The demographic impacts of browsing on woody plants in savannas: from individual branches to whole populations

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Front cover: *Acacia nigrescens*, heavily browsed by giraffe, in the Makhohlolo region of Kruger National Park

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Abstract

Browsing ungulates can potentially have drastic impacts on vegetation patterns. This is particularly true in African savannas where many large browsers persist at high densities. Most of the theory and models outlining mechanisms of impact on plants and predicting responses are framed in terms of biomass impacts and responses. However, for trees in African savannas, fitness is more closely linked to height than aboveground biomass. Here I evaluate the demographic impacts of browsing, making explicit contrasts with impacts on biomass. I set out to identify aspects of herbivore foraging and plant response that are critical in determining how height is affected by browsing. I also evaluate population-level browser impact by measuring browser induced changes in plant form.

I describe the development of a function linking browser consumption to impacts on height growth. This function is developed from considerations of individual branch growth and branch population dynamics. It is then incorporated into a tree population model parameterized for giraffe browsing on *Acacia nigrescens* in Kruger National Park to explore its population level consequences. I show that browser impacts on height growth can be separated into the impacts resulting from bud-loss and the impact of biomass lost to browsers. Incorporating bud-loss impacts results in predictions of far greater impacts on height than would be expected from the loss of biomass alone. I then test the relative importance of consumption and bud-loss impacts with an *in situ* experiment on *Acacia karroo* in Hluhluwe-iMfolozi Park. In this particular instance, bud-loss impacts affect height growth far more than consumption impacts, while they both are important for the growth of aboveground biomass.

Concomitant with bud-loss is the alteration of plant architecture and allometry. I use height-diameter allometries of *Colophospermum mopane* and *Acacia nigrescens* in Kruger National Park to evaluate population level browser impacts, interpreted in the light of allometric theories developed without reference to herbivory. Strong patterns of browser modification are evident, with the nature of these changes dependent on the particular browser responsible.

These results highlight under-explored intrinsic aspects of plants and browsers that determine the degree of browser impact on plant demography, aspects that have been under-explored due to an emphasis on biomass responses. They also provide novel methods to measure and evaluate large-scale browser impacts, which have proved difficult to quantify until now.

Table of Contents

Chapter 1: General introduction

Glenn R. Moncrieff

Introduction

Herbivory is a ubiquitous natural disturbance, affecting almost all wild plants. Mammalian herbivory, in particular, encompasses a wide spectrum of plant life forms and a diverse array, both taxonomically and functionally, of mammals. Unsurprising it is then that a range of responses from affected plants are observed (Belsky 1986, Strauss and Agrawal 1999, Maron and Crone 2006, Skarpe and Hester 2008). Often herbivory has little effect on plant fitness, as plants have evolved a range of mechanisms to tolerate or resist herbivores. However, sometimes populations can be devastated by herbivores, or community composition greatly altered (eg Dublin *et al* 1990, Augustine and McNaughton 2004). Providing a general framework for predicting herbivore impacts on plant populations has proved elusive (Hawkes and Sullivan 2001, Skarpe and Hester 2008). This is not surprising in the light of the diversity of interactions that fall under the moniker of herbivory.

Although we lack a theory outlining contexts in which strong herbivore impacts would be expected, significant impacts are often observed (Maron and Crone 2006). The question now is not whether herbivores can ever severely impact plant populations, but rather: over what spatial and temporal scales are plant affected, or, can herbivores significantly alter vegetation over large enough scales to be considered major agents of ecosystem change? White (1993) has suggested that it is not possible for herbivores to control vegetation at large scales, arguing that the nutritive quality of plants is too low to support large enough herbivore populations. Bond (2005), however, argued that the apparent lack of herbivore controlled vegetation globally is a result of recent megafaunal extinctions eliminating most of the herbivores most likely to have significant vegetation impacts. Large herbivores (>1000 kg) are, owing to their size, relatively immune from population control through predation pressure (Sinclair *et al* 2003). They are also highly tolerant of low quality forage, as a result a low mass specific metabolic requirements (Nagy 1987, Owen-Smith

1988). The legacy of the extinct Pleistocene mammalian megafauna is still evident today (Janzen and Martin 1982), with some suggestions that vegetation impacts may have been severe. African savannas retain a largely intact Pleistocene mammalian megafauna, providing a template in which to study herbivore-vegetation interactions that may have once been of global importance for ecosystem structure and assembly.

Savannas are defined as ecosystems in the seasonally dry tropics having a continuous grass layer and a discontinuous tree layer. They are a biome of global importance, covering and eighth of the global land surface, and accounting for much of African livestock production (Scholes and Archer 1997). However, within the limits of the circumscription 'savanna' a vast amount of variation in grass productivity and woody biomass is encompassed. Even given a particular set of environmental variables such as rainfall, temperature and soil nutrient status, a large range in tree cover is still possible (Sankaran *et al* 2005). This is due to the modifying influence of fires and herbivores, which have been shown to greatly alter tree cover (Higgins *et al* 2008, Asner *et al* 2009,). Given the large potential variation in cover at a particular savanna site, and the large browsing herbivores such as Elephant (*Loxodonta africana*) and Giraffe (*Giraffa camalparadaris*) occurring at high densities in many African savannas, we are presented with an ideal study system in which to investigate the influence of large herbivores on ecosystem structure; this system being the foraging of large mammalian ungulates on woody plants, termed browsing.

In this thesis I approach browser impacts on vegetation from a plant demographic perspective. The role of tree demography in determining the functioning of savannas has been extolled by Bond (2008). Most of the critical processes acting over the lifetime of a savanna tree are highly height dependent: competition with grass, aboveground mortality due to fire, the production of flowers and fruit, and vulnerability to herbivores (figure 1 a and b). Thus, within the limits set by a particular climatic and edaphic scenario, the inherently variable tree cover is determined largely by the outcome of these demographic processes. Moreover, here I apply the definition of a tree as being a woody plant that delays reproduction until reaching a particular height, usually around 2-3 meters in African savannas (figure 1a). Thus, by definition, height determines reproductive fitness.

Aside from measuring browser impacts on tree height, biomass is also sometimes used to quantify plant response. Much of the work attempting to document and describe general mechanisms of tree response to browsing has been done in the light of biomass loss and recovery (e.g. Senn and Haukioja 1994, Hester *et al* 2004, Palacio *et al* 2008). The conclusions reached about patterns and processes of plant biomass response to herbivory need not necessarily apply to height. Plant height does not change simply as a result of an increase or decrease in aboveground biomass. It is the distribution and orientation of biomass loss or gain that will determine height response. The foraging behaviour of a particular browser will determine the distribution of lost biomass and height impacts, and the growth induced by buds will determine the distribution of new biomass following browsing. The ability of browsers to impact plant height long after the browsing event through altering the activity of buds (sinks) has received little attention.

The reorganisation and altered growth pattern induced by browsing should be detectable in the architecture of affected trees. Modification of tree architecture by browsing ungulates is well documented (du Toit *et al* 1990, Danell *et al* 1994). The individual- or branch-scale measurements used to measure change in architecture induced by herbivore are, not, however amenable to measuring population or landscape scale changes. Large scale herbivore impacts are usually investigated by interrogating size-class distributions (Birkett and Stevens-Wood 2005, Asner *et al* 2009) or measuring growth over a fixed period of time (Pellew 1983a, b, Vila *et al* 2001). Using plant architecture to investigate browser impacts at large spatial scale has many advantages when compared to other methods. Architecture has great functional significance, influencing, for example: carbon gain, vulnerability to disturbance and competition (Cooper and Owen-Smith 1986, Tremmel and Bazzaz 1993, Pearcy and Valladares 1999). Moreover, a plants' architecture reflects a lifetime of growth and disturbance.

Questions and Aims

The interaction between large savanna ungulates and the trees upon which they forage represents one of the best available natural systems in which to investigate the importance of herbivory at the landscape scale. Yet this interaction remains poorly studied, with little understanding of the crucial factors determining the intensity of impacts. In the chapters that follow I explore critical links between browser foraging and tree demographic impact from a botanical perspective. The responses of plants to the loss of tissues will be linked to the repeated, regular disturbance of a browser's bite. I decompose the impact of a browser's bite into separate elements, and investigate how plant response to browsing depends on different botanical and browser-related traits. I draw specific attention to the novel insights gained from considering the impact of browsing on plant height rather than biomass. Finally, I use the architectural modification resulting from plants' responding to herbivory to assess the impact of megaherbivore browsers at the population scale in an African savanna. Population-level quantification of architectural modification represents a rapid novel method to measure browsers impacts at large scales. I use height-stem-diameter allometry as a measure of tree architecture, allowing me to relate changes in tree form to predictions derived assuming the absence of herbivores.

Ultimately, I aim identify the aspects of herbivore foraging and plant responses that most influence demographic impacts, but have been overlooked due to a focus on biomass responses. By considering these impacts and their consequences for population architecture it may be possible to better predict where and when browsers impacts will be severe and better measure them when they occur.

In chapter 2 I provide a general description of the study sites, providing relevant background information and setting the scene. The current environmental template and historical setting necessary for the interpretation of results is described.

In chapter 3 I build a simple model of a well studied megaherbivore-tree interaction with the aim of addressing the question: can traditional ideas of herbivore impacts based on biomass adequately explain observed browser impacts in a system where tree height and population structure is the appropriate response variable? I then make modifications to the linkage of herbivore consumption and plant impact, incorporating novel elements of the impact of a bite, including the responses of buds to disturbance.

In chapter 4 I explicitly test some of the insights gained from the modelling exercise regarding two aspects of browsing relevant to plant height: the loss of buds and the loss of biomass (bud-loss impacts vs. coinsumption impacts). Herbivory was simulated by experimentally clipping saplings *in situ*, in an attempt to address the question: what is the relative importance of these two aspects of browser impact for both plant height and total aboveground biomass?

In chapter 5, using two megaherbivore-tree systems as illustrative examples, I show that tree population architecture, measured using height-diameter allometry, is modified by browsers. I look at the particular nuances introduced by the traits of the browser and tree involved in each interaction and consider the observed modifications in light of general theories of plant allometry.

I end by considering the implications of my findings for herbivore-vegetation systems modelling and reflect on my results in the light of contemporary ideas of plant responses to herbivores. Finally, I suggest how these ideas can be further interrogated through experiments and monitoring.

Figures

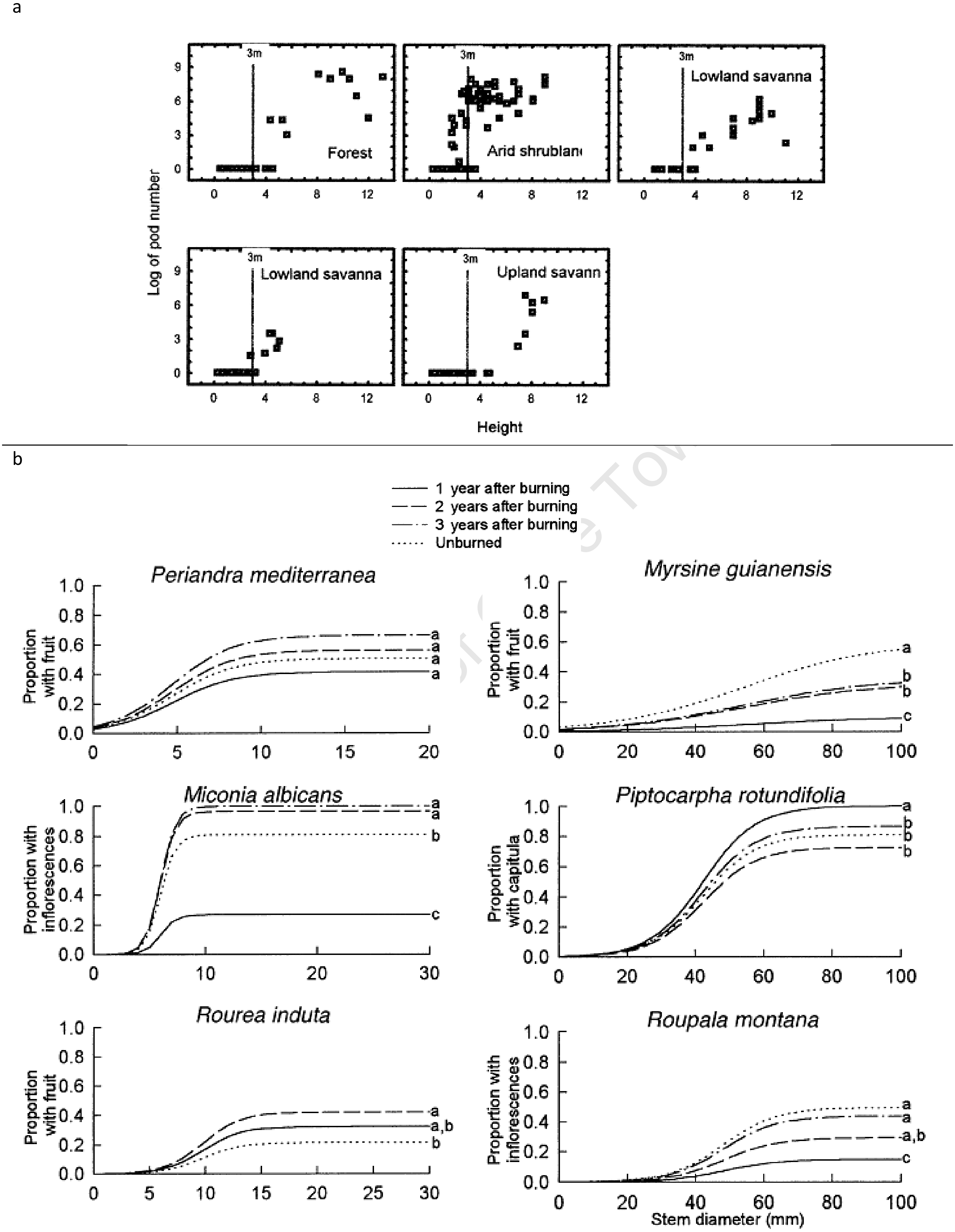

Figure 1. Height (or diameter) dependency of fruit and flower production for savanna trees. a) Shows pod production by height for *Acacia karroo* in South Africa (from Archibald and Bond 2003).b) Shows probability of producing flowers and fruit for 6 Brazilian cerrado tree species. Letters indicate significantly different groups (from Hoffmann 1998).

Chapter 2: Study Sites

Glenn R. Moncrieff

Introduction

All research described herein has been focussed on two savanna parks in South Africa: the Kruger National Park (KNP) and Hhluhluwe-iMfolozi Park (HiP), both replete with a large variety of mammalian herbivores. In order to contextualize the following chapters, or compare and consider their results amongst one another, it is necessary to have an understanding of each study site's template. The modelling study described in chapter 3 is done with reference to KNP and the field surveys of chapter 5 done within KNP and experimental enclosures therein. The experiments of chapter 4 were carried out within HiP. Here I will describe aspects of the history, abiotic template and ecology of these two parks relevant to the work conducted within them.

Kruger National Park

The Kruger National Park is located in the north-eastern corner of South Africa, spanning the provinces of Mpumalanga and Limpopo (Figure 1). Formal protection commenced when the Sabi Game Reserve was proclaimed in 1898. Since then the park has grown to encompass 18 989 km^2. Together with the adjacent Limpopo National Park (Mozambique) and Gonarezhou National Park (Zimbabwe), the Greater Limpopo Transfrontier Park covers approximately 35 000 km^2. Prior to the onset of formal protection game numbers throughout the region were low. Excessive hunting and the rinderpest epidemic of 1896 had decimated the once abundant wildlife (Mubunda *et al* 2003). After the proclamation of the national park in 1926, game numbers gradually increased as a result of protection and management interventions, such as the provision of artificial waterholes (beginning 1933) and fencing of the park (1959-1980). Protection of animals was so effective that concern began to arise that the park was becoming overpopulated. Elephant (*Loxodonta africana*) culling was thus introduced in 1967 with the management objective being to keep numbers around 7000 individuals (Whyte *et al* 2003). This policy continued until 1994 when a moratorium was called. Park managers have since sought other means to reduce elephant population numbers and their subsequent impact on vegetation and biodiversity, such as translocation, bringing down fences and promoting spatial heterogeneity in density (Whyte *et al* 2003).

Monitoring of animal numbers began in 1967 when an aerial census of elephant and buffalo number was conducted. Standardized annual aerial surveys of ungulates began in 1977 and continue to this day (Mabunda *et al* 2003, Owen-Smith and Ogutu 2003). The historical trends in population sizes of most large ungulates between 1965 and 1996 are presented in Redfern *et al* (2003), Owen-Smith and Ogutu (2003) and Whyte *et al* (2003). Most ungulates increased between 1965 and 1980, in association with increasing rainfall. Rainfall decreased between 1980 and 1996 and many ungulate population showed a concomitant decrease. Throughout this period giraffe (*Giraffa camelopardalis*) and blue wilderbeest (*Connochaetes taurinus*) population remained relatively stable, whereas zebra (*Equus burchelli*) were continuously increasing. Elephant numbers have been increasing since culling was halted in 1994, with the most recent (2008 - 2009) estimates putting the population at 13 353 individuals (Table 1). The giraffe population size is currently estimated to be 7091 individuals, the highest since monitoring began. Current population estimates for most large mammals are presented in table 1.

Kruger is positioned in the sub-tropical region of South Africa with hot, wet summers and mild, dry winters. The wet season lasts from October until April, and the dry from May until September. In general, rainfall decreases with deceasing latitude, though there is a region of comparatively higher rainfall around Punda Maria (22.68° S, 31.01° E). The lowest mean annual rainfall is received in the central and north-central region, where it falls below 400mm. The highest occurs in the Pretoriuskop (25.17° S, 31.26° E) area in the south-west, where mean annual rainfall exceeds 700mm. Rainfall is highly variable interannually, and a general trend of 10 years of extended dry conditions followed by 10 years of extended wet is observed (Tyson and Dyer 1978). January is the warmest month with mean maximum and minimum temperatures of 32.6° C and 20.6° C respectively in Skukuza (24.98 S, 31.60 E) in the south and 34.1° C and 20.6° C in Shingwedzi (23.10 S, 31.43 E) in the north. July is the coolest with mean maximum and minimum temperatures of 25.9° C and 5.6° C in Skukuza and 26.1° C and 7.4° C in Shingwedzi. The park is traversed by five perennial rivers running from the highlands in the west. From north to south these rivers are: the Levhuvhu, the Letaba, the Olifants, the Sabie and the Crocodile.

The park is divided along the north-south axis into two primary geological regions. Granite underlies most of the west and basalt the east (Figure 2). There are numerous gabbro intrusions in the east and a band of sedimentary rocks separates the granites and basalts across most of the park (Venter *et al* 2003). Strong catenal sequences are present on granite-derived soils. Upland soils are sandy with alluvium at the valley bottom. Often a distinctive high clay-high sodium zone is found at footslopes. No catenary sequences are apparent on the basaltic soils, which generally have a high clay content (>35%). Soil fertility and water holding capacity is high on basaltic soils, while granitic soils are infertile with low water holding capacity. Geological and edaphic patterns are reflected in the structure and composition of vegetation (Venter *et al* 2003, Figure 3).

Both broad-leaved and fine-leaved savanna types occur within KNP, with 75% being broad-leaved and 25% fine-leaved (Venter *et al* 2003). The broad-leaved savanna type occurs mainly on the granites and fine-leaved on the basalts. Grass productivity is higher on the basalts than the granites. This results in more frequent, higher intensity fires (Trollope and Potgieter 1986). This difference in fire regime contributes to there being higher tree cover on the granites. Kruger is further subdivided into 11 so-called land systems, with groupings based on geomorphology and vegetation patterns (Venter 1990, Figure 3). Dominant tree and shrub species on the southern granite land systems include *Combretum* spp., *Terminalia sericea*, *Dichrostachys cinerea* and *Euclea divinorum*. Common grasses include *Hyparrhenia filipendula*, *Panicum maximum*, *Themda triandra* and *Eragrostis* spp. North of the Olifants river *Colophospermum mopane* dominates the tree and shrub layer on both the granites and basalts, forming vast monodominant stands. In amongst the matrix of *C. mopane*, *Combretum imberbe, Combretum apiculatum* and *Acacia nigrescens* can be found. On the southern basalts *Acacia nigrescens* often dominates both the tree and shrub layer, with large *Sclerocarya birrea* trees commonly occurring. *Themeda triandra, Urochloa mossambicensis* and *Bothriochloa radicans* are common grasses. Across KNP tree cover varies widely, with some areas appearing as open grasslands and others as closed canopy woodlands. Within this overall vegetation patterning there is substantial variability in tree cover at fine-scales. Woodland patches can be juxtaposed with open, almost treeless savanna, with no apparent edaphic or abiotic differences to explain the contrast.

Park management has erected multiple animal exclosures and enclosures throughout its history in order to serve both management and scientific objectives. Three exclosures have been erected with the purpose of determining herbivore impacts on vegetation. These are the Nkuhlu, Letaba and Makhohlolo exclosure erected in 2002, 2002 and 1974 respectively. Nkuhlu and Letaba are both on the granite substrate and are 129ha and 139 ha respectively. Various combinations of fire exclusion and differing types of herbivore exclosures are included at each exclosure site. Extensive baseline data regarding vegetation structure and composition and soil characteristics were collected when these exclosure were constructed. The much smaller Makhohlolo exclosure is 2.4 ha and situated on the southern basalts in the Satara land system. The exclosure fence was breached in 1992 and only repaired in 2004. Thus it does not represent a site fully protected from herbivory; rather it has been subjected to greatly reduced herbivory. Until 2002 the fire regime within the exclosure was similar to that outside. In 2002 1.2 ha of the exclosure was allocated to a fire exclusion treatment. In addition to the three experimental exclosures described above KNP maintains three rare antelope enclosures. Various antelope species, locally rare in KNP, have been kept in these enclosures to bolster declining populations across the park. While these fenced areas do contain low numbers of animals, they serve as exclosures for all other large mammals. The N'washitshumbe enclosure is the most northerly, located on the northern basalts. This enclosure was erected in 1967 and extended in 1984, beginning at 254 ha and expanding to cover 302 ha. It has housed roan antelope (*Hippotragus equines*), Lichtenstein's hartebeest (*Alcelaphus lichtensteinii*) and sable antelope (*Hippotragus niger*), all grazer species. The number of individuals of each species has fluctuated in time, but none has exceeded 50 individuals. The Capricorn enclosure is on the northern basalts and was completed in 2002. It is 500 ha and contains roan antelope and tsessebe (*Damaliscus lunatus*). The Hlangwine enclosure is found in the southern granites near the Pretoriuskop restcamp. Erected in 1972, it is 220 ha and has contained roan, sable and tsessebe. The woody and herbaceous vegetation structure of N'washitshumbe, Hlangwine, Nkuhlu and Letaba and adjacent unfenced areas is described by Asner *et al* (2009). A fourth animal enclosure is present near the Satara rest camp on basalt derived soils. This 900 ha enclosure was completed in 2002 to house and breed Tuberculosis free buffalo. The enclosure has housed approximately 50-60 buffalo from 2002 until present (Burns *et al* 2009). An additional 9 ha within the buffalo enclosure is fenced to exclude all herbivores including the buffalo.

Table 1. The most recent (2008 – 2009) population size estimates for large mammals in Kruger National Park. (http://www.sanparks.org/parks/kruger/conservation/scientific/ff/biodiversity_statistics.php, accessed 15/04/2010)

Species		**Number**
Lion	*Panthera leo*	700
Leopard	*Panthera pardus*	1 000
Cheetah	*Acinonyx jubatus*	200
Wild dog	*Lycaon pictus*	350
Spotted hyaena	*Crocuta crocuta*	2 000
Elephant	*Loxodonta africana*	13 573
White rhinoceros	*Ceratotherium simum simum*	12 158
Black rhinoceros	*Diceros bicornis minor*	627
Burchell's zebra	*Equus burchelli*	20 868
Hippopotamus	*Hippopotamus amphibius*	3 000
Warthog	*Phacochoerus aethiopicus*	2 316
Giraffe	*Giraffa camelopardalis*	7 091
Buffalo	*Syncerus caffer*	37 462
Eland	*Taurotragus oryx*	300
Roan antelope	*Hippotragus equinus*	50
Sable antelope	*Hippotragus niger*	325
Greater kudu	*Tragelaphus strepsiceros*	8 045
Nyala	*Tragelaphus angasii*	>300
Bushbuck	*Tragelaphus scriptus*	>500
Waterbuck	*Kobus ellipsiprymnus*	5 000
Reedbuck	*Redunca arundinum*	300
Mountain reedbuck	*Redunca fulvorufula*	150
Blue wildebeest	*Connochaetes taurinus*	8 963
Tsessebe	*Damaliscus lunatus*	160
Impala	*Aepyceros melampus*	127 788

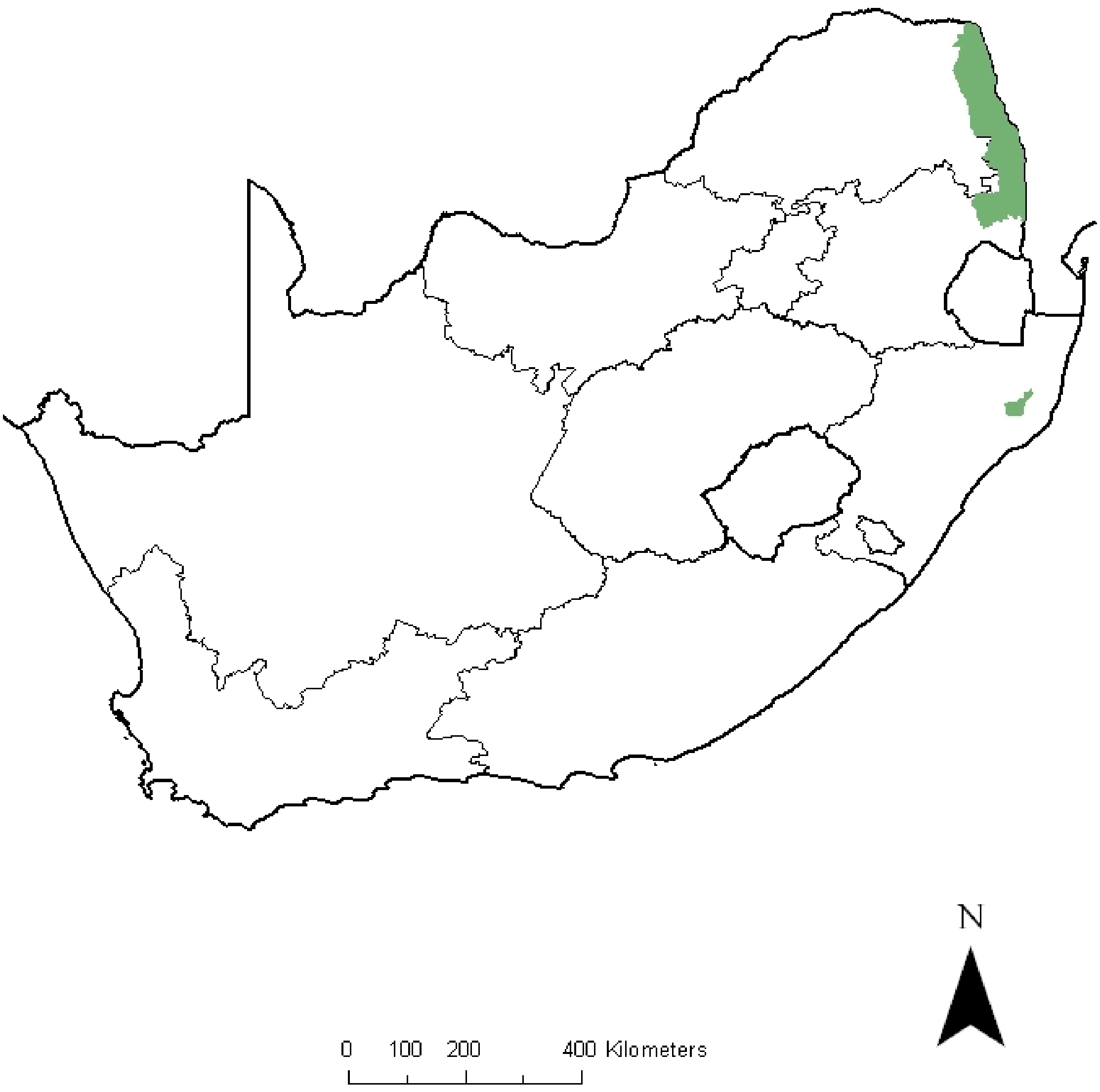

Figure 1. The location of Kruger National Park and Hluhluwe-iMfolozi Park within South Africa.

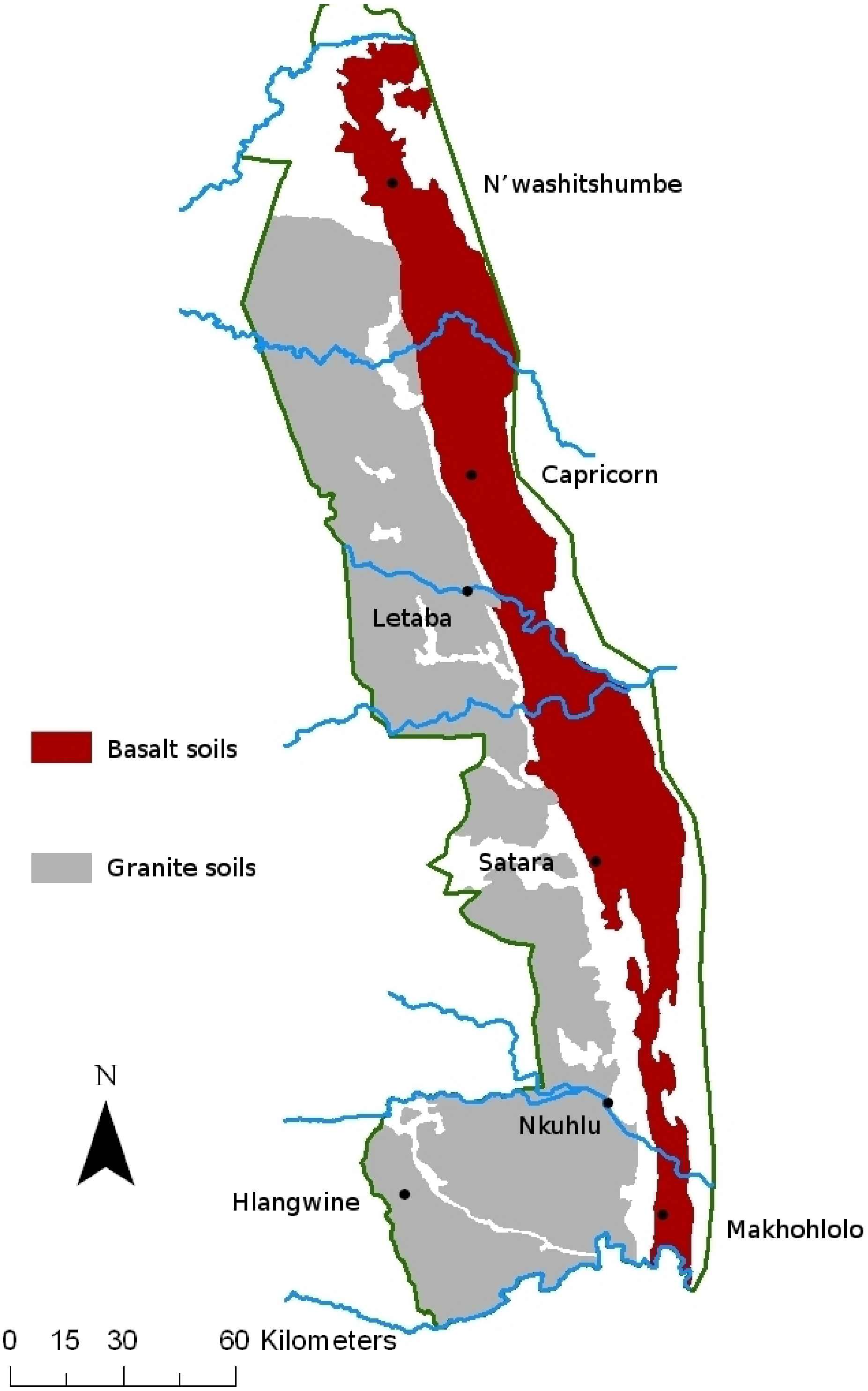

Figure 2. Kruger National Park, with the extent of the basaltic and granitic geological regions shown. The location of all animal exclosures and enclosures mentioned in the text is also shown.

