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THE ROLE OF SMALL ANTELOPE IN ECOSYSTEM FUNCTIONING IN THE MATOBO HILLS, ZIMBABWE

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ABSTRACT

The 28-month study assessed the impacts of five syntopic medium-sized mammalian browsers and one fire event in a woodland savanna in the Matobo Hills, Zimbabwe. Aspects of herbivory, mechanical pressures, seed dispersal and nutrient cycling were investigated for three species of small antelope (common duiker [*Sylvicapra grimmia*][1], klipspringer [*Oreotragus oreotragus*] and steenbok [*Raphicerus campestris*]) and two medium-sized species (bushbuck [*Tragelaphus scriptus*] and greater kudu [*T. strepsiceros*]).

Focusing on *Burkea africana*[2] woodland, in a system that does not include elephant (*Loxodonta africana*), effects of browsing antelope on woody and herbaceous vegetation development were investigated using exclusion plots. Browsers regulated woody plant cover (measured as basal stem area), with smaller antelope having a greater impact than larger species. This was linked to feeding height, feeding selectivity and mechanical pressures (e.g. twig breakage and trampling).

Fire caused an initial reduction in above-ground standing biomass, but in the presence of fauna, pre-fire equilibria were attained within 15 months. In antelope exclosures, herbaceous biomass increased and woody biomass decreased following fire.

Responses by woody vegetation to browsing varied among species, with highly palatable species typically exhibiting compensatory regrowth. Woody species richness and abundance (especially of palatable species) increased in the absence of browsers, but species richness of the herbaceous layer was promoted by moderate disturbance (trampling or fire).

Faecal deposition behaviour, primarily the use of latrines by small antelope, resulted in localised soil enrichment within defended territories. Decomposition rates (and therefore return of nutrients to the soil) varied among species and seasons, due to defecation site selection, accessibility to decomposers and desiccation rates of faecal pellets.

[1] Fauna authorities given in Appendix 1
[2] Flora authorities given in Appendix 3

Controlled seed germination experiments indicated that ingestion by small antelope enhances germination rates of large, hard-seeded fruits such as *Sclerocarya birrea.* However, germination of savanna seeds may require multiple cues.

This study demonstrated the critical roles of small antelope in ecosystem functioning, and highlights the importance of the less visible impacts of frequently overlooked smaller mammalian herbivores. Perturbations to the faunal community, especially small antelope, are predicted to have substantial impacts on woody plant cover.

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PREFACE

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DEDICATION

This thesis is dedicated to the memory of my grandfathers, who loved the Zimbabwean bush and encouraged my interest in wildlife

OWEN BARTON LUNT
(1911-1995)

ALBERT HENRY PENTON
(1925-2004)

1. GENERAL INTRODUCTION

1.1. LITERATURE REVIEW

Savannas are ecosystems that occur in summer-rainfall regions of the tropics and subtropics, and are characterised by a well-developed continuous herbaceous layer that is intermingled with trees and shrubs (Skarpe, 1992). They are complex, dynamic systems that are shaped by the interaction of a large number of physical and biological factors which operate at a variety of spatial and temporal scales. Soil nutrients and rainfall are largely responsible for overall physiognomy, e.g. open/ closed woodland, or grassland (Sankaran *et al.*, 2005; Scholes, 1990), primarily due to resource competition between woody and herbaceous plants (Meyer *et al.*, 2008; Vandenberghe *et al.*, 2008). Areas with high rainfall and low-nutrient soils (moist dystrophic savannas) tend to be dominated by woody species, whilst at the other extreme, high nutrient low rainfall regions (dry eutrophic savannas) tend to be open woodland or grassland (McNaughton and Georgiadis, 1986; Sankaran *et al.*, 2005; Scholes, 1990); however patchiness in soil fertility is mirrored by plant community structure regardless of mean annual rainfall (Scholes, 1990). However, the ratio of woody to herbaceous vegetation is influenced at a more local scale by disturbances in the form of fire, frost, herbivory, trampling, biotic ecosystem engineering and manure deposition (Chidumayo, 2006; Cumming and Cumming, 2003; Govender *et al.*, 2006; Hulme, 1996; McNaughton *et al.*, 1988; Mills and Fey, 2005; Roques *et al.*, 2001; Sankaran *et al.*, 2005; Savadogo *et al.*, 2008; Sawadogo *et al.*, 2005; Scholes, 1990; Waldram *et al.*, 2008; Zida *et al.*, 2007). Disturbance stochasticity produces the mosaic of vegetation types and concomitant variability of faunal assemblages that are typical of savannas (Fuhlendorf and Smeins, 1998; Laris, 2005; Skarpe, 1992).

1.1.1 Disturbance

Disturbance is any event that causes a directional change in a system (Skarpe, 1992), and is an important determinant of savanna structure. It can occur at a range of spatial and temporal scales, from the individual to the biome, and from a single point in time (e.g. a lightning strike) to an extended period (e.g. climate change), and may even be an iterative process (e.g. drought, fire and disease cycles) (King *et al.*, 1997; McNaughton, 1992; McNaughton and Georgiadis, 1986; Sankaran *et al.*, 2005).

The timing of disturbance in relation to the successional stage of the plant community and the phenology of affected species affects both the probability of recovery by existing vegetation and the species available to fill gaps. Early colonists concentrate energy into growing parts, have rapid leaf turnover and are often able to compensate for moderate defoliation (Davidson, 1993). Species of later successional stages usually have lower leaf turnover rates, and because of this longevity are more likely to experience damage, which is why many invest in anti-herbivore defences to limit defoliation (Davidson, 1993). Late-succession savanna species, being long-lived, tend to develop substantial below-ground reserves and are fire-adapted: disturbance by fire may therefore result in coppicing or resprouting (Klimešová and Klimeš, 2007), while early successional species may be obligate seeders (Hanley *et al.*, 2001) with persistent seed banks that can take advantage of newly created gaps (Pakeman *et al.*, 2002). As a result, there is usually a mix of successional stages in savanna systems, creating a mosaic effect (Dublin *et al.*, 1990; Fuhlendorf and Smeins, 1998).

In savanna systems, typical disturbances consist of shifts in herbivore pressure, drought and fire cycles, and anthropogenic changes (e.g. bush clearing, overgrazing by domestic livestock) (Fuhlendorf and Smeins, 1998; Gambiza *et al.*, 2005; King *et al.*, 1997; McNaughton, 1992; Savadogo *et al.*, 2009; Sheuyange *et al.*, 2005). Within the constraints imposed by geological (e.g. soil type and depth), climatic (primarily rainfall), abiotic (e.g. fire, drought) and biotic (e.g. stocking rate) factors, disturbed systems move towards a new equilibrium point mediated by interactive and feedback responses (Dublin et al., 1990; McNaughton, 1992). Perhaps the most noticeable changes to savanna vegetation are in the relative abundance of herbaceous and woody vegetation (Sankaran et al., 2005), and several generalisations have been made concerning the roles of herbivores and fire on this proportion.

1.1.1.1 Fire and fauna as disturbance and nutrient cycling agents

Fire is a great equaliser in ecosystems, although its effects depend on the successional stage of the system, the intensity of the fire, and the frequency at which fires occur (Favier *et al.*, 2004; Gambiza *et al.*, 2005; Govender *et al.*, 2006; King *et al.*, 1997). Fire combusts moribund material and accelerates the return of minerals that are not vaporised to the soil, thus contributing to the “fast” and “pulsed” nutrient cycles (McNaughton et al., 1988). Nutrient enrichment shifts competitive advantage to late-succession perennial plants that are often fire-resistant (Eriksson *et al.*, 2003; Favier *et al.*, 2004), while removal of litter creates gaps that can be filled by pioneer plant species or by resprouts of established fire-resistant

perennials (Eriksson *et al.*, 2003; Hanley *et al.*, 2001; Pellew, 1983; Yu *et al.*, 2009); these processes promote vegetation heterogeneity. While bark thickness confers some fire tolerance in woody plants, exposure of juveniles to fire may be lethal, and for this reason fire has been used historically as a shrub control tool in livestock rangelands (Eriksson *et al.*, 2003; Hough, 1993; Sheuyange *et al.*, 2005). However, very high fire frequency or intensity may negatively affect soil properties, ultimately causing degradation and erosion (Mills and Fey, 2004; Scott and Van Wyk, 1990; Snyman, 2003).

Grasslands are regulated by a number of factors, including a combination of soil nutrients, duration and timing of water stress and evolutionary history with generalist grazers (Milchunas *et al.*, 1988). In savannas, heavy, sustained grazing especially by domestic livestock, favours the establishment of woody vegetation (Dunham *et al.*, 2003; Otuoma *et al.*, 2009; Roques *et al.*, 2001; Strang, 1973; Weber and Jeltsch, 2000) resulting in reduced forage availability for grazers and subsequent grazer population crashes (Dunham et al., 2003).

While fire may temporarily arrest woody development, in the presence of grazers, woody growth may be further accelerated due to reduced competitive ability of grazed herbaceous vegetation (Sheuyange *et al.*, 2005; Strang, 1973), especially in moister savannas (Scholes, 1990). By contrast, the presence of mammalian browsers can arrest or reverse the development of a mature woody layer and promote grassland or the development of "shrubby" growth forms (Augustine and McNaughton, 2004; Belsky, 1984; Dublin *et al.*, 1990; Levick and Rogers, 2008; Makhabu *et al.*, 2006; Strang, 1973). Such an effect has been evident along the Chobe River in Botswana: a crash in the browser guild and heavy elephant hunting in the late 1800s promoted the development of riverine woodland but subsequent increases in elephant and impala (*Aepyceros melampus*) populations have resulted in reversion to a preponderance of shrubs (Moe et al., 2009)

1.1.2 Nutrient cycling

Nutrient cycling is an integral part of ecosystem dynamics, and occurs through a number of pathways. Nutrients in mineralized or soluble form are more accessible to plants (Raven *et al.*, 1986). The primary source of most nutrients is from weathering of rock and soil, but gaseous and aerosol components produced by respiration or combustion can be incorporated back into a system via precipitation (wetfall), settling of solid particles (dryfall) or direct

uptake by plant leaves (e.g. carbon dioxide for photosynthesis) (Begon *et al.*, 1996). Ultimately, nutrients are lost from the system either through respiration, combustion, leaching or streamflow (Begon et al., 1996).

