CHAPTER 1

Introduction

1.1 BACKGROUND AND JUSTIFICATION

The African savanna biome includes more large mammalian herbivores (> 5 Kg) than any other continent (McNaughton and Georgiadis 1986; Owen-Smith and Cumming 1993), as would be expected from the suitable combination of precipitation and soil fertility (see du Toit 1995; Olff et al. 2002). The exceptional species richness in African savannas likely depends on the high degree of specialization of ungulate species to particular habitats and the highly variable savanna ecosystem over temporal and spatial scales (du Toit and Cumming 1999; du Toit 2003).

It has been proved that large mammalian herbivores influence terrestrial ecosystem processes both directly by consuming plant material and indirectly by altering litter quality and nutrient cycling (McNaughton et al. 1988; Hobbs 1996). In African savannas the literature on mammalian herbivory in relation to the composition and structure of vegetation communities has been dominated by studies on the grazing guild (Sinclair and Norton-Griffiths 1979; Sinclair and Arcese 1995). Former studies have shown that grazing induces changes in reallocation of nutrients within individual plants and indirectly stimulates soil mineralization processes (McNaughton 1979, 1983). Moreover grazing increases root exudation in grassland plants, which in turn stimulates microbial biomass and activity in the rhizosphere (Hamilton and Frank 2001). Hence, grazing may enhance net primary productivity at the community level and create a positive feedback loop within the grazer-plant-soil system that improves grazing efficiency at moderate herbivore densities (McNaughton et al. 1988).

The only studies of browsing as an ecosystem process have been conducted in boreal forests, where the evidence is that the long-term consequences of intensive browsing are opposite to those for grazers (Naiman et al. 1986; Pastor et al. 1988; Kielland and Bryant 1998). The difference appears to be that selective browsing on palatable deciduous woody plants provides a competitive advantage to chemically defended slow-growing evergreens, which produce leaf litter that decomposes slowly (Pastor et al. 1988). Consequently, with slow nutrient uptake by slow-growing plants,

combined with leaching and reduced microbial activity, there could be a net loss of nutrients down the soil profile (Bryant and Chapin 1986).

So far, I'm not aware of previous studies that have addressed ungulate browsing as an ecosystem process in eutrophic southern African savannas, where the set of environmental key drivers are different from those of boreal and temperate forest ecosystems (see Scholes et al. 2003). Moreover, it is important to uncouple the effects of browsing from those of grazing on aspects related to the ecosystem nutrient cycling. Finally, plant-animal interactions and their effects on ecosystem properties assume particular importance in protected areas where management decisions have to be taken according to vegetation status and animal distribution and density. Naiman et al. (2003), highlight the exceptional habitat diversity in the Kruger National Park, South Africa, due to the interactions between soil characteristics, rainfall regime and animal activities. They also suggest that, although soils determine the composition of plant communities, individual plants may influence soil characteristics at the local scale. I therefore addressed the responses of savanna woody plants to ungulate browsing at different hierarchical levels from (1) plant to, (2) population, (3) community, and (4) ecosystem level.

1.2 UNGULATE BROWSING AND *ACACIA* TREE RESPONSES

Plants may reduce herbivore damage through resistance, tolerance and/or changes in phenological traits (see Agrawal 2000). Specifically, (1) plant resistance traits (i.e. thorns) reduce herbivore performance or damage, (2) tolerance traits (i.e. mass compensatory growth ability) reduce negative effects when herbivore damage has already occurred, and (3) phenological "escape" reduces plant availability when herbivores are most active. Plant responses to herbivory likely depend on levels of habitat resource availability (Coley et al. 1985; Bryant et al. 1983; Herms and Mattson 1992; Bardgett and Wardle 2003), as well as on interspecific competition and/or frequency and intensity of disturbance events.

Indications of compensatory growth abilities (tolerant trait) after herbivore damage have been found in woody plant species under ungulate browsing in different ecosystems (Bergström and Danell 1987; du Toit et al. 1990; Dangerfield and Modukanele 1996; Bergström et al. 2000; Gadd et al. 2001). Resistance traits such as spine and thorns are quite common in woody species of arid eutrophic savannas (Huntley 1982) and represent an efficient physical protection against tree pruning (Cooper and Owen-Smith 1986; Young 1987). In general, defensive traits vary across plant

communities depending on the interactions between different environmental factors. A useful approach is to compare populations or stands of vegetation with very different histories of attack from herbivores (Agrawal 1998, 2000).

In Chapter 5, I examine defensive traits of two stands of *A. nigrescens* Miller in a eutrophic southern African savanna under a natural regime of ungulate browsing. *Acacia nigrescens* Miller, is a staple food resource for ungulate browsers and is very common throughout all my study area (see Chapter 2). The leaves are characteristics of this species and quite different from other common *Acacia* species, being double pinnately compound and having 4-6 leaflets per leaf which are comparatively large with oblique (lopsided) bases (Fig. 1.1a). Trees bear prickles and are usually leafless for two-three months during the dry season (June to September). Mass compensation after artificial clipping, tree branching, prickle spacing and size, annual shoot growth, leaf N, specific leaf area (SLA), and seed production, were measured over a two-year survey (see Chapter 5) among stands of *Acacia* trees that have undergone very different levels of browsing presumably for centuries (see du Toit 2003; Naiman et al. 2003; see Fig. 1.1 and Fig. 1.2).

Similarly, I tested compensatory growth abilities of 120 suppressed juveniles forms of two common woody species, *Acacia nigrescens* Miller and *Acacia tortilis* (Forsk.), Hayne, after severe artificial clipping (see Chapter 6). I also measured five gulliver morpho-functional traits including net annual height growth and plant density variation throughout a study area where fire had been absent for 13 years.