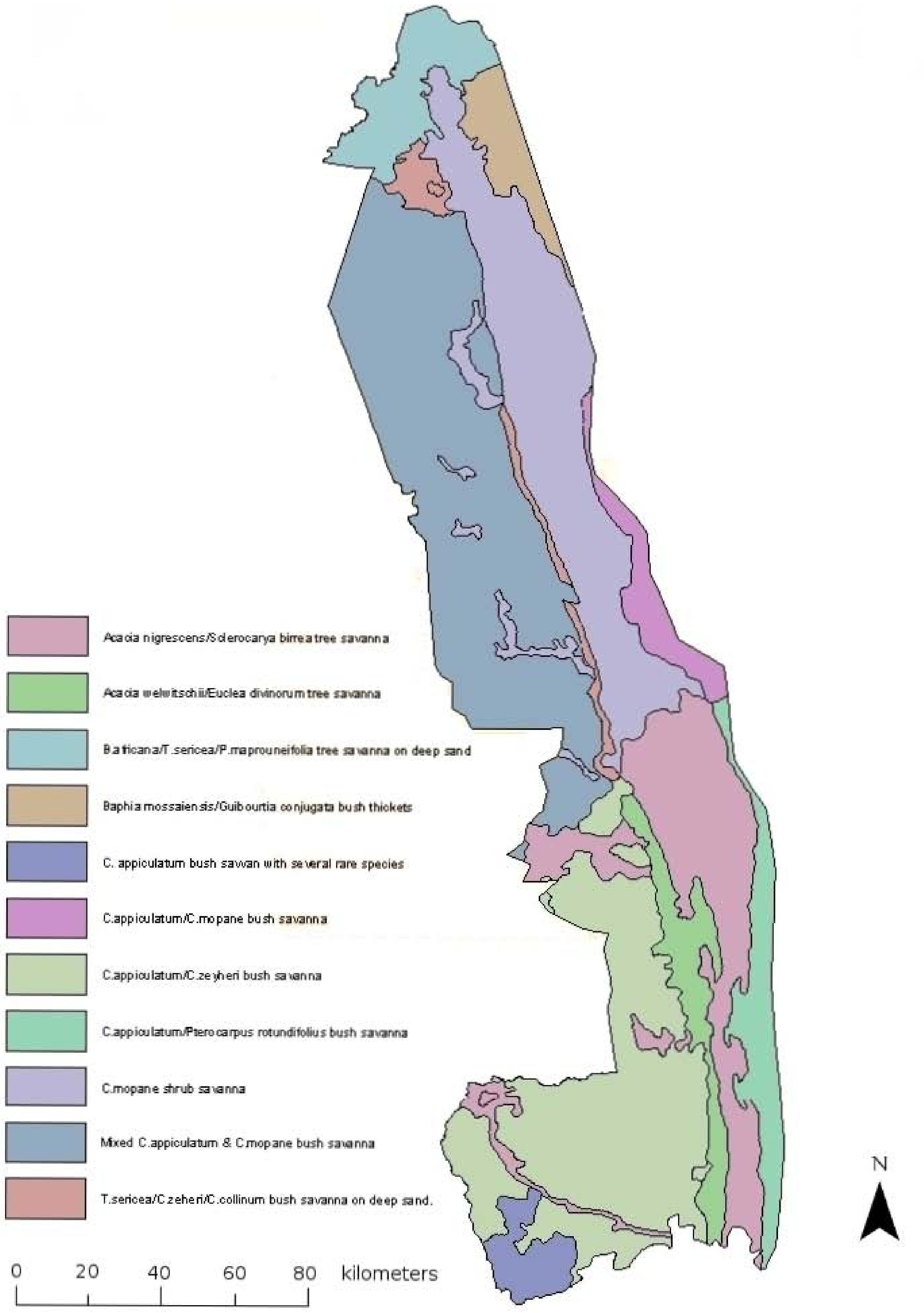

Figure 3. The vegetation of Kruger National Park. Vegetation types are classified into land systems as defined by Venter (1990). Adapted from http://www.sanparks.org/parks /kruger/conservation/scientific/maps/map_images/landsystem.jpg

Hhluhluwe iMfolozi Park

Hhluhluwe- iMfolozi Park is in the north of KwaZulu Natal, in the east of South Africa (Figure 1). Hluhluwe and iMfolozi were declared separately in 1895, and in 1982 the corridor area separating them was incorporated into these parks. Prior to the declaration of these parks humans used the area extensively (Staver 2008). Most notably, Shaka, king of the Zulus, declared the area around the confluence of the Black and White iMfolozi rivers his royal hunting ground. Before the park was created and in its early years, game numbers were low due to hunting and the rinderpest epidemic. Most large mammal populations remained low for the first half of the 20th century, as many ungulates were slaughtered to control *nagana* (livestock sleeping sickness) and predators were eradicated (Lincoln 1995) Animals continued to be culled after the *nagana* campaigns to prevent perceived overgrazing. Most populations have, however, increased since the 1950's or at least remained at similar levels (Staver 2008). Throughout the parks history, protection of threatened species has been a high priority. In particular, the white rhinoceros (*Ceratotherium simum simum*) has been assiduously protected from the threat of poaching, and the efforts of the park and its staff have almost certainly single-handedly saved this species from extinction.

HiP covers an area of approximately 89 000 ha (28°00' - 28°26'S, 31°43' - 32°09' E). HiP has a subtropical climate, with hot, wet summers and warm, dry winters. Mean maximum daily temperatures in Hluhluwe and iMfolozi are 39°C and 40°C respectively in summer and 32°C and 34°C in winter. Mean minimum daily temperatures in Hluhluwe and iMfolozi in summer are 15°C and 14°C respectively and 9°C and 6°C in winter. There is a strong rainfall gradient from the north-east (Hluhluwe) to the south-west (iMfolozi). Mean annual rainfall is 910mm in the north-east and 671mm in the south-west. Rainfall also varies with elevation, which is higher, with greater relief in Hluhluwe (maximum 540 m) than in iMfolozi (minimum 40 m). Multiple geological substrates are present, predominantly shales and sandstones with occasional dolerite intrusions.

A variety of vegetation types occur, heterogeneously distributed within the park. Whatley and Porter (1983) recognize savanna, grassland, thicket and forest biomes within the park and describe sub-types within these biomes (Figure 4). Thicket and forest are common in Hhluhluwe, whereas grassland and savanna are relatively more common in iMfolozi. A trend of grassland and savannas converting to thickets through woody plant encroachment has been observed in the park and throughout the region, and may be linked to global changes in atmospheric CO_2 (Wigley *et al* 2009). Common woody species in Hluhluwe include *Acacia karroo* and *Acacia nilotica* (in savannas) and *Euclea divinorum* (thickets). More arid adapted species are found in iMfolozi such as *Acacia nigrescens* and *Acacia tortilis*. *Dichrostachys cinerea* is common throughout the park.

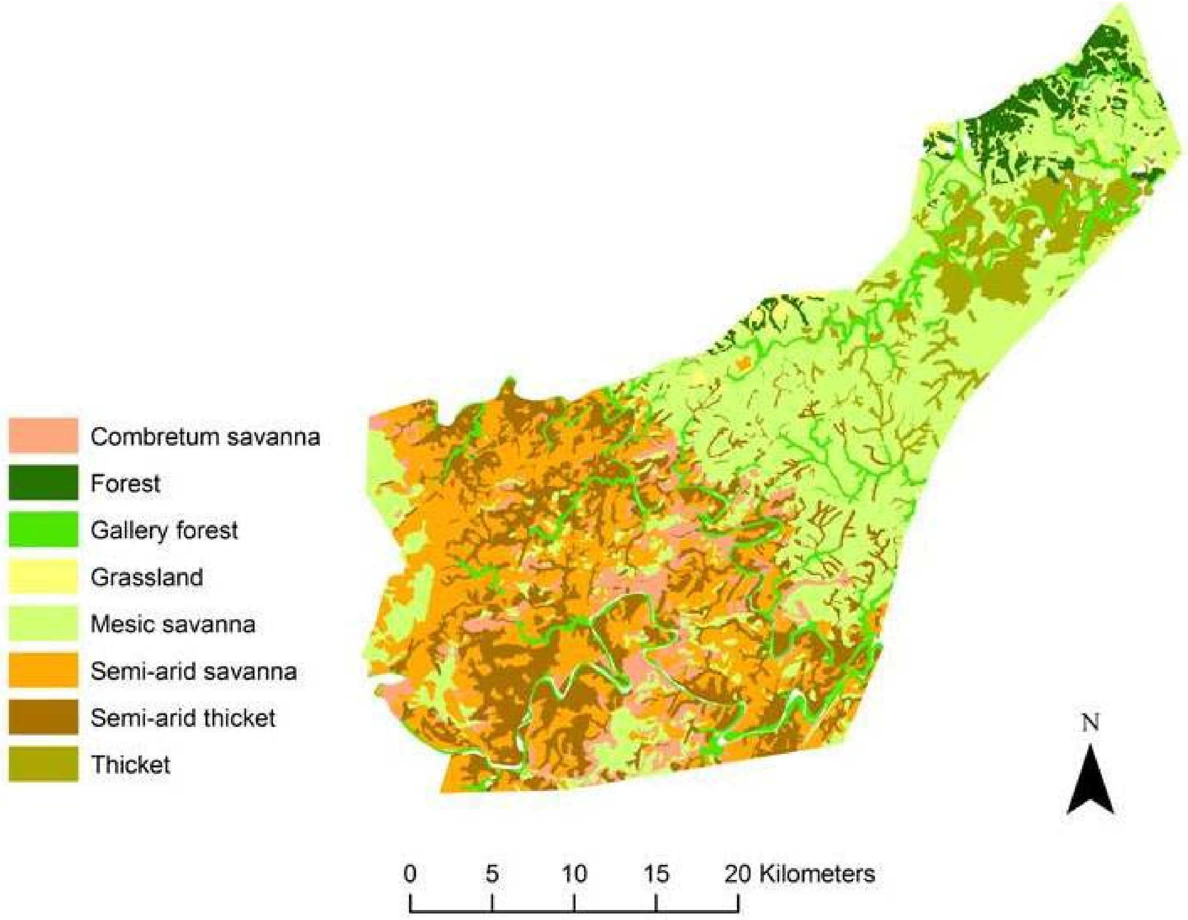

Figure 4. Hluhluwe-iMfolozi Park, with the distribution of vegetation types according to Whateley and Porter (1983).

Chapter 3: Beyond Biomass: linking browser consumption to demographic impacts on woody plants in savannas.

Glenn R. Moncrieff

Introduction

Models and theory concerning consumer-resource interactions traditionally use numbers or biomass to measure the size of resource pools. This is the approach used in the classical Lotka-Volterra predator-prey models, where the size of both the consumer and the resource populations are represented by numbers of individuals (Lotka 1925, Volterra 1926). Caughley (1976) extended this approach to modelling herbivore-vegetation dynamics in the form of elephants and tree populations in African savannas. Recently, Owen-Smith (2002 a,b) used systems of differential equations based on similar principles to Caughley (1976) to model herbivore-plant interactions, representing populations as biomass pools. In the context of herbivore-vegetation dynamics, these approaches may be appropriate for grass and grazers as the homogenous structure of a grass population is adequately described by its biomass. Characterising a population of woody plants as a pool of biomass does not, however, adequately describe the population. For woody plants, individual size is critically important in determining susceptibility to browsing and other disturbances (Trollope 1984, Shannon *et al* 2008). Thus, structured population models are required to accurately represent woody plant dynamics.

Existing structured models of woody plant-browser interactions usually represent browser impacts phenomenologically. Impacts on recruitment, transitions and mortality observed at a particular population density of browsers and plants are used to interpolate impacts in unobserved scenarios (Pellew 1983, Dublin *et al* 1990, Baxter and Getz 2005, Holdo 2007, Holdo *et al* 2009). This is unrealistic, as it has been shown that herbivore intake rates are nonlinearly dependent on factors such as bite size, the spatial arrangement of forage and the abundance of forage (Owen-Smith and Novellie 1982, Spalinger and Hobbs 1992, Hobbs *et al* 2003). Non-structured models do take into account this functional response of herbivore intake to forage (eg Owen-Smith 2002a, de Knegt *et* al 2008, Sheffer *et al* 2008).

These models, however, fall short of representing the response of vegetation to herbivory as anything other than directly proportional to the herbivore intake. Using this approach, the direct impact of herbivory on plants is easy to calculate: it is simply the amount of biomass consumed by the browser population. While this may be a reasonable assumption for biomass (but see Senn and Haukioja 1994, Gadd *et al* 2001, Hester *et al* 2004, Persson *et al* 2007), it may be less tenable for demographic impacts on plant populations. Is it reasonable to assume that the elongation of a branch and ultimately the height growth of a tree decreases linearly in response to the loss of biomass to browsers? Some models use allometries to translate modelled biomass pools into height structured populations (e.g. Scheiter and Higgins 2009). Using allometries when modelling browsing relies on the assumption that browsing simply removes biomass, and does not alter growth patterns following the browsing event. Thus the allometries used are fixed, and particularly, not affected by browsing (but see Holdo (2007)). However, allometries have been shown to vary in responses to a number of factors, including herbivory (Henry and Aarssen 1999, Henry and Thomas 2002, Levick and Rogers 2008, Kaianiemi and Lintunen 2008, Chapter 5 herein).

A theoretical framework, such as that which exists for herbivore intake response to plant abundance, is sorely needed for plant demographic response to browser intake. Progress is confounded by the fact that biomass consumed is often compensated for, and the degree of compensation has complex and difficult-to-predict relationships with factors such as resource abundance, competitive neighbourhoods and timing (Senn and Haukioja 1994, Hester *et al* 2004, Persson *et al* 2005, 2007). However, linking demographic responses to browser intake has not been as extensively explored. A tree is a highly organized, hierarchical structure built from fairly uniform, repeated components (branches, leaves, buds). Given the highly organized architectural structure of woody plants and the regular nature of an individual foraging event – a bite – generalities may emerge.

The focus here is on a particular system where a single browser maybe causing severe demographic impacts on a tree population. The tree layer in the Makhohlolo region of Kruger National Park (hereafter KNP) has been shown to be severely altered by the presence of browsers. Levick *et al* (2009) showed that within the confines of a 2.4 ha animal exclosure the tree layer was well developed with many trees taller than 8 meters and most at around 6 meters in height. Outside the exclosure, however, there were almost no trees taller than 5 meters, with most at around 3-4 meters in height. Giraffe have been shown to influence tree growth and population structure in the Serengeti ecosystem of east Africa (Pellew 1983), and also limit tree species distribution in South Africa (Bond and Loffell 2001). In KNP, Fornara and du Toit (2007, 2008) showed that giraffe browsing reduced growth rates of *Acacia nigrescens* Oliv. and resulted in strong architectural modification of browsed trees. Although elephants are often implicated in the alteration of savanna tree population structure and it is widely accepted that they have the potential to regulate the structure of ecosystems on large scales (Dublin *et* al 1990, Cumming *et al* 1997), the concentration of structural impacts on trees between 2 and 6 meters and the severely modified architecture of the dominant species in this region (*Acacia nigrescens*) suggests that giraffe are largely to blame (du Toit 1990, Fornara and du Toit 2007, 2008).

I begin by asking the question: can the direct impact of tree biomass consumption by giraffe account for observed structural impacts on the tree layer in the Makhohlolo region of KNP? This question is addressed by building a matrix model of a tree population parameterized to maximise the potential impacts of biomass removal. The impacts of giraffe are incorporated by linking their consumption and tree production to tree growth rates. Modelling the impact of giraffe alone is appealing because their foraging height range is beyond the reach of other browsers (du Toit 1990). Moreover, if it is assumed that fires of average intensity only kill trees below 2m, then - because giraffes feed largely above 2m –

these two factors can be assumed not to affect an individual tree simultaneously (Bond and van Wilgen 1996, Bond 2008). This allows the confounding effects of these two factors to be ignored in a model-based investigation.

The shape of the relationship between browser intake and demographic impact on tree population is perhaps the most challenging and novel aspect of this population-level approach. Initially it is assumed that demographic impacts are linearly related to consumption. The consequences of this assumption for giraffe effects on population structure are then explored. This relationship is investigated further by developing response curves for individual plant modules (branches) to browser intake, incorporating not only the loss of biomass or branch length, but also simple assumptions about the nature of the browsing disturbance and plant response. As the primary concern in this demographic approach is whole-plant growth and not branch elongation, the consequences of browsing on these branch level-phenomena for whole plant growth are explored with a simple whole-plant simulator. The purpose of this is to confirm that behaviours described at the branch level emerge when considering whole plants. The functions emerging from this analysis are then integrated into a matrix population model to explore the population level consequences of the novel processes incorporated.

Methods

In the models and formulae described below, parameters in the matrix model and whole-plant simulator appear as italicised lowercase Roman letters, while state variables are uppercase. Vectors are represented as bold lowercase Roman letters while matrices are bold uppercase. In the derivation of the relationship between browsing and plant growth response parameters used in the derivation of the relationship appear as lowercase Roman letters and those that appear in the final formulation as lowercase Greek letters.

Matrix population model

Model structure

The dynamics of a tree population in a 1 km^2 block foraged upon by giraffes is simulated with an annual time step. The model is designed and parameterized for the *Acacia nigrescens* – giraffe browsing system on the southern basalts of Kruger National Park, South Africa (KNP). *Acacia nigrescens* is the dominant tree species over large tracts of this landscape. The model is designed to address the question of whether biomass consumption alone can possibly account for the reported impact of browsers on the tree layer in the Makhohlolo region by choosing parameters that maximise the possible affect of giraffe consumption on tree population structure. This parameter choice ensures that biomass consumption can only be rejected as a possible cause of vegetation structural modification if it is extremely unlikely. The dynamics of only trees taller than 2m are simulated. Trees taller than 2m are approaching fire-invulnerable size and heights beyond the reach of most savanna browsers, excluding elephant and giraffe (du Toit 1990**)**. By excluding smaller trees the effect of fire, smaller browsers and seedling dynamics can be ignored in the model. The impact of elephant browsing is excluded from the model. Although elephants significantly alter the structure of the tree layer over larger areas of KNP (Shannon *et al* 2008, Asner *et al* 2009), the evidence for elephant browsing of tree canopies in the Makhohlolo region of Kruger National Park is significantly less than the obvious pattern of giraffe browsing (*pers. obs.*). Furthermore, inter-tree competition is also excluded from the model.

Tree population dynamics

The tree population is represented by a population vector **v** divided into 26 evenly spaced size classes between 2 m and 15 m, thus leaving a 50 cm interval for each size class. The high degree of subdivision is to facilitate comparison with size-class distributions reported for the region. Reported densities of trees above 2 m on the southern basalts of KNP range between 1000 and 10000 km^{-2} (Brits *et al* 2002). Densities of 1000 km^{-2} are not representative of the greater landscape as they are recorded from areas directly adjacent to water points. I chose an estimate of the average at 6000 trees km^{-2}. The modelled population size remains constant by replacing all trees dying as a result of background mortality with new recruits into the smallest size class. Background mortality is modelled by removing a constant proportion from each size class annually. Height growth, q_i, is described as a decreasing function of current height (Higgins *et al* 2000):

$$q_i = \left(1 - \frac{m_i}{h_{max}}\right) g_{max} \tag{1}$$

Where h_{max} is the maximum attainable height and g_{max} is the maximum growth rate. This formula is used to calculate the average height growth of trees in each size class by using the median height of the size class as m_i. This number was then converted into a transition probability by dividing by the size class interval:

$$t_i = \frac{q_i}{h_{int}} \tag{2}$$

Where t_i is the transition probability from size class i to size class i + 1 and h_{int} is the size class interval. These t_i form the transition vector, **t** , before modification by browsing.

Foraging

The dynamics of the browser population are not explicitly simulated. Rather, a fixed density is used to calculate vegetation impacts and the sensitivity of the model to the parameter explored. This is equivalent to assuming that the browser population visits the modelled patch at a fixed rate from a larger metapopulation. Giraffe densities reported for African savannas range between 0 and 3 giraffe km^{-2}, with approximately 0.25 km^{-2} in KNP (Pellew 1983, du Toit *et al* 2003). Giraffe are known to concentrate on the southern basalts, so it is likely that their densities are significantly higher here than the whole-park average (Redfern *et al* 2006). Giraffe population densities range between 0 and 3.5 km^{-2} in the model (Table 1 contains a full description of all parameters used and their sources). While it is assumed that giraffe are the sole browsers foraging above 2m, it cannot be assumed that all giraffe browsing occurs above two meters. The giraffe population is subdivided into males, females and juveniles, with 30%, 30% and 40% of the total population in each respective category. The maximum browsing height of males, females and juveniles is 5m, 4m and 3m, while the total proportion of foraging occurring above 2m is 1, 0.8, and 0.5 respectively (du Toit 1990). The average annual forage intake of the giraffe population is calculated by assuming an average daily intake of 2% of body mass, with a mean body mass of 1000 kg, 800 kg and 500 kg for males, females and juveniles respectively (Owen –Smith 1988). The maximum intake, l_i, in each vegetation height class is calculated as:

$$l_i = \left(w_m\, b_m\, s_m + w_f\, b_f\, s_f + w_j\, b_j\, s_j\right) z\, v \qquad i \leq 2 \qquad (3)$$

$$l_i = \left(w_m\, b_m\, s_m + w_f\, b_f\, s_f\right) z\, v \qquad 3 \leq i \leq 4 \qquad (4)$$

$$l_i = \left(w_m\, b_m\, s_m\right) z\, v \qquad 5 \leq i \leq 6 \qquad (5)$$

Where z is annual intake as a proportion of weight; v is the giraffe population density km^{-2}; w_m , w_f and w_j are mean weights for males, females and juveniles respectively; s_m, s_f and s_j are the proportions of the total population made up of males, females and juveniles; b_m, b_f and b_j are the proportions of browsing occurring above 2m.

Production

Foraging impacts the tree population by reducing growth rates. Transition rates between classes are reduced by foraging according to how much of the forage produced in a particular height stratum is consumed. Forage production is calculated by modelling tree canopies as cylinders and summing the production of trees across height strata. Canopy dimensions are based on tree height; canopy bottom height is 1/3 and canopy width is 2/3 of tree height. It is assumed that all forage is produced within 50 cm of the canopy edge and that giraffe can acquire all production within their browsing height range. The total amount of forage produced by each tree canopy, p_i, is then:

$$p_i = d\ \pi\, m_i \left[\left(\frac{c_w m_i}{2}\right)^2 (1 - c_h) - \left(\frac{c_w m_i - e}{2}\right)^2 \left(1 - c_h - \frac{2e}{m_i}\right)\right] \tag{6}$$

Where d is the production in kg.m^{-3}, c_w is the canopy width as a proportion of height, c_h is the canopy bottom height as a proportion of height and e is the depth of forage production.

Using the simplifying assumption that total forage is uniformly distributed vertically along the canopy, the distribution of forage across height strata is calculated. First, the number of height strata over which the production of size class i is distributed is calculated:

$$n_i = \left\lceil \frac{m_i - \frac{h_{int}}{2} - c_h m_i}{h_{int}} \right\rceil + 1 \tag{7}$$

For $m_i c_h > u$, where u is the height at which trees enter the model

$$n_i = \left\lceil \frac{m_i - u}{h_{int}} \right\rceil \tag{8}$$

For $m_i c_h \le u$

The lowest stratum in which forage is produced, j_{min}, by size class i for which $m_i c_h > u$ is:

$$i, j_{min} = \left\lceil \frac{m_i c_h - u}{h_{int}} \right\rceil \tag{8}$$

The forage produced in this stratum is:

$$f_{i,j_{min}} = \left[\frac{h_{int} - \left(m_i c_h - \left\lfloor \frac{m_i c_h}{h_{int}} \right\rfloor h_{int}\right)}{(1-c_h)\, m_i}\right] p_i \tag{9}$$

The forage produced in highest stratum, j_{max}, reached by size class i is:

$$f_{i,j_{max}} = \left(\frac{\frac{h_{int}}{2}}{(1-c_h)\, m_i}\right) p_i \tag{10}$$

The remaining forage produced by size class i above escape height is distributed equally among height strata:

$$f_{i,j} = \frac{p_i - f_{i,j_{min}} - f_{i,j_{max}}}{n_i - 2} \tag{11}$$

For $j_{min} < j < j_{max}$ and $m_i c_h > u$ and $n_i > 2$

$$f_{i,j} = \frac{\left(\frac{m_i - u}{(1-c_h)\, m_i}\right) p_i - f_{i,j_{max}}}{n_i - 1} \tag{12}$$

For $1 \leq j < j_{max}$ and $m_i c_h \leq u$ and $n_i > 1$

The total production in each height strata is then calculated:

$$\mathbf{h} = \mathbf{F}\mathbf{v} \tag{13}$$

Where **F** is a matrix of production by a single individual of each height class across height strata and **v** is the tree population vector. A diagrammatic representation of the calculation of production is provided in figure 1.

Browser impacts

After the total forage consumed and produced in each height strata is calculated, the proportion production consumed is:

$$\mathbf{r} = \min\left(\mathbf{1}, \frac{\mathbf{l}}{\mathbf{h}}\right) \tag{14}$$

Where **l** is a vector of consumption across height strata.

Transitions between height classes are assumed to be dependent only upon growth occurring at the top of trees. Transition rates are thus scaled according to the remaining production in the transitioning size class i.e. *browser impacts on transition rates are modelled as linear functions of browser intake*. The browser altered transition probability matrix becomes:

$$\mathbf{U} = \mathrm{diag}(\mathbf{t})\big(\mathbf{I} - \mathrm{diag}(\mathbf{r})\big) \tag{15}$$

Where $\mathbf{t}$ is the unaltered transition vector and **I** the identity matrix.

Finally mortality is included and the final transition probability matrix acquired:

$$\mathbf{Y} = \mathbf{U}\,\big(\mathbf{I} - \mathrm{diag}(\mathbf{o})\big) \tag{16}$$

$$\mathbf{Y}_{i=1} = \mathbf{o}^{T} \tag{17}$$

Where $\mathbf{o}$ is the mortality vector.

Simulations

The model is implemented in R 2.9.0 (R foundation 2009). The initial tree population structure is determined using the right eigenvector corresponding to the dominant eigenvalue of the Lefkovitch matrix constructed using only the fundamental transition and mortality rates without browser influence (Caswell 2001). Each year the population projection matrix is recalculated, updating the distribution of forage production and consumption. The model is run for 500 years or until the population reaches a steady, stable state. The temporal trajectory of population structure is followed by recording the mean height of trees and Simpson’s index of dominance annually. Model sensitivity to a range of giraffe densities is tested. The influence of the shape of the relationship between giraffe intake and tree growth response is further examined by using both the linear relationship described above and a mechanistically determined non-linear relationship derived below.

Validation

Model output is assessed for qualitative agreement with observed changes in vegetation structure following herbivore exclusion. The results presented in Levick *et al* (2009) for the vegetation in and surrounding the 2.4 ha Makhohlolo exclosure following 34 years of partial herbivore exclusion are used. The giraffe densities at which modelled impacts on vegetation begin to resemble the impacts observed by Levick *et al* (2009) are then compared to actual densities to assess whether they represent realistic scenarios.

Plant growth response to browser consumption – implications for height growth

As a first approximation, assuming a linear relationship between browser consumption and growth impact on tree growth appears reasonable. When studying the impacts of browsers on plant fitness if biomass is used as a proxy for fitness, the relationship between browser intake and plant impact is essentially linear (for every gram of biomass eaten, a gram of biomass is lost). This linear relationship is then modified by the plant's response to the loss of biomass; termed compensation. In many environments, however, fitness is far more closely related to plant height than biomass (particularly savannas, see Hoffmann 1998, Archibald and Bond 2003). For example, trees that delay reproduction until they reach a particular height will fail to reproduce if browsers prevent them from growing taller. How might the relationship between intake and impact change when browser impact on height is considered, rather than biomass?

The growth in length of a population of branches with consumption of growth by browsers can be expressed as:

$$g(p) = m(\alpha - p\omega) \tag{18}$$

where α is the total growth within a season per branch (cm), m is the number of branches, p is the probability that a branch is bitten and ω is length removed in a single bite (cm).This gives the total growth of all branches. If the growing season is divided into N time-steps, equation 18 becomes:

$$g(p, N) = \frac{\alpha}{N}m - \frac{p}{N}\omega m \tag{19}$$

where $g(p, N)$ now represents growth within each period of the growing season. Total growth within the season is the sum of growth within each period, which is simply equation 18. Thus, considering that growth and browsing do not occur in a single, instantaneous pulse does not change the prediction of herbivore impact *ie.* impacts remain linearly related to intake. Consider then a single branch ($m = 1$), growing from an apical bud. It then grows within a season divided into $N = 1$ periods according to equation 19. However, within a season, if the branch is bitten the apical bud is lost and growth of that particular branch ceases (at first assume for the rest of that season). Thus if the season is divided into N periods, a branch bitten in a given period will be unable to grow in subsequent periods within the growing season. In the first period growth is described by equation 19 with m =1, however, for all subsequent periods there is a certain probability that the branch bud has been lost and thus subsequent growth cannot occur. The probability that the potential for growth remains in period 2 is given by:

$$f(p, N) = 1 - \frac{p}{N} \tag{20}$$

Thus the growth in each subsequent period is limited by the probability that the potential for growth no longer remains. This potential becomes larger for latter periods. The sum of growth within each period can thus be modelled by the following series:

$$a + ar + ar^1 + ar^2 + \cdots + ar^{N-1}$$

where a is equation 19 and r is equation 20. This is a geometric series, with the sum of N terms represented by:

$$g(p) = \sum_{k=0}^{N-1} \left(\frac{\alpha}{N} - \frac{p}{N}\omega\right)\left(1 - \frac{p}{N}\right)^k \tag{21}$$

This simplifies to:

$$g(p) = (\alpha - p\omega)\frac{\left[1 - \left(1 - \frac{p}{N}\right)^N\right]}{p} \tag{22}$$

Here, the range of p depends on the bite size ω and growth α. p Can be reexpressed as a function of ω, α and a new nondimensional parameter τ that varies from 0 to 1 and represents the proportion of growth removed:

$$p = \frac{\tau\, \alpha}{\omega} \tag{23}$$

Equation 22 then becomes:

$$g(\tau) = \alpha(1 - \tau)\frac{\left[1 - \left(1 - \frac{\tau\, \alpha}{N\, \omega}\right)^{N}\right]}{\frac{\tau\, \alpha}{\omega}} \tag{24}$$

Now impacts are not linearly related to intake, as would be expected for biomass. Regardless of N the total growth within a season is constant if $\tau = 0$ and the total probability of the branch being bitten is constant. Indeed, setting $N = 1$ (*ie*. all growth and consumption occurs in a single, instantaneous pulse) in equation 24 we arrive back at equation 19 with $m = 1$, where impacts remain linearly related to intake. In a realisitic implementation $N \gg 1$. This expression can be generalized to the case where the removal of the apical bud resistricts growth for a variable fraction of the period over which growth is defined, until a new bud can establish:

$$g(\beta, \tau) = \alpha(1 - \tau)\left(1 - \frac{\tau\, \alpha}{N\, \omega}\right)^{\beta N} \tag{25}$$

Where β is the fraction of time it takes to re-establish the growing tip in units of time over which α is defined. Both equation 24 and 25 consist of two term: the first is a linear term, describing the direct impact of *consumption* (τ) on growth; the second term is nonlinear and describes the impact of *bud-loss* on growth. This second term is a multiplier of the first and describes the fraction of the growth not consumed that is translated into extension. A simplified diamgramtic representation of these bud-loss impacts and biomass-loss impacts is shown in figure 2.