The rate of recycling of an element depends on the pathway it enters. "Long" cycles generally involve geochemical processes; that is deposition of minerals, incorporation into sediments and subsequent release following rock and soil weathering (Begon *et al.*, 1996; McNaughton *et al.*, 1988). This process may take decades or millennia (McNaughton et al., 1988), and for terrestrial systems, rock weathering is the primary source of minerals (Begon et al., 1996). Ultimately, the productivity of the system is reliant on the nutrients available; shortage of one element can have limiting effects throughout the food web (van Ryssen, 2001).

Fast pathways usually involve biota and/or fire. Considering nitrogen, which is often limiting in terrestrial systems, nitrogen-fixing bacteria convert atmospheric oxygen into nitrates and nitrites that can be utilised directly by plants (Begon et al., 1996). Conversion of organic compounds into mineralised forms readily accessible to plants can also occur during digestion by herbivores, with subsequent deposition of urine and faeces rich in compounds such as nitrates and urea (Begon *et al.*, 1996; Mohr *et al.*, 2005; Pastor and Cohen, 1997). Dead organic matter (of both plant and animal origin) is broken down by micro-organisms, also with the release of nutrient ions (Begon et al., 1996; Lechmere-Oertel et al., 2008). Fire accelerates mineralization of some nutrients, but volatile compounds are released into the atmosphere and may result in a net loss from the system (Aranibar *et al.*, 2003; Hobbs, 1996; McNaughton *et al.*, 1988). Interactions between fire and herbivory can be complex, either accelerating or decelerating nutrient cycling rates (Aranibar *et al.*, 2003; Kay *et al.*, 2008).

In many systems, nutrient cycling is relatively faster through herbivore dung and urine than through decomposition of senescent plant material (McNaughton et al., 1988), primarily because structural materials such as cellulose are partially broken down during digestion. Decomposition of animal tissue also returns elements to the soil rapidly (Begon et al., 1996). However, the animal-mediated route can be highly complex. Nutrients may be exported from the local site if animals are large or highly mobile (de Mazancourt and Loreau, 2000b), and plants' production of secondary metabolites in response to herbivory may impact on

decomposers and result in slow decomposition and nutrient cycling rates (Harrison and Bardgett, 2004; Kay *et al.*, 2008; McNaughton *et al.*, 1988; Pastor and Cohen, 1997).

1.1.3 Animals and plants

1.1.3.1 Feeding strategies of herbivores

The majority of plant tissue is structural material, which has a high insoluble cell wall: soluble content ratio (Raven et al., 1986) and is therefore of limited digestibility (Davidson, 1993; Wenninger and Shipley, 2000). High-quality, easily digestible components such as new shoots and leaves, flowers, fruits and storage organs (e.g. tubers), are frequently only seasonally available, are rare, are typically surrounded by a matrix of lower-quality forage or buried, and are often defended by chemical or physical means (Hanley *et al.*, 2007; Wilson and Kerley, 2003b). As a result, the distribution of high quality plant tissues is spatially and temporally heterogeneous, so herbivores have evolved physiological and behavioural strategies to optimise energetic gain and reduce processing time. Allometric scaling of body volume with surface area impacts on thermoregulation, and results in larger mammals having lower basal metabolic rates (BMR) than small mammals, despite having higher absolute energetic requirements (Bell, 1971; du Toit and Yetman, 2005; Jarman, 1974; Rueda *et al.*, 2008). This has important implications for foraging behaviour due to gut capacity and digestive efficiency in relation to the quantity of energy required (McNaughton and Georgiadis, 1986): the Jarman-Bell principle states that larger animals can therefore tolerate lower quality diets than small animals (Bell, 1971; Geist, 1974; Jarman, 1974). There are two major strategies adopted by ungulates to ensure that sufficient food is ingested to meet energetic requirements. It is important to note, however, that a continuum exists between these strategies: most animals exhibit a degree of selectivity and continually make foraging decisions to optimise energetic gain (O'Connor *et al.*, 2007; Searle *et al.*, 2005; Shipley *et al.*, 1994; Woolley *et al.*, 2009).

The first strategy is to increase intake rate, i.e. ingest more food per unit time (Bergman *et al.*, 2001; O'Connor *et al.*, 2007; Searle *et al.*, 2005; Shipley *et al.*, 1994; Ungar and Noy-Meir, 1988). Digestion rates in ungulates that employ this strategy tend to be relatively rapid, and the animals spend a large proportion of the day feeding, especially if they are large and require large quantities of food (du Toit and Yetman, 2005; O'Connor *et al.*, 2007). Search time for high quality items, which are highly dispersed and have low relative biomass, is prohibitive for such animals. Consequently, optimal foraging theory predicts that such

animals will be generalist feeders, maximising intake and reducing handling time (which is the sum of search and cropping time) (Bergman *et al.*, 2001; Emlen and Emlen, 1975; Trudell and White, 1981; Wilson and Kerley, 2003b). However, a threshold is reached at which an animal will move to another feeding patch to maximise intake rate (O'Connor *et al.*, 2007; Searle *et al.*, 2005), and this is a major driver of the migration patterns of East African ungulates (Bell, 1971). Examples of this strategy include the so-called "bulk feeders" and hind-gut fermenters, such as elephants, equids and very large bovids (Demment and van Soest, 1985). Many of these species are not actively territorial, and tolerance of relatively low-quality forage allows the formation of large herds (Caro *et al.*, 2004; Jarman, 1974).

The second strategy involves selecting high quality forage, which is both rich in energy and easily digestible (Searle et al., 2005). As already described, such forage is irregularly distributed, and large animals are unlikely to use this as a default strategy. However, smaller animals with lower energetic requirements can feed selectively on patchily distributed, high-quality forage without compromising their metabolic requirements. Such animals include hindgut fermenters that exhibit coprophagy to maximise nutrient uptake (e.g. leporids), and smaller ruminants (Demment and van Soest, 1985). Among smaller ruminants, physical adaptations such as a narrow premaxilla, facilitates removal of selected items from within a generally low-quality sward (Spencer, 1995). Rumination, which involves a series of mechanical and chemical breakdown phases, acts as a bottleneck in the digestive process. Thus, although digesta passage rate is relatively slow, food items are comprehensively broken down and absorbed (Wenninger and Shipley, 2000). Furthermore, the animal need not forage for extensive periods (where it may be conspicuous to predators) but can instead feed for brief periods, then retreat to thick cover to ruminate (du Toit and Yetman, 2005). The coupling of low absolute requirements with slow throughput rates (which limits intake rate) favoured the evolution of territoriality and the maintenance of a relatively small home range (Jarman, 1974). Territoriality is advantageous to a ruminant in that it becomes familiar with local resources and does not have to travel far to forage.

1.1.3.2 Herbivory

There has been much debate in the literature pertaining to the effects of herbivory and herbivore activity on plant fitness and productivity. Several studies have shown that, under moderate disturbance conditions, productivity is unaffected or even enhanced (Agrawal, 2000; de Mazancourt and Loreau, 2000a,b; du Toit *et al.*, 1990; Thompson Hobbs, 1996).

This is adaptive and linked to herbivore size and residence time (de Mazancourt and Loreau, 2000b), the hypothesis being that tolerance of herbivory results in attraction of animals that promote nutrient cycling rates and reduce intra- and interspecific stem competition through tissue removal and trampling (Berger *et al.*, 2008; du Toit *et al.*, 1990; Jacobs and Naiman, 2008; Meyer *et al.*, 2008; Thompson Hobbs, 1996; van der Koppel and Prins, 1998; Veblen, 2008). Some authors have even suggested that plant-herbivore interactions can be mutualistic (e.g. Agrawal, 2000), although Belsky (1987) contends that tissue loss will always reduce fitness of the affected plant. Overcompensation, that is, the enhancement of productivity or growth in response to herbivory, is therefore likely to be a tolerance strategy rather than a form of mutualism. Considering the diversity of herbivores in African savannas, it can be expected that the long co-evolutionary history of plants and herbivores will have resulted in a range of plant defence and tolerance strategies. Similarly, herbivores have developed tolerance to plant defences, although the quantity of tissue that can be ingested at one time may be limited by toxicity levels or bite-size limitations invoked by physical defences (Hooimeijer *et al.*, 2005; Wilson and Kerley, 2003b).

The mechanisms by which plants apparently cope with herbivory can be separated into two broad categories which are not mutually exclusive: tolerance and defence or avoidance. Resistance to herbivory may take the form of chemical or physical adaptations. Many early successional plants develop few defences and instead favour rapid growth and production of reproductive tissues (Davidson, 1993); such plants rely more heavily on tolerance.

Chemical defences, for example the production of tannins, saponins and other secondary metabolites, reduce the palatability of the plant and may even be lethal to herbivores at high concentrations (Aschfalk *et al.*, 2000; Freeland *et al.*, 1985; Kumar and Vaithiyanathan, 1990; Scogings, 2005). Such defences may be induced when plants are subject to stress (e.g. drought, or high herbivore pressure) (Hooimeijer et al., 2005) or be always present (i.e. constitutive) regardless of herbivory pressure (Glynn et al., 2003). Chemical defence is an energetically costly strategy and can, under conditions of poor nutrient status, negatively affect growth rates (Glynn et al., 2003). Tolerance of chemical defences has evolved in herbivores, as demonstrated by the heavy utilisation of *Euphorbia* spp. by black rhinoceros (*Diceros bicornis*) (Ganqa and Scogings, 2007) and high preference shown for alkaloid-rich *Diplorhynchus condylocarpon* by antelope (pers. obs.) and rhinoceros (C. Foggin, pers. comm.). Browsers tend to have larger salivary glands and produce more saliva than grazers

or mixed feeders (Codron et al., 2008), which has been linked to tannin-rich diets; salivary enzymes bind preferentially with tannins and render leaves more readily digestible (Clauss *et al.*, 2005; Faurie and Perrin, 1995).

Physical defences include spinescence, leaf waxes, pubescence, and sclerophylly (Archibald and Bond, 2003; Guillermo, 1992; Hanley *et al.*, 2007; Navarro *et al.*, 2006; Sarmiento, 1992) and have the result of limiting bite size (Wilson and Kerley, 2003a,b), increasing tooth wear (Kaiser et al., 2009) or reducing digestibility (Hanley et al., 2007). Again, although herbivory may not be avoided, tissue removal rates are limited. Defence tends to be energetically expensive to plants, and may therefore affect their productivity (Hooimeijer et al., 2005); thus, there is a potential trade-off between limiting tissue loss and promoting growth (Glynn et al., 2003).

