and *C. mossambicense* (Fig. 3c) trees did not differ between different accumulated elephant impact levels (Table 1).

3.2. Mesoherbivores foraging patterns in relation to shoot abundance and elephant impact

The observed frequencies of browsing by kudu and impala in different height sections differed from expected for all plant species (Table 2). The residuals obtained in the Chi-square test indicated that both kudu and impala browsed less than expected in height sections with few shoots (Table 2). Impala browsed in height sections below 0.8 m less than expected. Impala browsed more than expected in height sections with high numbers of shoots, except that they browsed less than expected in the 1.2 - 1.6 m height section of *C. tomentosa* (Table 2). However, even if impala browsed more than expected in 1.2 – 1.6 m height sections of *C. mossambicense* and *F. virosa* the difference between observed and expected (residuals) was less than for 0.8 – 1.2 m height section (Table 2). Kudu browsed more than expected in height sections within 1.2 – 2.0 m but in the 1.6 - 2.0 m height section of *C. tomentosa* it was just above expected (Table 2).

Both impala and kudu preferred trees with accumulated elephant impact over trees without accumulated elephant impact. This held for all species except *C. tomentosa* (Table 3). The preferred accumulated elephant impact level for each tree species by either kudu or impala had more shoots in lower heights than trees at other accumulated elephant impact levels. However, *C. tomentosa* trees with no accumulated elephant impact were preferred by both impala and kudu (Table 3); these had more shoots than individuals with accumulated elephant impact (Fig. 3a). Further, impala preferentially browsed *C. mossambicense* with low accumulated elephant impact (Table 3), which was the highest impact level for this species. The number of shoots in height sections below 1.6 m on individuals of *C. mossambicense* with low accumulated elephant impact were slightly higher than on individuals with no accumulated elephant impact level (Fig. 3c) but not significantly different (Table 3). Impala preferentially browsed *F. virosa* and *M. zanzibarica* individuals with high accumulated elephant impact level (Table 3). *Flueggea virosa* individuals with high accumulated elephant impact level had more shoots in height sections below 1.8 m than individuals with low accumulated elephant impact level (Fig. 3e). *Markhamia zanzibarica* individuals with high accumulated elephant impact level had more shoots in height sections below 1.8 m high than individuals with no and with low accumulated elephant impact level (Fig. 3f). Kudu also preferentially browsed *F. virosa* individuals with high accumulated elephant impact level. Kudu further preferentially browsed *E. zambesiacum* and *M. zanzibarica* kudu individuals with low accumulated elephant impact level (Table 3).

4. Discussion

4.1. Tree height and distribution of shoots on trees with different accumulated elephant impacts

In this study we found supporting evidence to our first two and the forth hypotheses. This indicates that feeding and breakage of stems and branches by elephants promote what might be called “browsing lawns” (Owen-Smith, 2003), whereby tall trees are transformed to short trees (1 - 3 m tall). Such ‘browsing lawns’ are analogous to the ‘grazing lawns’ produced by wildebeest grazing in the Serengeti (McNaughton, 1976, 1984). Our results agree with those of Guy (1981) who found that in Sengwa Wildlife Research Area, Zimbabwe, elephant foraging resulted in more browse within reach of browsing mesoherbivores. *Capparis tomentosa* and *C. mossambicense* that did not agree with our first two hypotheses had few individuals with high accumulated elephant impact and the comparison was between trees with no impact and those with low impact. For the other species it could be argued that the difference in tree height depends on that elephant preferentially feeds on small/young trees. However, Makhabu (1994) found that elephant in neighbouring Moremi Wildlife Reserve browse trees of the same species with stem diameters at breast height of 2 cm to 16 cm without preference.

Elephants use the study area mostly during the dry period and the majority of them move out of the area during the wet season (Gibson et al., 1998), which is the plants' growing period. This gives coppiced and regrowth shoots time to grow with minimal interruptions. The increase in the number of shoots at low height levels of trees with high accumulated elephant impact is explained by the activation of dormant lateral buds with reduced apical dominance following the removal of leading shoots (Järemo et al., 1996; Smit and Bolton, 1999). The resprout shoots then grow with minimal disturbance during the growing season when most elephants are absent being in their wet season ranges. In most situations elephants do not directly damage the tree’s root system (Makhabu, 1994). Trees might then grow in such a way as to re-establish the former root/shoot ratio (Bergström and Danell, 1987). Some plant species have been found to produce fewer but larger shoots that are more branched after real or simulated browsing (Danell et al., 1985; Bergström and Danell, 1987). In this study we counted twig ends < 6 mm, and the high numbers of shoots at low height levels we report here may be a combination of main current season's shoots and branches on such shoots. The high capacity of these trees to resprout following browsing may be an adaptation evolved in response to browsing by large herbivores and/or to frequent fires (Bond and Midgley, 2001). Fewer shoots high in the canopies of trees with high accumulated elephant impact is more likely a consequence of changes in tree architecture following repeated elephant browsing than the result of elephants actually cropping the shoots at these levels. Elephant preferred browsing level in the area is 1.0 - 1.5 m (Stokke and du Toit, 2000).

The change in the distribution of the number of shoots on trees due to elephants' browsing could be beneficial to mesoherbivores like impala and kudu, in that more shoots become available for them at low heights of tree canopies (Guy, 1981). Makhabu (2005) found that the woody species browsed by elephant do not significantly overlap with those browsed by impala and kudu, but there are some woody species like *F. virosa* and *M. zanzibarica* they both browse. Therefore the increase in shoot availability at lower heights in such woody species might benefit browsing mesoherbivores.

4.2 Mesoherbivores foraging patterns in relation to shoot abundance and elephant impact

Impala and kudu selected between height sections with different browse availability, seemingly treating them as separate patches (Senft et al., 1987; Spencer et al., 1995). Their browsing frequencies in different height sections were generally a non-linear function of the number of shoots, "over-match". Thus, our third hypothesis is rejected. This finding may contradict the suggestion that browsers would show a linear relationship between the available biomass and intake rate (Renecker and Hudson, 1986; Spalinger and Thompson Hobbs, 1992). The difference could depend on the used scale and the measured variables. In this study, selection was between different height sections (patches) within a plant and the compared variables were number of shoots and frequency of browsing in height sections. Even with a linear response, browsers would spend most time browsing in height sections with high shoot densities, thus increasing the probability for observation. Thus, the overmatch response might be influenced by the method used. In other studies selection was between plants or bushes and the variables being biomass and intake rate. The likely explanation to the pattern we observed is that animals select height sections (patches) with high number of shoots to optimize intake and reduce searching time (Schoener, 1971; Stephens and Krebs, 1986). A complex interaction of several components such as mean bite rate, bite size and movement rate determine the intake rate of food by herbivores (Renecker and Hudson, 1986; Spalinger and Thompson Hobbs, 1992). Renecker and Hudson (1986) suggested that for large herbivores to meet their daily requirements they must either occupy rich habitats (or at least those with dense forage patches) or reduce selectivity so that a greater proportion of available forage is selected as food. By selecting a height section with dense shoots, a browser might increase intake rate since it has an opportunity to take more bites without the need to move, but intake rate also depends on shoot size, which was not recorded. Food intake rate however, could be limited by the need to ruminate while bite rate and size are often dictated by vegetation characteristics (Renecker and Hudson, 1986). It could be argued that an animal could search for browse while it chews bites it has taken (Spalinger and Thompson Hobbs, 1992; Illius et al., 2002). However, some animal species like impala feed in a group (Fritz and de Garine-Wichatitsky, 1996) hence suitable sites might be occupied by other individuals. In this study we did not consider animal group size, which is vital in selection of patches by animals in a group (Fritz and de Garine-Wichatitsky, 1996). Fritz and de Garine-Wichatitsky (1996) reported that an impala in a group appears to adapt its ‘prey’ choice to minimize intraspecific competition.