Equation 25 describes not only the dependency of plant response to browsing as a function of plant dependent traits (α, β), but also a specific attribute of the browser, bite size, ω. Integrating over τ, we obtain an expression for the impact of browser consumption, independent of intake, as a function of ω:

$$h(\omega) \; = \; \int_0^1 N \left(\frac{\alpha}{N} - \frac{\tau \; \alpha}{N}\right)\left(1 - \frac{\tau \; \alpha}{N \; \omega}\right)^{\beta N} \; d\tau \qquad (26)$$

$$= \frac{2 \, N^2 \, \omega^2 \, \left(1 - \frac{\alpha\tau}{N\omega}\right)^{N\beta+1}}{\alpha(2N\beta + 1)} - \frac{N\omega \, \left(1 - \frac{\alpha\tau}{N\omega}\right)^{N\beta+1}}{N\beta + 1} - \frac{2 \, N^2 \, \omega^2 \, \left(1 - \frac{\alpha\tau}{N\omega}\right)^{N\beta+2}}{\alpha(2N\beta + 4)} \qquad (27)$$

Incorporation into population model

The dependence of growth on browser consumption in the population model is linear *i.e.* browsing decreases growth in direct proportion to consumption. However, the form of the relationship between consumption and impact described by equations 24 and 25 is non-linear. Equation 15**,** expressing the form of the dependence of growth on consumption in the population model, is thus modified to incorporate this insight. The form of equation 24 is used for simplicity, but it is simply a special case of equation 25. Equation 15 thus becomes:

$$u_i = \left(\frac{t_i}{N} - \frac{t_i \; r_i}{N}\right) \frac{\left[1 - \left(1 - \frac{t_i \; r_i}{N \; \omega}\right)^N\right]}{\frac{t_i \; r_i}{N \; \omega}} \qquad (28)$$

and the transition probability matrix is formed:

$$\mathbf{U} = \mathrm{diag}\;(\mathbf{u}) \qquad (29)$$

Scaling from branch-level responses to whole-plant growth

Before applying models of individual branch functional response to whole-plant growth in a matrix population model, validation of the assumption that the functional relationships explored above hold true for hierarchically organized, vertically structured populations of reproducing branches, or trees, is needed. Although equations 24 and 25 have been developed by considering the dynamics of growth and browsing on a single branch, they can also be thought of as describing the height growth of a whole tree. Height growth is a result of the elongation of the leading branch at the top of a tree. If this leading branch is browsed with a certain probability τ, and its growth curtailed due to the loss of its bud, the time between the browsing event and a new branch becoming the leader and continuing height growth can be thought of as the parameter β in equation 25.

This assertion, that the growth and response to browsing of a whole tree, follows the same form as that of its branches, as described in equation 24 and 25**,** is tested by implementing a 1D plant growth simulator following the growth, survival and reproduction of a population of branches through time. Each annual time step is divided into N periods in which growth, browsing, new branch production and self-pruning occur. For simplicity, initially it is assumed conditions among all time steps are uniform (i.e. aseasonal), no compensation for lost biomass occurs and browsing does not affect the branching process itself, only individual branch growth.

Growth and new branch production

Every branch capable of growth grows by a fixed branch length, a, each year, independent of the number of branches on the tree. Length increase is equivalent to height increase because the model is 1 dimensional. The growth, h, that occurs in each period n of the total N periods is:

$$h = \ a/N \tag{30}$$

New branches are produced along parent branches at a fixed internode distance, z. Every time the length of a terminal branch segment exceeds z two new branches of length 0 are added to the model with their starting height calculated as their height of attachment on the parent.

Browsing and self-pruning

Browsing is modelled as removing a fixed length, z, from affected branches, simulating repeated biting. The annual number of bites taken, b, is proportional to the size of the whole plant:

$$b = \ q\,T \tag{31}$$

Where q is the proportionality constant and T is the total number of branches. The range of q is between 0 and a/w, where w is the bite size. When $q = a/w$, all growth on every branch is consumed. Using this formulation allows the intensity of browsing to remain independent of plant size and constant per branch, as in the formulation of derived response curves. The actual number of bites occurring in each time period n is calculated from b by dividing by N. Branches previously unbrowsed in a given year are randomly selected for browsing first, after which, if more bites are required, previously browsed branches are randomly selected. Browsing cannot reduce the length of a branch to below the point of attachment of daughter branches. Once a branch has been bitten it is flagged and its growth is curtailed for a number of times steps until the apical bud can re-establish. It is assumed that growth is halted for the remainder of the year, beginning again the following year, as described in the derivation of equation 24.

Branches are pruned off to improve the computational efficiency of the model. The pruning process does not affect the outcome of browsing impacts, as the browsing intensity is calculated as a proportion of the number of branches. Branch pruning occurs when branches are attached below a critical point along the parent axis given by:

$$k_i = s\, V_i \tag{32}$$

Where k_i is the critical point of attachment, s is the proportion of a parent axis along which it retains branches and V_i is the length of the parent axis. When a daughter branch is pruned off, it and all of its daughter branches are removed from the model.

Adding seasonality and varying the branching process

An additional layer of complexity is added to the model by introducing seasonality. This is achieved by forcing all annual growth as described above to occur within the first half of each year. In the dry season, browsing continues to occur while growth does not. Browsing has been shown to alter the production of branches, often decreasing the internode length between branches (du Toit *et al* 1990, Gadd *et al* 2001). Thus, in this implementation internode distance decreases from 20cm to 10cm in line with observations of *Acacia nigrescens* (du Toit *et al* 1990). This is achieved by reducing the amount of growth required proximal to the last branching point of branches flagged as being browsed within a given year.

Implementation

At the beginning of each intra-annual time step branches are first grown, after which browsing occurs. Following this, new branches are produced if necessary and finally self-pruning occurs. The model begins with a single branch of length and height 0, the plant is allowed to grow for 8 years without browsing after which multiple bites proportional to the number of branches occur. Model sensitivity to the number of times steps taken within a year is explored in order to ensure convergence occurs with increasing sub-division. The form of the relationship between consumption (the number of bites) and bite size is explored and comparisons to predictions based on the models of individual branch growth made. The model is run for 30 years after which the final tree height is recorded. The model is implemented in R 2.9.0 (R foundation 2009).

Results

The behaviour of the derived function for growth response to intake is presented first. The matrix model results are then shown, comparing results when using the simple linear response to browsing and the derived response.

Branch-level responses

Modelled branch growth (eq. 24) for varying degrees of subdivision of the period over which growth is defined (integer values of the parameter N) is presented in figure 3. Growth decreases linearly with increasing consumption when N =1. This is expected, as when N =1 all growth and consumption occurs in a single time period, and there are no periods following browsing for bud-loss impacts to arise. When N =2 or 3 the equation is inconsistent with reality, predicting negative growth for N =2 or lower impacts on growth at high levels of consumption. These parameter values do not however, reflect any situation near reality. As N grows larger the equation converges and stabilizes. A situation where N is large is a better representation of reality, with the growth season divided into many small steps. A nonlinear response of branch extension to browser consumption is thus expected when using equation 24. The effects of browser consumption are far greater than if it is assumed that impact on growth is directly proportional to consumption. This is due to the modification of the branch growth function; which simulates a loss of growth for a period following browsing on a branch as a result of bud loss.

The effect varying the proportion of the growing season over which growth is curtailed by bud loss (β) on the impact of browser consumption (τ) on growth (eq. 25) is shown in figure 4. For $\beta = 1$ it behaves similarly to equation 24, with growth curtailed for a single growth season following browsing. As $\beta \rightarrow 0$ growth decreases less rapidly with increasing consumption and the relationship approaches linearity. When $\beta = 0$, a browser's bite has no effect on subsequent growth, and thus the relationship is linear. Only in the special case of $\beta = 0$ are growth impacts of browsing linearly related to consumption. For all other cases, there is a degree of nonlinearity, with impacts greater than expected for a linear relationship.

The effect of bite size on browser impact, evaluated using equation 27, is shown in figure 5. The simple interpretation of this figure is that $h(\omega)$ is the area under the curve in figure 4 when $\beta = 1$. Lower values of $h(\omega)$ indicate higher browser impacts over all possible levels of consumption. When bite size (ω) is equal to the total growth of a branch there is no difference between the shape of equation 25 and the linear form and browsing impacts are at their minimum. As bite size decreases, impacts increase, with $h(\omega)$ eventually becoming 0 when bite size is infinitely small. This analysis thus suggests, somewhat unexpectedly, that for any given level of browser intake, impacts on plant growth will be higher for smaller bite sizes (see discussion).

Whole-plant growth

The final height of the simulated tree after 30 years of growth is shown in figure 6. The pattern of growth achieved for whole-plants under a range of browsing intensities and time periods within a season is very similar to the form predicted for individual branches when browser impact is nonlinearly related to consumption, as a result of the inclusion of bud-loss impacts (eq. 24). When all growth and browsing occurs in a single time period (N = 1), the relationship between consumption and growth achieved is essentially linear, although growth declines slightly slower than expected initially. However, as the number of periods a season is subdivided into increases, the relationship becomes increasingly nonlinear, with greater impacts on growth for a given level of consumption. The relationship converges for N > 6. When seasonality and varying internode distances are included in the model, these same relationships among consumption and growth achieved once again emerge despite the added complexity (figure 7). The patterns in figure 7 appear noisier than those of figure 6; this is because the data in figure 6 result from the average of 10 simulations and those of figure 7 from a single simulation due to computational limitations. The impacts of bite size on the shape of the relationship between growth achieved and consumption are in accordance with predictions for individual branches, with smaller bite sizes resulting in greater impacts for a given level of consumption (figure 8).

Impacts on population structure

The stable tree population structure in the absence of giraffe shows most individuals in the size classes between 2 and 8 m (figure 10, 11; 0 giraffe . km^{-2}). The number of individuals per size class declines slowly initially, then rapidly declines to a minimum of 10 trees in the 15 – 15.5m size class. Mean population height and structural diversity (shown using a rescaled Simpsons index) remain unaltered through time (figure 9, 10; 0 giraffe . km^{-2}).

When using the assumption that browser impact is linearly related to consumption, little impact on population structure through time is evident when giraffe densities vary between 0.5 and 2 km^{-2} (figure 9). Mean population height and structural diversity are very similar to that observed when no giraffe are present. The stable population structure reached after 500 years varies little between giraffe densities of 0 and 2 km^{-2} (figure 10). More individuals are present in the smaller size classes when densities reach 2 km^{-2}, however, trees taller than 3.5 m are little affected. When densities reach 2.5 km^{-2} giraffe consumption rapidly limits transitions to taller size classes and the population becomes bottlenecked, with no structural diversity as all individuals are in the smallest size class (2-2.5 m) with no tall trees present.

When a nonlinear function incorporating bud-loss impacts (eq. 28) is used to link giraffe consumption to plant growth impacts, top-down control of vegetation structure occurs at lower giraffe densities. When density is 0.5 giraffe km^{-2} there is little difference in the stable population structure from the case when no giraffe are present and very little change occurs through time (figure 11,12). At 1 giraffe km^{-2}, although many more trees are in the smaller size classes and the number of large trees has also decreased substantially, there are still many individuals in the large size classes. However, when densities of 1.5 giraffe km^{-2} or greater is used, all trees are rapidly bottlenecked into the 2-2.5 m size class, with none any taller. Thus, modelled giraffe densities required to generate major structural impacts on the tree population (as observed by Levick *et al* (2008)) are almost halved when bud-loss impacts are incorporated into the relationship between intake and impact.

Figures and Tables

Table 1. Model variables and parameters with their respective sources.

Parameter	Symbol	Units	Value	Source
Tree density		Individuals . km^{-2}	6000	Brits *et al* (2002)
Escape height	u	cm	200	du Toit *et al* (1990), Trollope (1984)
Canopy bottom height	c_h	proportion of height	1/3	
Canopy width	c_w	proportion of height	2/3	
Foliage depth	e	cm	50	Pellew (1983b)
Forage Production	d	kg. m^3	0.5	Pellew (1983b)
Forage produced by a single individual in size class *i*	p_i	kg		
Forage produced by a single individual in size class *i* in height strata *j*	$f_{i,j}$	kg		
Number of trees in size class *i*	V_i	trees	0 - 6000	
Proportion of production consumed in height strata *i*	r_i	proportion	0 - 1	
Total production in height strata *i*	h_i	kg		

Size class interval	h_{int}	cm	50	
Median size of size class *i*	m_i	cm	225 - 1475	
Maximum tree growth rate	g_{max}	cm . yr^{-1}	30	Pellew (1983a,b), Birkett and Stevens-Wood (2005), Fornara and du Toit (2007).
Maximum tree height	h_{max}	cm	1500	
Transition probability	t_i	probability	0 – 0.51	
Growth rate	q_i	cm . yr^{-1}	0 – 25.5	
Mortality	o_i	Proportion of size class . yr^{-1}	0.03	Baxter and Getz (2005), Higgins *et al* (2000), Le Houérou (1980)
Maximum foraging height	f_m , f_f , f_j	cm	500, 400, 300	du Toit (1990)
Occurrence of browsing above escape height	b_m , b_f, b_j	Proportion of total browsing	1, 0.8, 0.5	
Giraffe intake in size class *i*	l_i	kg		
Giraffe population structure	s_m , s_f , s_j	Proportion of population	0.3, 0.3, 0.4	Pellew (1983c), Owen-Smith (1988)
Giraffe Weight	w_m ,w_f ,w_j	kg	1000, 800, 500	Owen-Smith (1988)

Annual intake	z	proportion of weight . year^{-1}	7.3	Owen-Smith (1988)
Giraffe density	v	Individuals . km^{-2}	0 - 3	Redfern *et al* (2003), du Toit *et al* (2003)
Browser altered transition probability	$u_{i,j}$	probability	0 – 0.51	
Final transition probability	$y_{i,j}$	probability		
Growth rate	a	cm . yr^{-1}	25	Pellew (1983a,b), Birkett and Stevens-Wood (2005), Fornara and du Toit (2007).
Internode distance – unbrowsed branches	z_u	cm	20	du Toit *et al* (1990)
Internode distance – browsed branches	z_b	cm	10	du Toit *et al* (1990)
Bite size	w	cm	0 - 25	Fornara & Du Toit (2007), Pellew (1983b)
Number of time steps in a year	N		1 - 8	
Proportion growth consumed	q	Proportion	0 - 10	
Proportion of parent axis along which branches retained	s	Proportion	0.5	
Growth in period *n*	h	cm		
Number of bites taken per branch	b	Bites. yr^{-1}		

Number of branches	T			
Length of branch i	V_i	cm		
Critical attachment point	k_i	cm		

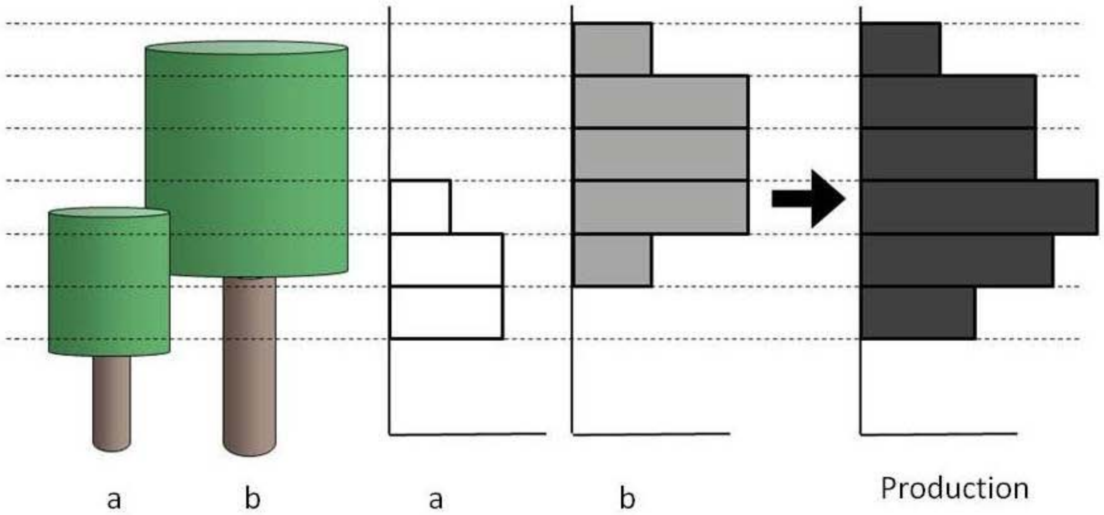

Figure 1. A diagrammatic representation of the calculation of forage production across height strata. The production of tree *a* within each height strata is added to that of tree *b* to calculate the total production per height strata.

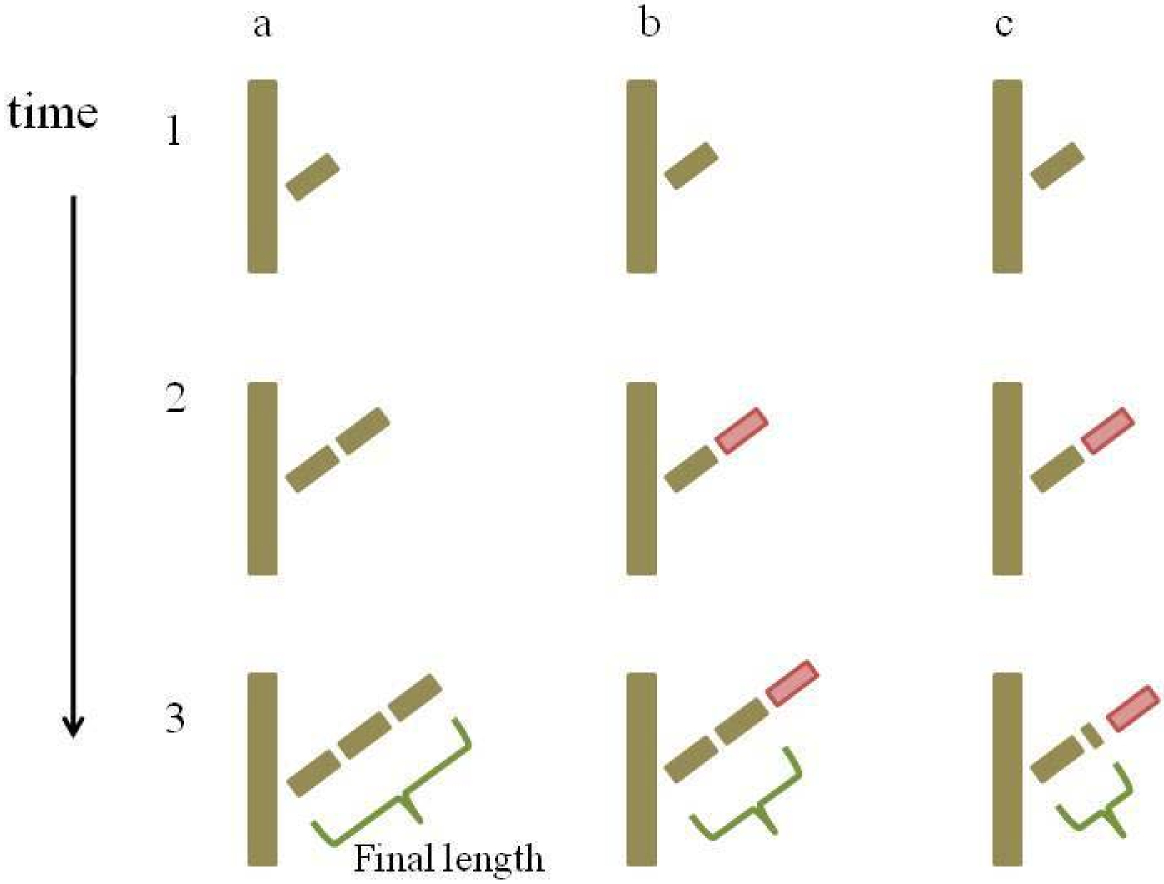

Figure 2. Diagrammatic representation of branch growth impacts from biomass-loss and bud-loss. Rows represent the progression of time and columns *a* – no browsing, *b* – biomass-loss impacts only, and *c*) – biomass- and bud-loss impacts. In *a* growth proceeds regularly and continuously though time. In *b* browsing occurs at time 2, with the length removed shown in red, but growth continues unaffected in time 3. The final length reached is thus simply the final length of the unaffected branch minus the length (or biomass) removed. In *c* browsing again occurs at time 2, but growth is delayed (or the pattern of elongation altered) following browsing such that less growth occurs in time 3. This compounding of biomass-loss with an growth alteration impact of bud-loss results in lower final length than in *a* or *b*.

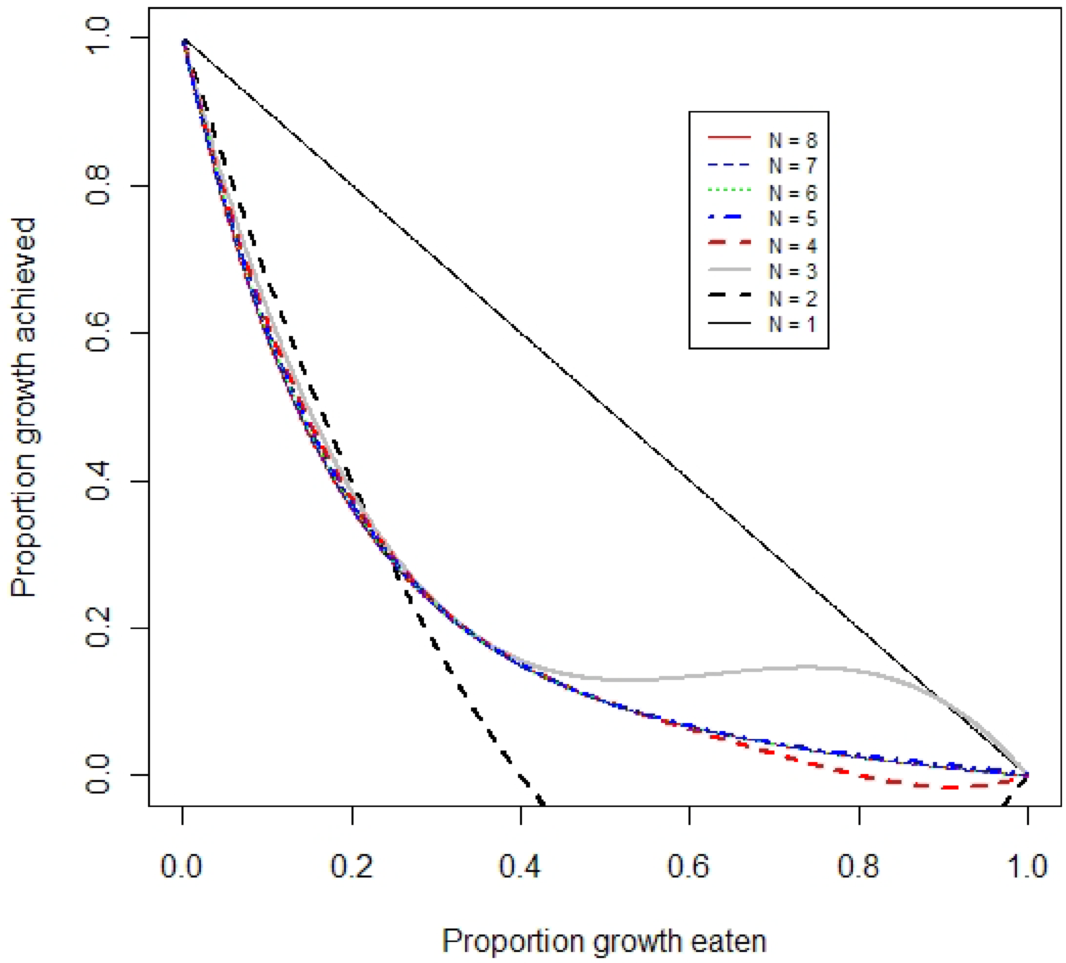

Figure 3. The relationship between branch growth and consumption (τ) for increasing subdivision of the growing season (N) (eq. 24). Consumption is defined here as the proportion of growth within a season consumed. Parameters used were total growth (α) = 1 and bite size (ω) = 0.1. When N = 1 all growth and consumption occur instantaneously.

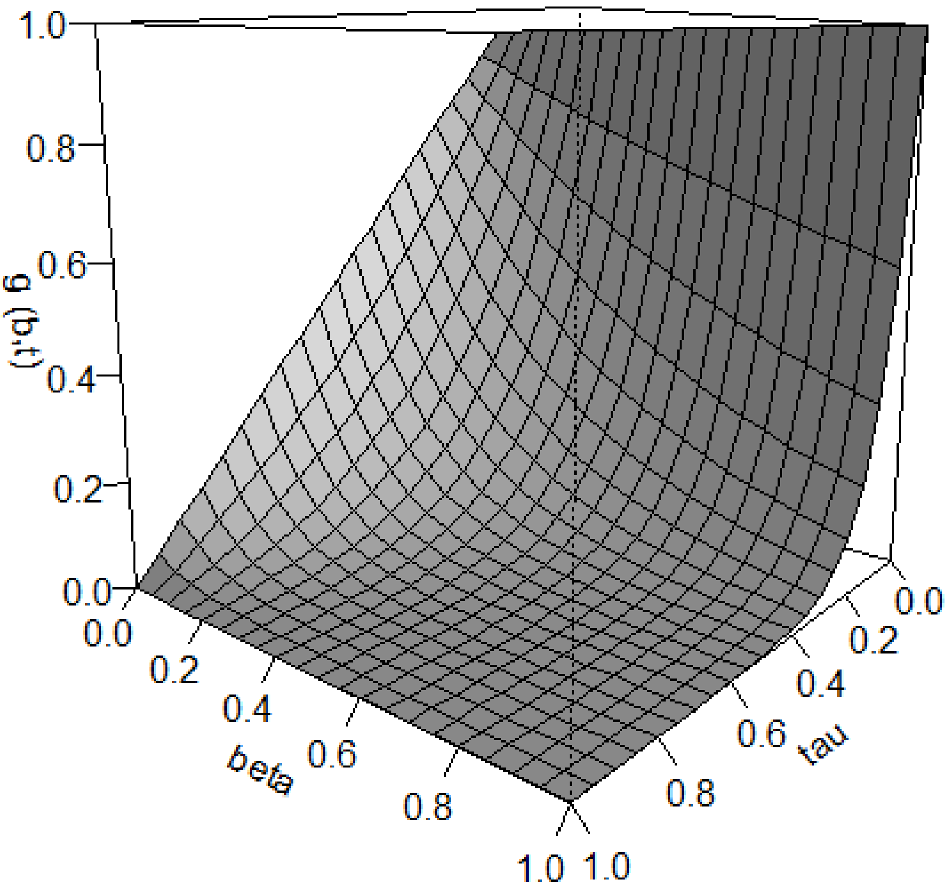

Figure 4. Growth (g (β,τ)) as a function of consumption (τ), defined as the proportion of total growth removed, and the duration of growth delay (β), defined as a proportion of the growing season (eq. 25). Parameters used were $\alpha = 1$, $N = 100$ and $\omega = 0.1$. When $\beta = 0$ a bite has no subsequent affect on growth. When $\beta = 1$, following a bite, growth is delayed for a period of time equal to the length of the growing season.

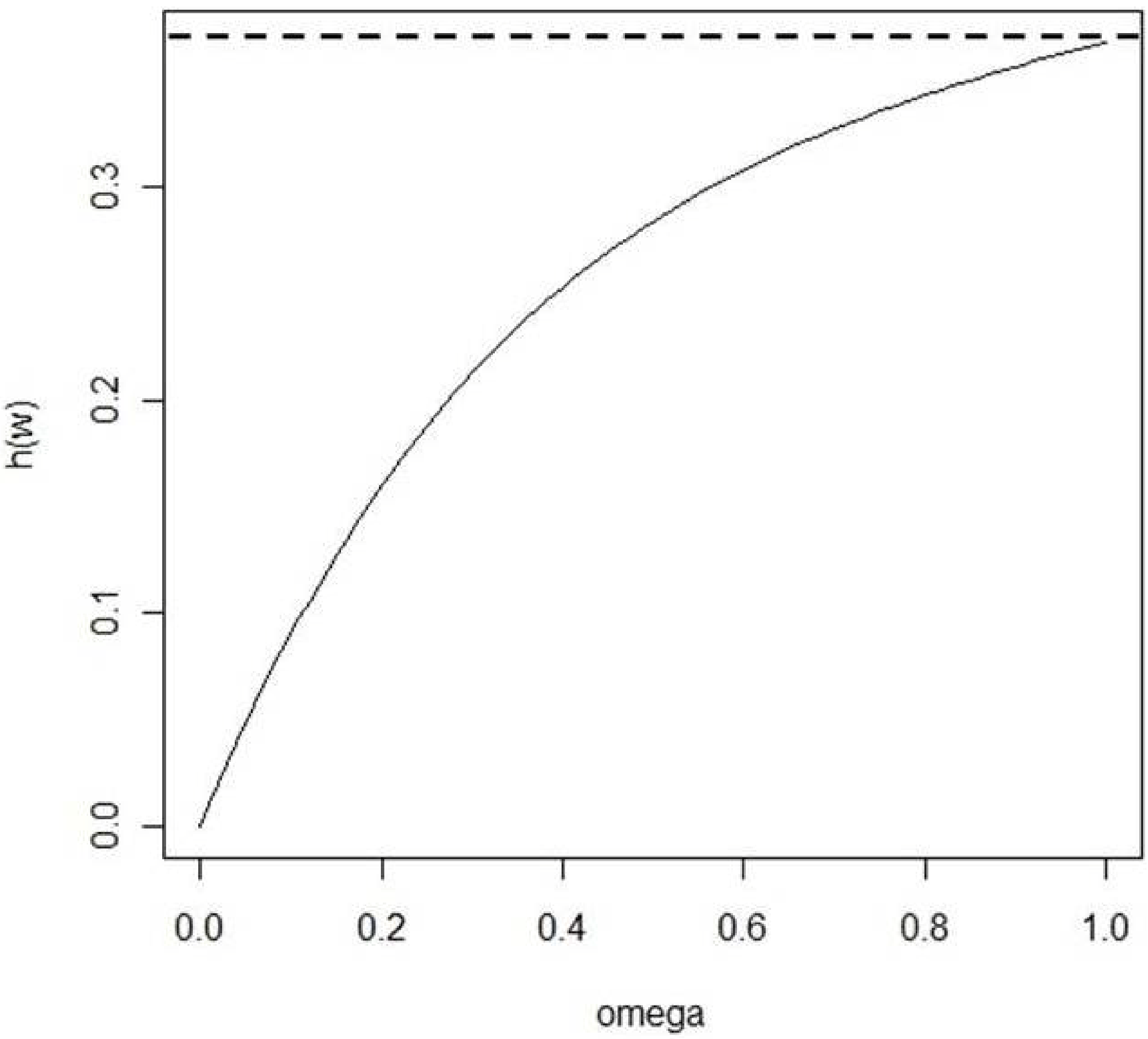

Figure 5. Predicted browser impact independent of the level of intake. The solid line shows the value of *h*(ω) (eq. 27) - the area under the curve in figure 4 when branch growth is curtailed for the duration of a single growing season after being bitten, as a function of browser bite size (ω) - integrated over all values of consumption (τ). The minimum browser impact, corresponding to the linear relationship between consumption and growth impact, is shown by the dotted line. Values of *h*(ω) below this line indicate impacts greater than in the linear case. Parameters used were total growth (α) = 1, number of time subdivisions (N) = 100 and bite size (β) = 1.