Tolerance is the ability of plants to tolerate and/or compensate for tissue loss through enhanced shoot growth, redistribution of resources away from affected tissues, resprouting or coppicing (Agrawal, 2000; du Toit *et al.*, 1990; Focardi and Tinelli, 2005; Vandenberghe *et al.*, 2008). A wide range of species use this strategy, sometimes reducing chemical defences to optimise biomass production (du Toit et al., 1990; Scogings, 2005). Further, herbivore saliva stimulates growth of some savanna plants (Rooke, 2003), although complete compensation may not be achieved. Some plants may be sensitive to herbivory but compensate in less obvious ways such as shifting nutrients to underground storage organs (Ritchie *et al.*, 1998) or responding rapidly to herbivory release.

Avoidance, as distinct from defence, is a strategy that limits the quantity of palatable or accessible tissues available to herbivores, and often involves growth-form plasticity. For example, graminoids in heavily grazed areas may have lower shoot density, smaller leaf size and exhibit a more prostrate growth form compared with the same species in ungrazed regions (Painter *et al.*, 1993). Woody plant morphology may also differ among sites with high and low browser pressure, where rapid growth can remove the crown from the browsing range of terrestrial herbivores, or leaf arrangement is suboptimal for cropping (Archibald and Bond, 2003; Renaud *et al.*, 2003). Adventitious buds produced through a range of heights on the plant have also been hypothesized to counteract damage (Klimešová and Klimeš, 2007).

1.1.3.3 Frugivory, dispersal and seed predation

Mature plants are sessile organisms, and are only able to distribute their genes more widely via propagules (seeds and vegetative sprouts). Being unable to move their propagules appreciable distances themselves, plants have evolved a variety of dispersal mechanisms that utilise other agents. These include using abiotic motile components of the environment such as wind (anemochory) or water (hydrochory), producing dehiscent pods that catapult seeds some distance (explosive dispersal), or taking advantage of mobile animals (zoochory) (Aparicio *et al.*, 2008; Calviño-Cancela, 2004; Couvreur *et al.*, 2005; Couvreur *et al.*, 2008; Traveset, 1998).

Two main categories of animal seed dispersal exist: (i) epizoochory, in which seeds temporarily attach to the skin or fur of passing animals (Couvreur *et al.*, 2008; Heinken *et al.*, 2006b), and (ii) endozoochory, where seeds are ingested and are spat out later ("spit dispersal", Bodmer, 1991; Feer, 1995) or pass through the digestive system of the animal and are deposited in faeces (Milton and Dean, 2001; Mouissie *et al.*, 2005b; Pakeman *et al.*, 2002; Traveset, 1998). An important component of dispersal is that seeds are deposited in suitable sites for germination and establishment (Baythavong *et al.*, 2009), which has led to the coevolution of many plants and their animal dispersers.

Seeds are typically highly nutritious, containing oils that provide the embryo with energy for germination. This energy-rich resource benefits animals able to access the endosperm, but damage is lethal to the embryo. Animals that cause seed mortality are therefore termed “seed predators”. While some groups feed exclusively on seed endosperm and are obligate predators (e.g. seed beetles, Coleoptera: Bruchidae) (Barnes, 2001; Ernst *et al.*, 1990; Miller, 1994), other animals, such as granivorous and frugivorous rodents, carry out some incidental dispersal by caching seeds that may germinate before the rodent returns (Christianini and Galetti, 2007; Davidson, 1993; Li and Zhang, 2003; Pérez-Ramos and Marañón, 2008). Even for plants reliant on endozoochory, ingestion by the wrong species of animal may be fatal due to extended gut retention time, excessive mastication force, or incorrect gut chemistry (Calviño-Cancela, 2004; Feer, 1995; Traveset, 1998).

Epizoochory is a random process, as plants cannot control to which animals seeds attach. However, the attachment mechanism may determine residence time on the disperser, ensuring that seeds are deposited at suitable distances from the maternal plant, and

epizoochorous species usually produce large numbers of seeds (Couvreur et al., 2005; Couvreur et al., 2008) to compensate for the high probability of seeds being deposited at unsuitable sites.

Endozoochorous dispersal is better suited to coevolution of plants and animals than epizoochory. Seeds must be presented in a way that ensures that dispersers are attracted and ingest them, but the endosperm and embryo must be protected from damage. To meet these criteria, endozoochorous seeds are usually encased in a matrix of palatable fruit pulp or an edible pod, which is often brightly coloured or strongly scented to attract dispersers (van Wyk and van Wyk, 1997). However, smaller-fruited species may be ingested incidentally by herbivores feeding on other plant parts (Janzen, 1984). Endozoochorous seeds typically have thick, hard seed coats, and are often larger than wind- or water-dispersed species (Feer, 1995; Gonthier, 2009; Traveset *et al.*, 2008; Tremlová and Münzbergová, 2007). The hard coat provides some resistance to tooth action and exposure to digestive chemicals in the gut, and large seeds may have better post-germination growth success (Bonfil, 1998; Coomes and Grubb, 2003).

A disadvantage of the hard seed coat is that water and gas exchange are limited. Seeds must absorb water before they can germinate, and germination is an aerobic process. Scarification of the seed coat is therefore vital for germination. Mechanical scarification during mastication and/ or chemical scarification in the gut can achieve this, and germination success may be improved following gut passage (Argaw *et al.*, 1999; Cosyns *et al.*, 2006; Razanamandranto *et al.*, 2004; Traveset, 1998; Traveset *et al.*, 2008). Coevolution between a plant and its endozoochorous dispersers can be very sophisticated. For example, passage rate of seeds through the gut may be controlled by chemicals to ensure that seeds are deposited before lethal damage occurs (Wahaj et al., 1998), and germination of some seeds may not occur without first passing through a suitable disperser (Dudley, 2000). However, enhanced germination following ingestion is not assured, and germination is inhibited in some species (Cosyns et al., 2005; Traveset et al., 2008). Neutral or reduced germinability after ingestion may imply that other germination cues are necessary to break dormancy (e.g. fire or heat shock, Banda *et al.*, 2006; Danthu *et al.*, 2003; Dayamba *et al.*, 2008; Hanley *et al.*, 2001; Luna *et al.*, 2007), or that the animal and plant are mismatched, resulting either in lethal damage to the seed (seed predation, e.g. Barnes, 2001; Bodmer, 1991) or insufficient scarification of the seed.

1.1.4 History of the Matobo Hills

The Matobo Hills, an exposed granite batholith 3000 km^2 in extent that has been subject to extensive weathering (Lightfoot, 1981), have been inhabited by humans for approximately forty thousand years (Ranger, 1999). Stone-age hunter-gatherers (the San) were ultimately replaced by agro-pastoralists towards the middle of the second millennium AD, with concomitant anthropogenic alterations to the environment (Ranger, 1999; Tredgold, 1956). Due to the long association with humans and the importance of the hills in traditional religion and mysticism (e.g. Stone Age "rock art", and the habitation of sacred areas by oracles and sacred spirits), the hills in their entirety were designated as an IUCN World Heritage Site in 2003 (UN, 1992-2010).

During the colonial period, indigenous people were relocated from the core of the hills, and the 416 km^2 Rhodes Matopos National Park was proclaimed in 1924. However, the Park remained populated by people and livestock until 1962, at which time inhabitants were relocated to Reservations in the South of the Hills, and the Park was run as a natural heritage concern (Ranger, 1999). Since then, the National Park has been a popular tourist destination (Ranger, 1999).

Utilisation of some natural resources in the Park continue. Thatching grass is collected under licence in the dry season, livestock graze (illegally) in the peripheral areas of the Park since the fence was destroyed, and unmeasured but potentially significant illegal hunting of wildlife and harvesting of wood for sculpture occurs (pers. obs.; C. Zhuwao, pers. comm.).

1.2. MOTIVATION

Despite savanna dynamics and the relationships between herbivores and plants being investigated over many years, identification of the key determinants of savanna structure remains equivocal. This is termed the "savanna problem" (Sarmiento, 1984 cited in Mills and Fey, 2005), and has given rise to a number of detailed studies. At the landscape scale, rainfall and soil nutrients are the most important determinants of savanna structure (Coe *et al.*, 1976; Sankaran *et al.*, 2005), enabling broad generalisations to be made. However, the interactions of domestic and wild animals, fire and anthropogenic factors, at varying spatiotemporal scales, result in complex effects that are difficult to interpret, and the roles of individual components are often impossible to separate from the whole (Favier *et al.*, 2004; Fuhlendorf and Smeins, 1998; Georgiadis *et al.*, 2007; Laris, 2005; McNaughton *et al.*, 1988;

Mills and Fey, 2005; Roques *et al.*, 2001; Savadogo *et al.*, 2009; Sheuyange *et al.*, 2005; Skarpe, 1992).

The majority of previous detailed studies of savanna dynamics have been in grazer-dominated systems and/or in the presence of megaherbivores such as elephants (*Loxodonta africana*) that are well-known "ecosystem engineers" (e.g. Augustine and McNaughton, 2004; Bell, 1971; Dublin *et al.*, 1990; Jacobs and Naiman, 2008; Levick and Rogers, 2008; McNaughton *et al.*, 1988; Norton-Griffiths, 1979; Pellew, 1983; Roques *et al.*, 2001; Sheuyange *et al.*, 2005; Sinclair, 1979; Weber and Jeltsch, 2000). The significant impacts of smaller browsing ungulates (e.g. small antelope) on savannas have been recognised (Augustine and McNaughton, 2004; Belsky, 1984; Strang, 1973), but few environments lend themselves to direct study of this guild due to sympatry with very large species.

The Rhodes Matobo National Park is situated in a unique, highly heterogeneous environment (Chapter 2). Its inclusion in the Matobo Hills World Cultural Heritage Site area requires that appropriate resource management is implemented. Understanding plant-herbivore and fire dynamics in the system is therefore integral to management decision-making.

1.3. AIMS AND SCOPE

For appropriate management to be carried out in line with an area's management plan, knowledge of the local determinants of vegetation structure is vital. This study, although carried out on a relatively small spatial and temporal scale, aims to provide information on the effects that medium-sized mammalian herbivores (antelope) have on vegetation and ecosystem functioning in the eastern section of the Rhodes Matobo National Park, Zimbabwe.

Focus was primarily on the resident small antelope (*viz.* common duiker *Sylvicapra grimmia*, klipspringer *Oreotragus oreotragus* and steenbok *Raphicerus campestris*), with other ungulates included in field studies for comparative purposes. Both field experiments and controlled *ex situ* experiments using captive antelope were undertaken.

Although not part of the original field study plan, accidental fires during the experimental period unavoidably altered the progression of the study and negatively affected the experimental design: two sites were burnt but the third was not and could not be since it was

not part of the National Park's burning plan, resulting in an unreplicated unburnt control site. Unequivocal determination of the effects of fire in the system was therefore impossible, but the fires provided some insight into the effects of a late-season fire on vegetation in the presence and absence of medium and large herbivores.