It is not evident why impala browse less than expected in 1.2 m – 1.6 m height section of *C. tomentosa* whereas they browse at the same height slightly more than expected on other species. Even for those species browsed as expected in 1.2 - 1.6 m height sections the residual was less than in the 0.8 m - 1.2 m height section possibly because impala have difficulties reaching heights above 1.5 m. For *C. tomentosa*, the numerous sharp hooked spines it possesses possibly inhibit impala from leaning against the tree in order to reach the browse at high levels. The same tendency is observed for kudu in heights between 1.6 and 2 m of *C. tomentosa*. *Flueggea virosa* does not have spines while *C. mossambicense* has spines (Coates Palgrave, 2002) but they are not hooked or as sharp and dense as those of *C. tomentosa.*

Impala and kudu mostly preferred plant individuals with accumulated elephant impact to those without, supporting our fourth hypothesis. Preference for trees with accumulated elephant impacts by impala and kudu suggest that browsing by these species is facilitated by elephant. The browsing facilitation for impala and kudu by the impact of elephants appear to be by conversion of tall trees to short trees and a change in tree growth form. This leads to that in some species more shoots are produced in heights reachable by impala and kudu. Other studies have shown that browsed trees of some species produce shoots with increased biomass per shoot (Bergström and Danell, 1987; Molvar et al., 1993), increased nitrogen concentration and decreased concentration of secondary compounds like tannins (du Toit et al., 1990) compared with unbrowsed individuals. If the tree species we studied respond to browsing in the same way, then it is likely that increased bite-size and nutrient advantages, besides availability of shoots, contributed to the observed preference for elephant impacted trees. However, large shoots might not benefit browsers if they are not branched, because their diameters may be larger than the maximum bite diameters of the twig biting ungulates (Makhabu et al., in press**)**. More branching on regrowth shoots of trees previously browsed than on shoots of unbrowsed trees, as found in some species (Bergström and Danell, 1987), is likely to result in more shoot ends within the bite diameters of impala and kudu. The high density of shoots with preferred diameters (< 6 mm) recorded on elephant impacted trees is likely to contribute to the preference by impala and kudu for these trees. Rutina et al. (2005) reported that impala prefer elephant impacted habitats and we suggested that it might be due to the facilitation effect we report.

Facilitation for impala and kudu by the modification of tall trees through the browsing activity by elephants to 'browsing lawns' probably is beneficial to them, but only if the rebrowsing of the elephants are not so intense as to deplete available shoots on those trees. Although elephant do not share many preferred woody food species with other browsing herbivores in the study area, the overlaps in resource use between elephants and other browsers do not significant differ between seasons (Makhabu, 2005). This suggests that although elephants rebrowse trees, other browsing herbivores continue to browse tree species they share with elephants. However, the amount of browse taken by herbivores from trees elephant browse may differ between seasons, but was not recorded by Makhabu (2005). Browsers are not the only species facilitated by elephant in our study ecosystem. The African buffalo (*Syncerus caffer*) has been shown to prefer to graze on patches grazed more heavily than average by elephants 3 – 10 days before (Halley et al., 2003; Taolo, 2003). Gallinaceous birds prefer areas with high elephant impact (Motsumi, 2002).

This study has implications for management of coexisting megaherbivores and mesoherbivores. It highlights the need for a careful balanced assessment of the ecological role of major species in the ecosystem before decisions to manipulate population and distribution of any of them can be done. Elephant impact on vegetation has been indicated to be either detrimental (Cumming et al., 1997; Fritz et al., 2002) or beneficial (Owen-Smith, 1987, 1989; Skarpe et al., 2004) to other animal species. We found evidence that they might be beneficial for other species and thereby this study gives some support to the suggestion of Owen-Smith (1989) that elephant is a ‘keystone herbivore’.

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Table 1

Non-parametric MANOVA results of number of shoots within 20 cm height sections on trees with no accumulated elephant impact (0), low accumulated elephant impact (1) and high accumulated elephant impact (2). P-values are calculated by Monte Carlo randomisation, and for pairs they have been adjusted using sequential Bonferroni procedure (Holm, 1979).

Species	All impact levels				Between pairs of accumulated elephant impact levels											
					0 and 1				0 and 2				1 and 2			
	df_1	df_2	F	P	df_1	df_2	F	P	df_1	df_2	F	P	df_1	df_2	F	P
Capparis tomentosa	1	147	10.29	0.001												
Combretum apiculatum	2	102	1.01	0.432												
Combretum mossambicense	1	185	0.90	0.423												
Erythroxylum zambesiacum	2	37	4.02	0.007	1	15	3.19	0.110	1	28	15.74	0.006	1	32	2.57	0.255
Flueggea virosa	1	53	4.09	0.004												
Markhamia zanzibarica	2	57	5.71	0.001	1	44	0.95	0.822	1	36	7.52	0.003	1	35	6.33	0.012

Table 2

Observed and expected frequencies of browsing in height sections 0-0.4 m, 0.41- 0.8 m, 0.81-1.2 m, 1.21-1.6 m and 1.61-2.0 m by (a) impala *(Aepyceros melampus* Lichtenstein*)* and (b) greater kudu *(Tragelaphus strepsiceros* Pallas).

Species	Height section, m	Browsing frequency			χ^2	p
		Observed	Expected	Residual		
(a) Impala						
Capparis tomentosa	0.41-0.8	13	37.9	-24.9	44.656	<0.001
	0.81-1.2	88	51.3	36.7		
	1.21-1.6	54	65.8	-11.8		
Combretum mossambicense	0-0.4	1	6.1	-5.1	23.383	<0.001
	0.41-0.8	4	18.9	-14.9		
	0.81-1.2	39	26.9	12.1		
	1.21-1.6	41	33.1	7.9		
Flueggea virosa	0.41-0.8	5	15.2	-10.2	10.502	0.005
	0.81-1.2	25	17.4	7.6		
	1.21-1.6	19	16.4	2.6		
(b) Kudu						
Capparis tomentosa	0.81-1.2	4	11.9	-7.9	8.233	0.016
	1.21-1.6	24	17.0	7.0		
	1.61-2.0	17	16.1	0.9		
Combretum mossambicense	0.41-0.8	1	8.8	-7.8	21.569	<0.001
	0.81-1.2	3	13.1	-10.1		
	1.21-1.6	31	21.9	9.1		
	1.61-2.0	34	25.2	8.8		

Table 3

Preference of trees of different accumulated elephant impact levels by impala *(Aepyceros melampus* Lichtenstein*)* and greater kudu *(Tragelaphus strepsiceros* Pallas). Bold faced indices indicate the most preferred impact level within a plant species