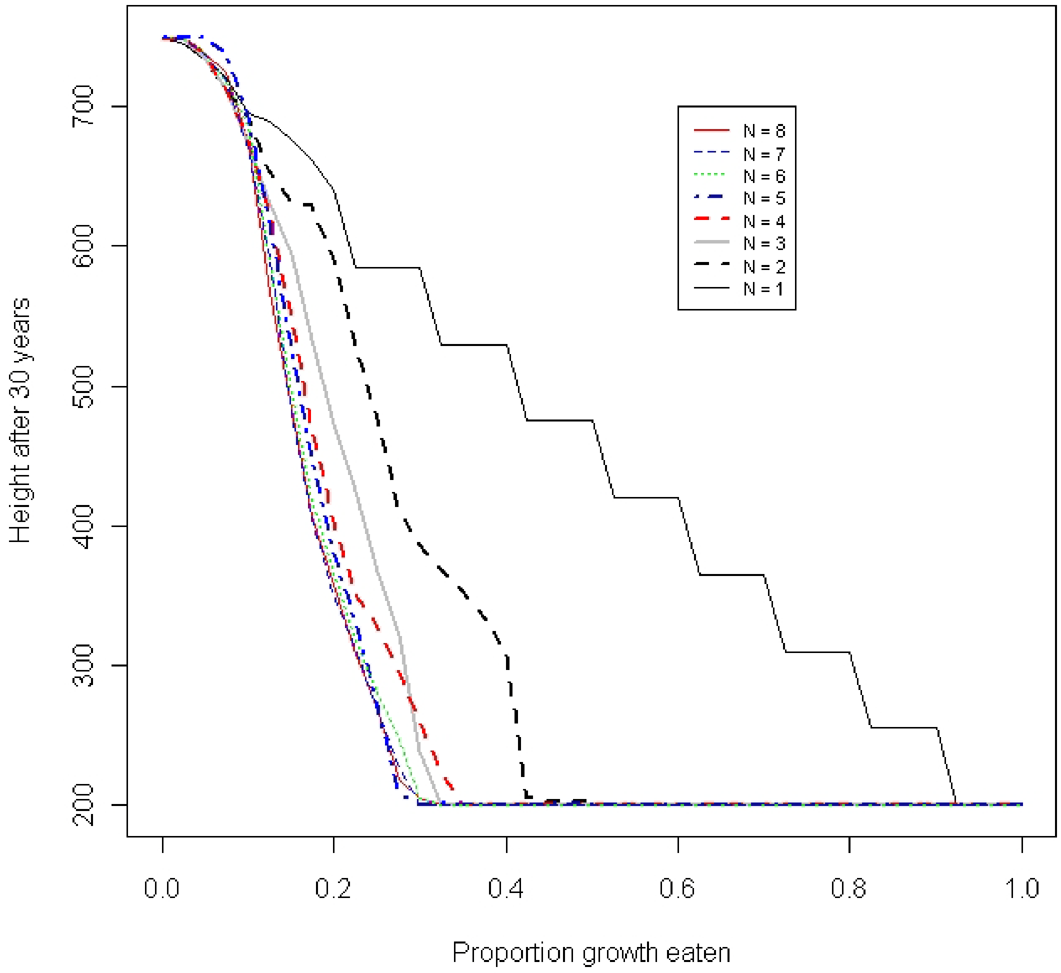

Figure 6. Simulated final height of whole-plants in cm after 30 years in response to varying intensities of consumption with aseasonal conditions and invariant internode distance. Results are shown for different numbers of subdivisions of the growing season (*N*). Parameters used were internode distance (*z*) = 10 and bite size (*w*) = 2.5. The presented values are the average of 10 simulations.

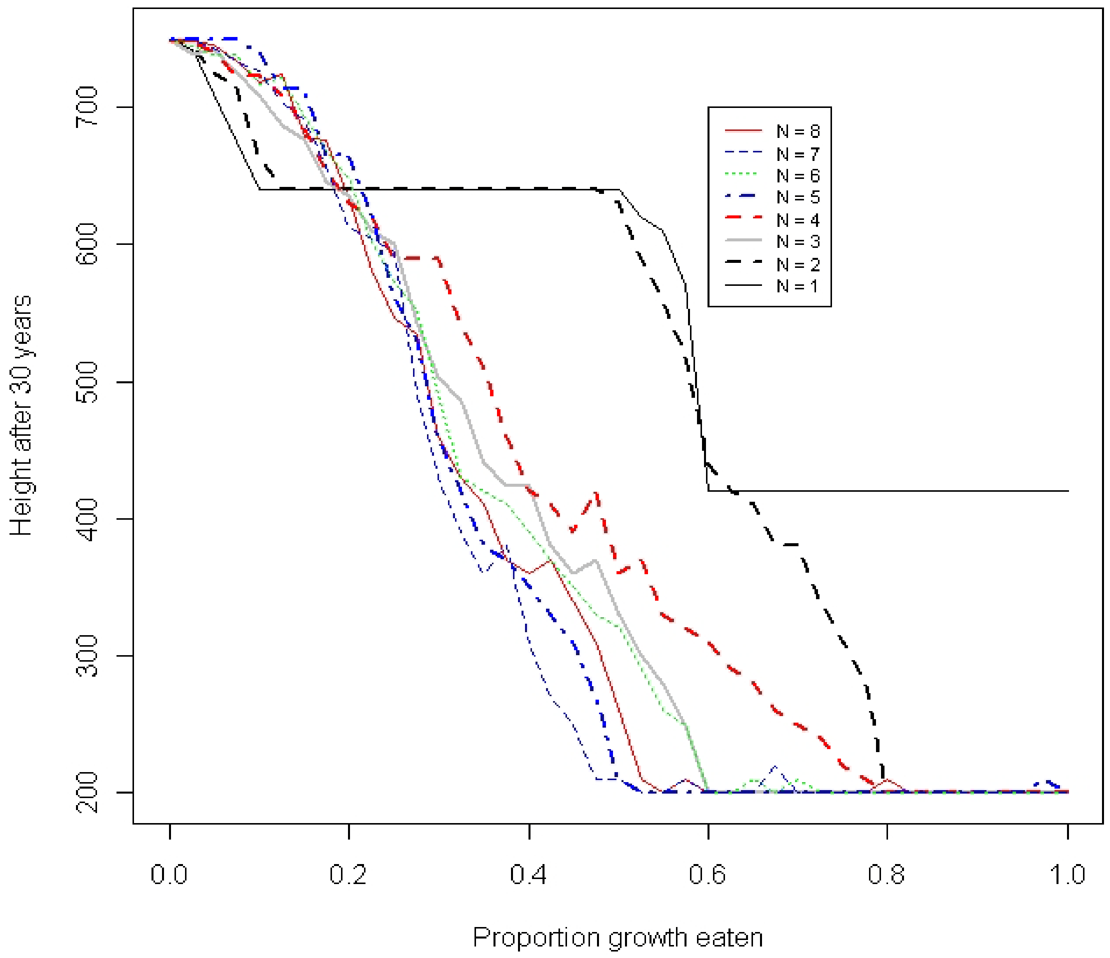

Figure 7. Simulated final height of whole-plants in cm after 30 years in response to varying intensities of consumption with seasonality and internode distance responsive to browsing with bite size (w) = 2.5. Results are shown for different numbers of subdivisions of the growing season (N). Results from a single simulation are presented.

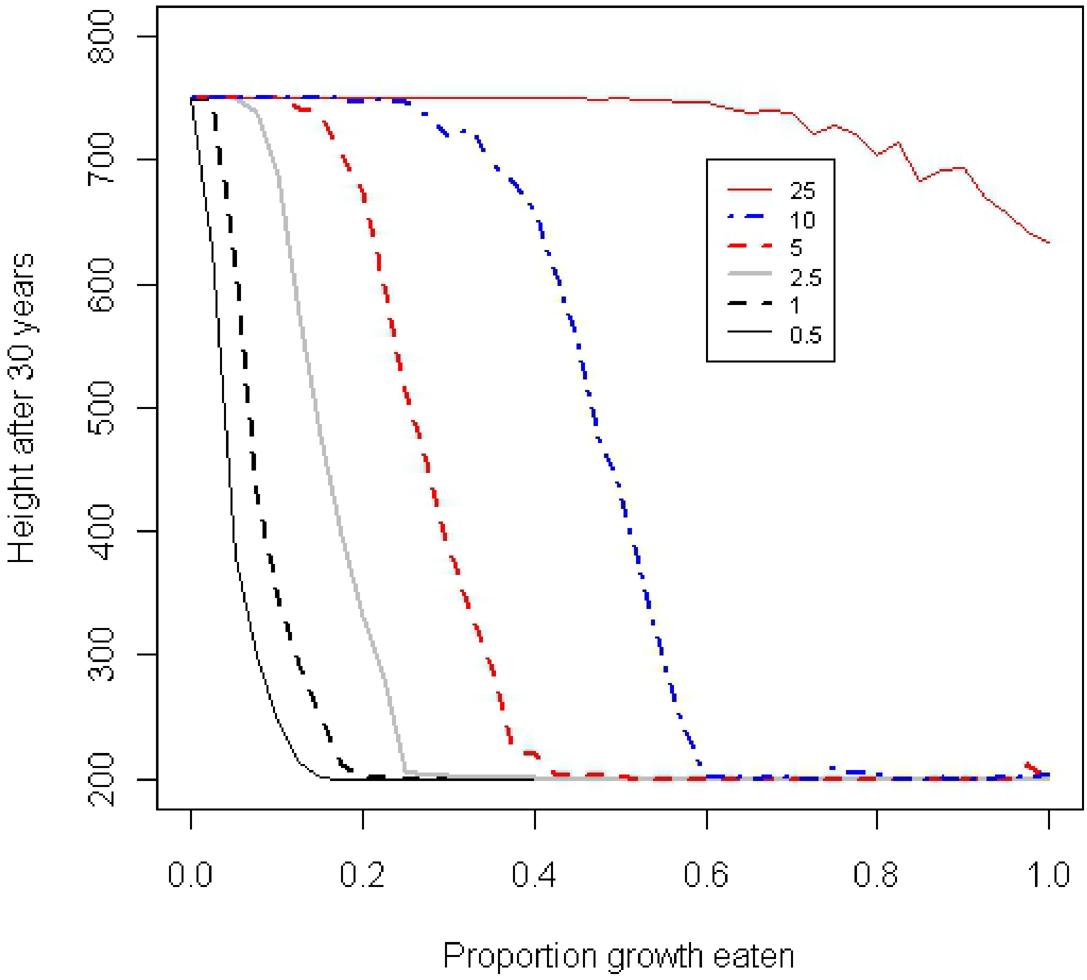

Figure 8. Simulated final height of whole-plants in cm after 30 years in response to varying intensities of consumption for a range of bite sizes between 0.5 and 25 cm. The presented values are the average of 10 simulations with no seasonality and fixed internode distance. Parameters used were internode distance (*z*) = 20 and number of periods within a season (*N*) = 16.

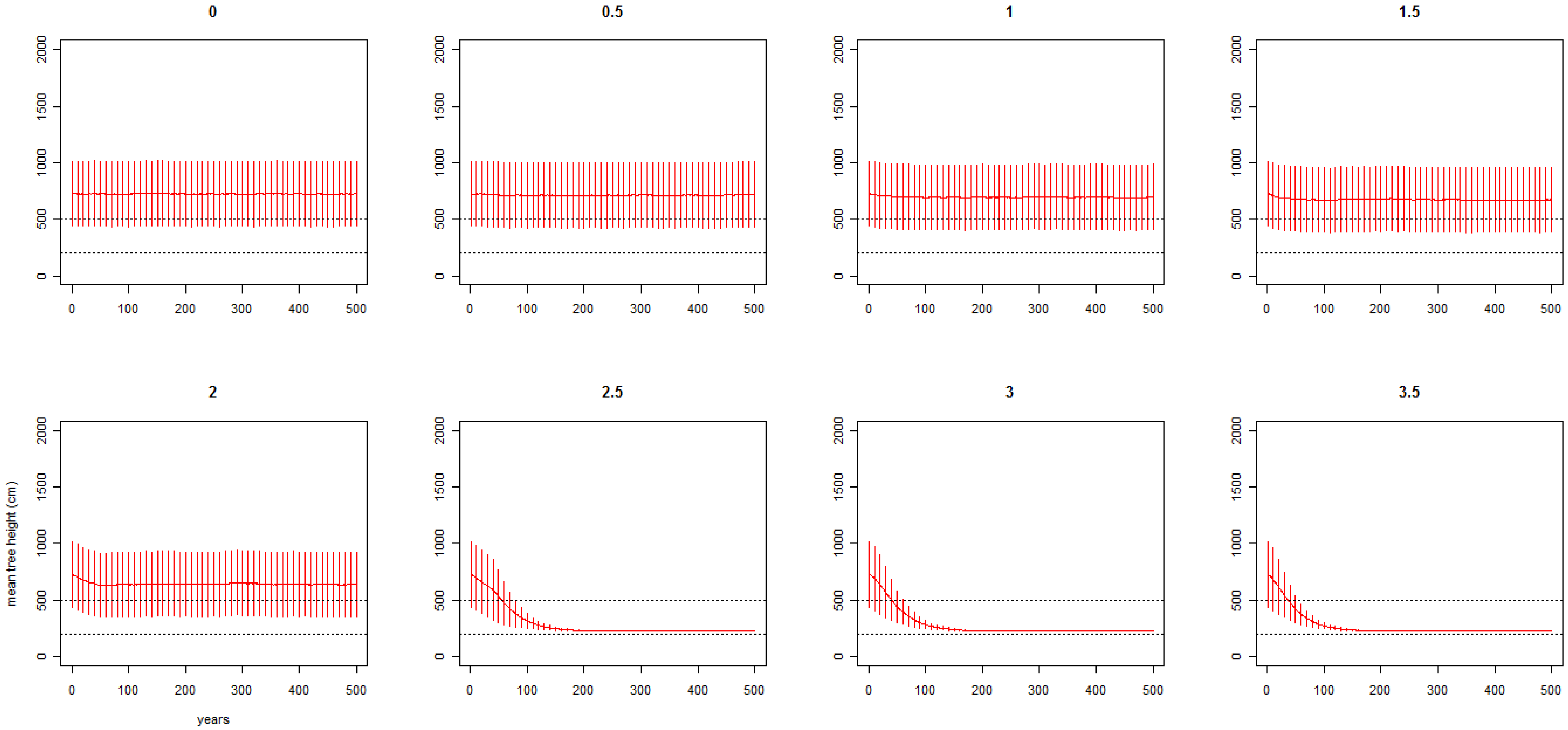

Figure 9. The temporal trajectory of tree population structure in the matrix model over 500 years for giraffe densities ranging between 0 and 3.5 km^{-2}. In this implementation browser impacts on height growth are directly proportional to consumption. The solid red line is the mean height of all trees and the red bars are 1-Simpson’s index scaled to the vertical axis. Longer bars indicate more even spread of trees among size classes.

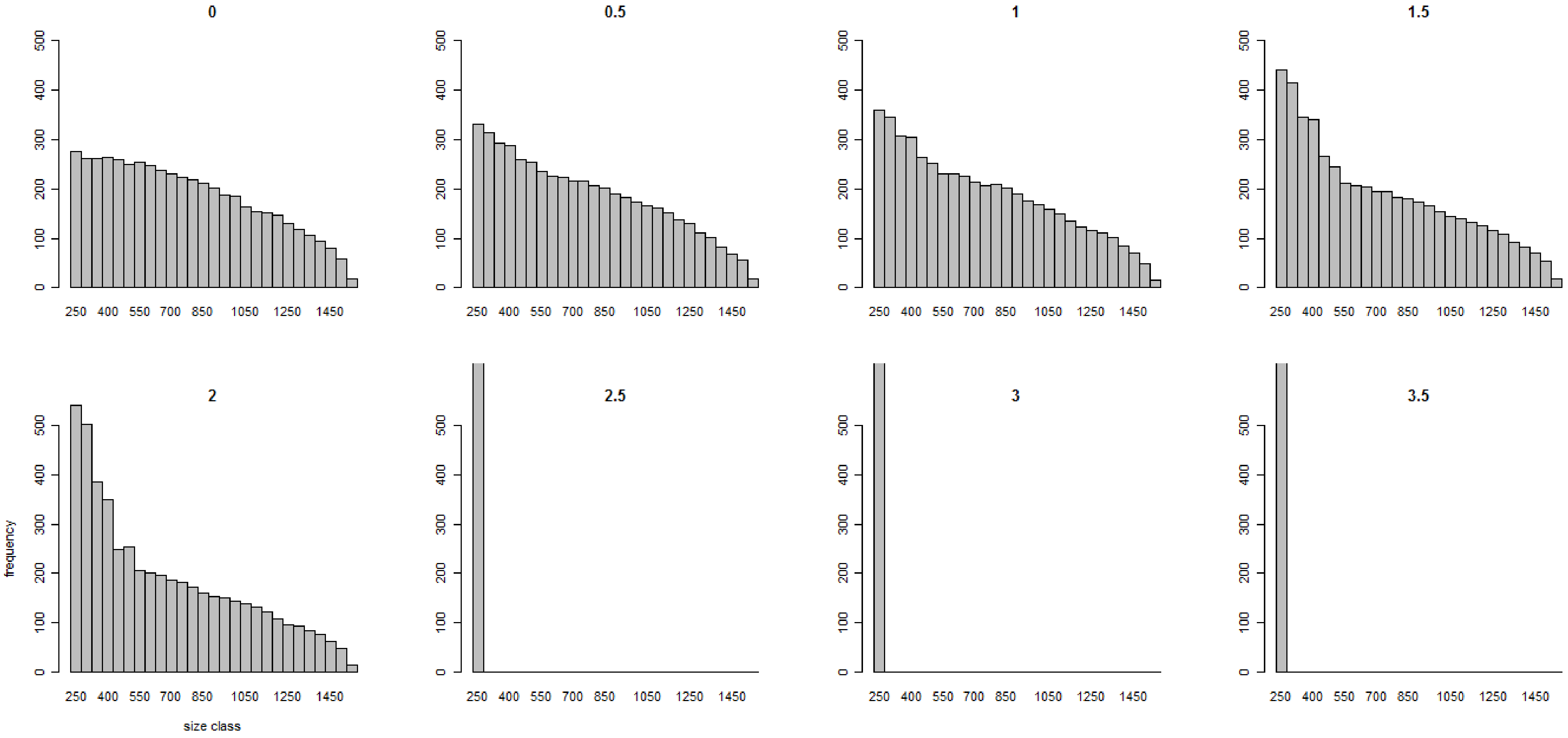

Figure 10. The stable population structure of trees in the matrix model after 500 years for giraffe densities ranging between 0 and 3.5 km^{-2}. Here browser impacts on height growth are directly proportional to consumption.

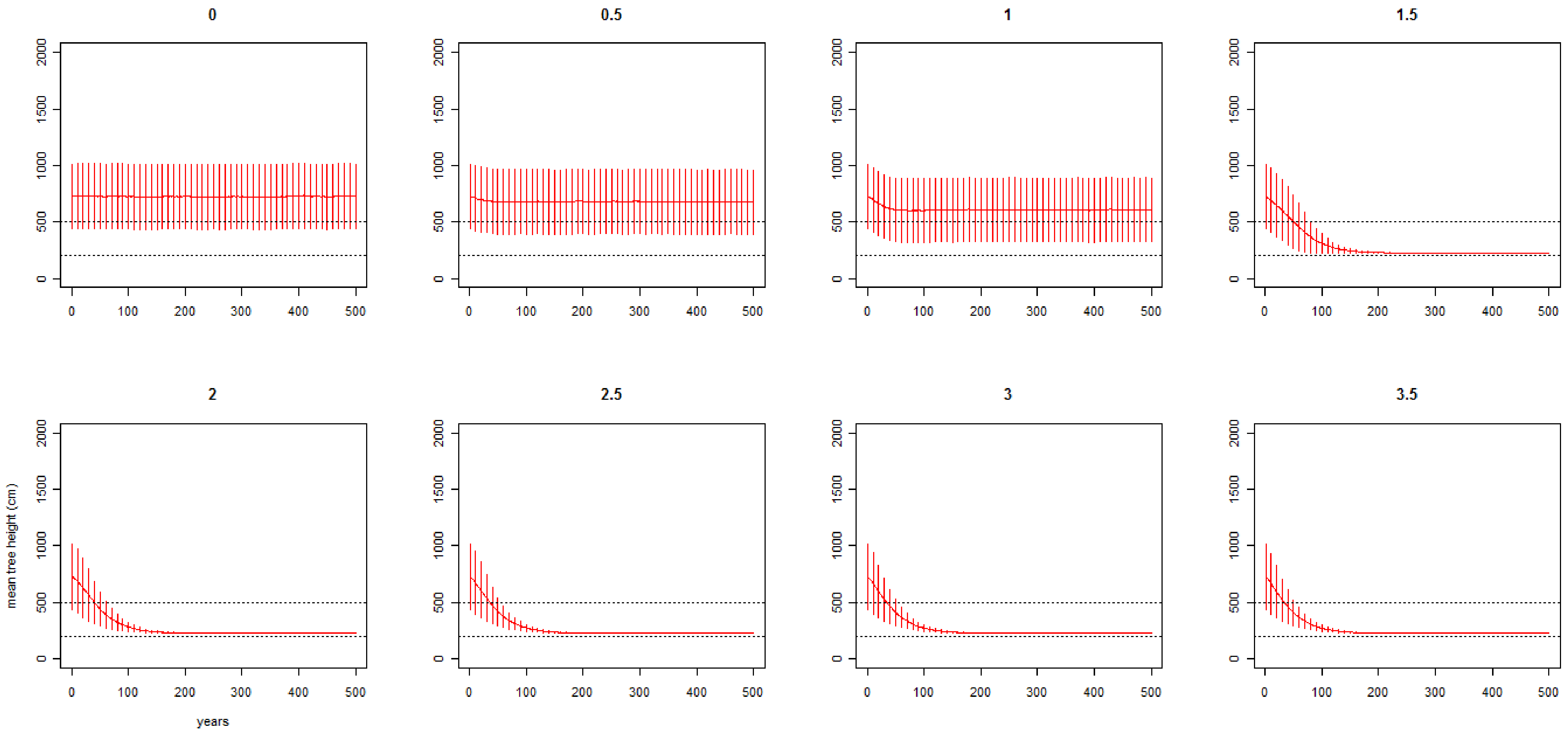

Figure 11. The temporal trajectory of tree population structure in the matrix model over 500 years for giraffe densities ranging between 0 and 3.5 km^{-2}. In this implementation browser consumption is linked to impacts on height growth using a nonlinear function which includes bud-loss impacts (eq. 28). The solid red line is the mean height of all trees and the red bars are 1- Simpson's index scaled to the vertical axis. Longer bars indicate more even spread of trees among size classes.

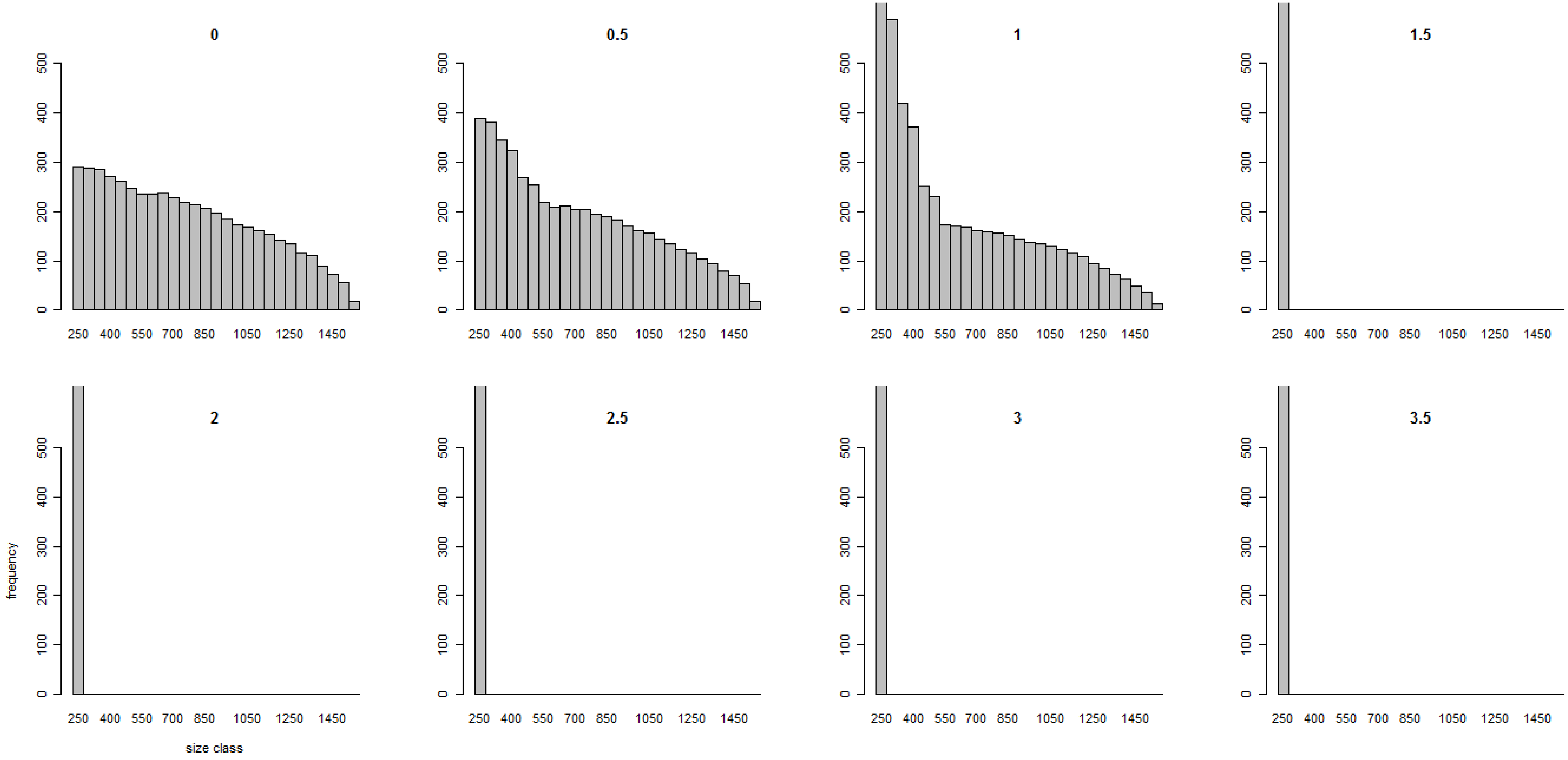

Figure 12. The stable population structure of trees in the matrix model after 500 years for giraffe densities ranging between 0 and 3.5 km^{-2}. Here browser consumption is linked to impacts on height growth using a nonlinear function which includes bud-loss impacts (eq. 28).

Discussion

Browser impacts on plant growth have previously been assumed to be proportional to the amount of plant biomass consumed (eg. Caughley 1976, de Knegt *et* al 2008, Akashi 2009). However, if in the process of removing biomass a browser disturbs the growing branch bud, this disturbance can have major consequences for the pattern and organization of plant growth. Here it is shown that when height is used to measure browser impacts, incorporating bud-loss effects alters the relationship between browser consumption and plant impacts. The relationship becomes nonlinear, with less growth occurring than in the case where impacts on height are assumed to be directly proportional to browser consumption for all potential levels of intake (eq. 25). The mechanism of bud-loss impact provided here is based on the inclusion of a parameter that describes a period of time following a browsers bite over which a branch does not elongate. The fundamental notion upon which this relation is based is that after a branch is bitten a new bud must be formed, or dormant buds activated and elongated beyond the site of the old bud, before any net elongation can occur. This period of time is expressed in the parameter β. In all cases, except the unlikely one of growth resuming instantaneously following a bite, the inclusion of this parameter results in browser impacts greater than one would expect if impact were directly proportionally to intake.

The mechanisms of bud-loss impact are slightly different when equation 25 is thought of as a description of whole-plant impacts. The impact of a browser bite is again the multiplicative affect of the length of branch removed when a bite occurs (consumption impact) and the subsequent curtailment of elongation (bud-loss impact). However, when considering whole-plants, a bite will only immediately impact height if it occurs on the leading branch. The probability that the leading branch is bitten is, however, assumed to be equal to the probability for any other branch. The case of whole-plant impacts differs from that of individual branches as the leading shoot can be overtaken if it is bitten or not growing and a new branch can become the leader. This is evident in the graphs of figure 6, 7 and 8. Initially impacts on height are less than linear and later increase, ultimately following the nonlinear pattern described by equation 24, with impacts on height greater than expected when using a linear relationship**.** This initial flattening is a result of a new branch becoming the leader after the old leader is bitten. The distance between the tip of the new branch and the old leader may be less than the bite size of a browser, thus resulting in the browsers bite impacting plant height less than expected. This example highlights that the formulation provided here is one of many possible mechanisms for including bud-loss impacts into a description of browser effects on plant height growth. While a growth-delay parameterization is used, alternate forms using, for example, a statistical description of the distance to the nearest growing tip or dormant bud below the leader might also provide an adequate framework for including bud-loss impacts in herbivore-vegetation models.