Investigation of the effects of fire and herbivores on vegetation structure and species complements was restricted to a single plant community (*Burkea africana*) over a twenty-eight month period. Ecosystem services, such as nutrient cycling (faecal decomposition) and post-ingestion seed viability (a component of seed dispersal), were studied across the study site and under controlled *ex situ* conditions over a longer period, therefore facilitating extrapolation to a larger scale.

Since this was a short-term study, the suite of answerable research questions was limited to relatively short-term effects. The overarching hypothesis of the study is that the physiological, morphological and behavioural attributes of small antelope result in measurable impacts on the structure and function of plant communities. Such attributes include (i) feeding selectivity and the height at which feeding occurs, (ii) digestive efficiency and passage rate, and (iii) longevity and territoriality. Other disturbance effects, such as fire, interact in complex ways with antelope activities, resulting in different response trajectories in the presence and absence of ungulates. Based on this hypothesis, the following predictions can be made, some of which are investigated further in this thesis:

Prediction 1: *Small antelope are enhance germination of hard-coated seeds and are thus potentially important dispersal agents*

In African forests, duikers (Cephalophini) are important seed dispersal agents (Eves, 2003), although dispersal of soft-seeded species is limited due to repeated oral mastication (Feer, 1995). In savanna ecosystems, a large number of woody plants produce fleshy, palatable fruits that are eaten by antelope (Coates-Palgrave, 1996; Prins *et al.*, 2006; Wilson, 1966) and savanna antelope play a similar role to their forest counterparts. By ingesting fruits, antelope transport seeds away from the parent plant, and either egest them in their faeces, or expel them orally during rumination (Bodmer, 1991; Feer, 1995). Chemical and mechanical scarification of the seed coat, which occurs during mastication and digestion, may stimulate germination of hard-seeded species (Raven et al., 1986; Traveset et al., 2008), but be lethal to soft-seeded species (Feer, 1995). Faecal matter acts as a fertiliser, which can promote

seedling growth (Argaw et al., 1999; Cosyns et al., 2006), and removal of seeds from the vicinity of the parent plant may reduce intraspecific competition and promote gene flow (Berger *et al.*, 2008; Calviño-Cancela *et al.*, 2006; Wiegand *et al.*, 2008).

Prediction 2: *Small antelope are selective browsers and feed at low levels, and therefore potentially alter plants' interspecific and intraspecific relationships. Being selective browsers, they (a) influence seedling recruitment, (b) alter competitive interactions among woody plants of differing palatability and between woody and herbaceous plants; (c) in the medium term alter the structure of the understorey, which in turn (d) may affect canopy structure in the long term*

The leaves of seedlings and new growth are high in protein, and during this rapid-growth phase, little indigestible or unpalatable material is produced (Cebrian and Duarte, 1994). Feeding on a seedling is energetically advantageous to the herbivore, but may easily be lethal to a plant, especially if it is completely defoliated. Thus, small antelope may have a negative effect on seedling recruitment, even of species that are unpalatable when mature, and are likely to influence the competitive relationships among species. However, at the community level, removal of seedlings can be advantageous, reducing stem competition (Duncan *et al.*, 2009; Wiegand *et al.*, 2008) and limiting woody development (Augustine and McNaughton, 2004; Belsky, 1984; Roques *et al.*, 2001). In the medium term, and depending on the species browsed, the structure and density of the understorey may also be altered.

Prediction 3: *Plants may compensate for moderate defoliation, but possibly at the expense of overall growth (biomass gains) or propagule production.*

Low to moderate browsing and grazing intensity has been demonstrated to stimulate primary production in some plant species (Agrawal, 2000; du Toit *et al.*, 1990; Rooke, 2003). However, a mutualistic relationship between a plant and its herbivore is unlikely (Belsky, 1987), and loss of tissue likely impacts negatively on propagule production or biomass gains by individuals.

Prediction 4: *Incidental impacts of faunal presence, such as trampling and mechanical damage, affect vegetation development*

Despite being small, the unit pressure exerted on the ground by small antelope such as cephalophines and neotragines is substantial, although the effect is necessarily limited in spatial extent because of short stride length, small hoof size and small group size (Cumming

and Cumming, 2003). Whilst low faunal densities may not result in large-scale trampling effects, frequently-used areas (e.g. resting/ rumination sites and paths to defecation sites) may cause localised soil compaction and thereby limit plant establishment (Boelhouwers and Scheepers, 2004; Savadogo *et al.*, 2007; Thrash, 1998). Frictional effects of animals moving through vegetation also occur, potentially causing damage to apical meristems of dicotyledonous plants and increasing litter fall. Furthermore, for antelope such as steenbok that bury their dung, or others that dig up below-ground foodstuffs, soil turnover may create gaps for colonisers or arrest development of existing plants (Cosyns *et al.*, 2006; Neill *et al.*, 2007).

Prediction 5: *Small antelope are important recyclers of nutrients*

Ruminants egest large quantities of well-digested (i.e. fine textured) plant matter. Faeces are rapidly broken down by microbial and insect activities and mechanical erosion (such as raindrop impact) (Masunga *et al.*, 2006; Plumptre and Harris, 1995). The nutrients present in the dung are therefore returned to the soil in forms that can be readily utilised by plants (McNaughton et al., 1988). Animal-mediated nutrient cycling is typically faster than via the plant decomposition cycle (de Mazancourt and Loreau, 2000b; McNaughton *et al.*, 1988; Thompson Hobbs, 1996), although herbivory-induced secondary metabolite production may limit decomposition rates (Pastor and Cohen, 1997). Furthermore, small antelope tend to utilise latrine sites or middens (Kingdon, 1997; Lunt *et al.*, 2007), which results in local concentration of nutrients in the soil. This may promote plant growth and vegetation succession, and maintain habitat heterogeneity by generating pockets of nutrient-rich soil (Davidson, 1993; McNaughton *et al.*, 1988; Thompson Hobbs, 1996).

Prediction 6: *Territoriality and longevity of small antelope results in localised plant community dynamics being continually affected over several years*

Most small antelope are territorial, and are relatively long-lived (Dunbar and Dunbar, 1979; Kingdon, 1997; Roberts and Lowen, 1997). In MNP, mean (± SE) male common duiker home range size was 0.47 ± 0.25 km^2 (Lunt et al., 2007), and this species frequently exceeds 10 years of age in captivity (N. Lunt, unpubl. data). Continual impacts – including nutrient cycling, trampling and herbivory – in a defined area over a period of years, may have medium- to long-term implications for plant community structure.

Prediction 7: *Fire interacts with faunal pressures to shape the plant community*

Savanna systems are fire-adapted, and the structure of the savanna is determined in part by fire frequency, intensity and timing (Bucini and Lambin, 2002; Joubert *et al.*, 2008; Roques *et al.*, 2001; Sankaran *et al.*, 2005). Individual fires are generally limited in spatial extent and relatively patchily distributed (Ehrlich *et al.*, 1997; Laris, 2005), which leads to a mosaic pattern of burnt sites. Fire interacts with other disturbances (e.g. herbivory, drought) and determinants (e.g. climate) (Sankaran et al., 2005) so that the trajectory of vegetation recovery following fire can vary substantially. Under conditions of similar abiotic conditions, post-fire vegetation recovery is likely to differ with herbivory pressure (Fuhlendorf and Engle, 2004).

Research questions

Based on the predictions outlined above, the following research questions were investigated in this study:

1. To what extent, and in what ways, do browsers of two size classes (small and medium) affect (i) herbaceous cover and species richness; (ii) woody cover and species richness, (iii) seedling density, and (iv) shoot development of woody plants in a savanna system?
2. What are the short-term interactive effects of fire and browsing antelope on vegetation structure (as defined in (i) to (iii), above)?
3. Do small browsing antelope enhance or inhibit germination of seeds of three savanna tree species (*Sclerocarya birrea*, *Grewia monticola* and *Euclea divinorum*)?
4. At what rate do small antelope faeces decompose under natural conditions, and what are the implications for nutrient cycling rates?
5. What effect does diet have on defecation rate (and ultimately on nutrient cycling rate) in small antelope?

1.4. STRUCTURE OF THE THESIS

The chapters that follow consists of one chapter combining information obtained from the literature with original background research data (Chapter 2), one field-research chapter (Chapter 3) and one chapter containing *ex situ* and field experimental data (Chapter 4). Chapter 5 extracts the main findings from the three research chapters. Due to the large quantity of visual material, tables and figures are included sequentially after the text of each chapter, to avoid disrupting the flow of the document.

2. STUDY SITE AND STUDY ANIMALS

This chapter provides background to the study sites and animals under study, and combines information obtained from the literature with original data collected between 2004 and 2008.

2.1. INTRODUCTION

2.1.1. Study sites

The study was divided into *in situ* and *ex situ* components, carried out in the Matobo National Park, and at Dambari Field Station, respectively. The sites are situated approximately 50 km apart in Matabeleland South Province of Zimbabwe (Fig. 2.1).

2.1.1.1. Matobo National Park

In situ studies were carried out in the Matobo National Park (MNP) in southern Zimbabwe (20º20' to 40'S; 28º25' to 45'E), in a *c*. 48 km^2 study area in the Togwe Wilderness Area in the East of the Park. The study site was assigned by the Zimbabwe Parks and Wildlife Management Authority (PWMA), and supported good populations of all antelope under investigation.

The Matobo Hills, which cover approximately 3000 km^2 and incorporate the 300 km^2 MNP (Fig. 2.1), comprise an exposed granite batholith dissected by deep drainage systems carved down into NNW to NW trending joints and faults (Lightfoot, 1981). A sub-rectangular system of jointing and consequent erosion predominates, resulting in parallel steep-sided rocky outcrops ('kopjes') and bornhardts ('whalebacks' or 'dwalas') interspersed with narrow valleys (Lightfoot, 1981). Outcrops may exceed 100 m in height. Rainfall in MNP averages 601.1 $mm.yr^{-1}$ (60-year mean, Zimbabwe Parks and Wildlife Management Authority, unpubl. data), with the majority falling between mid-November and March (hereafter referred to as the hot, wet season); however, the timing and quantity of rainfall are erratic. Mean daily temperatures reach a minimum in the cool, dry season (April to August) and a maximum towards the end of the hot, dry season (mid-August to mid-November) (Fig. 2.2).