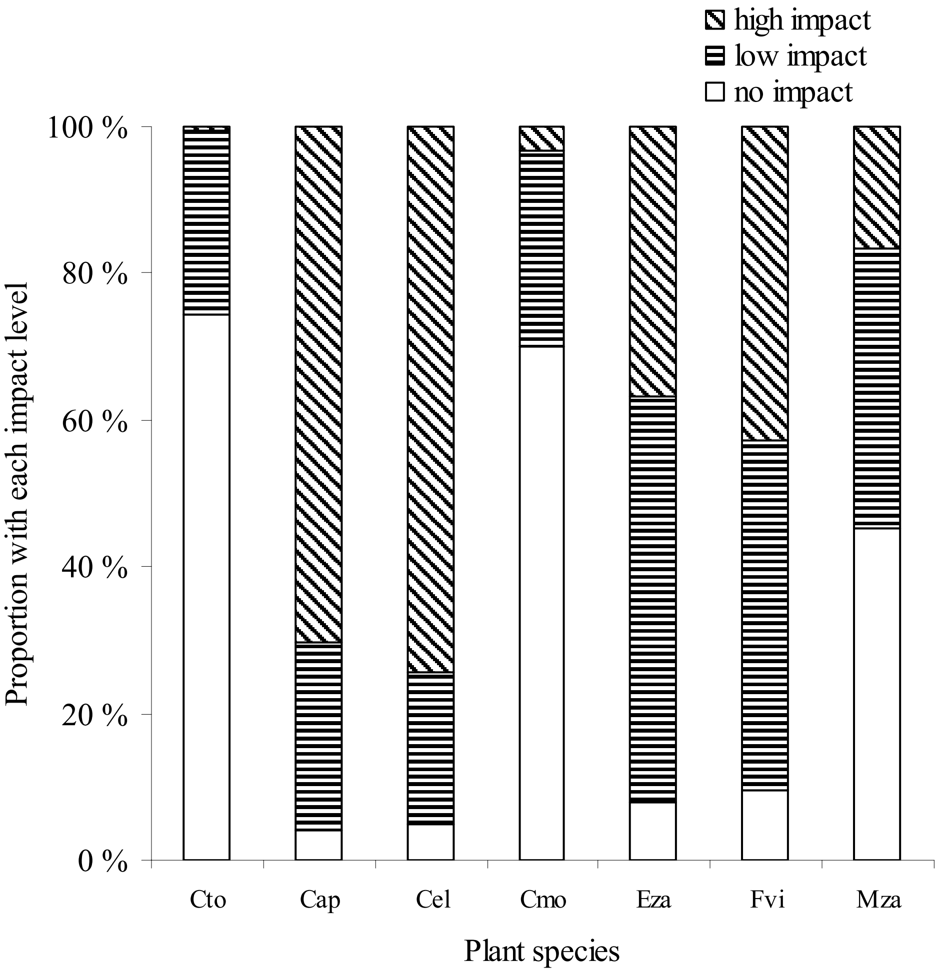
Animal species	Browsed plant species	Preference index		
		no impact	low impact	high impact
	Capparis tomentosa	**1.216**	0.263	
Impala	*Combretum mossambicense*	0.546	**2.307**	
	Flueggea virosa		0.263	**2.042**
	Markhamia zanzibarica	0.158	1.678	**1.732**
	Capparis tomentosa	**1.253**	0.154	
Kudu	*Combretum elaeagnoides*		0.210	**1.287**
	Combretum mossambicense	0.856	**1.499**	
	Erythroxylum zambesiacum	0.469	**1.340**	0.603
	Flueggea virosa		0.447	**1.837**
	Markhamia zanzibarica	0.130	**1.997**	1.070

Legends of figures

Fig. 1. Percentage of tree/shrub individuals divided in three accumulated elephant impact levels as assessed in Chobe National Park, Botswana excluding trees sampled in a nearby village. Abbreviations are *Capparis tomentosa (Cto), Combretum apiculatum* (Cap), *Combretum elaeagnoides* (Cel), *Combretum mossambicense* (Cmo), *Erythroxylum zambesiacum* (Eza), *Flueggea virosa* (Fvi) and *Markhamia zanzibarica* (Mza).

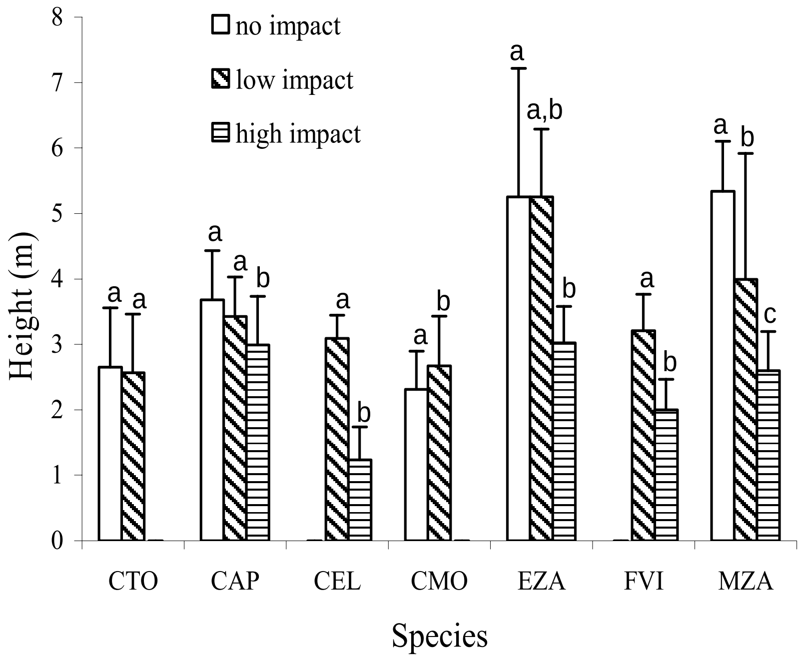
Fig. 2. Mean (± SD) heights of trees divided in three different accumulated elephant impact levels. Within each species, different letters show significant differences ($p<0.05$). The abbreviations of the plant species are as in Fig.1.

Fig. 3. Relationships between tree height and number of shoots ($\log_{10}$) available on tree individuals with no (●, dash curve), low (■, thin continuous curve) and high (▲, thick continuous curve) accumulated elephant impact on (a) *Capparis tomentosa* (b) *Combretum apiculatum,* (c) *Combretum mossambicense,* (d) *Erythroxylum zambesiacum,* (e) *Flueggea virosa* and (f) *Markhamia zanzibarica*. Quadratic regression models have been fitted to the data and the R^2 presented is the adjusted value.



high impact
low impact
no impact
100 %
80 %
60 %
40 %
20 %
0 %
Proportion with each impact level
Cto
Cap
Cel
Cmo
Eza
Fvi
Mza
Plant species

Fig. 1.



8
7
6
5
4
3
2
1
0
Height (m)
no impact
low impact
high impact
a
a
a
a
b
a
b
a
b
a
a,b
b
a
b
a
b
c
CTO
CAP
CEL
CMO
EZA
FVI
MZA
Species

Fig. 2.