1.3 BROWSING EFFECTS ON PLANT COMMUNITY COMPOSITION

Impacts of ungulate browsing on vegetation structure and dynamics have been recognized as significant in boreal forests (Kielland and Bryant 1998; Horsley et al. 2003) where historically, much emphasis had been given to abiotic factors as main responsible for vegetation structure and dynamics (see Bryant and Chapin 1986). Indeed selective browsing negatively affects species with nutrient rich tissues (Ritchie et al. 1998; Peinetti et al. 2001), and contributes to a shift in dominance towards unpalatable evergreen species within the vegetation community (Pastor et al. 1988; Kielland and Bryant 1998; Wardle et al. 2001; Horsley et al. 2003). In African savannas browsing induced effects have been described as limiting woodland regeneration (Belsky 1984), affecting vegetation structure (Pellew 1983) or influencing species composition and distribution (Bond and Loffell 2003).

However, there is a lack of information on how functional type composition might change along a strong browsing gradient in an extensive wildlife area where mammalian browsers are free to move according to resource availability. Vegetation responses under permanent browsing pressure are sometimes contradictory and do not always lead to a clear dominance of unpalatable species especially when trees and shrubs rely on compensatory growth abilities (Augustine and McNaughton 1998). Therefore we may expect different responses from woody plants in a eutrophic savanna where soil N concentration is relatively high due to the basaltic igneous substrate (Scholes 1990). Browsing impact on vegetation communities assumes particular importance in protected areas where management decisions have to be taken according to vegetation status, and animal distribution and density.

For example, in the Kruger National Park, one of the largest conservation areas in Africa, trends in woody vegetation structure and composition have been historically explained by the reciprocal effects of fire and elephants (see Eckhardt et al. 2000; Whyte et al. 2003), but the few published studies on the effects of browsing on woody plant ecology have been restricted to the central region of the Park (du Toit et al. 1990; du Toit 2003; Naiman et al. 2003). Hence, in Chapter 3 I test the following prediction derived from browser-woody plant interactions that have been elucidated in boreal and temperate forests:

- Ungulate browsing influences vegetation traits and species composition within woody plant communities through selective damage to palatable woody plants, resulting in increases in number of spinescent, evergreen and unpalatable species at increasing levels of browsing.

1.4 PLANT-BROWSER-SOIL INTERACTIONS: NUTRIENT CYCLING AT THE ECOSYSTEM LEVEL

To test predictions based on hypotheses proposed for boreal and temperate forest ecosystems I examine (Chapter 4) aspects of aboveground nutrient cycling between two stands of *Acacia nigrescens* with very different histories of attack from. herbivores. I specifically measured (1) leaf litter decomposition rates of five common savanna woody species, (2) leaf chemistry (mainly N) of *A. nigrescens* in wet and dry seasons, (3) soil chemistry (total N, NH_4, NO_3, P, Ca, K, Mg, Na, cation exchange capacity, pH) and (4) litter biomass and composition distributed across browsing and grazing gradients. If long-term selective browsing has a negative effect on ecosystem properties and nutrient

cycling as shown in boreal forests we might expect that: (1) leaf litter among heavily browsed sites has lower decomposition rates than litter placed in lightly browsed sites, (2) soil nutrient pool in heavily browsed sites is more depleted than in lightly browsed sites.

Nonetheless, the 'top-down' effects, exerted by large mammalian herbivores on ecosystem properties (Pastor and Naiman 1992; Kielland et al. 1997; Scholes et al. 2003; Bardgett and Wardle 2003) are likely mediated by "bottom up" effects exerted by soils and climate since large herbivores use their landscapes according to the spatio-temporal distribution of food resources. For example, in N limited boreal forest ecosystems, browsers are responsible to decrease number of palatable species with N rich tissues (see above) contributing to increase the number of unpalatable species over a long-term scale (McInnes et al. 1992).

However, the overall effects of browsing on ecosystem properties are likely more complex and driven by the interactions of different environmental factors. For example, although soils determine the composition of plant communities, individual plants may influence soil characteristics and nutrient concentrations at the local scale (Naiman et al. 2003). Indeed, Persson et al. (2005) found that in a N-limited Swedish boreal forest, selective browsing on medium preferred woody species, negatively affected ecosystem productivity through a reduction of litter quantity returned to the soil, rather than changes in plant community composition and litter chemical quality.

Alternatively, relatively fast-growing, highly-palatable woody plants of semi-arid eutrophic savannas, according to the resource economics of chemical and structural defences along a nitrogen gradient (Craine et al. 2003) may have evolved different defence strategies (e.g. increased physical defence) to cope with browsing damage. This in turn influences plant responses to tree pruning as, for example, enhancing compensatory growth abilities in savanna tree and shrub species (Augustine and McNaughton 1998), which therefore may have important consequences on nutrient cycling and ecosystem functioning.

Finally, I propose a simulation model that makes predictions on the effects of ungulate browsing on changes in plant productivity and soil nutrient availability according to varying plant defensive traits (see Chapter 7). The modelling results are confronted with empirical data and predictions are made in terms of nutrient cycling and functional type composition within a semi-arid eutrophic savanna.

a)

b)

Fig. 1.1. Unbrowsed shoot of *Acacia nigrescens* showing pairs of prickles and the double pinnately compound leaves with 4-6 leaflets each (a). Heavily browsed branches of *A. nigrescens,* 60% to 80% of the shoots have been browsed in the current growing season.

a)

b)

Fig. 1.2. Examples of heavily browsed *A. nigrescens* trees that show different canopy shapes due to the impact of different browsers species. Note the clear height limit for the giraffe's reach in the second tree (b).

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