Several mammalian ungulates larger than 2 kg are resident in the study site, and several others are seasonal visitors (Appendix 1). Potential predators of antelope – especially of smaller species and calves – include leopard (*Panthera pardus*), brown hyaena (*Hyaena*

brunnea), Chacma baboon (*Papio ursinus*), crowned eagle (*Stephanoaetus coronatus*), Verreaux's eagle (*Aquila verreauxii*), rock python (*Python sebae*) and humans (*Homo sapiens*). Steenbok (*Raphicerus campestris*) lamb remains have been found below nests of crowned eagles in the Matobo Hills (R. Hartley pers. comm.).

Nine antelope species belonging to six subfamilies are represented in the study site (Appendix 1). Subfamily classification, based on molecular and morphological data, follows Matthee and Davis (2001). Sable (Hippotraginae: *Hippotragus niger*), tsessebe (Alcelaphinae: *Damaliscus lunatus*) and blue wildebeest (Alcelaphinae: *Connochaetes taurinus*) are infrequent dry-season visitors that occur in small numbers. Apart from antelope, other herbivores include white rhinoceros (Rhinocerotidae: *Ceratotherium simum*), domestic cattle (Bovidae: *Bos taurus*), hyraxes (Procavidae: *Procavia capensis* and *Heterohyrax brucei*), and lagomorphs (Leporidae: *Lepus saxatilis* and *Pronolagus rupestris*).

2.1.1.2. Dambari Field Station

Ex situ experiments were carried out at Dambari Field Station, a 25 ha property situated approximately 25 km SE of Bulawayo on the Beitbridge Road (20º15.0' S; 28º46.5' E). Mean annual rainfall in the wetter than normal decade between 1999 and 2009 was 687 ± 68 mm per annum, with the majority falling between November and March (Fig. 2.3). Soils are of a sandy-loam type, and vegetation is dominated by open *Acacia nilotica* and *Dichrostachys cinerea* scrubland on well-drained soils, and *Hyparrhenia filipendula, Andropogon gayanus* and *Hyperthelia dissoluta* in seasonally water-inundated (dambo or vlei) areas.

Antelope were housed as single animals, pairs or small family groups (pair plus immature offspring) in fenced, semi-natural enclosures in species blocks. Experimental enclosures varied in size from 168 m^2 to 1050 m^2 and were primarily situated in *Acacia nilotica* scrubland. The animals were seldom handled (except for necessary veterinary treatment or routine examination), and minimal disturbance occurred beyond daily enclosure cleaning and food provision routines. Thus, the antelope were semi-wild, and their behaviour was assumed to mirror that of their wild counterparts. Where possible, observations were made from hides to prevent observer presence from influencing antelope behaviour.

A standard diet of domestic vegetables, game nuts (National Foods, Bulawayo, Zimbabwe) and indigenous browse (Plowman, 2002) was provided at approximately 15h30 daily; additional naturally growing edible plants in enclosures were available *ad libitum*. Soluble vitamin supplements (Agrimix, Harare, Zimbabwe) were added to drinking water, which was freely available.

2.1.2. Antelope species

The systematics of the Bovidae is currently unclear, especially at intermediate taxonomic levels. I will follow Matthee and Davis (2001) for most subfamily and tribe classifications. Six species of antelope, representing four subfamilies are resident in the Matobo study site, and are described here. The other three species (Appendix 1), being transient and present at very low densities, will not be considered further.

2.1.2.1. Small antelope: Neotragini (Antilopinae) and Cephalophinae

The Neotragini (dwarf antelope) and Cephalophinae (duikers) are collectively referred to as "small antelope". Both taxa are essentially African, although there are fossil records of neotragines in Asia (Kingdon, 1997). A massive radiation of both tribes occurred independently in the late Miocene between 4 and 6 m.y.a. (Brashares *et al.*, 2000; van Vuuren and Robinson, 2001) due to a combination of climate change and concomitant habitat fragmentation (which resulted in continual expansion and contraction of biomes and metapopulation fragmentation) and dwarfism (which facilitated survival in small patches of habitat) (van Vuuren and Robinson, 2001). As a result, there are extant small antelope representatives in most biomes in Africa, from forest (montane, rain and coastal), through eutrophic and dystrophic savanna, to desert (Kingdon, 1997).

Neotragini (Antilopinae)

Based on nuclear and mitochondrial DNA (mtDNA) analysis, the subfamilial and tribal classification of the klipspringer (*Oreotragus oreotragus*) and suni (*Neotragus moschatus*) are unclear, although historically they have been placed with the neotragines (Matthee and Davis, 2001). In the absence of a suitable alternative, I will retain the historical classification here. There are thirteen recognised species of neotragines, in six genera. Mean body mass ranges from 1.5 kg to 15 kg (Kingdon, 1997). Apart from the royal antelope (*Neotragus pygmaeus*) and dwarf antelope (*Neotragus batesi*) that inhabit forests, most species are found in thickets (e.g. *Neotragus moschatus*, *Raphicerus melanotis* and *R. sharpei*), savanna (e.g.

Raphicerus spp., *Ourebia ourebi*, some *Madoqua* spp.), rocky outcrops and scree slopes (*Oreotragus oreotragus* and *Dorcatragus megalotis*) and semi-arid or arid areas (*Madoqua* spp., *Rhynchotragus* spp.) (Kingdon, 1997).

i. Klipspringer (*Oreotragus oreotragus* Zimmerman 1783)

Klipspringer are powerfully built, with well-developed haunches that facilitate jumping. The muzzle is foreshortened, and the eyes are set wide apart and are partially forward-facing, which imparts a degree of binocular vision which is essential for judging distances when jumping between rocks and boulders. The preorbital scent glands are well developed, and contrasting-colour markings on the ears and face are used for visual communication. The tail is vestigial, and, unlike other small antelope, little tail flagging is carried out. Pelage colour is generally a brindled grey/ brown, which provides camouflage against rock. The fur is thick and hollow shafted, which is believed to provide insulation in cold environments (Kingdon, 1997). Unique amongst antelope, the klipspringer walks on the tips of its rubbery hooves, improving traction on slippery surfaces. Males possess short, straight horns, but beyond this, sexual dimorphism is limited; adults of both sexes stand up to 60 cm at the shoulder and weigh up to 18 kg (average 10 to 15 kg).

Behaviour: Klipspringer are monogamous and form a strong pair bond. Individuals remain within visual or auditory range of each other, and females tend to initiate travel within the territory (Estes, 1991; Roberts, 1998; Roberts and Dunbar, 2000). Trios are usually pairs with immature offspring, although female offspring may occasionally remain in their natal ranges until after sexual maturity (Estes, 1991). When sexual maturity is reached, offspring tend to be chased from the territory by the same-sex parent.

Both sexes are territorial, and mark vegetation within their territories with secretions from their preorbital glands. Encountering scent marks of intruders within the territory results in over marking with preorbital glands (Roberts, 1998; Roberts and Lowen, 1997). Dung is deposited at latrine sites near territorial boundaries, and this species tends to urinate and defecate simultaneously (pers. obs.). Aggression is not ritualised in klipspringer, and direct conflict may occur between territory-holders and intruders, with rivals butting and biting each other. In an unnatural social grouping in captivity, a female klipspringer was chased aggressively and had her ears bitten off by her three mature offspring (pers. obs.). Both sexes, but especially males, carry out “sentry duty” during the day, standing almost

motionless in areas with good visibility and surveying access points. When predators are sighted, an alarm call is given (sharp whistles and snorts) and the pair escapes uphill (Estes, 1991), often scaling extremely steep rocks and slopes in the process.

Home ranges vary in size with resource availability, and in the Ethiopian Highlands, density was positively correlated with herbaceous cover, ranging from fewer than 20 individuals km^{-2} to approximately 44 individuals km^{-2} (Dunbar, 1979). Klipspringer are primarily diurnal – with a peak in feeding activity in the early morning and late afternoon – but are known to be active at night (Estes, 1991). In cooler climes, or at sites with high diurnal ranges in temperature, individuals may sun themselves on exposed rocks in the early morning (Dunbar, 1979).

Klipspringer are selective mixed feeders, and they reach greatest densities in areas with a well-developed herbaceous layer (Dunbar, 1979). Due to their ability to scale rocks, they are able to reach woody vegetation beyond the reach of most other terrestrial ungulates, and their main competitors for food are probably hyraxes (*Procavia capensis*, *Heterohyrax brucei* and *Dendrohyrax* spp.). When food resources are limited in the hills, klipspringer may descend into valleys to feed (Estes, 1991), but are rarely encountered more than a few hundred metres from their preferred rocky habitat (pers. obs.).

Breeding is typically aseasonal, and a single lamb is born after a gestation of about five months. The juveniles are hidden and cryptically coloured, and do not flee in the face of danger (Estes, 1991). Juveniles remain hidden for two to three months, after which they remain in constant contact with their mothers and suckle until four to five months of age (Estes, 1991). Sexual maturity is reached at a year in females, and slightly later in males (Kingdon, 1997).

Habitat, distribution and status: The klipspringer is highly adapted to mountainous and rocky habitat, and is rarely found far from rugged slopes. *Oreotragus* is a monotypic genus and has a discontinuous distribution in Africa, from the Horn of Africa down the Rift Valley to south western Africa, with several isolated populations in Central West Africa (Fig. 2.4). Klipspringer have been recorded from near sea level to 4500 m.a.s.l., but are always associated with rocky or mountainous areas.

The current IUCN status is “Conservation Dependent” (Baillie and Groombridge, 1996), which implies that the species is reliant on protected areas for continued survival. Threats include poaching and competition with domestic livestock such as goats, especially in regions where klipspringer are seasonally reliant on valley vegetation (Kingdon, 1997).

ii. Steenbok (*Raphicerus campestris* Thunberg 1811). Alternative name: Steinbuck

These are small savanna-dwelling antelope that reach a maximum size of 15 kg and stand up to 60 cm at the shoulder. Males are horned. Pelage colour is light to reddish brown, with a whitish belly. The ears are large, and venation within them is prominent. Pre-orbital glands are less obvious than in the klipspringer. The hooves, which are straight-sided and pointed, facilitate rapid running. Contrasting light markings on the ears, around the eye and on the rump may be used for visual communication (Estes, 1991).

Behaviour: Like many other small antelope, steenbok are monogamous, but the pair bond is not necessarily very strong except when the female is in oestrus (Smithers, 1983). Reproduction is aseasonal (Estes, 1991) although there may be a birth peak in the early wet season. The gestation period is approximately 170 days, and sexual maturity is reached at seven (females) to nine (males) months. Juveniles remain hidden until they are fairly large, and are weaned at about three months (Estes, 1991).