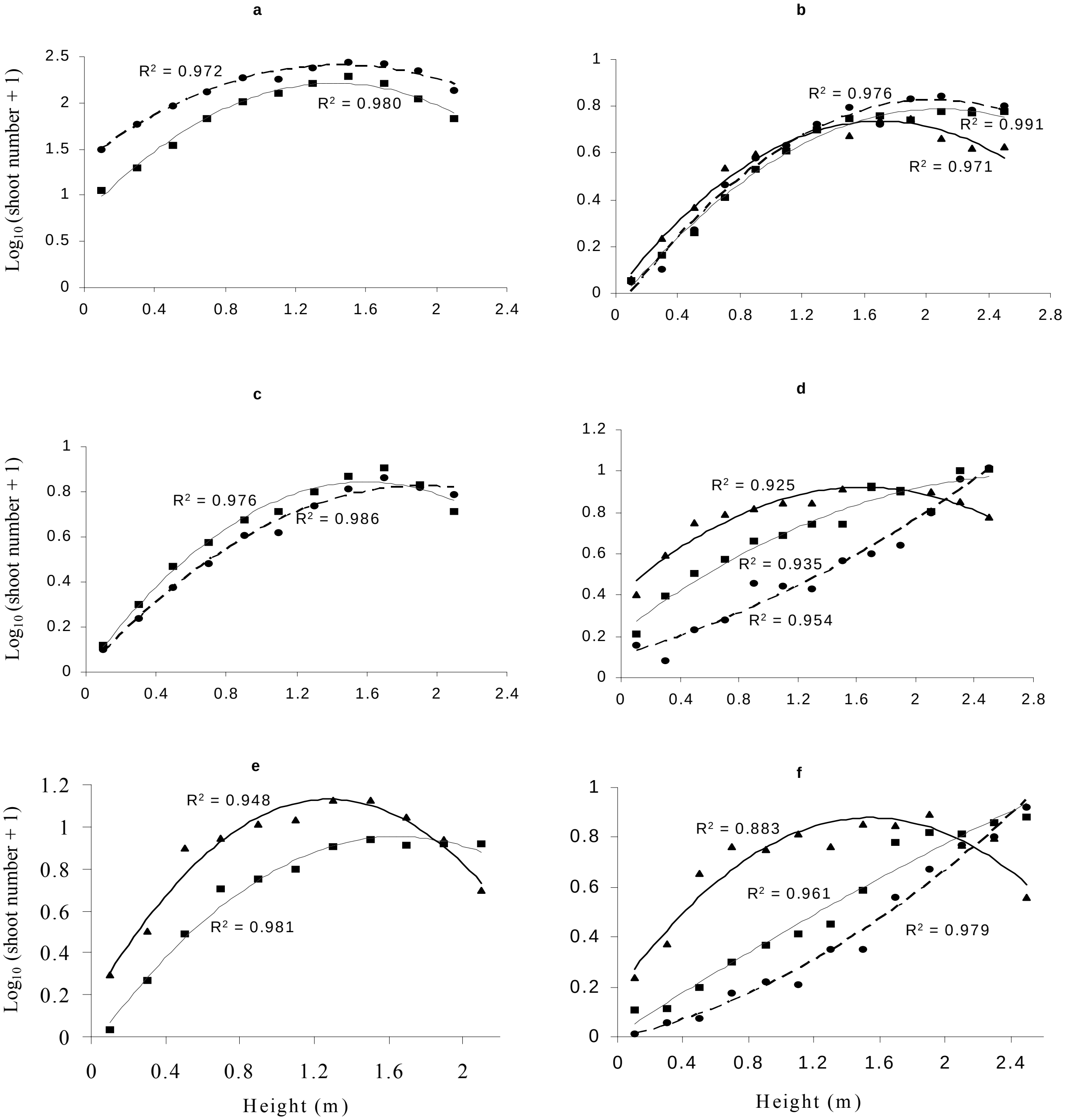

a
R² = 0.972
R² = 0.980
b
R² = 0.976
R² = 0.991
R² = 0.971
c
R² = 0.976
R² = 0.986
d
R² = 0.925
R² = 0.935
R² = 0.954
e
R² = 0.948
R² = 0.981
f
R² = 0.883
R² = 0.961
R² = 0.979
Log10 (shoot number + 1)
Height (m)
0
0.2
0.4
0.5
0.6
0.8
1
1.2
1.5
1.6
2
2.4
2.5
2.8

Fig. 3.

Paper IV

An Elephant browsing

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

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Abstract

Utilisation of five tree species by the African elephant (*Loxodonta africana* Blumenbach) was assessed on trees used 3 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 3 years, elephants broke into the area and their browsing of the experimental trees was assessed one month later. Four of the 5 species were browsed by the elephants, and for 3 of the species, percentage utilisation was higher on individuals subjected to simulated browsing 3 years before than on control trees. Treatment effects were strongest on the species intermediately preferred by the elephants. There was no difference in percentage utilisation 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 3 years with protection from browsing.

Key words: Chobe, percentage utilisation, 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 available 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 possible to a 'browsing lawn' when the tree or tree stand is kept short and coppicing, producing high quality browse (Owen-Smith 2003). Jachmann and Bell (1985) described elephants in the Kasungu National Park, Malawi, pushing over and repeatedly browse selected trees, maintaining highly productive coppicing 'browsing lawns'. Elephants seemed to select trees with high concentration of protein and sodium and low concentration of fibre.

Our aim was to assess whether treatment effects on trees were discernable by elephants after 3 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 tree 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 done in Kasane in northern Botswana. Annual average rainfall is about 640 mm with the wet season in summer mainly between November and April (Botswana Meteorological 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 has been protected from large herbivores. The vegetation is a 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 of these sites, three individual plants each of *Baphia massaiensis, Baikiaea plurijuga, Bauhinia petersiana, Combretum apiculatum* and *Markhamia zanzibarica* were selected. None of these species possess spines or thorns and they are all deciduous. The selected individuals were from 2.15 m (*B. petersiana*) to 3.5 m (*B. plurijuga*) and as similar, within species, as possible. 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. The experiment was evaluated in May 2000, but is not published. However, in all species treated trees had heavier and/or longer shoots than control trees.

Three years after the experiment was setup, 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 utilised trees of each species with different treatments. In November 2002 we revisited the marked trees. Of the initial 26 replicate areas twelve had been cleared by man and some of the remaining plants had lost their tags in the meantime. The average number of replicates remaining for species and treatments in November 2002 was 10, and the smallest number 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 was arcsine transformed and a two-way ANOVA applied to test for over-all 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 utilisation by elephants of trees with different treatments within species, a one-way ANOVA was used, and for those that were different, multiple comparison using a Tukey's 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

Elephant heavily browsed (in decreasing order) *Baphia massaiensis, Bauhinia petersiana* and *Combretum apiculatum.* They utilised *Markhamia zanzibarica* a little and *Baikiaea plurijuga* hardly at all (Fig.1). The percentage utilisation of trees by elephant was different between species ($F_{4,129}$ = 130; P < 0.001) and between treatments ($F_{2,129}$ = 14.43; P < 0.001). There was a significant interaction between species and treatment ($F_{8,129}$ = 5.21; P < 0.001). The rank order of browsing by elephants differed from that found by Omphile (1997) and Stokke and du Toit (2000), who ranked the three most used species (in decreasing order) *Combretum apiculatum, Baphia massaiensis* and *Bauhinia petersiana. Combretum apiculatum* and *Baphia massaiensis* had lowest concentration of fibre, and *Baphia massaiensis, Baikiaea plurijuga* and *Bauhinia petersiana* had the highest and *Combretum apiculatum* the lowest concentration of nitrogen (Makhabu *et al*. in press). The data suggest that it was more important for elephants to avoid intake of fibre than to maximise intake of nitrogen. Elephant food selection against fibre is also recorded by Jachmann and Bell (1985).

Analysing the species separately showed that for the 3 heavily browsed species, *Combretum apiculatum*, *Baphia massaiensis* and *Bauhinia petersiana*, the percentage utilisation differed between treatments (Table 1). The multiple comparisons showed that elephant browsed more on trees that had been subject 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 our own preference ranking, this was true, with the strongest treatment effect in *Combretum apiculatum* and *Bauhinia petersiana,* intermediate effect in the most preferred species, *Baphia massaiensis,* of which most shoots had been browsed both on treated trees and on controls, and no effect in the little browsed *Markhamia zanzibarica* and *Baikiaea plurijuga.* However, with the ranking by Omphile (1997) and Stokke and du Toit (2000) the most preferred species, *Combretum 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 and Danell 1987 (12 months); Bowyer and Bowyer 1997 (about 12 months); Bergström *et al*. 2000 (8 months); Cooper *et al*. 2003 (12 months); Rooke 2003 (3 months)]. We found treatment effects to remain after 3 years in the species browsed by elephant. 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 might have been different one or two years earlier, and might have differed in the future.