The approach outlined here ignores compensatory growth in response to browsing. Compensation occurs when growth is stimulated following browsing such that the impact of herbivory is reduced, and it is well documented in woody plants (Gadd *et al* 2001, Hester *et al* 2004, Persson *et al* 2007, Fornara and du Toit 2007). *Acacia nigrescens* has been shown to compensate for the biomass lost to browsers to such an extent that regrowth following browsing has been likened to grazing lawns (du Toit *et al* 1990, Fornara and du Toit 2007). Taken at face value this would appear to confound any relationship described herein, as branch regrowth is stimulated by browsing. However, as a result of browsing and the activation of dormant buds from which compensatory growth occurs, the architecture of a tree is often modified (Martínez and López-Portillo 2003). This is particularly true for *Acacia nigrescens* (du Toit *et al 19*90, Fornara and du Toit 2007). Often architectural modification is analogous to clipping a hedge: with increased branching and a concomitant increase in canopy density (du Toit *et al* 1990, Danell *et al* 1994, Martínez and López-Portillo 2003, Fornara and du Toit 2007**)**. Thus, although biomass lost may be compensated for, browsing alters the redistribution of this biomass. If compensatory growth is allocated to increased branching and canopy densification and not the elongation of current branches, there will be no height growth compensation. Ultimately, compensatory growth may not compensate at all for lost height. This was demonstrated for *Acacia nigrescens* in KNP, where despite high regrowth stimulated by browsing, heavily browsed trees experience a net decrease in height, whereas lightly browsed trees producing less regrowth had a net height increase (Fornara and du Toit 2007).

Although a browsers bite is measured here as the length of branch it removes, it is not suggested that the bite consists only of twig biomass. In reality not only do browser bite sizes vary, so to do the proportions of leaf and twig in a bite (Wilson and Kerley 2003). The nature of a bite will depend on the architecture of the plant being browsed and on herbivore morphology and body size (Shipley *et al* 1999, Wilson and Kerley 2003)**.** In the models presented here browser impact is highly dependent on bite size, ranging from direct proportionality between impacts and consumption when bite sizes are large, and almost no growth at very low levels of intake when bites are very small. For a fixed level of consumption, the smaller the bite, the more bites needed to meet dietary needs. When more bites are taken to remove the same amount of branch length, the time required to re-establish buds or leader growth is compounded, compounding impacts. This relationship, if real, has implications for the scaling of body size and herbivore impact on vegetation, implying that many small browsers will have a greater impact than an equal amount of browser biomass in few large browsers, all else being equal. In reality however, this relationship would be obfuscated by numerous factors. As browser bites get smaller, they contain a larger portion of leaf biomass, and eventually may not contain any twig biomass - although this varies seasonally (Owen-Smith and Cooper 1989). Moreover, large bites may shorten branches to diameters from which epicormic sprouting is not possible, due to thick bark or lack of buds. Larger bites will also be associated with large bodied animals, whose impacts will be heightened by decreasing vulnerability to predation and incidental damage to plants unrelated to dietary needs (Midgley *et al* 2005, Sinclair *et al* 2003).

Most existing models of herbivore-vegetation dynamics assume direct proportionality between herbivore consumption and plant impacts (Caughley 1976, Rietkerk and van der Koppel 1997, Illius and O'Conner 2000, Owen-Smith 2002a,b, van Langevelde *et al* 2003, de Knegt *et* al 2008, Sheffer *et al* 2008, Akashi 2009). When direct proportionality for demographic impacts is assumed here, substantial browser impacts only emerge at densities of 2.5 giraffe km^{-2}. Currently, the park-wide density of giraffe in KNP is approximately 0.25 km^{-2} (http://www.sanparks.org/parks/kruger/conservation/scientific/ff/ biodiversity_statistics.php). Densities have remained between 0.2 and 0.3 km^{-2} for the past 30 years (Redfern *et al* 2003). However, it has been shown that giraffe are not uniformly distributed throughout the park; they are concentrated in the landscapes on basalt derived soils in the central and southern regions (Redfern *et al* 2006), and have been reported to reach local densities approaching 2.5 km^{-2} (du Toit 1988). Though, given that they are not highly concentrated around water sources (Redfern *et al* 2003), it is unlikely that they reach 10 times their park-wide density at the broad scale over which the demographic impacts reported in Levick *et al* (2009) are observed. The model was parameterised choosing parameter values to maximize giraffe impact; even with these parameter values and assuming spatial aggregation of browsers in the areas in which impacts are observed it does not appear possible that the direct effects of biomass intake by giraffe at current and historical densities can account for their observed impacts on the tree layer in the Makhohlolo region of KNP (figure 9, 10).

When linking consumption to demographic impacts using the nonlinear relationship in equation 28, demographic impacts qualitatively similar to those reported by Levick *et al* (2009) emerge at giraffe densities between 1 and 1.5 km^{-2}. These are realistic densities for KNP; it is likely that giraffe occur at these densities over large areas in KNP that they favour. These estimates of densities at which considerable impacts appear, and the magnitude of the impacts themselves, should not be thought of as quantitative predictions of browser effects. The uncertainty in parameter values and lack of data for the system focused on here resulted in a choice of parameter values that maximized the possible impact of giraffe. However, what can be concluded is that even when parameters that maximize giraffe impact are chosen, the loss of biomass alone cannot explain observed impacts. Top-down control of vegetation structure by giraffe in KNP, therefore, is far more plausible when bud-loss impacts - beyond the direct loss of biomass - are considered.

Savannas are temporally and spatially very heterogeneous systems (du Toit *et al* 2003), and thus the matrix model is unrealistic in the sense that it represents an equilibrium system. Temporal variability in rainfall will cause growth and mortality rates to vary, and the occurrence of fire will cause pulses and depressions in tree recruitment rates. The outcome of these pulses is that there will be periods in which trees are severely impacted upon by browsers and others where many escape to become large and invulnerable to most browsers.

Many studies consider the impacts of herbivores on plants from the point of view of changes in biomass of individual plants or populations (eg de Knegt *et al* 2008, Akashi 2009). In this context, the quantity of biomass lost directly to herbivores and the compensatory response to biomass removal are the key factors in determining the ultimate impact of herbivores. However, when vegetation structure is of interest, the proximal cause of impacts is browser induced changes in height growth. Height growth of plants occurs as the result of branch elongation. If, as a result of a browser bite, the timing and pattern of branch elongation is altered, then plant demography will be altered. This mechanism is not directly dependent on the actual loss of biomass itself, but rather the ancillary effects of the event in which biomass is lost. Thus, when considering the demographic impact of browsers on tree populations, suppression of height growth, simulated here by disturbances to bud banks can be more important than the loss of biomass itself. Identifying intrinsic characteristics of browsers and tree species that determine height growth responses will advance capacity to predict and manage impacts on trees across diverse environments and taxa.

Chapter 4: Impacts of simulated browsing on *Acacia karroo*: the relative importance of biomass consumption and bud loss.

Glenn R. Moncrieff

Introduction

The impact of herbivory on a plant's fitness includes both the direct impact of lost tissues and the consequences of the plants' response. Plants can respond either through induced change in resistance to future herbivore attack or by tolerating herbivory through compensation for reduced fitness (Haukioja and Koricheva 2000). Factors such as light and nutrient availability, competition and the timing of herbivory have been shown to influence the degree of compensation and the overall impact of herbivory on plant fitness (Hester *et al* 2004, Persson *et al* 2007, Häsler *et al* 2008, den Herder *et al* 2009). Initially, studies focussed on the responses of grasses and other herbaceous plants, and the degree to which they compensate for herbivory (McNaughton 1983, 1984, Belsky 1986). With grasses and herbs, it is often possible to measure fitness directly, in the form of reproductive output (Mauricio *et al* 1997, Stowe 1998**)**. However, when this is not possible, biomass can serve as a useful proxy for fitness and compensation due to the structural homogeneity of grasses and herbs. For iteroparous woody plants, it is very difficult to directly measure the lifetime impact of herbivory on reproductive output and thus proxy measures must be used (Haukioja and Koricheva 2000).

Often change in biomass is used to quantify woody plant response to browsing. In many environments this can be a good measure of plant fitness. For example, when light competition is not strong, the size of a plant - measured as its biomass - can serve as an approximate measure of its ability to intercept light and capture carbon (Aarssen 1995). If pollinators or dispersal agents are not limiting, reproductive potential will be correlated with plant size (sensu biomass) (Aarssen and Jordan 2001). Biomass, however, is not always a useful measure of plant fitness. Plant height is often more closely related to fitness than biomass - when competition for light is strong the tallest trees are the most successful, or, when pollinators or dispersal agents are more likely to visit the most apparent individuals

(Aarssen 1995). Moreover, plant height determines susceptibility to browsing by many mammalian herbivores. In savannas where fire is a major driver of woody plant dynamics, the susceptibility of trees to fire induced stem mortality is closely linked to their height. If a tree's canopy is within the reach of flames aboveground biomass will be lost (Trollope 1984). Once out of the flame zone and above the feeding height of all large mammalian browsers, the fecundity of trees greatly increases **(**Hoffmann 1998, Archibald and Bond 2003, Fleming *et al* 2006, Bond 2009). Here we limit our discussion to savannas trees, defined as woody plants delaying reproduction until reaching a minimum height. Thus, for savanna trees within the reach of browsers and fire, height is by definition the best measure of fitness. Many studies of plant biomass response to browsing do also measure plant height, which often responds similarly to biomass, but can also show different patterns (Bergstrom and Danell 1987, Hester *et al* 2004**)**. Explicit comparison of height and biomass responses is however lacking. Determining the underlying causes for diverging responses of height and biomass will help in understanding browser impact on woody plants and how plants compensate for herbivory.

Plant height growth is the result of branch elongation, and browser impact on whole plants is the result of foraging on individual branches. Thus to understand and compare how biomass and height of whole plants respond to browsing, branch-level processes need to be studied. The release of branch growth from apical dominance has been postulated as a mechanism accounting for the compensation of biomass lost to browsers (Strauss and Agrawal 1999). However, even if release from apical dominance results in the stimulation of branch growth that compensates for lost branch length and biomass, elongation parallel to the vertical axis will not necessarily compensate for the lost height. In this way the response of biomass and height to browsing may diverge. Processes that control how frequently apical dominance is disturbed and re-established will affect how branch elongation, and plant height, respond to browsing.

When a browser removes a bite from a plant, the plant not only loses the biomass contained in the bite, but very often it also loses a bud. After a bud is lost to a browser there may be a period between the loss of the original bud and the activation of new buds in which there is no active leading bud (see Chapter 3, figure 2). In addition, newly activated buds may be at a lower height than the most proximal point of the browsed branch, further compounding the loss of growth (figure 1). Thus, the impact of a bite on branch extension and height growth is two-fold. The first aspect is loss of biomass/length (consumption impact) and the second the delay of growth or modification of growth form resulting from loss of buds and apical dominance (bud loss impact). The relative importance of these two factors can be determined by varying the intensity and frequency of simulated browsing. Holding the absolute amount of biomass or length removed constant, if all browsing occurs in a single event it would be predicted that this would have less impact on the orthotropic growth of the original axis, and ultimately plant height, than if browsing occurred in multiple events throughout the season. This is because multiple removals of the bud on the leader branch will result in more time spent not elongating as buds are activated or re-establish (assuming that dormant buds are available). Moreover, dormant lateral buds will be less suppressed if apical buds are constantly being removed and having to re-establish **(**du Toit *et al* 1990, Fornara and du Toit 2007). Altering the frequency of browsing would therefore reveal the importance of bud loss impacts for height growth. To control consumption impacts, increasing length or biomass removal should increase consumption impacts in direct proportion.

I studied responses of height growth and biomass to both consumption and bud-loss impacts for whole-plants while simultaneously measuring branch-level impacts. I attempt to relate changes in height growth and biomass to responses of individual branches. I expect that the longest axis of branch extension will determine tree height increment and that total branch extension will determine biomass growth. Any factor that reduces length extension will reduce height growth and similarly a factor that reduces total extension will reduce biomass growth. Moreover, they need not respond in the same direction or with the same magnitude. The effects on growth of two factors are investigated: the frequency of clipping and the intensity (defined as the length or biomass removed). If all simulated browsing occurs as a single event at the end of the growing season, and the responses measured directly thereafter, there can be no scope for bud losses to alter plant growth. Conversely, if browsing is simulated throughout the growing season, buds will be continually removed and their loss will impact growth. The intensity of clipping will determine the magnitude of consumption impacts by removing more or less plant material.

I expect that bud-loss impacts are of greater importance than consumption impacts in determining the response of branch length extension and ultimately height growth to browsing. Thus, the frequency of clipping will affect branch length extension and height growth more than intensity. Biomass may respond to frequency and intensity quite unlike height, with the intensity of consumption having greater importance. I simulate browsing over a single growing season on *Acacia karroo* Hein., a common forage species in southern African savannas.

Methods

Acacia karroo is a widespread and abundant savanna tree species. It occurs throughout southern Africa and has a wide range of growth forms. Here we study the savanna form (sensu Archibald and Bond 2003), which has a small canopy and a low degree of branch ramification relative to the other varieties. This growth form reflects adaptation to rapid vertical growth to escape above-ground mortality following fire. *A. karroo* has been found to be susceptible to suppression of both biomass increase and height growth by browsing (Mopipi *et al* 2009, Staver *et al* 2009). Branch elongation is definite and episodic, with extension occurring after rains and apical buds dying at the end of the growing season and new buds forming at the beginning of the following growing season (Edelin 2010).

A. karroo saplings inside the 1 ha Gunjaneni exclosure (28.202°S, 32.042°E) in the Hluhluwe section of Hluhluwe-Umfolozi park were used in this experiment. The exclosure was last burnt in 2006. Mean annual rainfall at the Gunjaneni site is 620mm. The stems used in this experiment had begun growing after the 2006 fire, which occurred after the exclosure had been erected and thus have never been exposed to mammalian browsing. Other common tree and shrub species in the exclosure include *Acacia nilotica* and *Dichrostachys cinerea*. The grass layer is dominated by *Cymbopogon excavatus*, *Eragrostis curvula* and *Themeda triandra* (Schutz *et al* 2009). The dominant browser in the area is the impala (*Aepyceros melampus*), though nyala (*Tragelaphus angasii*) and giraffe (*Giraffa camelopardalis*) are also common.

Six groups of 20 trees between 1 and 2 meters in height were assigned to simulated browsing treatments varying in intensity and frequency on October 15th 2009. Clipping was conducted monthly on 40 individuals and exclusively at the end of the season for another 40. The 40 trees within each of these two frequency treatments were then subjected to two intensity treatments: 20 received full intensity clipping and 20 received half-intensity clipping (figure 2). A further 20 individuals within the exclosure were enumerated and left untreated for the duration of the experiment. Outside of the exclosure 20 trees were marked and used to compare growth impacts of natural and simulated herbivory. Within each treatment group, 5 trees were selected for enumerating branch-level responses. Four branches per tree were marked at 30cm from the tip, selecting only unbranched modules. Branches were selected at random throughout the canopy.

Prior to experimental manipulation all trees were enumerated to control for pre-treatment state. The total length of all branches, tree height, stem diameter at 10cm above the ground and number of branch tips were measured. These variables were measured for an additional 20 trees, not part of the experimental group, which were subsequently harvested at the beginning of the experiment. Allometric analyses were then performed and the best predictors of biomass used as covariates in subsequent analyses to control for pre-treatment variation in aboveground biomass.

A common method for simulating realistic browsing intensities is to trim all shoots at the point where the shoot diameter equals the maximum diameter observed to be browsed by natural herbivores in a single event (eg Hester *et al* 2004). This method cannot be applied directly to this experiment as here I attempt to trim trees and remove buds repeatedly and in a single event, controlling for intensity. If attempting to reduce intensity when cutting branches down to a set diameter, a reduced proportion of shoots would need to be cut (Hester *et al* 2004, Edinus *et al* 1993). However, I wished to compare the effect of monthly bud loss against a single bud removal event while simultaneously varying intensity. A fixed length was therefore removed from the tip of branches. The length removed was decided on by measuring the diameter to which branches of *Acacia karroo* were browsed outside the exclosure. The allometry of branch length and diameter was determined by measuring the diameter of branches and the length following that diameter on trees within the exclosure. The length removed in full intensity treatments was then calculated as the length of branch following the maximum diameter to which branches were browsed. This length was determined to be 30 cm (see results). Clipping was applied beginning with the highest order branches. Lower order branches would only be clipped below the point of attachment of higher order branches if the attached branch had already been completely removed. Figure 2 shows the experimental design and clipping procedure diagrammatically.

In the low (half) intensity, high (monthly) frequency treatment all material (leaves, stems and pods) 3 cm from the tip of every branch was removed monthly for five months. In the low intensity, low (single) frequency treatment 15 cm was removed from the tips of branches at the end of the experiment before harvesting of trees. In the high (full) intensity, high frequency treatment 6cm was removed from branch tips monthly for five months. In the high intensity, low frequency treatment, 30 cm was removed from the tips of branches at the end of the experiment before harvesting. For every tree, all trimmed material was separated into leaves, stems and pods, dried until mass had stabilized and weighed.

Tree and branch response to experimental manipulation was evaluated on the 10th, 11th and 12th of March 2010, after which all aboveground mass was harvested to measure aboveground biomass response. The final height and diameter at 10cm aboveground was measured. For trees with marked branches, the total branch length distal to the original marking and the length along the longest single axis were measured. After harvesting, trees were separated into leaves, stems and pods and dried until mass had stabilized after which they were weighed.

Analysis

All analyses were done using a Bayesian framework. The Bayesian approach focuses on effect size rather than their ‘significance’ thus facilitating exploration of the relative importance of factors rather than the binary significance test (McCarthy 2007**)**. In all analyses the unclipped control treatment and the treatment exposed to natural herbivory were not included as they are not part of a crossed design. The responses of these two treatments are used as a baseline to compare the absolute effect of other treatments and their comparability to natural herbivory impacts. The height and diameter growth response of the four treatments exposed to crossed effects of intensity and frequency were separately evaluated using a

Bayesian analogue for two-factor fixed effects ANOVA (Qian and Shen 2007). An accessible introduction to Bayesian ANOVA with examples is provided by Qian and Shen (2007). The data distribution was modelled as:

$$Y_{ij} \sim N\,(\mu_{ij}\,,\, \delta^{2})$$

and μ_{ij} is defined as:

$$\mu_{ij} = \beta_{1i} + \beta_{2j} + \beta_{3ij}$$

where Y_{ij} is the height or diameter of a plant with clipping intensity i and frequency j. β_{1i} is the effect of clipping intensity at the i_{th} level, β_{2j} is the effect of frequency as the j_{th} level and β_{3ij} is the interaction of intensity and frequency.

Branch response for total length and longest axis were evaluated using intensity and frequency as fixed factors and tree as a random effect. The data distribution was modelled as:

$$Y_{ijk} \sim N\,(\mu_{ijk}\,,\, \delta^{2})$$

and μ_{ij} is defined as:

$$\mu_{ijk} = \beta_{1i} + \beta_{2j} + \beta_{3k} + \beta_{4ij}$$

and the random effects term β_{3k} for tree k is modelled as:

$$\beta_{3k} \sim N\,(0,\, \tau^{2})$$

Covariates included in the analysis of biomass responses were selected using Bayesian regression. The best combination of predictors that showed negligible covariance was selected. Leaf biomass, stem biomass and pods mass was analysed collectively as total aboveground biomass. Again, a Bayesian ANCOVA analogue was employed using frequency and intensity as fixed factors and variables selected with multiple regressions as covariates. The data distribution used was:

$$Y_{ijk} \sim N\,(\mu_{ijk}\,,\ \delta^{2})$$

and μ_{ij} is defined as:

$$\mu_{ijk} = \beta_{1i} + \beta_{2j} + \beta_{3}\,x_{ij} + \beta_{4ij}$$

where β_3 is effect of the of the selected covariate, x_{ij} .

Uninformative priors were used for all parameters in all analyses. Where data were observed to be non-normal appropriate transformations were used. Models were fitted using MCMC algorithms implemented in WinBUGS 1.4 (Lunn *et al*. 2000). Diagnostic analyses were performed in R 2.11.0 (R Development Core Team 2010). All MCMC chains aside from those used to test branch growth responses ran for 500 000 iterations, discarding the first 250 000 steps. The branch growth response chains ran for 2 000 000 iterations, discarding the first 1 000 000. Three parallel MCMC chain were run and visual inspection of diagnostic plots indicated that chains had converged and mixed.

Results

The maximum diameter branch browsed was estimated to be 4mm, the 3rd quartile of measured branch tip diameters. Using the constructed branch length-diameter allometry, 4mm corresponds to a branch length of approximately 30cm (figure 3). All variables measured for use as covariates were highly collinear, and thus the best single covariate (as determined by a Bayesian R^2) was selected for use in further models (figure 4). The best predictor of total biomass (leaf, stem and pod biomass) was total branch length ($R^2_{bayesian}$ = 0.828 [0.660, 0.913]; all statistics and parameters reported are presented as: mean [95% credible interval]), followed by diameter ($R^2_{bayesian}$ = 0.819 [0.639, 0.908]), height ($R^2_{bayesian}$

= 0.709 [0.420, 0.852]) and number of branches ($R^2_{bayesian}$ = 0.313 [0, 0.652]). The relationship between total branch length and total biomass is shown in figure 5.

The average total mass of leaves, stems and pods removed over the duration of the experiment for each of the treatment groups is shown in figure 6. The amount of total biomass removed in the single clipping treatments was similar to the amount removed over the entire duration of the monthly clipping treatments. The biomass removed in the high intensity single clipping treatment was much greater than the low intensity treatments, particularly for stem biomass, which was approximately double (31.5 g high intensity vs. 14.7 g low intensity). In the monthly treatment, although more total biomass was removed in the high intensity treatment it was not much greater than the low intensity treatment. However, stem biomass removal was greater in the high intensity treatment (27.3 g high intensity vs. 19.5 g low intensity).

Similar response patterns were observed for branch growth whether measured as the length of the longest axis or total extension (figures 7a and b). Medians are used to summarize data due to outliers in untransformed data. For both measures, monthly clipping treatments grew the least, with the high intensity monthly clipping growing slightly less than the low intensity (monthly high intensity: T = -29.3 cm, L = -29.3 cm; monthly low intensity: T = -13.5 cm, L = -13.5 cm; T = total branch growth, L = longest axis of extension). Only the control treatment and single low intensity clipping achieved median net positive shoot growth (control: T = 37.05 cm, L = 28.55 cm; single low-intensity: T = 30.05 cm, L = 30.05 cm). Total extension and longest axis extension for the trees exposed to natural herbivory were slightly less than the single high intensity treatment, but not as low as either of the monthly clipping treatments (natural herbivory: T = 0.05 cm, L = -3.5 cm; single high-intensity: T = 0.25 cm, L = 0.25 cm).

The analysis of these patterns reveals that both frequency and intensity of clipping affected branch growth. Frequency and intensity both accounted for a large amount of the variation in both total branch growth and longest axis extension (figure 8a and b). However, wider posterior credible intervals surround estimates for total branch extension (figure 8 and table 1). Monthly clipping reduced mean growth response of both measures, with a slightly greater effect than high intensity clipping, while single clipping had the greatest positive effect relative to the mean response (figure 9a and b). Effects of individual trees on branch growth outcome show no systematic patterns with most 50% credible intervals overlapping zero (figure 10a and b). The residual variation (within-tree variation) is far greater than the among tree variation for both measures, suggesting that most variation is at the level of branches within trees.

Height growth was lowest for the monthly clipping treatments (monthly low intensity (mean, median): 6.5 cm, 10 cm; monthly high-intensity: 0 cm, 0 cm). Mean control and single clipping height growth was similar and higher than monthly clipping, regardless of intensity (control: 50.7 cm, 47.5 cm; single low-intensity: 48.5 cm, 45 cm; single high-intensity: 47.75 cm, 55 cm). Growth of trees exposed to natural herbivory was lower than both single clipping treatments, but higher than both clipped monthly (13 cm, 15 cm). Patterns of medians and quartiles are shown in figure 11a.

The frequency of clipping accounted for far more variation in height growth than intensity, with a negligible interaction effect (figure 12a). The 95% posterior credible intervals for frequency and intensity effect do not overlap, with frequency being far greater (table 2). Monthly clipping had a strong negative effect on height growth, while the intensity of clipping had little effect (figure 12b). All posterior credible intervals for effect sizes are narrow, with intensity effects overlapping zero.

Differences in diameter growth, though slight, are evident (figure 11b). Average diameter increment for monthly clipped trees was slightly lower than for other treatments (monthly high-intensity: 0.27 cm, 0.26 cm; monthly low-intensity: 0.41 cm, 0.39 cm). All other treatments had similar diameter increments (control: 0.62 cm, 0.55 cm; single high-intensity: 0.65 cm, 0.65 cm; single low-intensity: 0.5 cm, 0.48 cm; natural herbivory: 0.57 cm, 0.5 cm). Frequency and its interaction with intensity accounted for most of the variation in diameter growth (figure 13a). The monthly treatment has a considerable negative effect on growth (figure 13b, table 2).

The response patterns of total aboveground biomass to clipping treatments were similar to the patterns observed for branch growth, though data were highly variable (figure 14). Unclipped control trees had on average greater biomass for a given initial size at the end of the season than those experimentally clipped. Unexpectedly, the greatest final biomass was observed in the unclipped trees exposed to natural herbivory (figure 14). Clipping frequency was again the most important factor, though intensity accounted for nearly as much variation (figure 15a). Credible interval surrounding these variance estimated are, however, wide, overlapping with one another. Again, clipping had the greatest negative effect on biomass in the monthly clipping treatment (figure 15b). High intensity clipping also reduced biomass considerably. A full summary of estimated effects and parameters is given in table 3.

Figures and Tables

Table 1. Summary of variance components and treatment effects from statistical analyses on total length and longest axis response to clipping of *Acacia karroo* branches within trees at two levels of intensity and two frequency levels. Rhat is the potential scale reduction factor, and equals 1 when chains converge. Low = half intensity clipping, High = full intensity clipping, Monthly = monthly clipping, Single = clipping at end of experiment. Credible intervals are reported as 0.025 – 0.975 posterior density. Effect sizes are reported as the difference from the mean response.

		Total Length mean	sd	95% CI	Rhat	Longest axis mean	sd	95% CI	Rhat
Variance components	Frequency	0.767	0.118	0.544 - 0.992	1.00	0.829	0.083	0.672 - 0.997	1.00
	Intensity	0.570	0.120	0.329 - 0.795	1.00	0.591	0.084	0.422 - 0.747	1.00
	Tree	0.160	0.101	0.008 - 0.373	1.00	0.107	0.070	0.005 - 0.259	1.00
	Interaction	0.249	0.095	0.061 - 0.437	1.01	0.255	0.069	0.123 - 0.389	1.00
	Residual	0.619	0.020	0.580 - 0.657	1.00	0.454	0.013	0.427 - 0.480	1.00
Effect size (cm) (4th root transformed)	Single	0.542	0.083	0.385 - 0.702	1.00	0.586	0.059	0.475 - 0.705	1.00
	Monthly	-0.542	0.083	-0.702 - -0.385	1.00	-0.586	0.059	-0.705 - -0.475	1.00
	Low	0.403	0.085	0.232 - 0.562	1.00	0.417	0.060	0.298 - 0.528	1.00
	High	-0.403	0.085	-0.562 - -0.232	1.00	-0.417	0.060	-0.528 - -0.298	1.00

Table 2. Summary of variance components and treatment effects from statistical analyses on tree height growth and diameter growth response to clipping of *Acacia karroo* branches at two levels of intensity and two frequency levels. Low = half intensity clipping, High = full intensity clipping, Monthly = monthly clipping, Single = clipping at end of experiment. Effect sizes are reported as the difference from the mean response.

		Height mean	sd	95% CI	Rhat	Diameter mean	sd	95% CI	Rhat
Variance components	Frequency	31.970	3.474	25.130 - 38.235	1.00	0.160	0.030	0.103 - 0.216	1.01
	Intensity	3.137	2.354	0.090 - 8.624	1.01	0.025	0.019	0.001 - 0.071	1.00
	Interaction	2.685	1.940	0.108 - 7.359	1.00	0.082	0.024	0.036 - 0.130	1.01
	Residual	21.362	0.335	20.980 - 22.209	1.00	0.185	0.003	0.182 - 0.193	1.01
Effect size (cm)	Single	22.606	2.456	17.770 - 27.037	1.00	0.113	0.021	0.073 - 0.153	1.01
	Monthly	-22.606	2.456	-27.037 - -17.770	1.00	-0.113	0.021	-0.153 - -0.073	1.01
	Low	1.245	2.470	-3.441 - 6.093	1.00	-0.007	0.021	-0.049 - 0.034	1.00
	High	-1.245	2.470	-6.093 - 3.441	1.00	0.007	0.021	-0.034 - 0.049	1.00

Table 3. Summary of variance components and treatment effects from statistical analyses on aboveground biomass response (total final biomass in March 2010) to clipping of *Acacia karroo* branches at two levels of intensity and two frequency levels. Low = half intensity clipping, High = full intensity clipping, Monthly = monthly clipping, Single = clipping at end of experiment. Effect sizes are reported as the difference from the mean response.

		mean	sd	95% CI	Rhat
Variance components	Frequency	57.16	25.52	23.39 – 86.28	1.02
	Intensity	46.46	15.28	15.07 – 75.64	1.00
	Interaction	22.16	12.25	2.21 – 47.23	1.01
	Branch length	115.99	11.78	93.97 – 139.40	1.00
	Residual	124.34	1.41	122.60 – 127.70	1.00
Effect size (g)	Single	40.418	10.97	16.54 – 61.01	1.03
	Monthly	-40.418	10.97	-61.01 - -16.54	1.00
	Low	32.837	10.85	10.66 – 53.49	1.00
	High	-32.837	10.85	-53.49 –10.66	1.00

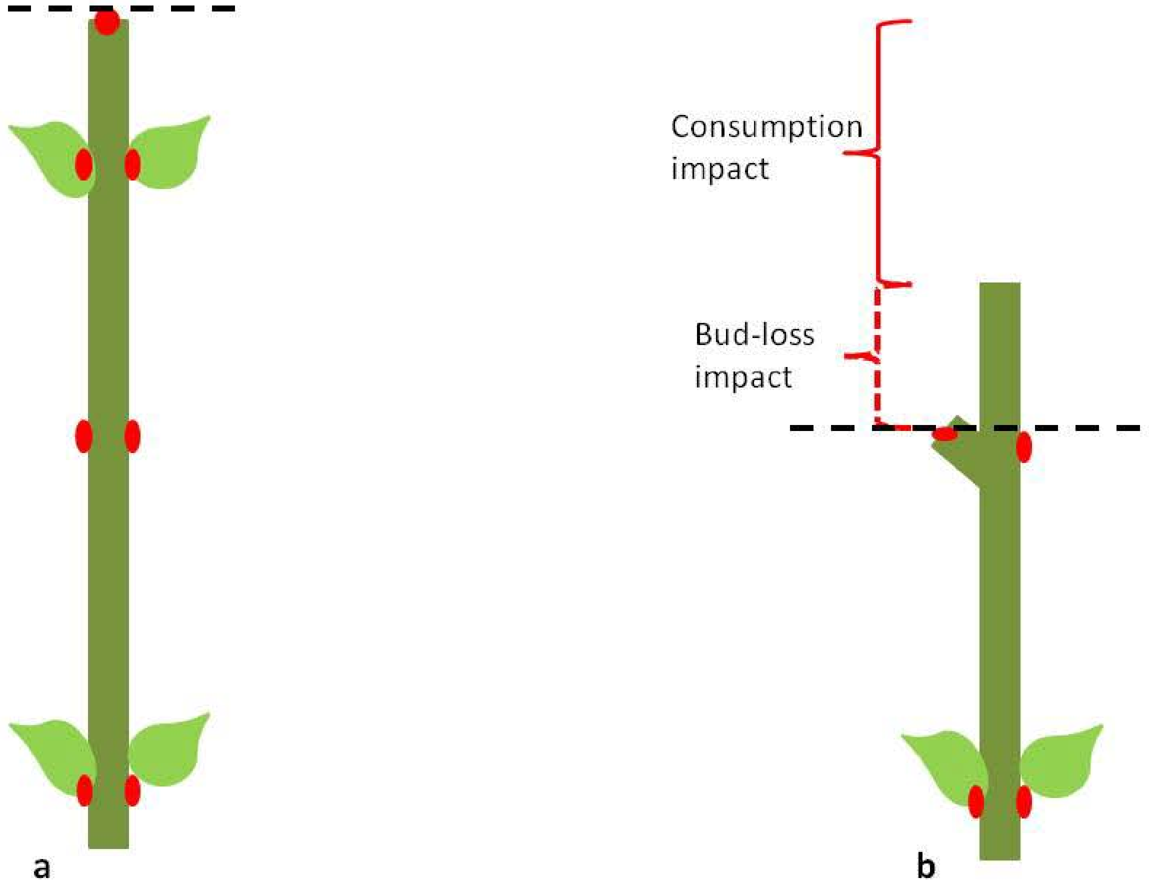

Figure 1. Diagrammatic representation of the two aspects of a browser's bite that impact plant height. Red ellipses represent buds and black dotted lines the highest point from which branch extension occurs. The plant in figure a represents the unbrowsed form. In figure b the apex of the plant has been bitten off. The solid red bracket outlines the length removed from the apex by the bite (consumption impact). The red dotted bracket represents the height lost because the most proximal bud does not occur at the highest point of the plant (bud-loss impact) and must elongate to this point before any height increase can occur.