Both sexes are territorial, and boundaries are presumably marked with pedal and preorbital scent glands (but Estes [1991] reports that preorbital gland marking has not been observed in either sex) and with dung latrines (Estes, 1991; Smithers, 1983). Like dik-diks, steenbok bury their dung: shallow holes are dug with the front hooves, dung and urine are deposited and then covered with sand or litter.

Predator avoidance tactics include immobility (relying on camouflage), or fleeing. Steenbok tend to run and bound directly to the nearest cover, and are capable of rapid direction changes (Estes, 1991). When in cover, they either freeze, or may adopt the juvenile tactic of lying prone, laying the ears back and remaining immobile. There are also reports of steenbok hiding in disused aardvark (*Orycteropus afer*) and warthog (*Phacochoerus africana*) burrows (Smithers, 1983).

Despite having relatively small salivary glands, an adaptation suited to grazing (Hofmann et al., 2008) steenbok are browsers and include a large proportion of forbs in their diets (Codron *et al.*, 2008; Codron *et al.*, 2007a; du Toit, 1993; Smithers, 1983). Codron *et al.* (2008) suggest that this species, over evolutionary time, changed from being a mixed feeder to a more specialist browser following extinctions and competitive release at the end of the Florisian Land Mammal Age 10,000 years ago. Approximately three-quarters of the diurnal activity budget is dedicated to resting (51%) and feeding (26%) (du Toit and Yetman, 2005).

Habitat, distribution and status: Steenbok are generally associated with low- to medium-density savanna woodland, for example *Acacia* veld (du Toit, 1993). They avoid mountainous regions and dense habitats. Steenbok have a disjunct distribution, occurring in southern Africa south of the Zambezi River, and in East Africa as far north at Mount Kenya (Fig 2.5, Estes, 1991). They are relatively common within suitable habitat.

Cephalophinae

The Cephalophinae is entirely African, with two recognised extant genera: *Cephalophus* (18 spp.), and the monotypic *Sylvicapra*. Some morphological and recent molecular studies have supported the recognition of a third genus – *Philantomba* – which is basal to both *Sylvicapra* and *Cephalophus* and contains two small duiker species – the blue (currently *C. monticola*) and Maxwell's (currently *C. maxwellii*) duiker (van Vuuren and Robinson, 2001).

The majority of species are forest specialists, occurring in Central, East and West African forests, while two species are found in southern African montane and coastal forests. *Sylvicapra*, the savanna-dwelling common duiker, is widespread throughout Africa's savanna biome. Duiker are selective feeders, choosing high-quality plant matter. In forest ecosystems, they are important frugivores, and have been demonstrated to disperse seeds through spit dispersal and in dung (Feer, 1995) .

i. Common duiker (*Sylvicapra grimmia* Linnaeus 1758) Alternative names: Grimm's duiker; crowned duiker; bush duiker; grey duiker

The fur is grey-brown with a brindled appearance, the belly and throat are whitish, and the anterior aspects of the forelegs and the muzzle have black blazes. Only males are horned, but both sexes have a long tuft of fur on the mid-crown, giving rise to the alternative common name of "crowned duiker". The tail has a conspicuous black longitudinal stripe, and the

underside is white. Preorbital and pedal glands are well developed. The hooves have slightly rounded exterior edges, which assist with rapid direction-changes (jinking) during escape from predators.

Behaviour: Common duiker are territorial, although males are more actively territorial than females: they hold exclusive territories that may include partial home ranges of one or more female (Dunbar and Dunbar, 1979; Lunt *et al.*, 2007), and control defecation volume (Mhlanga & Lunt in prep.) in much the same way as oribi (Brashares and Arcese, 1999).

In the MNP, mean home range size was 24 ha, but was widely variable among individuals (14 ha to 102 ha: Lunt et al., 2007). Pre-orbital scent glands and dung piles are used as territorial markers, and dung piles are often deposited at latrine sites (Lunt et al., 2007).

Activity shows a bimodal pattern, with peaks in activity in the early morning and in the early evening (Bowman and Plowman, 2002). The heat of the day is generally spent hiding in thick vegetation, sleeping and ruminating. Studies of captive animals suggested that territorial behaviour (i.e. preorbital scent marking) is predominantly carried out in the evenings (N. Lunt & B. Msimanga, unpubl. data), and peaks in defecation occur between 04h00 and 07h00 and from 16h00 to 22h00 (N. Lunt unpubl. data).

Breeding is aseasonal, with single lambs born at intervals of about 244 days in captivity (N. Lunt unpubl. data). Lambs remain hidden for some time after birth, but are mobile within three days. They suckle two to three times a day and are weaned by four to five months (Estes, 1991, pers. obs.). Sexual maturity is reached within the first year in both sexes (Estes, 1991, pers. obs.).

Habitat, distribution and status: Common duiker are widely distributed in sub-Saharan Africa (Fig. 2.6) and are tolerant of a wide range of habitats, but tend to prefer medium-density woodland with a well-developed herbaceous layer, e.g. *Terminalia* and mixed woodland (Lunt et al., 2007). They avoid primary forest, but may be found at high altitudes, up to the snow line (Smithers, 1983). Common duiker are not endangered (Baillie and Groombridge, 1996).

2.1.2.2. Larger resident antelope: spiral-horned antelope and reedbuck

Tragelaphini (Bovinae)

The spiral-horned antelope are a tribe of the Bovinae, with nine extant species occurring in Africa. Most species are woodland or grassland-dwelling mixed feeders or browsers. A recent molecular phylogeny produced three major clades – the basal *Tragelaphus imberbis* and *T. angasi*, a clade comprising forest-reliant species, which was a sister group to the savanna-dwelling greater kudu (*T. strepsiceros*), and the arid-adapted eland species (*Taurotragus derbianus* and *T. oryx*) (Willows-Munro *et al.*, 2005), which, being imbedded in *Tragelaphus* makes the current generic classifications paraphyletic. Radiation of the group occurred between 14 and 3.3 m.y.a, with relatively recent speciation events within the *T. strepsiceros*/ closed forest species clade.

i. Bushbuck (*Tragelaphus scriptus* Pallas 1766).

Bushbuck are medium-sized, sexually dimorphic antelope. Males are larger than females (80 cm at shoulder height, 40 kg c.f. females 70 cm at shoulder height, 30 kg) and possess relatively straight, spiralled horns. Pelage colour varies geographically, giving rise to several recognised subspecies. In the Matobo population (subspecies *T. s. ornatus*), adult males are dark reddish-brown with well-defined vertical stripes on their sides and pale spots on their haunches. They possess a whitish crest along the spine, and a distinct white transverse stripe on their dark faces. Younger males are redder in colour; the coat darkens with maturity. Females are reddish brown in colour, with distinct white spots on their sides. The underside of the tail is distinctly white and long-haired.

Behaviour: It was long believed that bushbuck were not territorial and that males had linear hierarchies, given their high densities in some habitats and apparent lack of agonistic encounters (Kingdon, 1997). However, recent studies indicate that adult male bushbuck are territorial, defending the 50% minimum convex polygon (MCP) area of their home ranges (Wronski, 2005; Wronski et al., 2006) and no linear dominance hierarchy has been detected (Wronski *et al.*, 2009). In Uganda, male bushbuck territories are 0.14 ± 0.04 km^2 (Wronski et al., 2006), while in Kenya, bushbuck diurnal home ranges average 0.19 km^2 (Estes, 1991) . Territorial boundaries are marked by olfactory secretions produced at the base of the horns and on the cheeks, and intruders into the defended area are aggressively challenged (Wronski et al., 2006). Bushbuck are solitary and polygynous (Estes, 1991; Wronski et al., 2006).

Bushbuck are mixed feeders, but primarily browse on shrubs and forbs, although they also ingest new grass shoots and fruits of a variety of trees (Estes, 1991; Kingdon, 1997; Simpson, 1974a; Smithers, 1983). Grazing tends to be a nocturnal behaviour (Estes, 1991). They are water dependent and are usually found near surface water, but may also drink dew from leaves (Estes, 1991; Kingdon, 1997). This species is primarily nocturnal and spends long periods resting and ruminating; however, activity periods vary with disturbance and predation levels. When alarmed, bushbuck utter a loud bark, and this call may also be used to challenge other males or advertise a male's presence (Kingdon, 1997). This species relies on its cryptic pelage to escape detection, but will flee with its tail raised if pursued (Estes, 1991).

Breeding tends to be aseasonal, although birth peaks may occur in April/May and October/November in more arid areas (Estes, 1991; Simpson, 1974b; Smithers, 1983). A single calf is born after a gestation of six to seven months, and is hidden by the female, only venturing into more open areas about four months after birth (Estes, 1991; Smithers, 1983). Males reach sexual maturity at about 11 months, and females at 14 months (Smithers, 1983).

Habitat, distribution and status: Bushbuck belong to the "closed forest" group of tragelaphines (Willows-Munro et al., 2005), and are restricted to dense woodland and thickets, usually close to water. They are widely distributed in Africa in regions with suitable habitat, and are therefore absent from the arid south-west, north-east, and north (Fig. 2.7). Bushbuck are not endangered, although some localised subspecies are vulnerable (Kingdon, 1997).

ii. Kudu (*Tragelaphus strepsiceros* Pallas 1766). Alternative names: Greater kudu

Distinct sexual size dimorphism is evident in this species, with males standing about 1.4 m at the shoulder and weighing about 250 kg, and females reaching 1.25 m (shoulder height) and attaining a maximum mass of 200 kg. Males possess large, corkscrew horns that may exceed 1.5 m in length. Both sexes are brown or greyish in colour (females usually more brown) as adults, with six to ten pale vertical stripes on their sides and pale crests along their spines. Juveniles are reddish brown, and the stripes are more distinct. Males have dark faces with a white V-shaped band, and a fringe of long hair on their throats. Females have similar facial markings but they are less distinct, and they lack the beard and throat fringe. The lips and chin in both sexes are white, and both sexes have large, rounded ears. The lower legs are paler in colour than the body, and the tail is boldly white beneath and acts as a signal to other

individuals during flight (Smithers, 1983). Kudu have false-hoof glands in the hind feet (Estes, 1991).

Behaviour: Kudu are loosely social antelope, with females and juveniles forming herds and males occasionally forming bachelor herds. Associations are often transient, and herd size may vary seasonally (Estes, 1991). Kudu are not territorial, and range over large areas; dominant bulls' home ranges average 10 km^2. A bull consorting with cows will challenge other adult bulls that move into his range (Kingdon, 1997).