Acknowledgements

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Table 1. Comparison of percentage utilisation means for species and treatments. 0 = control, 1= ‘cut’, 2 = ‘stump’ Species ranked from most (top) to least (bottom) browsed by elephants in our study.

Species	ANOVA between treatments			P of Tukey’s comparisons		
	df	**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	-	-	-

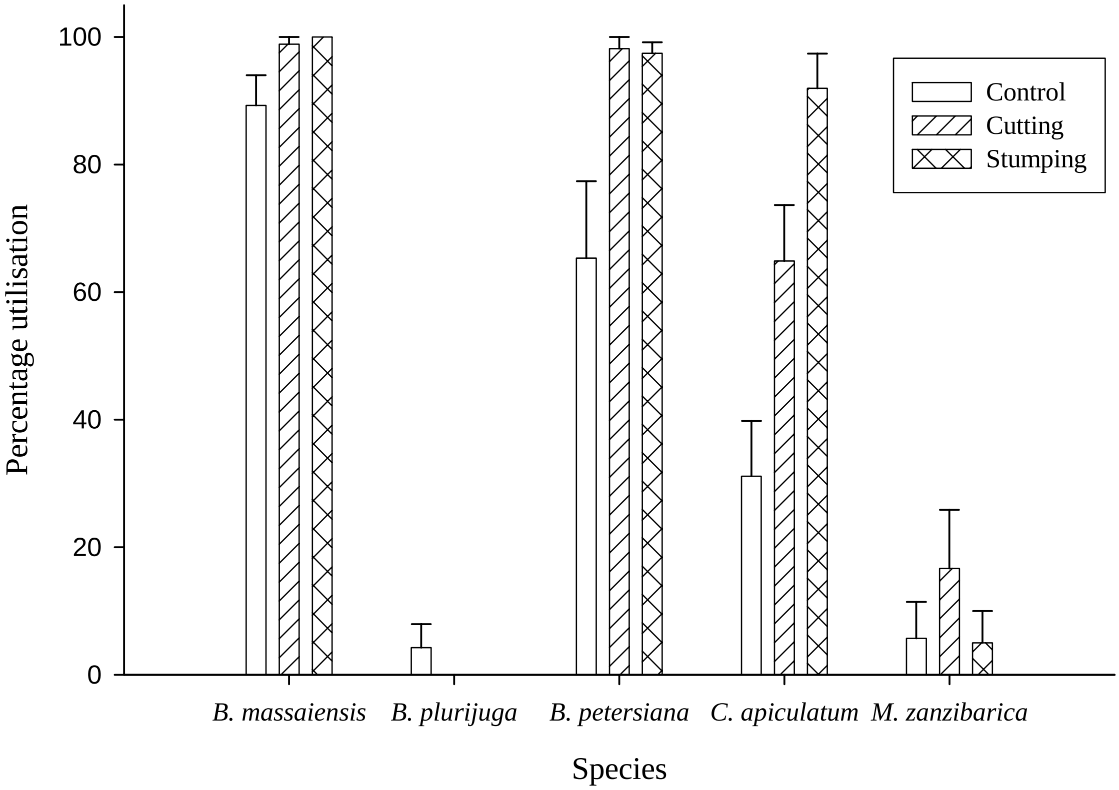

Fig. 1. Mean (± S.E.) browsing pressure by elephant on *Baphia massaiensis, Baikiaea plurijuga, Bauhinia petersiana, Combretum apiculatum* and *Markhamia zanzibarica* trees with different previous intensities of simulated browsing (control, cutting and stumping).

Doctoral theses in Biology
Norwegian University of Science and Technology

Year	Name	Degree	Title
1974	Tor-Henning Iversen	Dr. philos Botany	The roles of statholiths, auxin transport, and auxin metabolism in root gravitropism
1978	Tore Slagsvold	Dr. philos. Zoology	Breeding events of birds in relation to spring temperature and environmental phenology.
1978	Egil Sakshaug	Dr.philos Botany	"The influence of environmental factors on the chemical composition of cultivated and natural populations of marine phytoplankton"
1980	Arnfinn Langeland	Dr. philos. Zoology	Interaction between fish and zooplankton populations and their effects on the material utilization in a freshwater lake.
1980	Helge Reinertsen	Dr. philos Botany	The effect of lake fertilization on the dynamics and stability of a limnetic ecosystem with special reference to the phytoplankton
1982	Gunn Mari Olsen	Dr. scient Botany	Gravitropism in roots of *Pisum sativum* and *Arabidopsis thaliana*
1982	Dag Dolmen	Dr. philos. Zoology	Life aspects of two sympartic species of newts (*Triturus, Amphibia*) in Norway, with special emphasis on their ecological niche segregation.
1984	Eivin Røskaft	Dr. philos. Zoology	Sociobiological studies of the rook *Corvus frugilegus.*
1984	Anne Margrethe Cameron	Dr. scient Botany	Effects of alcohol inhalation on levels of circulating testosterone, follicle stimulating hormone and luteinzing hormone in male mature rats
1984	Asbjørn Magne Nilsen	Dr. scient Botany	Alveolar macrophages from expectorates – Biological monitoring of workers exosed to occupational air pollution. An evaluation of the AM-test
1985	Jarle Mork	Dr. philos. Zoology	Biochemical genetic studies in fish.
1985	John Solem	Dr. philos. Zoology	Taxonomy, distribution and ecology of caddisflies (*Trichoptera*) in the Dovrefjell mountains.

1985	Randi E. Reinertsen	Dr. philos. Zoology	Energy strategies in the cold: Metabolic and thermoregulatory adaptations in small northern birds.
1986	Bernt-Erik Sæther	Dr. philos. Zoology	Ecological and evolutionary basis for variation in reproductive traits of some vertebrates: A comparative approach.
1986	Torleif Holthe	Dr. philos. Zoology	Evolution, systematics, nomenclature, and zoogeography in the polychaete orders *Oweniimorpha* and *Terebellomorpha*, with special reference to the Arctic and Scandinavian fauna.
1987	Helene Lampe	Dr. scient. Zoology	The function of bird song in mate attraction and territorial defence, and the importance of song repertoires.
1987	Olav Hogstad	Dr. philos. Zoology	Winter survival strategies of the Willow tit *Parus montanus*.
1987	Jarle Inge Holten	Dr. philos Bothany	Autecological investigations along a coust-inland transect at Nord-Møre, Central Norway
1987	Rita Kumar	Dr. scient Botany	Somaclonal variation in plants regenerated from cell cultures of *Nicotiana sanderae* and *Chrysanthemum morifolium*
1987	Bjørn Åge Tømmerås	Dr. scient. Zoology	Olfaction in bark beetle communities: Interspecific interactions in regulation of colonization density, predator - prey relationship and host attraction.
1988	Hans Christian Pedersen	Dr. philos. Zoology	Reproductive behaviour in willow ptarmigan with special emphasis on territoriality and parental care.
1988	Tor G. Heggberget	Dr. philos. Zoology	Reproduction in Atlantic Salmon (*Salmo salar*): Aspects of spawning, incubation, early life history and population structure.
1988	Marianne V. Nielsen	Dr. scient. Zoology	The effects of selected environmental factors on carbon allocation/growth of larval and juvenile mussels (*Mytilus edulis*).
1988	Ole Kristian Berg	Dr. scient. Zoology	The formation of landlocked Atlantic salmon (*Salmo salar* L.).