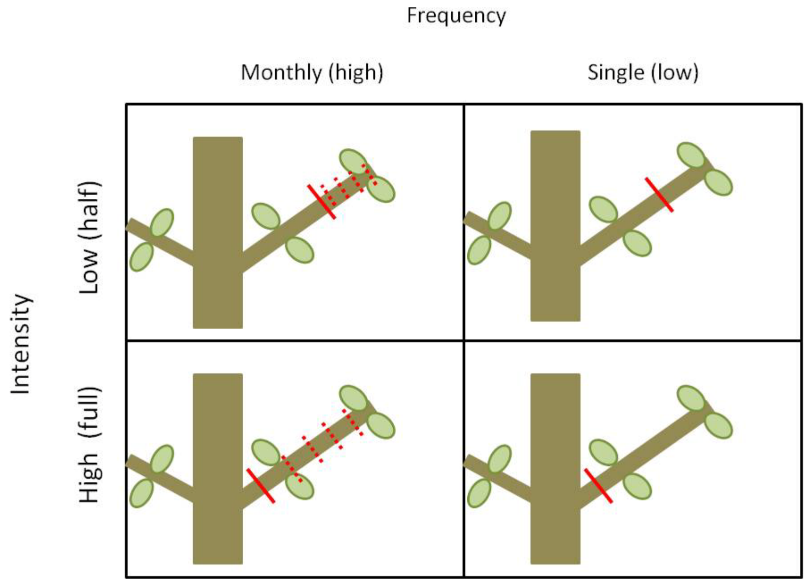

Figure 2. Diagrammatic representation of experimental design and herbivory simulation. Two factors (frequency, intensity) were investigated at two levels each (Frequency: Monthly, Single; Intensity: High, Low). Within each group represented by a block in the figure 20 trees were sampled. The dashed red lines show where clipping would occur on a branch in the monthly treatments in each successive month. The solid red line shows where clipping would occur in the final month. For clarity, the figure is drawn assuming that branches do not grow during the experiment.

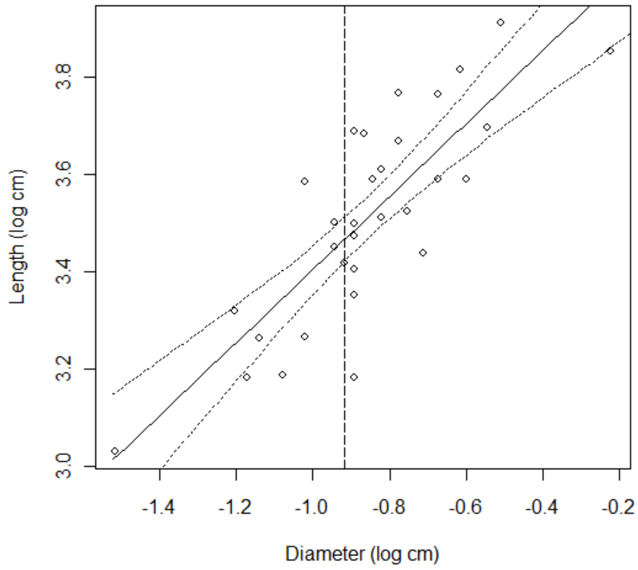

Figure 3. Allometry of branch length and diameter measured on *Acacia karroo* trees protected from natural browsing. Slope = 0.751 [0.560, 0.943], intercept = 4.15 [3.99, 4.33], $R^2_{bayesian}$ = 0.642 [0.398, 0.785]. Parameters are reported as: mean [95% CI].

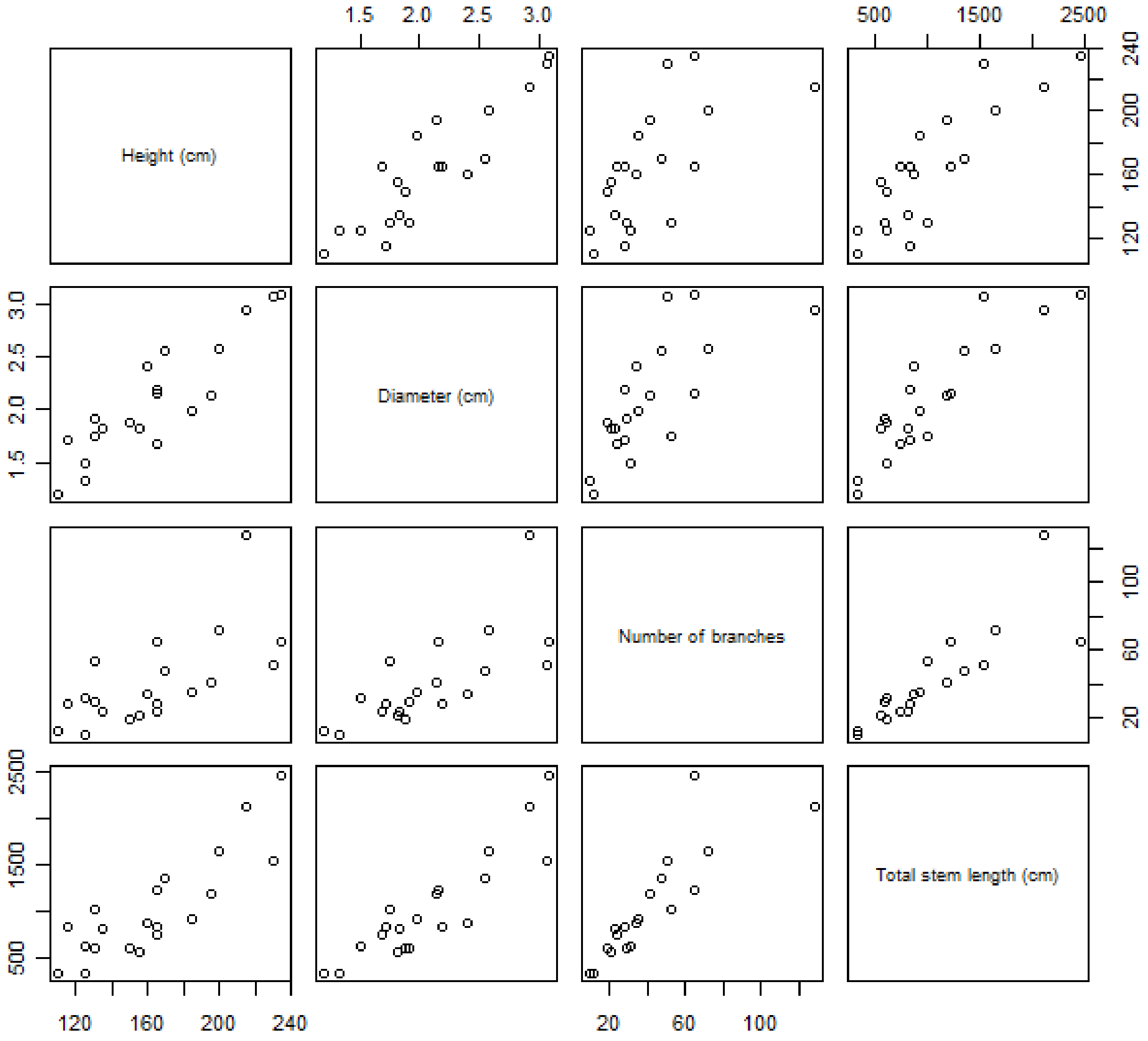

Figure 4. Scatter plot matrix of variables measured for use as predictors of initial tree biomass. All variables are highly correlated with one another.

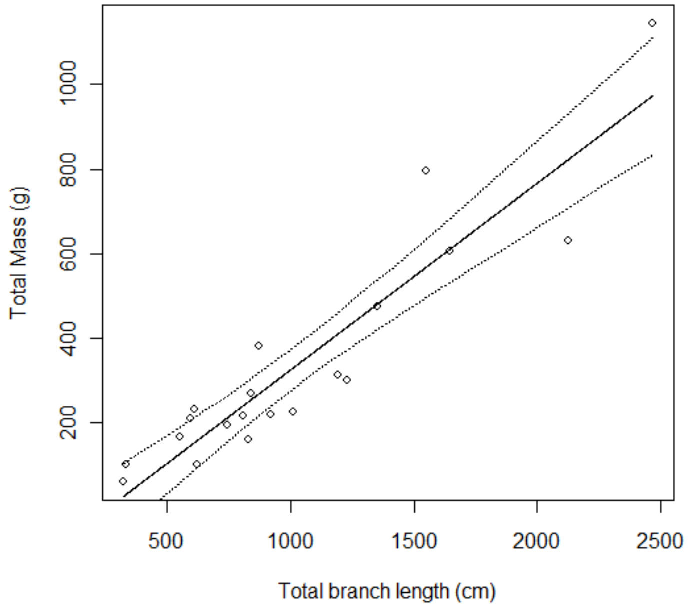

Figure 5. The relationship between total length of all branches on trees and total (leaf, stem and pod) biomass. Slope = 0.443 [0.353, 0.533], intercept = -117.6 [-230.4, -14.94], $R^2_{bayesian}$ = 0.828 [0.660, 0.913]. Parameters are reported as: mean [95% CI].

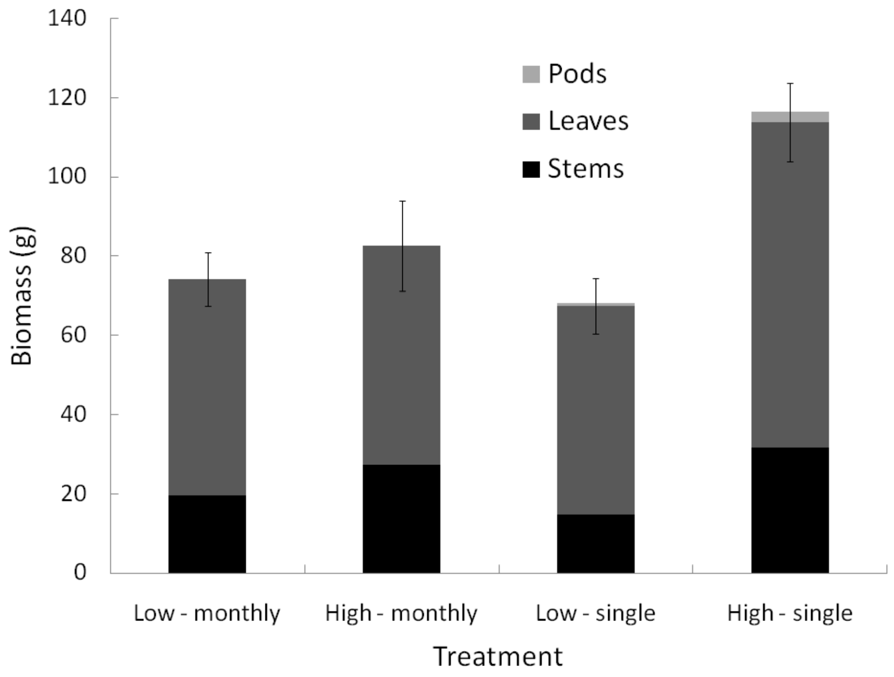

Figure 6. Mean biomass removed throughout the duration of experimental clipping for each treatment group. Error bars show standard error of the mean. Low = half intensity clipping, High = full intensity clipping, Monthly = monthly clipping, Single = clipping at end of experiment.

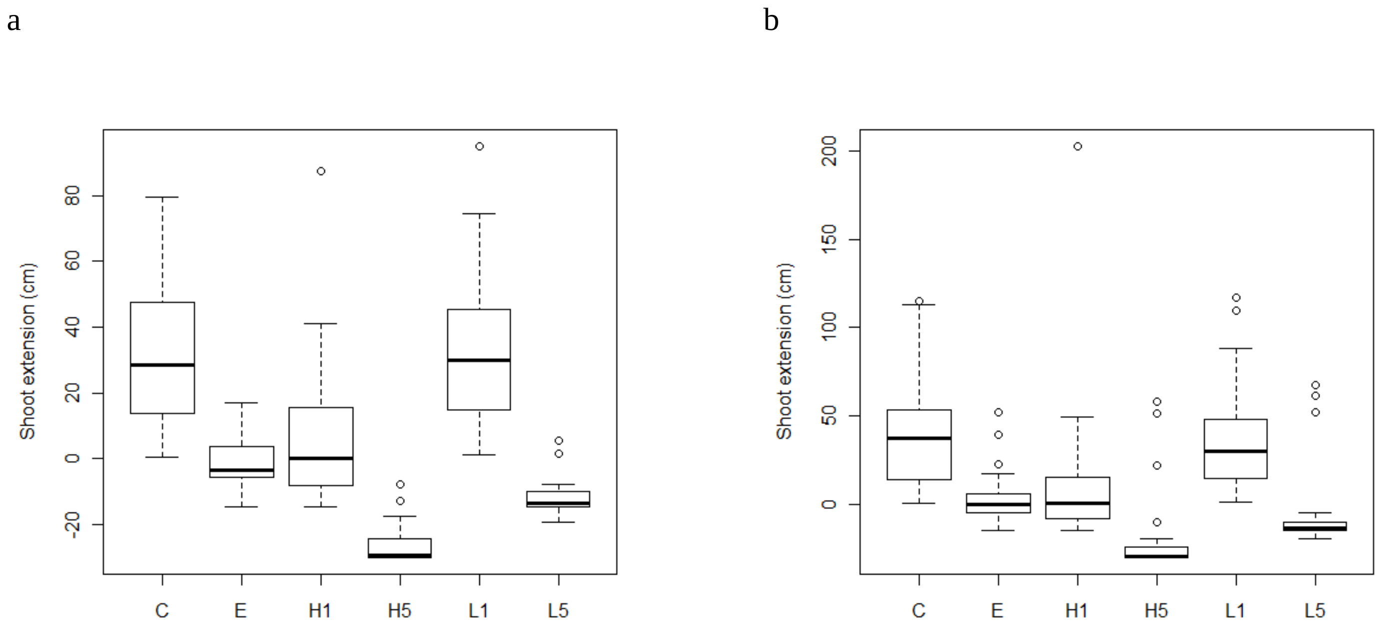

Figure 7. Box plots of net shoot extension for a) longest branch axis and b) total branch length measured at the end of the experiment for all treatments, including those not used in factorial analysis (C, E). Treatment codes are: C – control, E – Exposed to natural browsing, H1 – high intensity end-of-season clipping, H5 – high intensity monthly clipping, L1 – low intensity end-of-season clipping, L5 – low intensity monthly clipping.

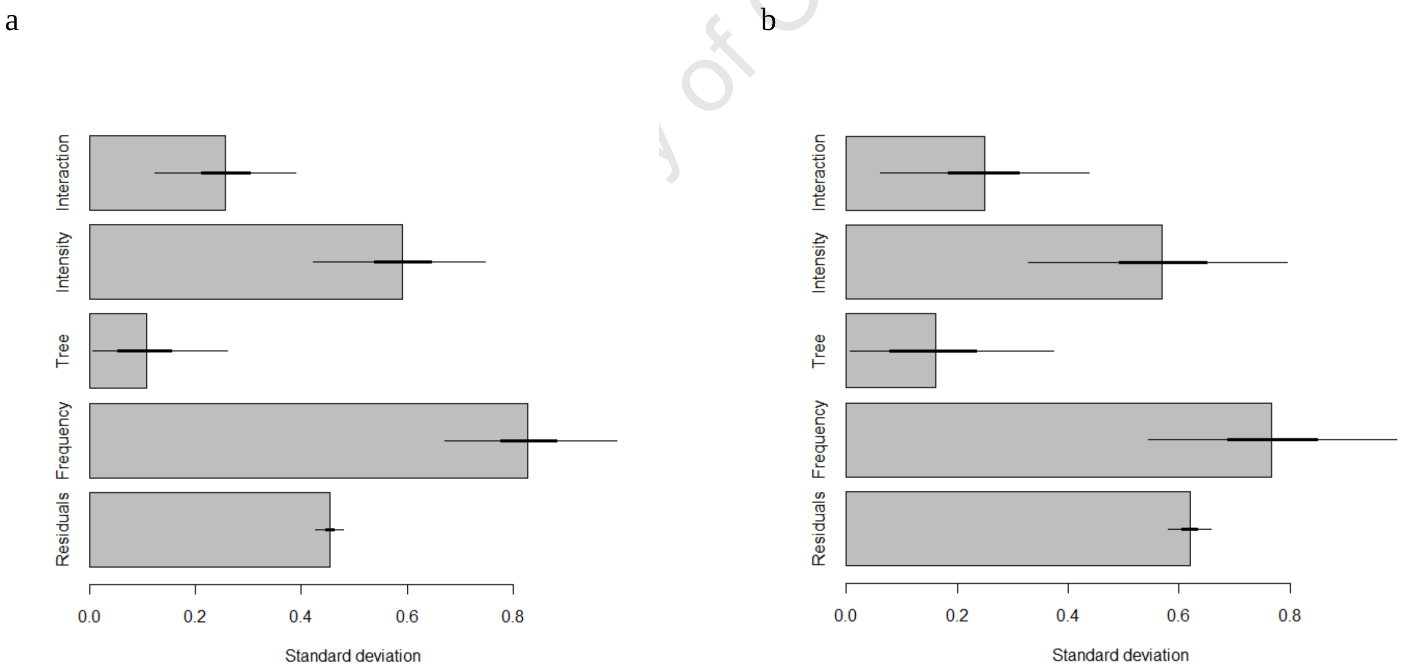

Figure 8. Variance components of a) longest branch axis and b) total branch length response to simulated browsing. Factors tested were clipping intensity, clipping frequency, individual tree effects and intensity*frequency interaction. Bars show estimated variance explained, dark lines 50% posterior credible interval around the estimate and thin lines 95% posterior credible intervals (see also table 1).

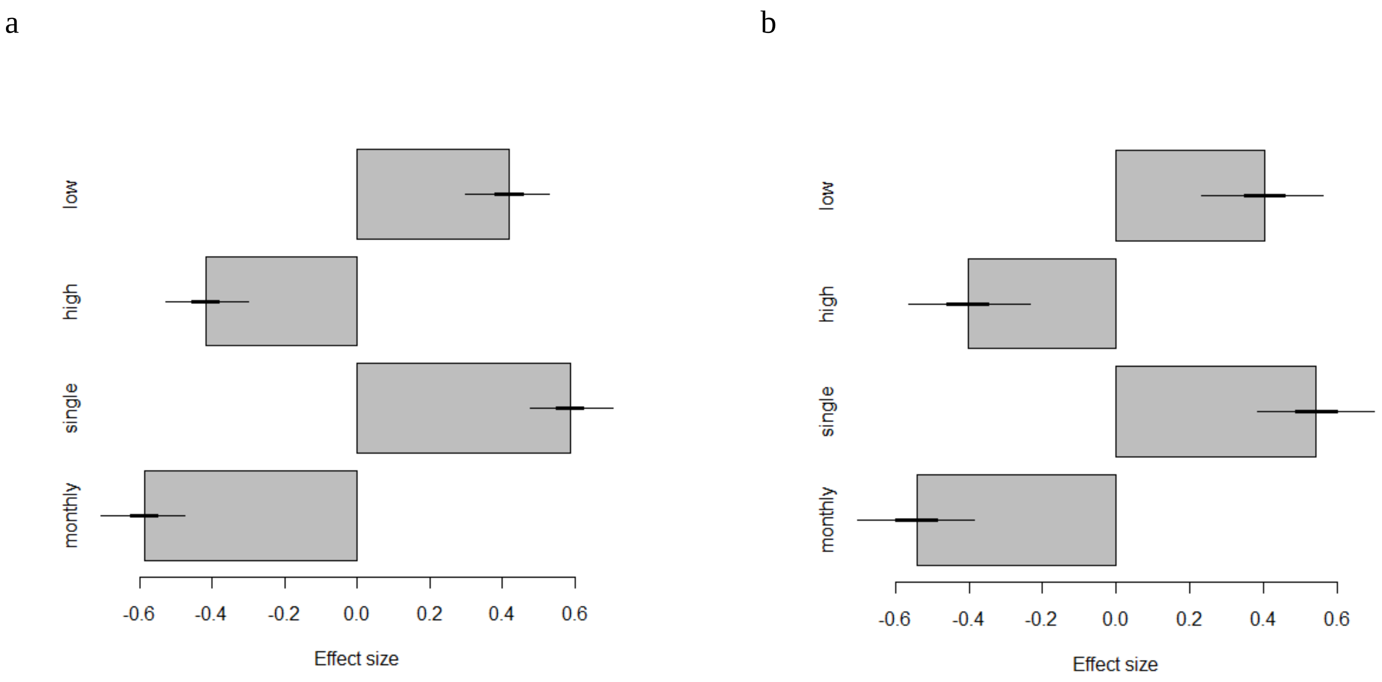

Figure 9. Effect sizes of intensity and frequency factor levels for a) longest branch axis and b) total branch length response to simulated browsing. Two factors levels were used for clipping intensity (low, high) and two for clipping frequency (single, monthly). Bars show estimated mean response, dark lines 50% posterior credible interval around the mean estimate and thin lines 95% posterior credible intervals (see also table 1). Effect sizes are shown as the group difference from the overall mean response.

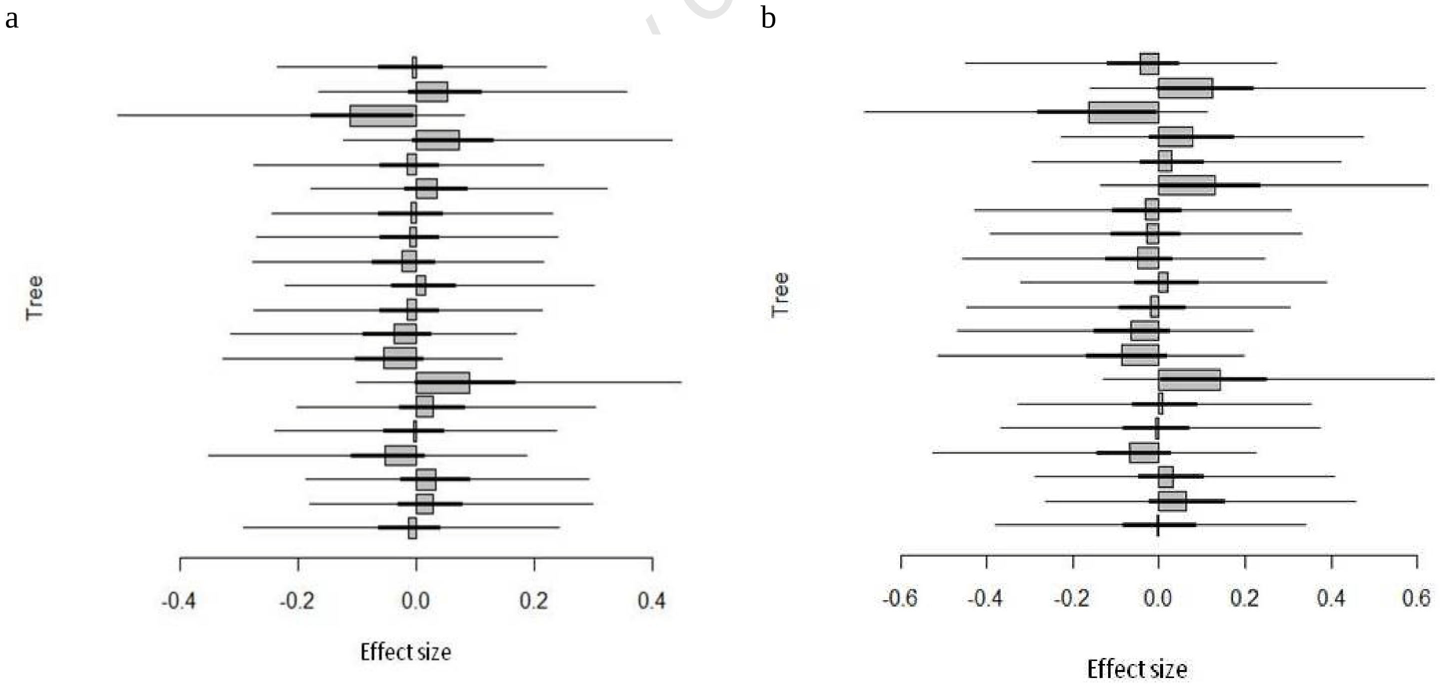

Figure 10. Individual tree effect on a) longest branch axis and b) total branch length response within trees. Each bar represents a single tree used in the study. Bars show estimated mean response, dark lines 50% posterior credible interval around the mean estimate and thin lines 95% posterior credible intervals.

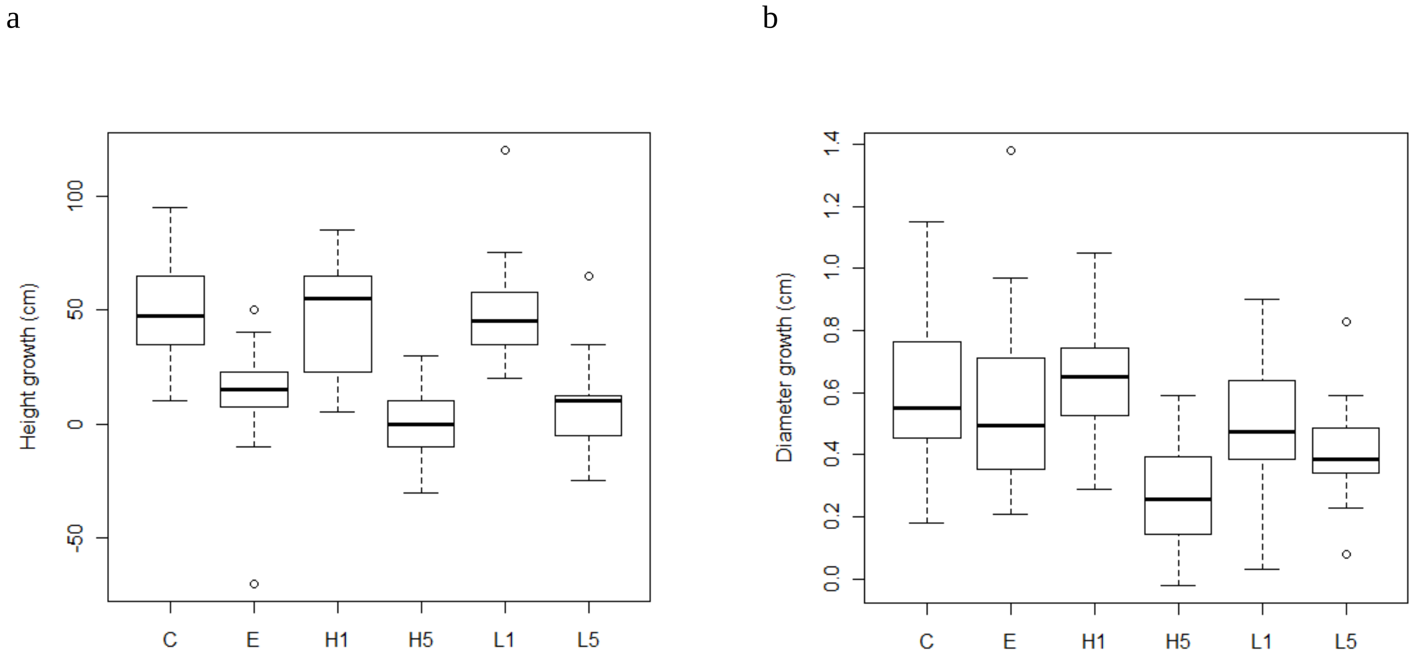

Figure 11. Box plots of a) height growth and b) diameter growth measured at the end of the experiment for all treatments, including those not used in factorial analysis (C, E).