Like bushbuck, kudu emit a loud bark alarm call when disturbed, and either freeze to escape detection or flee. When running, the tail is raised, showing the white underside, and males hold their heads back so that their horns lie along their backs. In flight, kudu can easily clear obstacles that exceed 2 m in height (Estes, 1991; Smithers, 1983).

Kudu spend more than half of their time foraging (Estes, 1991), and are primarily browsers and frugivores. Codron *et al.* (2007a) reported that 4 to 10% of intake in the dry and wet season, respectively, comprised grass but this is likely to be fresh growth. Kudu in Kruger National Park showed a marked preference for forbs, switching to woody browse when new growth was available (Smithers, 1983).

Breeding can be aseasonal, but calf mortality is high in the dry season and in southern Africa, there is a marked peak in births in January/February (Smithers, 1983). A single calf is born after a gestation period of 7.5 to 8 months and intercalf intervals average eight to ten months (Estes, 1991). Calves remain hidden for several days after birth, after which the dam and calf rejoin the cow herd. Calves are weaned by six months and reach sexual maturity at two to three years (females) or five years (males) (Estes, 1991).

Habitat, distribution and status: Kudu, being independent of surface water, have a wide distribution in southern and East Africa (Fig. 2.8), but are restricted to areas with suitable woodland. They are found from sea level to 2450 m.a.s.l. (Estes, 1991), and show preferences for riverine habitats. The kudu is not at risk, although isolated populations in East Africa may be vulnerable (Kingdon, 1997).

Reduncinae

This subfamily contains the genera *Kobus* (five species), *Redunca* (three species) and arguably *Pelea* (one species) (Kingdon, 1997; Matthee and Davis, 2001). Again, the intermediate level classification is unclear, with some authors granting the group subfamily status (Matthee and Davis, 2001), and others placing it as a tribe within the Antilopinae (Kingdon, 1997). However, molecular analysis indicates that the reduncines are the earliest divergence of the Caprinae/ Alcelaphinae/ Hippotraginae clade, which clearly separates them from the Antilopinae (Matthee and Davis, 2001). The earliest fossil reduncines in Africa date to 11 m.y.a., and this group was present in Asia by 5 m.y.a. (Kingdon, 1997).

Reduncines are water-dependent, grassland dwelling grazers. However, only the lechwe (*Kobus leche*) is adapted to permanent swamp conditions; the other species are generally found on the periphery of swamplands (Kingdon, 1997). All species are medium- to large antelope, and males have curved, ridged horns.

Social structure varies with species, ranging from monogamy to polygyny, and animals may be solitary or form loose herds (Estes, 1991). Males are often territorial, and all animals advertise their presence through olfactory means (faeces, urine and scent from inguinal glands). They lack preorbital glands (Kingdon, 1997).

i. Reedbuck (*Redunca arundinum* Boddaert 1785). Alternative names: Common reedbuck, southern reedbuck.

The reedbuck is a medium-sized antelope, standing 80 to 90 cm at the shoulder (male and female, respectively) and weighing 70 to 80 kg. Males possess horns that curve forwards and are ridged for the lower two-thirds of their length. Pelage colour is variable geographically, but tends to be a pale greyish-brown. The back is darker than the rest of the body, and the underparts are white, as is the underside of the tail (Kingdon, 1997; Smithers, 1983). Juveniles tend to be lighter in colour than adults.

Behaviour: Reedbuck are generally solitary or occur in monogamous pairs in the wet season, but home ranges contract in the dry season and small, loose groups may form (Estes, 1991; Kingdon, 1997). Unusually for a bovid, female offspring disperse before males (Estes, 1991). Individuals are fairly sedentary, which makes this species vulnerable to habitat change resulting from dry season droughts and fire (Estes, 1991); however, in such instances,

large aggregations may form when animals are displaced to suitable habitat near water sources and at unburned sites.

Dominant males are territorial, and they defend their territories using threat displays including defecation, urination, adopting the "proud" stance, whistling and stotting (Estes, 1991; Smithers, 1983). Antipredator behaviour takes the form of freezing or crouching, or sneaking into cover. If disturbed further, they will take flight, jumping and snorting, and producing a "popping" sound which is believed to be a result of the sudden opening of the inguinal glands (Estes, 1991; Smithers, 1983).

Reedbuck are primarily grazers, although forbs may be included in the diet in some localities (Smithers, 1983). Being reliant on good cover, they usually move away from burnt areas and therefore do not take advantage of new grass growth to the same extent as other grazers (Estes, 1991; Smithers, 1983). They are primarily nocturnal.

Breeding is aseasonal, with a birth peak in the wet season. A single calf is born after a gestation of about 7.5 months. Female reedbuck seek shelter about a month before calving, and the calf remains concealed for about two months after birth (Estes, 1991). Calves are suckled two to three times a day. The female and calf may rejoin the male when the calf is approximately four months old (Smithers, 1983). Sexual maturity is reached at around one year.

Habitat, distribution and status: Southern reedbuck are restricted to areas with good cover, access to good grazing, and water. Thus, they prefer vlei areas or medium- to tall-grassland, but avoid scrubland and woodland (Kingdon, 1997; Smithers, 1983). They are distributed in the moister regions of southern and central Africa (Fig. 2.9), and are not endangered although populations are fragmented due to habitat change (Kingdon, 1997).

2.2. MATERIALS AND METHODS

The characteristics of plant communities and their distribution and habitat use by and population density of antelope were investigated across the study site. These data were used to identify sites for specific experiments described in Chapters 3 and 4.

2.2.1. Characterisation of Matobo National Park study site vegetation

Plant communities were identified in the study site, based on woody plant composition and, to a lesser extent, dominant grass species. These communities could be further sub-divided using stem density, but a coarser separation was used for vegetation sampling. A vegetation map was developed using remote sensing (Fig. 2.10), as follows. Representative sites of each community were visited, and their positions recorded with a hand-held GPS device (Garmin III Plus, Garmin Corporation, Kansas, USA) with positional accuracy of 5 to 10 m. These locations were digitised against a June 2001 Landsat 7 image (Radarsat International) with a pixel size 15 m by 15 m, and used to create training sites and community signatures in Idrisi Kilimanjaro v.14.02 (Eastman, 2004). A vegetation map was created using the MAXLIKE algorithm, and map accuracy was tested by ground truthing. Refinements to the map were carried out on an *ad hoc* basis until less than 10% of randomly assigned groundtruth points were incorrectly assigned. However, separation of *Brachystegia/ Julbernardia* woodland and *Combretum* woodland was difficult to resolve, so these communities were combined on the map (Fig. 2.10).

Over one annual cycle (Appendix 2), from May 2004 to June 2005, characteristics of both woody and herbaceous vegetation were assessed in each community in the cool dry, hot dry and hot wet seasons. On each occasion, five sampling sites per community were generated in Idrisi Kilimanjaro (Eastman, 2004) using the SAMPLE module and random point generation. Points were uploaded onto a handheld GPS III Plus GPS (Garmin Corporation, Kansas, USA) and located in the field. Each sample site consisted of the area included in an approximate 30 m radius of the sample point.

At each sample site, up to five individuals of each species of woody plant that occurred were assessed using a nearest-neighbour method. Data were recorded for each individual, as follows:

- Dimensions: estimated height; estimated canopy diameter; height of lowest branch
- Composition (estimated on a logarithmic scale to a maximum of 10^5) of: flowers and fruits, both on the tree and on the ground; and leaves separated into green, senescent and fallen
- Utilisation: evidence of browsing by vertebrates or insects; minimum and maximum height of observed browsing damage

At the beginning of the study, during the wet season when species richness was highest, optimal quadrat size and replicates for herbaceous vegetation (i.e. grasses, sedges and forbs) in each community were determined using square nested quadrats with 0.5 m increments in linear dimensions. Assuming a linear increase in effort with size, and setting a cost of 1 to the smallest quadrat size (0.25 m^2), the Weigert method (Kenney and Krebs, 2002) was used to determine optimal quadrat sizes for each community, using species richness of (i) grasses and sedges only, (ii) forbs only and (iii) all herbaceous species as determinants. Optimal sizes varied from 4 m^2 to 6.25 m^2, so the conservative size (6.25 m^2) was used as the standard for assessment. Sample size (i.e. replicates) was calculated using the "continuous variables – means" module of Ecological Methodology (Kenney and Krebs, 2002), again using species richness of each herbaceous component, in isolation and combined, as determinants. Modal sample size was five.

In each quadrat, total aerial cover and moribund load and species complements of all herbaceous components were recorded. Mean height (cm) (of three individuals) and aerial cover were estimated for each grass and sedge species, along with reproductive stage data and evidence of grazing. Dimensions (height and canopy diameter) of up to five individuals of each species of forb were measured to the nearest 0.5 cm, proportion of green: senescent growth and presence of flowers and fruits were recorded, and note was taken of browsing signs. The number of forbs of each species was counted with the exception of prostrate, spreading individuals for which percent cover was recorded instead.

Data were used to determine species richness, relative frequency of palatable and unpalatable species, and extent of utilisation by ungulates in each plant community (Appendix 3).

2.2.2. Habitat selection by antelope

In May 2004, six routes that representatively sampled all plant communities were established in the study area (Fig. 2.11). Route length ranged from 5.8 km to 9.8 km (map distance), and totalled approximately 44 km. Routes were walked at monthly intervals until May 2005 (Appendix 2), at a speed of approximately 2 to 2.5 $km.h^{-1}$. The localities of field sign – spoor, dung, resting sites, feeding stations, marking posts – within one metre either side of the "line", together with visual sightings of all antelope species, were recorded using a hand-held GPS. To avoid pseudoreplication and temporal autocorrelation, only sign adjudged by an

For each month, the route walked was overlaid on the vegetation map, and the total distance walked in each plant community was calculated. Coordinates of antelope field sign were overlaid on the vegetation map, and the number of points that fell in each plant community was recorded. It was assumed that the rate of encountering field signs mirrored the level of habitat utilisation by each species. Although it is recognised that spoor recorded may have been of animals in transit between habitats, it was assumed that the probability of encountering such spoor was lower than encountering spoor of animals utilising the habitat for foraging/resting etc.

Habitat selection was estimated by means of density of sign per kilometre of transect (= encounter rate) and through the use of a standardised selection index ("SELECT v. 6.0" of Kenney and Krebs, 2002). The latter index illustrates relative selection and avoidance of habitats according to the prevalence of sign in proportion to the area covered by each habitat. Indices greater than the inverse of the number of categories indicate selection, and vice versa. Therefore, in this study, which comprised ten recognised habitat types, indices greater than 0.1 indicated selection.