1989	John W. Jensen	Dr. philos. Zoology	Crustacean plankton and fish during the first decade of the manmade Nesjø reservoir, with special emphasis on the effects of gill nets and salmonid growth.
1989	Helga J. Vivås	Dr. scient. Zoology	Theoretical models of activity pattern and optimal foraging: Predictions for the Moose *Alces alces*.
1989	Reidar Andersen	Dr. scient. Zoology	Interactions between a generalist herbivore, the moose *Alces alces*, and its winter food resources: a study of behavioural variation.
1989	Kurt Ingar Draget	Dr. scient Botany	Alginate gel media for plant tissue culture,
1990	Bengt Finstad	Dr. scient. Zoology	Osmotic and ionic regulation in Atlantic salmon, rainbow trout and Arctic charr: Effect of temperature, salinity and season.
1990	Hege Johannesen	Dr. scient. Zoology	Respiration and temperature regulation in birds with special emphasis on the oxygen extraction by the lung.
1990	Åse Krøkje	Dr. scient Botany	The mutagenic load from air pollution at two work-places with PAH-exposure measured with Ames Salmonella/microsome test
1990	Arne Johan Jensen	Dr. philos. Zoology	Effects of water temperature on early life history, juvenile growth and prespawning migrations of Atlantic salmion (*Salmo salar*) and brown trout (*Salmo trutta*): A summary of studies in Norwegian streams.
1990	Tor Jørgen Almaas	Dr. scient. Zoology	Pheromone reception in moths: Response characteristics of olfactory receptor neurons to intra- and interspecific chemical cues.
1990	Magne Husby	Dr. scient. Zoology	Breeding strategies in birds: Experiments with the Magpie *Pica pica*.
1991	Tor Kvam	Dr. scient. Zoology	Population biology of the European lynx (*Lynx lynx*) in Norway.
1991	Jan Henning L'Abêe Lund	Dr. philos. Zoology	Reproductive biology in freshwater fish, brown trout *Salmo trutta* and roach *Rutilus rutilus* in particular.

1991	Asbjørn Moen	Dr. philos Botany	The plant cover of the boreal uplands of Central Norway. I. Vegetation ecology of Sølendet nature reserve; haymaking fens and birch woodlands
1991	Else Marie Løbersli	Dr. scient Botany	Soil acidification and metal uptake in plants
1991	Trond Nordtug	Dr. scient. Zoology	Reflctometric studies of photomechanical adaptation in superposition eyes of arthropods.
1991	Thyra Solem	Dr. scient Botany	Age, origin and development of blanket mires in Central Norway
1991	Odd Terje Sandlund	Dr. philos. Zoology	The dynamics of habitat use in the salmonid genera *Coregonus* and *Salvelinus*: Ontogenic niche shifts and polymorphism.
1991	Nina Jonsson	Dr. philos.	Aspects of migration and spawning in salmonids.
1991	Atle Bones	Dr. scient Botany	Compartmentation and molecular properties of thioglucoside glucohydrolase (myrosinase)
1992	Torgrim Breiehagen	Dr. scient. Zoology	Mating behaviour and evolutionary aspects of the breeding system of two bird species: the Temminck's stint and the Pied flycatcher.
1992	Anne Kjersti Bakken	Dr. scient Botany	The influence of photoperiod on nitrate assimilation and nitrogen status in timothy (*Phleum pratense* L.)
1992	Tycho Anker-Nilssen	Dr. scient. Zoology	Food supply as a determinant of reproduction and population development in Norwegian Puffins *Fratercula arctica*
1992	Bjørn Munro Jenssen	Dr. philos. Zoology	Thermoregulation in aquatic birds in air and water: With special emphasis on the effects of crude oil, chemically treated oil and cleaning on the thermal balance of ducks.
1992	Arne Vollan Aarset	Dr. philos. Zoology	The ecophysiology of under-ice fauna: Osmotic regulation, low temperature tolerance and metabolism in polar crustaceans.
1993	Geir Slupphaug	Dr. scient Botany	Regulation and expression of uracil-DNA glycosylase and O^6-methylguanine-DNA methyltransferase in mammalian cells
1993	Tor Fredrik Næsje	Dr. scient. Zoology	Habitat shifts in coregonids.

1993	Yngvar Asbjørn Olsen	Dr. scient. Zoology	Cortisol dynamics in Atlantic salmon, *Salmo salar* L.: Basal and stressor-induced variations in plasma levels ans some secondary effects.
1993	Bård Pedersen	Dr. scient Botany	Theoretical studies of life history evolution in modular and clonal organisms
1993	Ole Petter Thangstad	Dr. scient Botany	Molecular studies of myrosinase in Brassicaceae
1993	Thrine L. M. Heggberget	Dr. scient. Zoology	Reproductive strategy and feeding ecology of the Eurasian otter *Lutra lutra*.
1993	Kjetil Bevanger	Dr. scient. Zoology	Avian interactions with utility structures, a biological approach.
1993	Kåre Haugan	Dr. scient Bothany	Mutations in the replication control gene trfA of the broad host-range plasmid RK2
1994	Peder Fiske	Dr. scient. Zoology	Sexual selection in the lekking great snipe (*Gallinago media*): Male mating success and female behaviour at the lek.
1994	Kjell Inge Reitan	Dr. scient Botany	Nutritional effects of algae in first-feeding of marine fish larvae
1994	Nils Røv	Dr. scient. Zoology	Breeding distribution, population status and regulation of breeding numbers in the northeast-Atlantic Great Cormorant *Phalacrocorax carbo carbo*.
1994	Annette-Susanne Hoepfner	Dr. scient Botany	Tissue culture techniques in propagation and breeding of Red Raspberry (*Rubus idaeus* L.)
1994	Inga Elise Bruteig	Dr. scient Bothany	Distribution, ecology and biomonitoring studies of epiphytic lichens on conifers
1994	Geir Johnsen	Dr. scient Botany	Light harvesting and utilization in marine phytoplankton: Species-specific and photoadaptive responses
1994	Morten Bakken	Dr. scient. Zoology	Infanticidal behaviour and reproductive performance in relation to competition capacity among farmed silver fox vixens, *Vulpes vulpes*.
1994	Arne Moksnes	Dr. philos. Zoology	Host adaptations towards brood parasitism by the Cockoo.
1994	Solveig Bakken	Dr. scient Bothany	Growth and nitrogen status in the moss *Dicranum majus* Sm. as influenced by nitrogen supply

1995	Olav Vadstein	Dr. philos Botany	The role of heterotrophic planktonic bacteria in the cycling of phosphorus in lakes: Phosphorus requirement, competitive ability and food web interactions.
1995	Hanne Christensen	Dr. scient. Zoology	Determinants of Otter *Lutra lutra* distribution in Norway: Effects of harvest, polychlorinated biphenyls (PCBs), human population density and competition with mink *Mustela vision*.
1995	Svein Håkon Lorentsen	Dr. scient. Zoology	Reproductive effort in the Antarctic Petrel *Thalassoica antarctica*; the effect of parental body size and condition.
1995	Chris Jørgen Jensen	Dr. scient. Zoology	The surface electromyographic (EMG) amplitude as an estimate of upper trapezius muscle activity
1995	Martha Kold Bakkevig	Dr. scient. Zoology	The impact of clothing textiles and construction in a clothing system on thermoregulatory responses, sweat accumulation and heat transport.
1995	Vidar Moen	Dr. scient. Zoology	Distribution patterns and adaptations to light in newly introduced populations of *Mysis relicta* and constraints on Cladoceran and Char populations.
1995	Hans Haavardsholm Blom	Dr. philos Bothany	A revision of the *Schistidium apocarpum* complex in Norway and Sweden.
1996	Jorun Skjærmo	Dr. scient Botany	Microbial ecology of early stages of cultivated marine fish; inpact fish-bacterial interactions on growth and survival of larvae.
1996	Ola Ugedal	Dr. scient. Zoology	Radiocesium turnover in freshwater fishes
1996	Ingibjørg Einarsdottir	Dr. scient. Zoology	Production of Atlantic salmon (*Salmo salar*) and Arctic charr (*Salvelinus alpinus*): A study of some physiological and immunological responses to rearing routines.
1996	Christina M. S. Pereira	Dr. scient. Zoology	Glucose metabolism in salmonids: Dietary effects and hormonal regulation.
1996	Jan Fredrik Børseth	Dr. scient. Zoology	The sodium energy gradients in muscle cells of *Mytilus edulis* and the effects of organic xenobiotics.