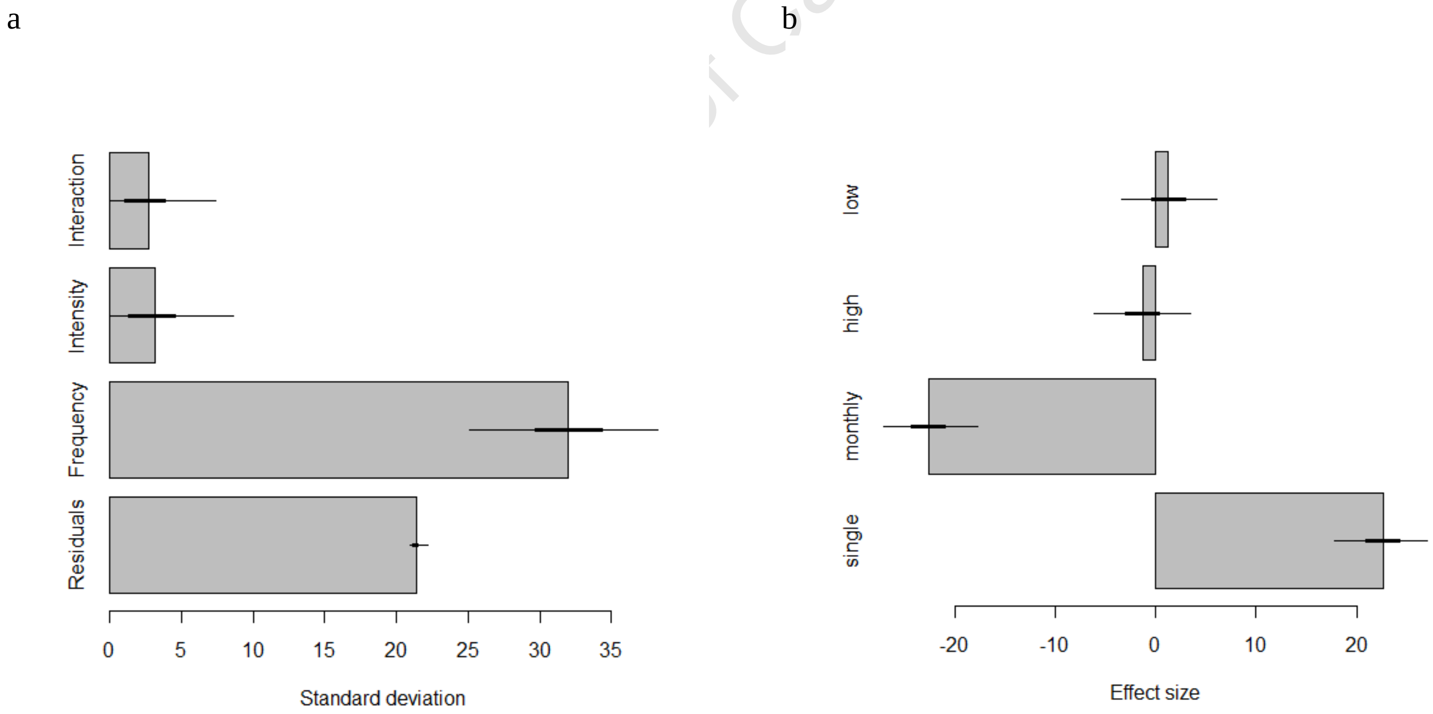

Figure 12. Variance components (a) and effect sizes (b) of height growth response to intensity, frequency and frequency*interaction factors. Two factors levels were used for clipping intensity (low, high) and two for clipping frequency (single, monthly). Bars show estimated mean, dark lines 50% posterior credible interval around the mean estimate and thin lines 95% posterior credible intervals (see also table 2). Effect sizes are shown as the group difference from the overall mean response.

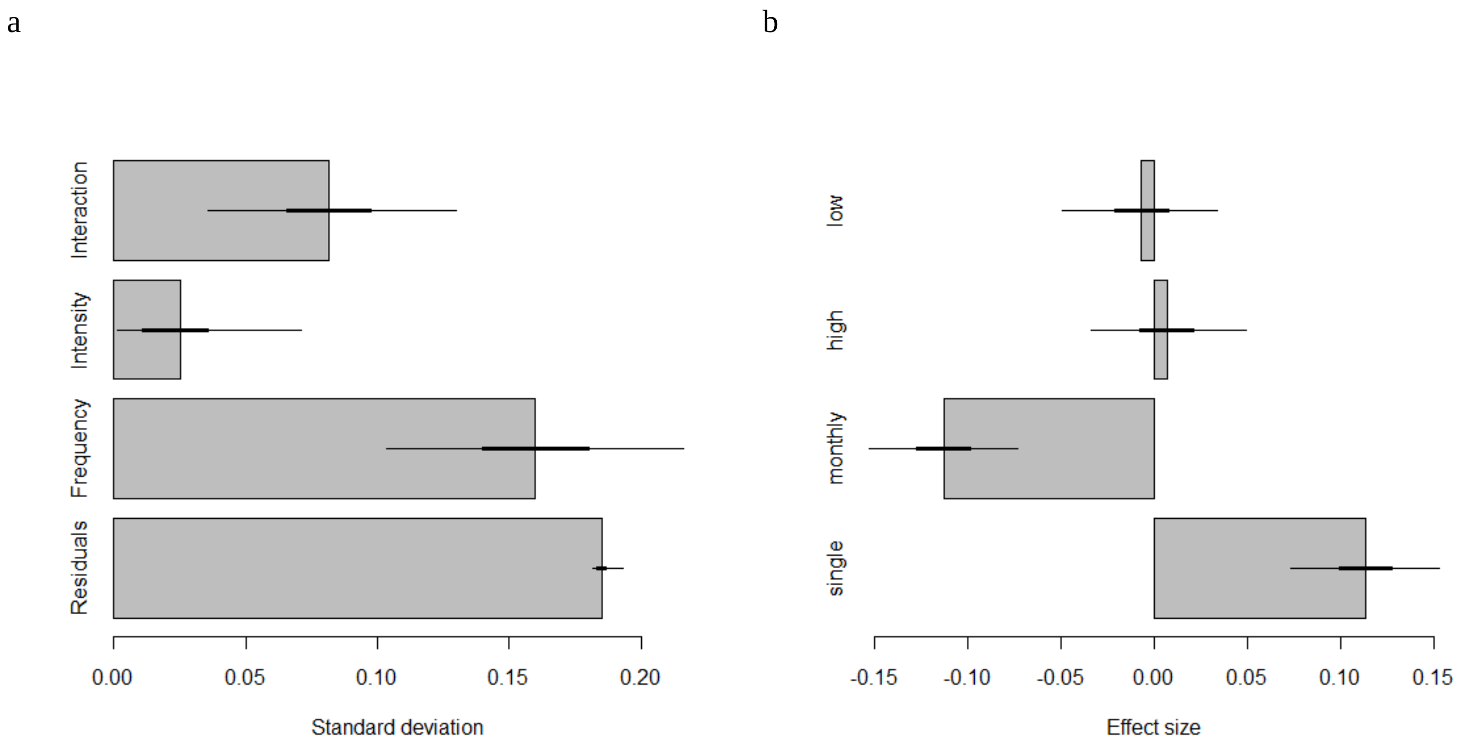

Figure 13. Variance components (a) and effect sizes (b) of diameter growth response to intensity, frequency and frequency*interaction factors Two factors levels were used for clipping intensity (low, high) and two for clipping frequency (single, monthly). Bars show estimated mean, dark lines 50% posterior credible interval around the mean estimate and thin lines 95% posterior credible intervals (see also table 2). Effect sizes are shown as the group difference from the overall mean response.

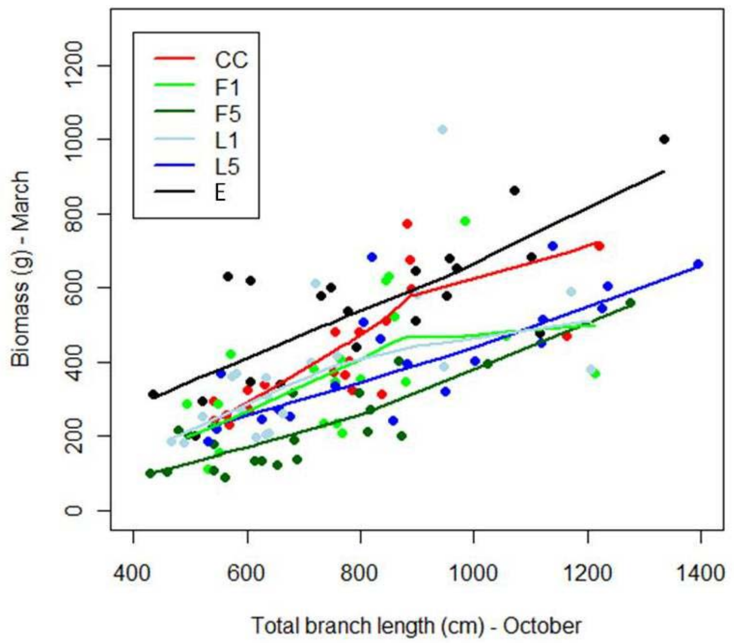

Figure 14. Total aboveground biomass measured at the end of the experiment plotted against total length of all branches measured at the beginning of the experiment for all treatments, including those not used in factorial analysis (C, E). The solid lines show overall trends fitted using a loess smoother.

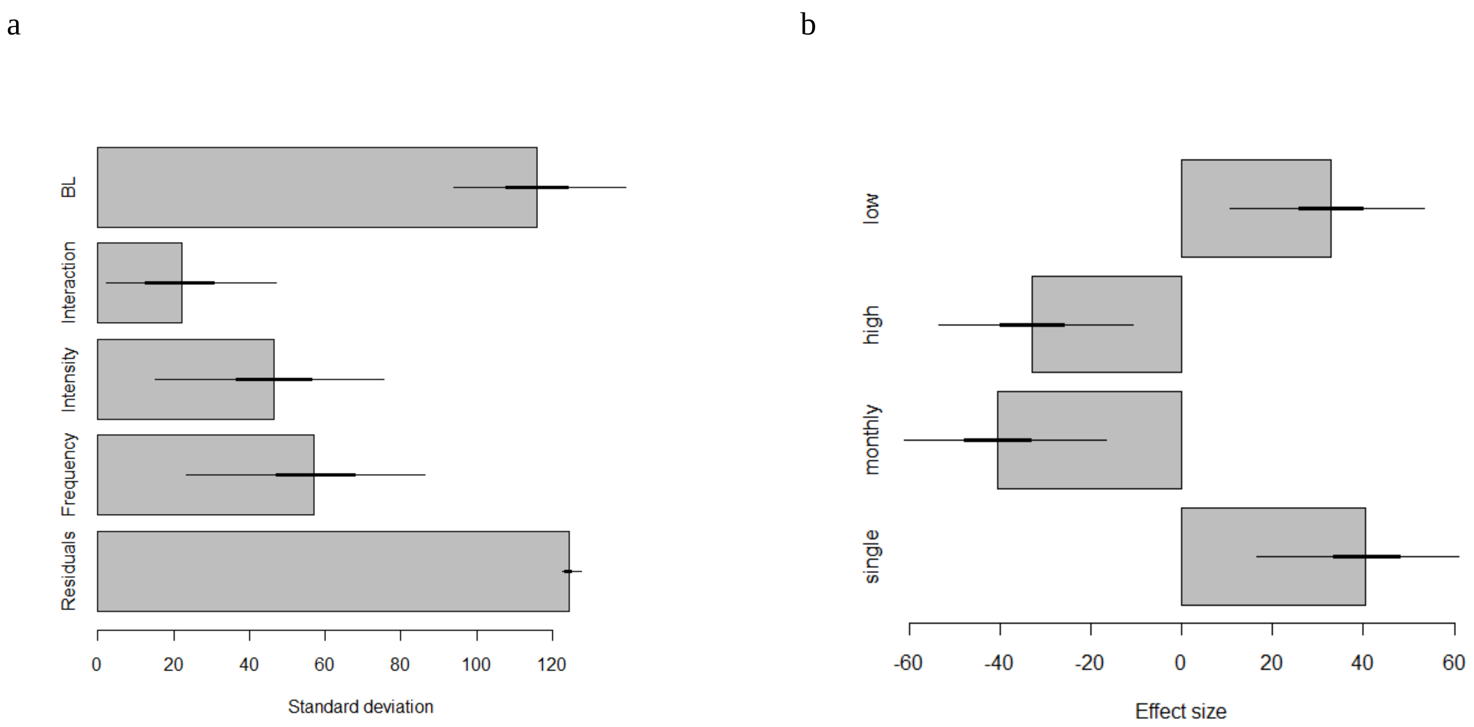

Figure 15. Variance components (a) and effect sizes (b) of total aboveground biomass response to intensity, frequency and frequency*interaction factors. The covariate of pre-treatment total branch length (BL) is included to control for variation in initial biomass. Bars show estimated mean, dark lines 50% posterior credible interval around the estimate and thin lines 95% posterior credible intervals (see also table 3). Effect sizes are shown as the group difference from the overall mean response.

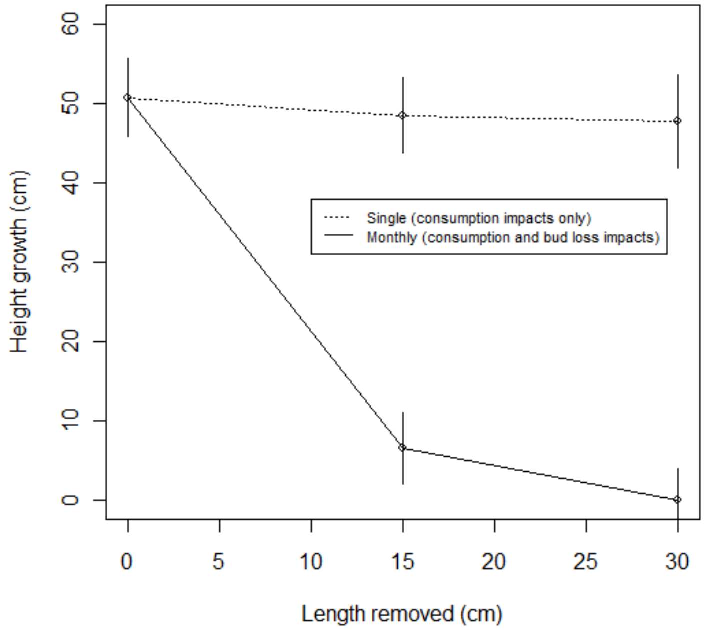

Figure 16. Mean height growth for trees clipped monthly and at the end of season plotted as a function of clipping intensity. Growth for unclipped plant (0 cm) was obtained from the control trees measured, but not included in the factorial analysis. Vertical lines indicate standard errors.

Discussion

Both bud-loss and consumption impacts negatively affect plant fitness. However, bud-loss impacts, manipulated by modifying the frequency of clipping, had a far greater effect on plant fitness measured as height. Though height growth is the direct product of branch elongation, observed patterns of height growth were not directly explained by factors affecting branch elongation, nor did biomass respond in a similar manner to height. These differences highlight the importance of understanding how the responses of height and biomass may diverge, and how factors such as the amount of plant material consumed and bud responses to browsing differentially affect biomass and height.

Clipping of trees at the end of the growing season provides a control treatment in which browsing occurs without inflicting bud-loss impacts. This treatment resulted in far more height growth than monthly clipped trees, comparable to the growth of unclipped controls. The height growth of monthly clipped trees was comparable to trees exposed to natural browsing. This suggests that the repeated browsing treatment is a more accurate simulation of natural herbivory at this site. This is an important observation as many experiments simulating browsing apply treatments as a single clipping treatment (eg Bergstrom and Danell 1987, Gadd *et al* 2001, Hester *et al* 2004**)**. However, the differences in biomass responses between experimentally clipped trees and trees exposed to natural browsing affirm the difficulty of realistically simulating natural herbivory (Baldwin 1990).

Frequent clipping, resulting in high bud-loss impacts, greatly reduced height growth. The proposed mechanism for this loss of height growth was the loss of apical growth - delaying or curtailing branch extension, and the activation of dormant lateral buds resulting in the diversion of growth to multiple points. The absence of any difference in patterns of total branch growth and longest axis extension suggests that loss of height growth is not due to activation of lateral buds. If lateral buds were activated by repeated clipping, greater total branch growth relative to the longest axis of extension would be expected in this treatment, though this was not observed. Thus, I suggest that the reduction in height growth resulting from multiple clipping events is as a result of the curtailment of branch extension. This curtailment may be due to the lack of a readily available dormant bud bank. The variety of *A. karroo* used experiment is adapted to frequent fire, rather than frequent browsing, and this may explain the proposed lack of resting buds for epicormic sprouting (Archibald and Bond 2003). A variety better adapted to frequent browsing would be expected to maintain a larger bank of dormant buds, and may perhaps respond by activating dormant buds and diverting biomass to multiple points of extension (Tuomi *et al* 1994, Archibald and Bond 2003).

Although I attempted to control for the intensity of clipping between the frequency treatments (eg. High intensity: 5 cm per branch monthly for 6 months = 30 cm once at the end of the experiment), for any given intensity level the monthly clipping treatment remains biased toward less growth. Although an equivalent amount of stem length or biomass was removed between the two treatments, the biomass removed from the end-of-season clipping treatment was allowed to remain on the plant – photosynthesising and contributing to new biomass growth – for the duration of the experiment, while in the monthly clipping treatment I began removing it from the outset. Thus, the monthly treatment had reduced capacity to grow for the season over which the experiment was conducted, even if the intensity is controlled for. I do not however consider this bias to significantly affect the outcome of this experiment. The leaf biomass removed monthly from each tree represents a small fraction of the total leaf biomass of the treated trees at any time (mean leaf biomass removed monthly – 11 g, mean leaf biomass of whole plants – 79 g), and was recovered quickly after clipping.

Surprisingly, consumption impacts, simulated by varying clipping intensity, affected height growth very little. Yet the intensity of consumption had a strong affect on both branch elongation and total aboveground biomass. The discrepancy between branch-level and whole plant response can be explained by age- and canopy position-dependent branch growth. It is well known that the physiological age of buds and their growth units determine branch growth and phenology (Barthelemy and Caraglio 2007). This is reflected in figure 8a and b, where far more variance is accounted for by within tree variation than between trees. At the canopy bottom, growth units were observed to extend very little, if at all, while at the top of the canopy, almost all branches extended greatly. Since little growth occurred on lower branches through the growth season, bud loss impacts were minor and the final length of branches was entirely determined by the intensity of clipping (consumption impacts). Without clipping, branches in the upper canopy grew far more than the maximum amount clipped (upper quartile of control trees in figure 6a and b). All of this growth could still be lost if bud-loss impacts are high, with repeated removal of apical buds preventing any extension from accruing. This was observed for both the high frequency clipping treatments, where little to no branch extension occurred. If consumption impacts are high for branches low in the canopy and bud-loss impacts important for those at the top, we would expect both to emerge as important when a random sample of branches are measured, as was observed.

This explains why consumption impacts on height growth are low and bud-loss impacts high, and why this is not reflected in patterns of branch growth or aboveground biomass. Browser impacts on biomass are the result of disturbance and responses of the whole canopy and stem. Impacts on height growth are, however, at least in the short term, entirely a result of impacts on branch extension in the upper canopy. Therefore, because bud-loss impacts are probably higher for branches in at the top of canopies, they will also be more important for height growth than for total aboveground biomass. The responses observed here thus show that the different growth and disturbance patterns in the upper canopy and whole-plant need to be considered when interpreting browser impacts.

Here I have shown that height growth of *A. karroo* is greatly affected by bud loss. By implication, plant fitness and tree demography will be impacted upon strongly. The models described in the third chapter of this thesis attempt to incorporate bud responses to browsers in a model of woody plant demography. These experiments do not explicitly test the browsing mechanisms described therein. Here, at each simulated browsing event, all branch tips were pruned simultaneously, while the model assumption was that branch pruning occurs at random in near-continuous time. This results in the exaggeration of bud-loss impacts in the experiment (relative to the model), as no branch is re-browsed until all others have been clipped again. This difference is intentional, with the desired outcome being the maximization of treatment effects in the short experimental time. The results can nonetheless be re-expressed to facilitate direct comparison to the predictions of chapter 3 (figure 16). We see that there is qualitative agreement between the results obtained herein and model predictions, with the inclusion of bud loss impact resulting in a nonlinear relationship between consumption and impact, and greatly depressed growth.

The strong influence of browser disturbance to buds on tree growth prompts speculation regarding what further factors may affect the severity of bud loss impacts, and ultimately the severity of browser impacts. Bud distribution through the canopy, activation intensity, longevity and the temporal rhythm of growth and development are just some of the factors that will determine how browsing impacts plants (Klimešova and Klimeš 2007). Aspects of plant growth and development important in characterising major axes of variation between woody plants are well described (Barthelemy and Caraglio 2007, Klimešova and Klimeš 2007). Factorial experiments that evaluate the responses of plants characterised by different suites of traits may lead to the discovery of systematic response patterns related to certain functional traits. Complex plant simulators tracking growth, architecture and bud dynamics already exist, with some amenable to the inclusion of growth disturbance agents (Allen *et al* 2004, Yan *et al* 2004, Barczi *et al* 2007). Simulation experiments and sensitivity analyses may help identify potentially important traits and correlations. Synthesizing the major axes of variation in woody plant architecture, development and bud dynamics into an understanding of how browsing impacts plants could lead to significant advances towards a better predictive understanding of mammalian control of vegetation structure.

Chapter 5: Herbivore-induced alteration of stem diameter-height scaling in an African savanna

Glenn R. Moncrieff

Introduction

The relationship between one measure of an organism's size (or the size of an organ) and another is known as allometry and is often described by the allometric equation:

$$Y = Y_0 X^b$$

Where Y_0 is a normalization constant and b is the allometric exponent, describing how Y grows in relation to X. A large body of theory exists examining the mechanisms governing the scaling of plant form, linking structure to the dynamics of internal resource supply or external physical limitations. These theories predict how stem height and diameter scale with one another (McMahon and Kronauer 1976, Dean and Long 1986, Rich *et al* 1986, Niklas 1992, West *et al* 1999, Niklas and Spatz 2002, Price *et al* 2007). Height is one of the most ecologically significant traits of trees. In closed canopy forests competitive fitness in the race to occupy light gaps is largely determined by height. In savannas, where light is not a limiting factor, height remains the primary determinant of tree fitness because fire and large mammalian herbivores limit the rate of transition to reproductive size classes. There are limits to how rapidly a tree can increase in height. Aside from limits imposed by resource availability there are also mechanical and hydraulic limits (Niklas 1994, Midgley 2003, Koch *et al* 2004). For a given height a tree must be able to support its own mass and resist wind stress. Thus growth in height must be matched with a concomitant increase in stem diameter. Moreover, the increase in metabolically active and photosynthesizing tissues as a result of growth requires the enlargement of supply networks. Hence growth necessitates an increase in sapwood, heartwood, and ultimately stem diameter.

The elastic similarity model, which models the theoretical buckling height of a self-supporting, taping column, predicts that heights should scale as the 2/3 power of stem diameter (McMahon 1973). The constant stress model predicts that if mechanical stress is equal along the stem height should scale as the ½ power of diameter (Dean & Long 1986). West, Brown and Enquist (1999) have proposed a model that predicts universal allometric scaling relationships in plants based on the fractal nature of supply and branching networks (henceforth referred to as WBE theory). This relies on the assumption that plant vascular systems are hierarchical branching systems and that plants (1) have a branching architecture which is volume filling; (2) minimize hydrodynamic resistance; (3) maintain constant leaf characteristics within a species during growth and development and (4) experience uniform biomechanical constraints.

The utility of allometric theories has been widely criticized, as often empirical data do not match the theoretical predictions (Glazier 2005, Muller-Landau *et al* 2006, White *et al* 2007). However, making comparisons between observed scaling exponents and theoretical predictions can yield information regarding how trees differ in form from architectures designed to optimally cope with mechanical and hydraulic constraints. Moreover, comparing allometry between populations can highlight important architectural and ontogenetic differences and the environmental drivers causing them. This is particularly true for stem diameter-height allometry because of the importance of height for trees in forest and savannas. Inter-specific variability about predicted scaling exponents has been interpreted as a result of differences in species-specific resource allocation patterns in response to the light environment and life-history strategies

(O'Brien *et al* 1995, Alves and Santos 2002, Poorter *et al*. 2006). Intra-specific variation in scaling exponents is often observed and has been attributed to factors such as stand age, stand density and neighbour effects (Henry and Aarssen 1999, Henry and Thomas 2002, Kaianiemi and Lintunen 2008).

The role of disturbance has been neglected in the interpretation of stem diameter-height allometry (but see Archibald and Bond 2003). Herbivory influences architecture by removing apical buds, resulting in the activation of dormant lateral buds and ultimately induces a decrease in internode distance and canopy densification (du Toit *et al* 1990, Bergström 1992). These architectural changes will be reflected in stem diameter-height allometry. The loss of apical dominance and removal of biomass reduces height growth (du Toit *et al* 1990, Danell *et al* 1994, Fornara and du Toit 2008). Diameter growth is also altered by herbivory (eg. Vila, *et al*. 2001, Bee *et al*. 2007). However, changes in diameter growth are unlikely to be related to disturbances to canopy bud banks, a major driver of height growth impacts. Thus, stem diameter-height allometry may change with herbivory as long as height and diameter responses are not in the same direction and of the same magnitude.

Traditionally, studies have used size-class distributions to investigate browser impact on tree populations (eg Pellew 1983, Asner *et al*. 2009). These size distributions result from two distinct processes: the population dynamics of recruitment and the individual dynamics of growth; both modified by browsing but also subject to environmental variations. Direct measurements of height growth over time can also reveal similar impacts, but such data necessitate large sampling effort and repeated measurements. Here stem diameter-height allometries are used to investigate browser impacts. Comparing allometry between impacted and unimpacted populations can reveal both the degree of browser impact and the possible implications of this impact for individual plant functioning. Stem-diameter height allometry is constructed from two ecologically significant traits, for which the data are easy to acquire and generate population level parameters that have a strong theoretical basis for interpretation.

Here I examine changes in stem diameter-height allometry induced by two megaherbivore browsers, African elephant (*Loxodonta africana*) and giraffe (*Giraffe camelopardalis*), on two regionally dominant savanna trees and compare our results to theoretical predictions. I expect differences to emerge in the allometric impacts on each species related both to herbivore foraging behaviour and plant response to herbivory. Specifically, I expect that when exposed to chronic herbivory, scaling exponents will be lower than those of paired populations protected from herbivory, with trees of a given diameter being taller inside exclosures than out. However, there may be a change in scaling, evident in allometric breakpoints, when trees grow beyond the reach of a browser or large enough to resist damage. Deviation from theoretical predictions and between impacted and umimpacted populations will then be used to explore the importance of herbivory and disturbance in general in causing plants to scale differently than predicted.

Methods

Study areas

All sampling was conducted within the Kruger National Park, South Africa on *Acacia nigrescens* Oliv. and *Colophospermum mopane* (Kirk ex Benth.) Kirk ex J.Léon. *A. nigrescens* is known to be heavily used by giraffe and is abundant throughout the southern regions of Kruger National Park, dominating in many landscapes. *C. mopane* forms extensive monodominant stands throughout the northern regions of the park, and is the staple forage elephants through the dry season in this region (Codron *et al*. 2006).

Much of the park falls within two distinct geological regions: granite and basalt. *A. nigrescens* was sampled at two sites: Satara (24.99 S, 31.50 E) and Makhohlolo (25.24 S, 31.90 E), both with basalt derived soils. MAP for Makhohlolo and Satara is approximately 600mm and 550mm respectively. The data collected at these two sites were combined and all subsequent analyses done on the pooled dataset. The site at Makhohlolo is paired with a 2.4 ha long term herbivore exclosure established in 1974. *C. mopane* was sampled in and around the 309 ha 'Nwashitsumbe exclosure (22.77 S, 31.27 E) on the northern basaltic plains established in 1968. Sampling in and around the 'Nwashitsumbe exclosure was conducted in upland areas to control for catenal soil differences. Elephant densities are high near the 'Nwashitsumbe exclosure and have been shown to drastically impact *C. mopane* populations through their foraging (Smallie and O'Conner 2000, Asner *et al*. 2009). Giraffe population densities are locally high on the southern basalts where *A. nigrescens* is common (Redfern *et al* 2003). Their impacts have been shown to be significant on both individuals and populations of *A. nigrescens* (Fornara and du Toit 2007, Levick *et al*. 2009). Two distinct browser vegetation interactions are therefore studied: giraffe foraging on *A. nigrescens* in the south of Kruger National Park, and elephant foraging on *C. mopane* in the north, with each plant population paired with a population protected from herbivory.

Sampling

At each site outside of an exclosure and within the 'Nwashitsumbe exclosure multiple transects were walked and stem diameter of the largest stem at 10 cm above ground level was measured for all *A. nigrescens* or *C. mopane* individuals encountered. Additional transects were walked measuring only large stemmed individuals in order to obtain a greater sample of large trees. All *A. nigrescens* individuals within the 2.4 ha

Makhohlolo exclosure were sampled. Height was measured to the nearest centimetre using a measuring tape for trees below 2m. The height of trees taller than 2m was measured using a clinometer. *A. nigrescens* individuals that showed obvious signs of elephant visitation were excluded, as the focus was on the giraffe - *A. nigrescens* interaction.

Data analysis

The statistical analyses were performed using a Bayesian framework, which is flexible and allows treatment effects on the scaling coefficient to be estimated. The resulting posterior distribution allows a full characterization of the uncertainty in parameter estimates. The growth change occurring when a tree grows beyond the reach of a browser represents a natural system breakpoint. This breakpoint should be reflected in the diameter-height allometry. Piecewise models were used to identify these breakpoints (Beckage *et al* 2007). Piecewise regression can be used to detect ecological thresholds, and has been successfully employed to identify breakpoints in tree architecture and allometry (Toms and Lesperance 2003, Beckage *et al* 2007, Ishii *et al* 2008). Both single and double breakpoint models were used when appropriate. Model fits were compared using the deviance information criterion (Spiegelhalter *et al* 2002). The following data distribution model was used when fitting a piecewise linear model after logarithmic transformation of both stem diameter and height, were y_i is the natural logarithm of height of tree *i* in a particular population and x_i the natural logarithm of diameter of tree *i*:

$$\mathrm{P}(y_i|\mu_i ,\tau) \sim N\,(\mu_i ,\tau)$$

Where μ_i is conditionally defined as:

$$\textit{if } (x_i < bp_1)$$

$$\textit{then } \mu_i = \alpha + \beta_1$$

$$\textit{else } \mu_i = \alpha + \beta_1 + (\beta_2 - \beta_1)(x_i - p_1)$$

For a single breakpoint model, and:

$$\textit{if } (x_i < p_1)$$

$$\textit{then } \mu_i = \alpha + \beta_1$$

$$\textit{else if } (bp_1 < x_i < p_2)$$

$$\mu_i = \alpha + \beta_1 + (\beta_2 - \beta_1)(x_i - p_1)$$

$$\textit{else } \mu_i = \alpha + \beta_1 + (\beta_2 - \beta_1)(x_i - p_1)$$

$$+ (\beta_3 - \beta_3)(x_i - p_2)$$

For a double breakpoint model.

Where α is the normalization constant, p_1 is the first breakpoint, p_2 is the second, β_1 the scaling exponent before the first breakpoint, β_2 the scaling exponent after the first breakpoint and β_3 the scaling exponent after the second breakpoint. Uninformative normal priors were used for scaling parameters and normalization constants. Uniform priors were used for breakpoints. For the single breakpoint model the maximum and minimum observed x_i were used to bound the uniform breakpoint prior. For the two breakpoint model, the prior for the first breakpoint was bound by the minimum observed

x_i and the tail-end of the posterior distribution for the breakpoint in the single breakpoint model. The prior for the second breakpoint was then uniform from this value to the maximum observed x_i. Models were fitted using MCMC algorithms implemented in WinBUGS 1.4 (Lunn *et al*. 2000). Diagnostic analyses were performed in R 2.11.0 (R Development Core Team 2010). For simulations using the simple linear model, chains ran for 100 000 iterations, with a burn-in of 50 000. When break-point models were used 1 000 000 iterations were performed discarding the first 500 000. Three parallel MCMC chain were run and visual inspection of diagnostic plots indicated that chains had converged and mixed. Although models were fitted in log-log coordinates all result presented are back-transformed for ease of interpretation.

Results

A full summary of all parameter estimates for all fitted models and their credible intervals is given in table 1. The simple linear model fitted the allometry for *A. nigrescens* within the exclosure and *C. mopane* outside the exclosure well (figure 1). However, simple linear models fitted to the allometry for *A. nigrescens* exposed to herbivory and *C. mopane* inside the exclosure did not fit well, with systematic departures from the predicted mean height for larger diameter trees (figure 2). Fitting piecewise-linear models for these two populations improved model fit in both (figure 2), with the DIC decreasing from -127.12 to -184.47 for the exposed *A. nigrescens* population and from 21.14 to -16.74 for *C. mopane* protected from herbivory (Table 1). Yet the height of the tallest trees was overestimated using a single breakpoint model for *A. nigrescens*. This bias was overcome by the addition of a second breakpoint (figure 2), which decreased the DIC to -195.07.

The posterior probability for the first breakpoint for *A. nigrescens* had a narrow credible interval (25.79 - 33.45 cm diameter; 522.8 – 683.3 cm height; [2.5% - 97.5%]; figure 2a) showing that the point where the scaling coefficient shifts is well defined. This was also true for *C. mopane* (7.31 - 10.8 cm diameter; 440.1 – 589.9 cm height; figure 2b). The credible interval was wider for the second breakpoint (40.04 - 73.7 cm diameter; 1014 – 2186 cm height; figure 2a), as a result of the paucity of data points occurring above it. It's inclusion in the allometry model for *A. nigrescens* was nonetheless supported statistically

The scaling coefficient for *A. nigrescens* when protected from herbivory was 0.74, far greater than predictions of 2/3 from McMahon and Kronauer (1976), West *et al* (1999) or Niklas and Spatz (2002) (figure 3). The scaling coefficient when exposed to herbivores was very similar to the value inside the exclosure, although this was only true for the linear model. (figure 3). When a single breakpoint was fitted, the scaling coefficient decreased considerably from 0.75 to 0.71. This was likewise true for the two-breakpoint model, decreasing again to 0.71. The exponent after the breakpoint then increased to 1.17 in the single breakpoint model, and 1.54 with two breakpoints, as height grows rapidly with diameter increase. After the second breakpoint the scaling exponent decreased; however, the uncertainty in the estimate was large, and included both 0.75 and 0 (figure 3.)

For *C. mopane* the scaling coefficients of simple linear models were very different between populations inside and outside of the exclosure (0.74 inside and 0.57 outside; figure 4). Height increased markedly less with increasing diameter when exposed to herbivores. When the piecewise model was used for the protected population the slope before the break point was 0.85 and 0.5 after the breakpoint (figure 4).

Again, some exponents exceed predicted values. However, for *C. mopane* exposed to herbivores and after the breakpoint in the protected population, exponents decreased to values close to the predicted 2/3.

Architectural differences, in the form of predicted height difference for a given diameter, between populations of *A. nigrescens* and *C. mopane* exposed to and protected from herbivores are shown in figure 5. The differences in predicted height are a result of differences in both scaling parameters and normalization constants, and include uncertainty in the estimates of these parameters and breakpoints in the models. As diameter increases, so does the predicted difference in height between *C. mopane* populations protected from, and exposed to, herbivores. The rate at which this difference increases, however, decreases after the breakpoint in the protected population's allometry. Associated with this increasing difference in height is an increasing variability about the mean prediction. Height differences between the protected and exposed population of *A. nigrescens* also increased as diameter increased, until the first breakpoint in the allometry of trees exposed to herbivores. For larger trees, as a result of an increase in the scaling exponent of exposed trees, height difference decreases towards zero.

Figures and Tables

Table 1. Summary of fitted models and parameters in log-log coordinates. All parameters are reported as means followed by 95% credible intervals [2.5%, 97.5%]. 1bp = first breakpoint, 2bp = second breakpoint.

Exclosure	Model	alpha		beta1		beta2		beta3		bp1		bp2	
A. nigrescens													
inside	linear	4.32	[4.28, 4.36]	0.74	[0.73, 0.76]								
outside	linear	3.96	[3.90, 3.99]	0.75	[0.74, 0.77]								
	1bp	4.01	[3.97, 4.06]	0.71	[0.69, 0.73]	1.17	[1.01, 1.35]			3.25	[3.03, 3.42]		
	2bp	4.02	[3.98, 4.06]	0.71	[0.69. 0.73]	1.54	[1.19, 2.05]	0.07	[-1.79,0.94]	3.40	[3.25, 3.51]	4.00	[3.69, 4.30]
C. mopane													
inside	linear	4.51	[4.43, 4.58]	0.74	[0.70, 0.77]								
	1bp	4.37	[4.29, 4.45]	0.85	[0.80, 0.91]	0.50	[0.41, 0.58]			2.17	[1.99, 2.38]		
outside	linear	4.56	[4.46, 4.66]	0.57	[0.53, 0.62]								

Table 1. Cont.

Exclosure	Model	sigma		DIC	
A. nigrescens					
inside	linear	0.16	[0.14, 0.18]	-158.13	[-160.90, -152.10]
outside	linear	0.22	[0.20, 0.23]	-127.12	[-130.00, -120.20]
	1bp	0.21	[0.19, 0.22]	-184.47	[-188.60, -177.40]
	2bp	0.20	[0.19, 0.22]	-195.07	[-200.90, -186, 10]
C. mopane					
inside	linear	0.25	[0.23, 0.28]	21.14	[18.46, 27.03]
	1bp	0.23	[0.21, 0.26]	-16.74	[-21.17, -8.47]
outside	linear	0.36	[0.34, 0.40]	192.95	[190.20, 199.09]

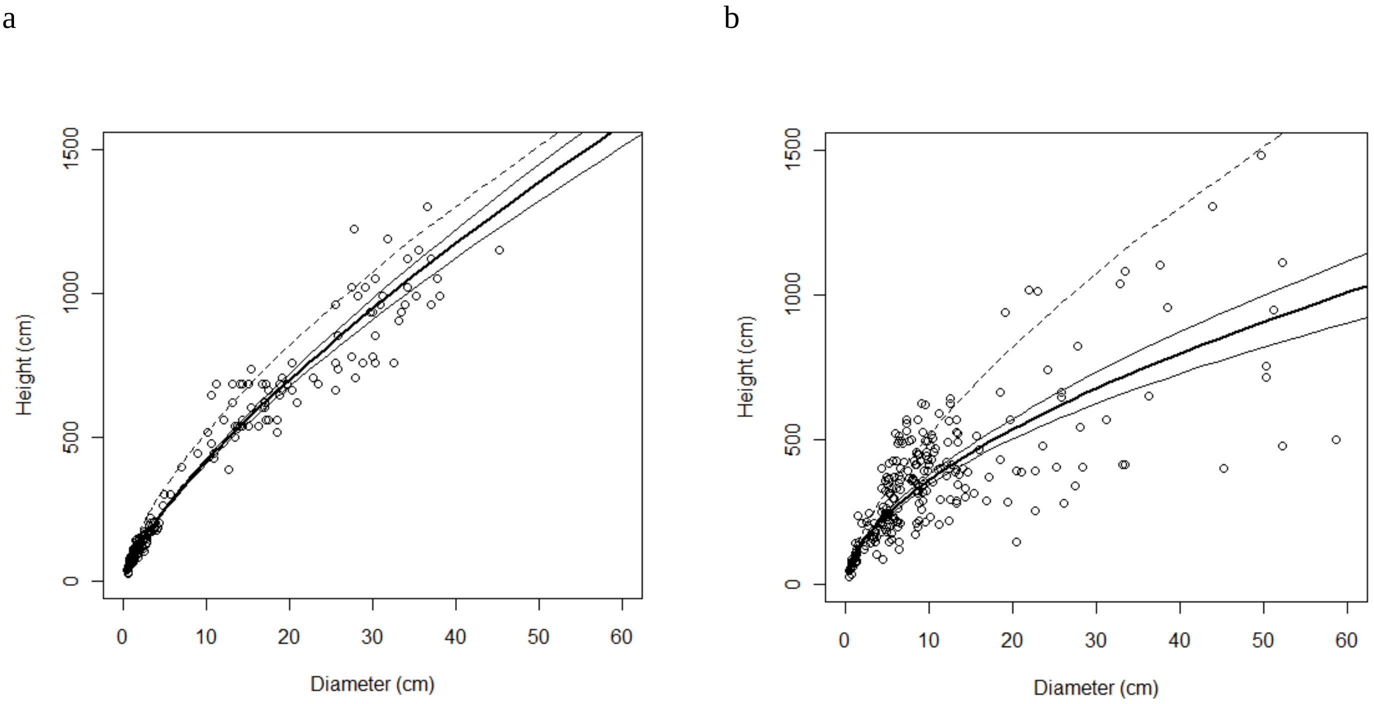

Figure 1. Height – stem diameter allometry fitted using simple linear models for a) *Acacia nigrescens* protected from herbivores and b) *Colophospermum mopane* exposed to herbivores. Thin solid lines show 95% credible intervals surrounding means (thick solid lines). The dashed line shows the prediction from mechanical theory of elastic similarity, with parameters from Niklas & Spatz (2004). Back-transformed model results are shown after fitting in log-log coordinates.

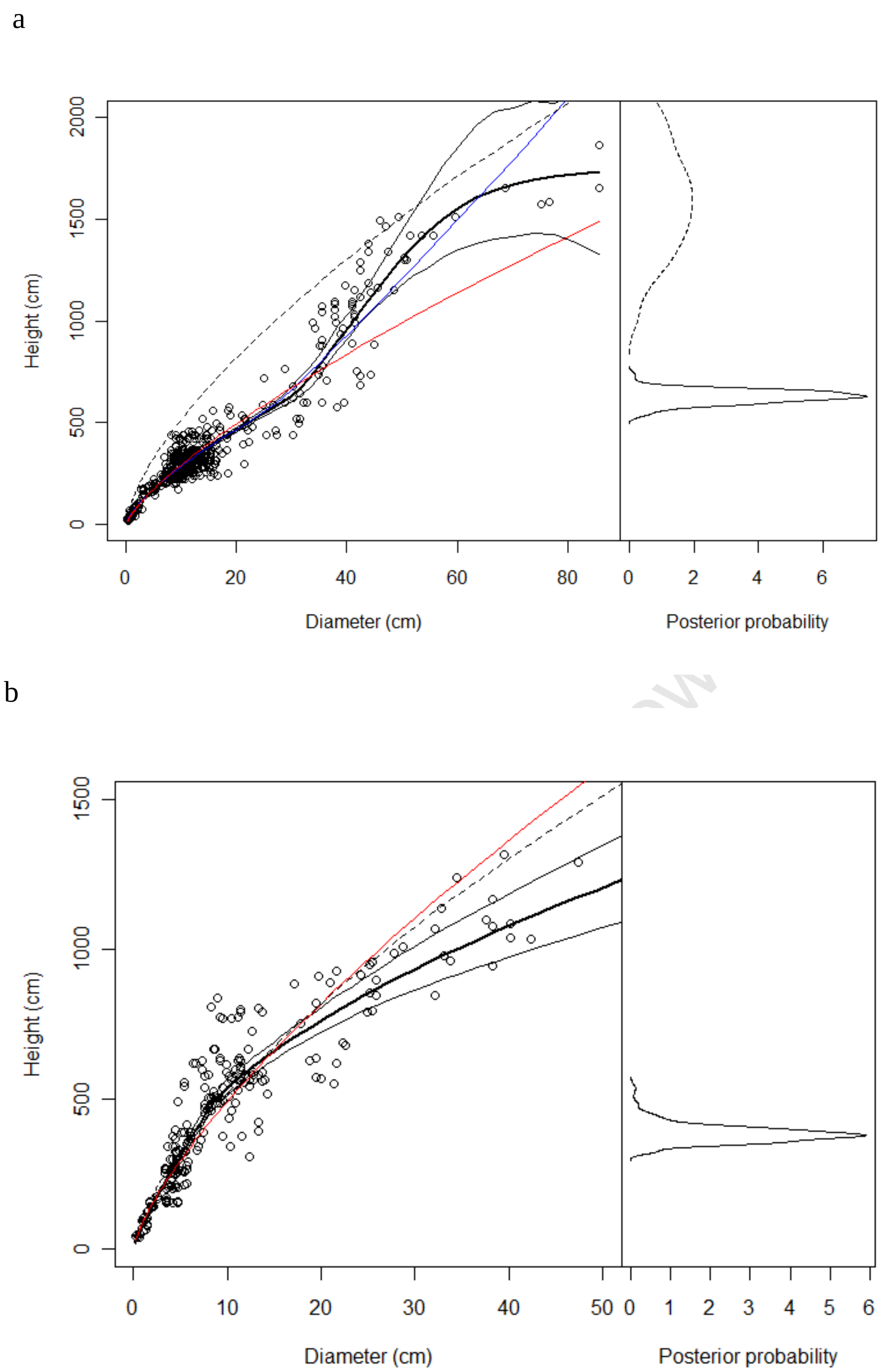

Figure 2. Height – stem diameter allometry fitted using piecewise-continuous linear models with posterior probability density plots for breakpoints translated into height. A two-breakpoint model fitted to *Acacia nigrescens* exposed to herbivores is shown in (a) and a single breakpoint model fitted to *Colophospermum mopane* protected from herbivores is shown in (b). Red lines show fitted curves when using simple linear models and the blue line shows the fit using a single breakpoint model for *Acacia nigrescens* exposed to herbivores. Thin solid lines show 95% credible intervals surrounding means (thick solid lines). The dashed line shows the prediction from mechanical theory of elastic similarity, with parameters from Niklas & Spatz (2004). Back-transformed model results are shown after fitting in log-log coordinates.

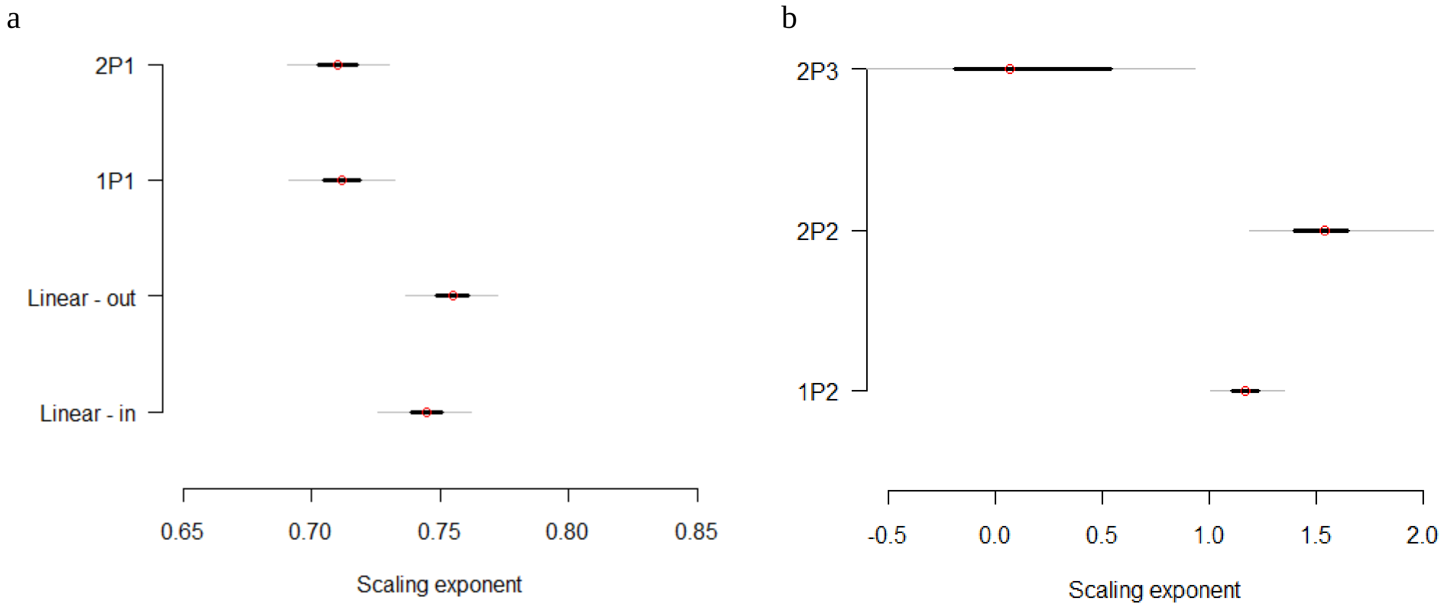

Figure 3. Scaling exponents estimated using various models for *Acacia nigrescens*. The thin grey tails represent 95% credible intervals, thick black tails 50% credible intervals and the red circle the mean. Codes used are: In = protected from herbivores (all other exponents are from exposed population); 1P1 = first exponent, single breakpoint model; 2P1 = first exponent, double breakpoint model; 1P2 = second exponent, single breakpoint model; 2P2 = second exponent, double breakpoint model; 2P3 = third exponent, double breakpoint model. Panel a) shows the exponents from the linear fit and first line segment. Panel b) shows exponents from the second and third line segments. Note the different scales used for the left and right panels.

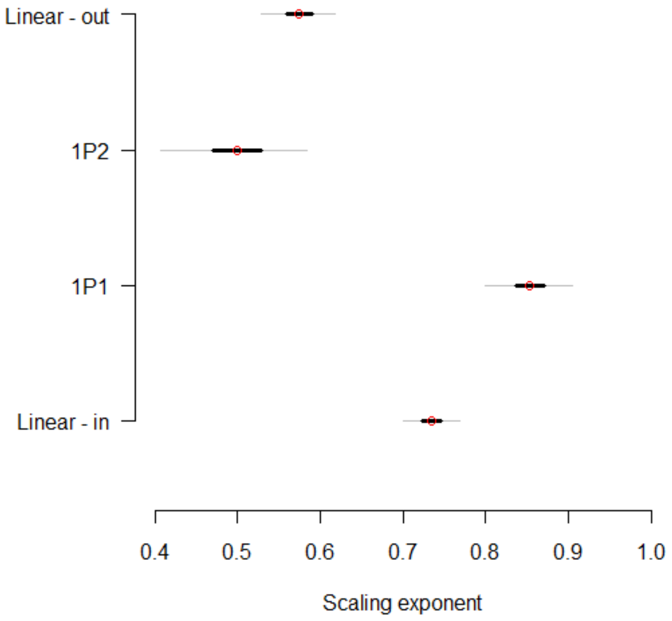

Figure 4. Scaling exponents estimated using various models for *Colophospermum mopane*. The thin grey tails represent 95% credible intervals, thick black tails 50% credible intervals and the red circle the mean. Codes used are: In = protected from herbivores; 1P1 = first exponent, single breakpoint model for protected population; 1P2 = second exponent, single breakpoint model for protected population; out = exposed to herbivores.

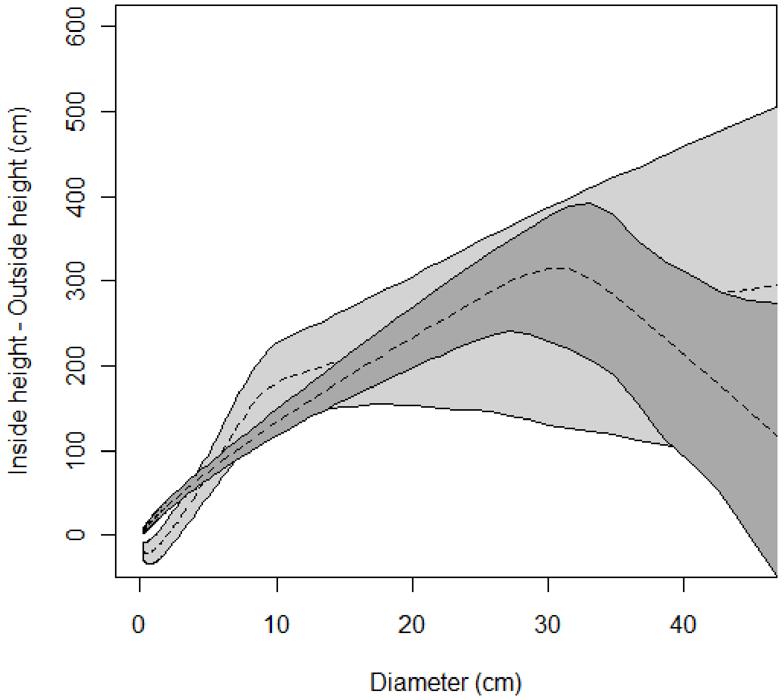

Figure 5. Predicted differences in height at a given diameter between populations exposed to and protected from herbivores for *Colophospermum mopane* (light grey) and *Acacia nigrescens* (dark grey) using the best fitted models for each species. The shaded area show the 95% credible interval surrounding the mean (dashed lines).

Discussion

Herbivores have a strong influence on height-diameter allometry and population-level patterns of herbivore impact are evident in the modified allometries. Height increases far less with increasing stem diameter in populations exposed to browsers and trees have a much lower height for a given stem diameter. These architectural differences accumulate over time in *C. mopane*, with the largest trees showing the greatest degree of modification, as even very large trees do not escape the influence of elephants. In *A. nigrescens*, trees eventually escape from the influence of giraffe and recover to the unmodified form. Thus patterns of modification differ between species, depending on the responsible herbivore and the corresponding plant response.

In the population of *C. mopane* protected from herbivory height increased rapidly with diameter for smaller individuals until the breakpoint at 5.06 m height, after which the scaling exponent decreased. *C. mopane* is highly multi-stemmed initially, with a single stem eventually dominating as trees become large (Hempson *et al* 2007). The observed breakpoint and concomitant change in scaling exponent is likely the result of a transition from multi- to single-stemmedness. Trees appear to be operating at the limits of mechanical stability near the breakpoint, suggesting strong inter-ramet competition (figure 1b). Thus this observed change in scaling is probably a reflection of non-uniform competition for light and other resources ontogenetically (Henry and Aarsen 1999). The inclusion of breakpoints in the allometry model for *A. nigrescens* exposed to herbivores resulted in a scaling exponent for the first line segment lower than that of the protected population. For trees above the breakpoint the exponent increased to a value far in excess of theoretical predictions (and the protected population). The breakpoint is at a height of 6.24m, which is close to the limit to which giraffe can browse (du Toit 1990). The lowered scaling below, and increase above the breakpoint, is a result of giraffe browsing (du Toit 1990). The restriction of height growth while within the foraging range of giraffe is the cause of the lowered scaling exponent below the breakpoint. For taller trees beyond this point trees height is gained rapidly with increasing diameter, suggesting that the limits to height growth imposed by structural support from stems or hydraulic supply are relaxed due to reduced height growth when within the range of giraffe. Height differences between protected and unprotected trees decrease after this breakpoint, showing recovery towards the form of protected trees.

There was no evidence for a breakpoint in the allometry of *C. mopane* when exposed to herbivores. Height was lower for a given diameter when compared to the protected population through the range of diameters observed, with the scaling exponent lower than the protected population. The absence of an escape size above which the scaling exponent would increase can be explained by the foraging behaviour of the responsible herbivore, elephants. Even the largest trees observed were still vulnerable to elephants (Shannon *et al* 2008). This is not because they can reach the canopy top of the tallest trees and reduce height growth. Rather, it is a result of the snapping of stems causing the immediate reversion to a much reduced height. Moreover, as trees become larger and the potential difference between the height of damaged and undamaged trees increases, we see that the credible range of height difference between protected and unprotected populations increases.

In almost all cases, even those involving the absence of browsers, scaling exponents are higher than predicted from mechanical or hydraulic considerations (McMahon and Kronauer 1976, West *et al* 1999, Niklas and Spatz 2002). It is interesting to note that most datasets used to test allometric theories of tree structure do not include savanna trees (eg Niklas and Spatz 2002, Muller-Landau *et al* 2006). The importance of stem diameter and height in determining fire vulnerability in savannas (Trollope 1984, Hoffmann and Solbrig 2003, Balfour and Midgley 2006) may result in trees compromising on mechanical stability or hydraulic efficiency. This is not to say that theoretical predictions constructed without reference to disturbance are not of use. In the example of *A. nigrescens* some canopies have grown above giraffe browsing height. After this point height scales rapidly with diameter. However, this is followed by a decrease in the scaling exponent. The reason for this decrease is likely to be that the change in scaling occurring after escape from giraffe - resulting in the recovery of architecture to the unmodified form - cannot be maintained due to eventual mechanical limits (figure 2a).

It is important to note that the ‘modified’ allometries of trees exposed to herbivores reported in this study do not represent aberrations, rarely found under natural conditions. Indeed, the allometries of trees protected from herbivores within exclosures represent a more atypical case in African savannas with an intact mammal fauna. A general predictive theory of plant form and functioning that does not account for the variation introduced by natural disturbance agents, such as herbivory, may prove to be neither general nor predictive in systems with frequent disturbances (eg. Coomes *et al* 2003).

Using stem diameter-height allometry to quantify browser impact has many advantages: the data are can easily be acquired for many individuals facilitating comparison between populations across broad spatial scales, allometry will contain information regarding the size related variation in impact, any change in the shape of the allometric curve has direct implications for plant fitness and demography and, as I have shown, the pattern of alteration contains information regarding the nature of the herbivores foraging behaviour. Furthermore, there exists a large body of theory outlining optimal allometric patterns for trees. Thus, a mechanistic understanding can be sought for comparisons between predicted allometry and patterns brought about by browsers. Variation in stem diameter-height allometry between species or populations has been used previously to investigate inter-specific differences in allocation patterns in response to local wind and light niches (O’Brien *et al* 1995). Here, allometries were successfully used to ascertain if tree populations were being severely impacted by browsing and which height ranges were most impacted. By comparing changes within and between observed and predicted allometries, mechanisms could be provided helping explain observed patterns.

Chapter 6: Summary and Synthesis

Glenn R. Moncrieff

Introduction

The 20th century saw great global changes in the abundance and distribution of mammalian herbivores, a result of changing land management, government policy and shifting vegetation patterns (Gordon and Prins 2008a). The 21st century will no doubt see further changes, and corollary changes in vegetation (IPCC 2007, Gordon and Prins 2008b). A better understanding of the role herbivores play in large-scale vegetation patterning, and advances in our ability to predict the outcome of herbivore – vegetation interactions is thus not a matter only of academic interest. It affects land management, tourism, carbon storage, agricultural production and conservation amongst others.

Progress towards identifying general patterns of browser impacts and plant responses has been slow, with few general patterns emerging (Hawkes and Sullivan 2001, Skarpe and Hester 2008). This is due to numerous factors, among them being the difficulty in measuring browser impacts and the framing of models and theory in the context of biomass responses. In this thesis I have attempted to overcome some of these problems by focussing explicitly on height as a measure of plant fitness and browser impact. I have also attempted to apply novel methods to quantifying and interpreting browser impact on plant populations. These approaches have led to fresh insights into the linkage of browser foraging and plant responses and to a potential new methodology for investigating impacts. Here I summarize my main findings, their significance and possible avenues for future research.

Linking biomass consumption to demographic impacts

Typically, the impacts of herbivores on plants are modelled by translating their nutritional requirements into an amount of biomass removed from the vegetation stock (eg Caughley 1976, de Knegt *et* al 2008, Akashi 2009). Here I used the novel approach of linking consumption to plant impacts not through biomass, but with browser bites. Using a bite as the unit of browser impact allows the actual browsing event to be modelled more realistically, incorporating the response of individual plant modules (branches) into a population model, without having to explicitly model every branch. The advance I have made, facilitated through using bites and bite responses, is to include not only the impact of tissue loss following browsing, but the subsequent branch growth response resulting from bud-loss. Within the modelling framework used, bud-loss impacts were very important in determining the demographic impacts of browsers on trees.

Further work is required on the importance of browser induced bud-loss for plant growth. The removal of these sinks results in the redistribution of acquired biomass and the modification of growth form. The influence of factors intrinsic to both the responsible browsers and target plant species on bud-loss impacts need to be investigated. Potential factors include: Bite size, leaf to stem ratio in bite, numbers of dormant lateral buds and bud activation intensity. These studies may reveal generalities in plant responses and browser impacts that are not apparent when focussing on consumption impacts and extrinsic factors, as has been the tradition (Strauss and Agrawal 1999, Hawkes and Sullivan 2001).

Much work has been done on herbivore foraging behaviour with reference to bite characteristics (eg. Owen-Smith and Novellie 1982, Spalinger and Hobbs 1992, Hobbs *et al* 2003). Can this body of work be unified with a botanical perspective, as presented here, to produce predictions relevant to both?

The relative importance of bud-loss and consumption impacts on *Acacia karroo*

The aboveground response of whole plants to browsing is largely the result of branch level impacts and growth. This applies both to biomass and height. I studied the relative importance of bud-loss and consumption impacts of both biomass and height from the level of individual braches to the individual plant. Experiments were designed with the formulation and predictions of the models in chapter 3 in mind, though they were not an explicit test nor suitable for estimating parameter values. It was found that bud-loss impacts strongly affected height and biomass, in line with model predictions. Consumption impacts affected biomass growth strongly, but had little impact on height growth. Branch level responses were a poor predictor of whole plant responses. This was due to the dependency of branch growth on canopy position, with factor effects resulting from a mixture of responses.

I thus demonstrated that bud-loss impacts of browsers on plant fitness are significant and can be separated from the impact of biomass or length removal alone. The response of biomass and height need not be in the same direction and of the same magnitude. Thus it is important that in herbivory studies, if both are not measured, the appropriate measure of fitness *in situ* is used. Factors resulting in the divergence of height and biomass responses require further investigation. I believe that the response of plants to bud-loss is a critical factor in controlling this. The architectural modification of plants by browsers is the ultimate result of bud removal (du Toit *et al* 1990, Danell *et al* 2003, Fornara and du Toit 2007). It is this architectural modification that causes height and biomass responses to diverge. When buds are lost the distribution of biomass throughout the canopy is altered, altering the relationship between canopy biomass and height (see chapter 5).

Herbivore-induced alteration of stem diameter-height scaling

The architectural modification that accumulates in a plant over a lifetime of exposure to browsers represents a possible metric to quantify browser impacts that has many appealing properties. Height – diameter allometry is an easily attainable quantification of architecture that has a strong theoretical basis for interpretation (McMahon and Kronauer 1976, Dean and Long 1986, Rich *et al* 1986, Niklas 1992, West *et al* 1999, Niklas and Spatz 2002, Price *et al* 2007). I have shown how allometry - and hence architecture - is indeed modified by browsers and that the degree and patterns of modification depends on properties specific to the target plant and responsible browser. The pattern of modification also contains information regarding demographic impacts (ie which size ranges are most vulnerable) and plant responses.

These results suggest that theories of plant allometry developed without reference to disturbances like browsing will fail to find general applicability in places like African savannas where large vertebrates can significantly alter plant form. However, interpreting allometries in the light of theoretical predictions based on assumptions of zero disturbances may aid interpretation and reveal herbivore impacts when making comparison between predicted and realized plant form.

Conclusion

With the current toolkit available to ecologists and the prevailing ideas pertaining to herbivore impacts much progress has been made. Significant browser impacts on plant populations have been observed in many different environments, involving a diverse array of vertebrates (Martínez and López-Portillo 2003, Bond *et al* 2004, Persson *et al* 2005, Fornara and du Toit 2007). Within some well studied ecosystems a few general patterns have emerged (Danell *et al* 1994, Skarpe and Hester 2008). The next step is to test the importance of browsers in structuring vegetation at regional scales. Identifying key traits and environmental variables that determine whether large scale impact emerge will require new methods of measurement impacts and new ideas regarding how plant respond, and how these responses feedback to browser behaviour and population dynamics. Here I hope to have made some progress to this end, proposing allometry as a means of interpreting browser impact and identifying bud-loss impacts as a critical aspect of plant response.

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