1996	Gunnar Henriksen	Dr. scient. Zoology	Status of Grey seal *Halichoerus grypus* and Harbour seal *Phoca vitulina* in the Barents sea region.
1997	Gunvor Øie	Dr. scient Bothany	Eevalution of rotifer *Brachionus plicatilis* quality in early first feeding of turbot *Scophtalmus maximus* L. larvae.
1997	Håkon Holien	Dr. scient Botany	Studies of lichens in spurce forest of Central Norway. Diversity, old growth species and the relationship to site and stand parameters.
1997	Ole Reitan	Dr. scient. Zoology	Responses of birds to habitat disturbance due to damming.
1997	Jon Arne Grøttum	Dr. scient. Zoology	Physiological effects of reduced water quality on fish in aquaculture.
1997	Per Gustav Thingstad	Dr. scient. Zoology	Birds as indicators for studying natural and human-induced variations in the environment, with special emphasis on the suitability of the Pied Flycatcher.
1997	Torgeir Nygård	Dr. scient. Zoology	Temporal and spatial trends of pollutants in birds in Norway: Birds of prey and Willow Grouse used as Biomonitors.
1997	Signe Nybø	Dr. scient. Zoology	Impacts of long-range transported air pollution on birds with particular reference to the dipper *Cinclus cinclus* in southern Norway.
1997	Atle Wibe	Dr. scient. Zoology	Identification of conifer volatiles detected by receptor neurons in the pine weevil (*Hylobius abietis*), analysed by gas chromatography linked to electrophysiology and to mass spectrometry.
1997	Rolv Lundheim	Dr. scient. Zoology	Adaptive and incidental biological ice nucleators.
1997	Arild Magne Landa	Dr. scient. Zoology	Wolverines in Scandinavia: ecology, sheep depredation and conservation.
1997	Kåre Magne Nielsen	Dr. scient Botany	An evolution of possible horizontal gene transfer from plants to sail bacteria by studies of natural transformation in *Acinetobacter calcoacetius*.

1997	Jarle Tufto	Dr. scient. Zoology	Gene flow and genetic drift in geographically structured populations: Ecological, population genetic, and statistical models
1997	Trygve Hesthagen	Dr. philos. Zoology	Population responces of Arctic charr (*Salvelinus alpinus* (L.)) and brown trout (*Salmo trutta* L.) to acidification in Norwegian inland waters
1997	Trygve Sigholt	Dr. philos. Zoology	Control of Parr-smolt transformation and seawater tolerance in farmed Atlantic Salmon (*Salmo salar*) Effects of photoperiod, temperature, gradual seawater acclimation, NaCl and betaine in the diet
1997	Jan Østnes	Dr. scient. Zoology	Cold sensation in adult and neonate birds
1998	Seethaledsumy Visvalingam	Dr. scient Botany	Influence of environmental factors on myrosinases and myrosinase-binding proteins.
1998	Thor Harald Ringsby	Dr. scient. Zoology	Variation in space and time: The biology of a House sparrow metapopulation
1998	Erling Johan Solberg	Dr. scient. Zoology	Variation in population dynamics and life history in a Norwegian moose (*Alces alces*) population: consequences of harvesting in a variable environment
1998	Sigurd Mjøen Saastad	Dr. scient Botany	Species delimitation and phylogenetic relationships between the Sphagnum recurvum complex (Bryophyta): genetic variation and phenotypic plasticity.
1998	Bjarte Mortensen	Dr. scient Botany	Metabolism of volatile organic chemicals (VOCs) in a head liver S9 vial equilibration system in vitro.
1998	Gunnar Austrheim	Dr. scient Botany	Plant biodiversity and land use in subalpine grasslands. – A conservtaion biological approach.
1998	Bente Gunnveig Berg	Dr. scient. Zoology	Encoding of pheromone information in two related moth species
1999	Kristian Overskaug	Dr. scient. Zoology	Behavioural and morphological characteristics in Northern Tawny Owls *Strix aluco*: An intra- and interspecific comparative approach

1999	Hans Kristen Stenøien	Dr. scient Bothany	Genetic studies of evolutionary processes in various populations of nonvascular plants (mosses, liverworts and hornworts)
1999	Trond Arnesen	Dr. scient Botany	Vegetation dynamics following trampling and burning in the outlying haylands at Sølendet, Central Norway.
1999	Ingvar Stenberg	Dr. scient. Zoology	Habitat selection, reproduction and survival in the White-backed Woodpecker *Dendrocopos leucotos*
1999	Stein Olle Johansen	Dr. scient Botany	A study of driftwood dispersal to the Nordic Seas by dendrochronology and wood anatomical analysis.
1999	Trina Falck Galloway	Dr. scient. Zoology	Muscle development and growth in early life stages of the Atlantic cod (*Gadus morhua* L.) and Halibut (*Hippoglossus hippoglossus* L.)
1999	Torbjørn Forseth	Dr. scient. Zoology	Bioenergetics in ecological and life history studies of fishes.
1999	Marianne Giæver	Dr. scient. Zoology	Population genetic studies in three gadoid species: blue whiting (*Micromisistius poutassou*), haddock (*Melanogrammus aeglefinus*) and cod (*Gradus morhua*) in the North-East Atlantic
1999	Hans Martin Hanslin	Dr. scient Botany	The impact of environmental conditions of density dependent performance in the boreal forest bryophytes *Dicranum majus*, *Hylocomium splendens*, *Plagiochila asplenigides*, *Ptilium crista-castrensis* and *Rhytidiadelphus lokeus*.
1999	Ingrid Bysveen Mjølnerød	Dr. scient. Zoology	Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon (*Salmo salar*) revealed by molecular genetic techniques
1999	Else Berit Skagen	Dr. scient Botany	The early regeneration process in protoplasts from *Brassica napus* hypocotyls cultivated under various g-forces
1999	Stein-Are Sæther	Dr. philos. Zoology	Mate choice, competition for mates, and conflicts of interest in the Lekking Great Snipe
1999	Katrine Wangen Rustad	Dr. scient. Zoology	Modulation of glutamatergic neurotransmission related to cognitive dysfunctions and Alzheimer’s disease

1999	Per Terje Smiseth	Dr. scient. Zoology	Social evolution in monogamous families: mate choice and conflicts over parental care in the Bluethroat (*Luscinia s. svecica*)
1999	Gunnbjørn Bremset	Dr. scient. Zoology	Young Atlantic salmon (*Salmo salar* L.) and Brown trout (*Salmo trutta* L.) inhabiting the deep pool habitat, with special reference to their habitat use, habitat preferences and competitive interactions
1999	Frode Ødegaard	Dr. scient. Zoology	Host spesificity as parameter in estimates of arhrophod species richness
1999	Sonja Andersen	Dr. scient Bothany	Expressional and functional analyses of human, secretory phospholipase A2
2000	Ingrid Salvesen, I	Dr. scient Botany	Microbial ecology in early stages of marine fish: Development and evaluation of methods for microbial management in intensive larviculture
2000	Ingar Jostein Øien	Dr. scient. Zoology	The Cuckoo (*Cuculus canorus*) and its host: adaptions and counteradaptions in a coevolutionary arms race
2000	Pavlos Makridis	Dr. scient Botany	Methods for the microbial econtrol of live food used for the rearing of marine fish larvae
2000	Sigbjørn Stokke	Dr. scient. Zoology	Sexual segregation in the African elephant (*Loxodonta africana*)
2000	Odd A. Gulseth	Dr. philos. Zoology	Seawater tolerance, migratory behaviour and growth of Charr, (*Salvelinus alpinus*), with emphasis on the high Arctic Dieset charr on Spitsbergen, Svalbard
2000	Pål A. Olsvik	Dr. scient. Zoology	Biochemical impacts of Cd, Cu and Zn on brown trout (*Salmo trutta*) in two mining-contaminated rivers in Central Norway
2000	Sigurd Einum	Dr. scient. Zoology	Maternal effects in fish: Implications for the evolution of breeding time and egg size
2001	Jan Ove Evjemo	Dr. scient. Zoology	Production and nutritional adaptation of the brine shrimp *Artemia* sp. as live food organism for larvae of marine cold water fish species

2001	Olga Hilmo	Dr. scient Botany	Lichen response to environmental changes in the managed boreal forset systems
2001	Ingebrigt Uglem	Dr. scient. Zoology	Male dimorphism and reproductive biology in corkwing wrasse (*Symphodus melops* L.)
2001	Bård Gunnar Stokke	Dr. scient. Zoology	Coevolutionary adaptations in avian brood parasites and their hosts
2002	Ronny Aanes	Dr. scient	Spatio-temporal dynamics in Svalbard reindeer (*Rangifer tarandus platyrhynchus*)
2002	Mariann Sandsund	Dr. scient. Zoology	Exercise- and cold-induced asthma. Respiratory and thermoregulatory responses
2002	Dag-Inge Øien	Dr. scient Botany	Dynamics of plant communities and populations in boreal vegetation influenced by scything at Sølendet, Central Norway
2002	Frank Rosell	Dr. scient. Zoology	The function of scent marking in beaver (*Castor fiber*)
2002	Janne Østvang	Dr. scient Botany	The Role and Regulation of Phospholipase A_2 in Monocytes During Atherosclerosis Development
2002	Terje Thun	Dr. philos Biology	Dendrochronical constructions of Norwegian conifer chronologies providing dating of historical material
2002	Birgit Hafjeld Borgen	Dr. scient Biology	Functional analysis of plant idioblasts (Myrosin cells) and their role in defense, development and growth
2002	Bård Øyvind Solberg	Dr. scient Biology	Effects of climatic change on the growth of dominating tree species along major environmental gradients
2002	Per Winge	Dr. scient Biology	The evolution of small GTP binding proteins in cellular organisms. Studies of RAC GTPases in *Arabidopsis thaliana* and
2002	Henrik Jensen	Dr. scient Biology	Causes and consequenses of individual variation in fitness-related traits in house sparrows
2003	Jens Rohloff	Dr. philos Biology	Cultivation of herbs and medicinal plants in Norway – Essential oil production and quality control

2003	Åsa Maria O. Espmark Wibe	Dr. scient Biology	Behavioural effects of environmental pollution in threespine stickleback *Gasterosteus aculeatur* L.
2003	Dagmar Hagen	Dr. scient Biology	Assisted recovery of disturbed arctic and alpine vegetation – an integrated approach
2003	Bjørn Dahle	Dr. scient Biology	Reproductive strategies in Scandinavian brown bears
2003	Cyril Lebogang Taolo	Dr. scient Biology	Population ecology, seasonal movement and habitat use of the African buffalo (*Syncerus caffer*) in Chobe National Park, Botswana
2003	Marit Stranden	Dr.scient Biology	Olfactory receptor neurones specified for the same odorants in three related Heliothine species (*Helicoverpa armigera, Helicoverpa assulta* and *Heliothis virescens*)
2003	Kristian Hassel	Dr.scient Biology	Life history characteristics and genetic variation in an expanding species, *Pogonatum dentatum*
2003	David Alexander Rae	Dr.scient Biology	Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Artic environments
2003	Åsa A Borg	Dr.scient Biology	Sex roles and reproductive behaviour in gobies and guppies: a female perspective
2003	Eldar Åsgard Bendiksen	Dr.scient Biology	Environmental effects on lipid nutrition of farmed Atlantic salmon (*Salmo Salar* L.) parr and smolt
2004	Torkild Bakken	Dr.scient Biology	A revision of Nereidinae (Polychaeta, Nereididae)
2004	Ingar Pareliussen	Dr.scient Biology	Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohitantely Forest Reserve, Madagascar
2004	Tore Brembu	Dr.scient Biology	Genetic, molecular and functional studies of RAC GTPases and the WAVE-like regulatory protein complex in *Arabidopsis thaliana*
2004	Liv S. Nilsen	Dr.scient Biology	Coastal heath vegetation on central Norway; recent past, present state and future possibilities

2004	Hanne T. Skiri	Dr.scient Biology	Olfactory coding and olfactory learning of plant odours in heliothine moths. An anatomical, physiological and behavioural study of three related species (*Heliothis virescens, Helicoverpa armigera* and *Helicoverpa assulta*).
2004	Lene Østby	Dr.scient Biology	Cytochrome P4501A (CYP1A) induction and DNA adducts as biomarkers for organic pollution in the natural environment
2004	Emmanuel J. Gerreta	Dr. philos Biology	The Importance of Water Quality and Quantity in the Tropical Ecosystems, Tanzania
2004	Linda Dalen	Dr.scient Biology	Dynamics of Mountain Birch Treelines in the Scandes Mountain Chain, and Effects of Climate Warming
2004	Lisbeth Mehli	Dr.scient Biology	Polygalacturonase-inhibiting protein (PGIP) in cultivated strawberry (*Fragaria* x *ananassa*): characterisation and induction of the gene following fruit infection by *Botrytis cinerea*
2004	Børge Moe	Dr.scient Biology	Energy-Allocation in Avian Nestlings Facing Short-Term Food Shortage
2005	Matilde Skogen Chauton	Dr.scient Biology	Metabolic profiling and species discrimination from High-Resolution Magic Angle Spinning NMR analysis of whole-cell samples
2005	Sten Karlsson	Dr.scient Biology	Dynamics of Genetic Polymorphisms
2005	Terje Bongard	Dr.scient Biology	Life History strategies, mate choice, and parental investment among Norwegians over a 300-year period
2005	Tonette Røstelien	PhD Biology	Functional characterisation of olfactory receptor neurone types in heliothine moths
2005	Erlend Kristiansen	Dr.scient Biology	Studies on antifreeze proteins
2005	Eugen G. Sørmo	Dr.scient Biology	Organochlorine pollutants in grey seal (*Halichoerus grypus*) pups and their impact on plasma thyrid hormone and vitamin A concentrations.
2005	Christian Westad	Dr.scient Biology	Motor control of the upper trapezius

2005	Lasse Mork Olsen	PhD Biology	Interactions between marine osmo- and phagotrophs in different physicochemical environments
2005	Åslaug Viken	PhD Biology	Implications of mate choice for the management of small populations
2006	Ariaya Hymete Sahle Dingle	PhD Biology	Investigation of the biological activities and chemical constituents of selected *Echinops* spp. growing in Ethiopia
2006	Ander Gravbrøt Finstad	PhD	Salmonid fishes in a changing climate: The winter challenge