2.2.3. Antelope density

Antelope densities were estimated in the study site using the cleared plot method of dung-heap counts along twelve to fifteen strip transects (Fig. 2.11). Dung-heap counts were used in preference to direct counts, due to low detectability of cryptic small antelope (Schmidt, 1983). Strips were 1000 m long and 2 m wide, and were each subdivided into 50 m lengths (“plots”) using wooden pegs. Transects were assessed in the early dry season (April/May) and late dry season (September/October) of 2001, 2002 and 2004 to 2008 (Appendix 2). All

antelope sign encountered in each plot along each transect was recorded. Densities of each herbivore species were calculated using the formula

$$D = \frac{X}{A.T.R}$$

Where D = density (individuals.km^{-2}), X = no. dung heaps encountered along transect, A = area sampled per transect, T = days between clearing and assessing transect, and R = defecation rate (no. pellet groups produced per day). Defecation rates were obtained experimentally for common duiker, steenbok and klipspringer (Lunt et al., 2007), and estimated using a power-law function of (Ellis, 2003) for the other ruminants.

Relationships between antelope density and (i) annual rainfall and (ii) fire in the year of assessment and two years preceding assessment were investigated using Spearman's rank order correlation.

2.2.4. Antelope habitat overlap

To determine the extent of overlap in spatial habitat use, antelope sign in strip transect plots (100 m^2 areas) were collated for each transect assessment session. Shared habitat for a species was estimated as the total number of shared plots as a proportion of the number of plots containing sign of that species. Pairwise and multiple species comparisons were run using the formula:

Proportion overlap of species i with species j = $\sum(\sum i \cap j \cap \ldots n)/\sum i$

Where $(\sum i \cap j \cap \ldots n)$ is the number of 100 m^2 plots containing sign species i in addition to species j to n.

2.3. Results and Discussion

2.3.1. Vegetation

Ten plant communities were identified and mapped in the study area. The boundary between different communities was often soft, but transitions usually occurred within 30 m.

2.3.1.1. Burkea africana *woodland community (c. 2.5 km^2 of study site)*

This community typically comprised wooded grassland, dominated by *Burkea africana* and *Terminalia sericea* or *T. brachystemma*, with *Andropogon gayanus*, *Hyperthelia dissoluta* or *Hyparrhenia* spp., *Pogonarthria squarosa* and *Heteropogon contortus* dominating the herbaceous layer. It was moderately speciose and diverse, with 50 woody plants (Appendix

3), 29 species of grasses and 22 species of forb recorded. Between 40 and 50% of forb species encountered showed evidence of browsing. Although only 38% of woody plant species were browsed, the relative frequency of palatable individuals was relatively high (Fig. 2.12), and almost two-thirds of browsed species were heavily utilised (>20% of individuals browsed).

2.3.1.2. Kopje community (c. 12.6 km^2 of study site)

This mixed community was located at the bases and up the sides of kopjes. In many areas, it blended rapidly with *Pterocarpus* woodland, but was distinguishable by the absence of dominant tree species and a more depauperate herbaceous layer – fewer than six grass and forb species per 6.25 m^2 quadrat. However, a total of 16 forbs and 23 grass species were recorded in this community. Although no woody species was dominant, several were relatively common (Appendix 3), and this community had the highest woody species count (67 spp.) of all sampled communities.

A number of woody plants were palatable, but many of them were inaccessible to antelope besides klipspringer. Just over one third of woody plant species were browsed (Fig. 2.12). Forb density was relatively low (Fig. 2.13).

2.3.1.3. Terminalia *woodland community (c. 3.2 km^2 in study site)*

Structurally similar to the *Burkea* community, *Terminalia* woodland was dominated by *Terminalia sericea*. The herbaceous layer was dominated by *Pogonarthria squarrosa* and *Heteropogon contortus* with *Hyperthelia dissoluta/ Andropogon gayanus* occurring at some sites. The density of palatable forbs was high compared with all communities except *Combretum* woodland (Fig. 2.13). The proportion of woody plant species that were apparently palatable was low (33%), but 50% of those species were browsed heavily (Fig. 2.12). The dominant species, *Terminalia sericea* was generally not browsed, but the relative frequency of palatable woody plant species was moderate (Appendix 3).

2.3.1.4. Pterocarpus *woodland community (c. 7.8 km^2 of study area)*

This community was generally situated close to rocky outcrops on deep sandy soils, and was dominated by *Pterocarpus rotundifolius* and *Dombeya rotundifolia*. A total of 46 woody plants were identified in the community (Appendix 3). Forb diversity and species richness were intermediate, with a large percentage of unpalatable forb species (Fig. 2.13). Mean

relative frequency of palatable woody plant species was higher than for any other community (Fig. 2.12), despite the relatively low proportion of palatable species in the community. However, fewer than 50% of palatable species were browsed heavily.

2.3.1.5. Vlei community (c. 7.4 km^2 of study area)

Vleis had characteristically low tree densities, and occurred on seasonally water-inundated, clayey soil. The thatching grasses, *Hyperthelia dissoluta, Hyparrhenia filipendula* and *Andropogon gayanus* dominated, and scattered individuals of 27 woody plant species occurred in this community (Appendix 3). About 40% of the woody species encountered in vleis were browsed, and the low relative frequency of palatable species was a reflection of the limited abundance of trees in this community (Fig. 2.12; Appendix 3). The proportion of palatable forb species did not exceed 67%, although density of palatable forbs (no. individuals per m^2) was frequently very high if one of the dominant species was palatable (Fig. 2.13).

2.3.1.6. Dwala community (c. 0.7 km^2 of study area)

The distinctive dwala community comprised a primarily granite substrate, interspersed with pockets of weathered rock in which woody plants (e.g. *Elephantorrhiza goetzii, Entandrophragma caudatum* and *Ficus* spp.), resurrection plant (*Myriathamnus flabellifolius*) and *Coleochloa* sp. grew. Lichens dominate bare rock, attaining coverage of up to 98% on south-facing slopes. Some mosses grew on gravel substrates, but few or no forbs occurred in this community. Browsing intensity (primarily klipspringer and hyraxes) was extremely variable among localities, and was dependent on the species complement. However, 47% of species encountered on dwalas were apparently palatable, and 81% of those were heavily browsed (Fig. 2.12). Again, as seen in the vlei community tree density was low.

2.3.1.7. Combretum *community (c. 1.1 km^2 of study area)*

The *Combretum* community was variable among sites, but was characterised by occurring on rocky or gravel substrates, and being dominated by *Combretum apiculatum* and *C. collinum* or *C. hereroense*, with *Faurea saligna, Elaeodendron (Cassine) matebelicum* and *Grewia monticola* being fairly abundantly represented. It typically has a very diverse herbaceous layer, and density of palatable forbs was high in all seasons (Fig. 2.13). Of the 55 woody plant species identified in the community, 31% were palatable, but only 53% of those were

heavily browsed (Fig. 2.12). However, some of the species browsed were relatively abundant in the community, resulting in a high relative frequency of palatable species (Appendix 3).

2.3.1.8. Miombo community (c. 1.0 km^2 of study area)

Only small pockets of miombo woodland occurred in the study area, growing on sodic soils in the Mtsheleli Valley in the West of the study area. The community was heavily dominated by *Julbernardia globiflora* and *Brachystegia boehmii*. Although 58 woody plant species have been identified, the majority was uncommon. Approximately one third of the woody species were palatable, although neither of the dominant species was browsed, even as seedlings (Fig. 2.12; Appendix 3). Furthermore, because of the relatively limited numbers of non-dominant species, the mean relative frequency of palatable species was low (Appendix 3). However, the majority (79%) of browsed species were heavily utilised by ungulates. The herbaceous layer, although sparse, was relatively speciose, with 23 and 30 recorded species of grasses and forbs, respectively, and a relatively high density of palatable forb species (Fig. 2.13).

2.3.1.9. Mixed woodland (Mtsheleli) community (c. 7.2 km^2 of study area)

Another mixed woodland/ thicket community, the Mtsheleli community tended to be dominated by *Terminalia sericea* and *Grewia monticola* although several other species were also abundant (e.g. *Lippia javanica*, *Burkea africana* and *Dichrostachys cinerea*). Forb species richness, diversity and heterogeneity were all high in this community; a reflection of a diverse herbaceous layer with no truly dominant species. However, the relative frequency of palatable species was low relative to most other communities (Fig. 2.13) as a result of few individuals of each species being present. Two-thirds of the palatable woody species were browsed heavily, and more than half of all species were browsed (Fig. 2.12). Additionally, the frequency of palatable species was moderately high (Appendix 3)

2.3.1.10. Boulder slope community (< 3.1 km^2 of study site)

This community was restricted to steep, boulder-dominated slopes. Most sites were inaccessible, so detailed sampling was not carried out. Common woody species included *Ficus* spp., *Commiphora* spp. and *Albizia* spp.

2.3.2. Antelope density and habitat preference in the MNP study site

Antelope densities varied, both between sessions (April and October assessments) within years and among years. Although data since 2002 were available, the time frame was too short to statistically assess trends in densities. However, where strong trends were evident, they are discussed. All species showed strong habitat preferences (Table 2.1), which were generally related to structural characteristics and corresponded with other authors' observations (Estes, 1991; Jarman, 1974; Kingdon, 1982a,b,c,1997; Simpson, 1974b; Smithers, 1983).

The most abundant and habitat tolerant species in the MNP study site was the common duiker, which attained densities in the region of 6 to 20 individuals.km^{-2} (mean density across years = 12.7 individuals.km^{-2}; Fig. 2.14) and constituted 19.4 ± 2.9 percent of the total resident antelope biomass. The common duiker population fluctuated among years (Fig. 2.14), but variability was not significantly correlated with rainfall or fire (Spearman's rank correlation; $p > 0.05$).

In the MNP study area, common duiker were found in all habitats but avoided dense woodland at the base of hills, steep rocky slopes, and dwalas (Table 2.1). Habitat selection appeared to coincide with vegetation structure, with preference shown for open- and medium-density woodland such as *Burkea africana*, *Terminalia* spp. and *Combretum* spp. woodland (Table 2.1). Such plant communities provide diverse forage and shelter for rest and rumination. Common duiker spatial distribution overlapped with all other resident antelope species, but a large proportion (68%) of plots along strip transects that contained duiker sign were exclusive to this species (Fig. 2.16).

Klipspringer, whilst not abundant on a study-site wide basis (mean 2.0 ± 0.4 individuals.km^{-2}; Fig. 2.14), reached high densities of approximately 13 pairs.km^{-2} in preferred habitat (data from known groups along walked routes in 2004 and 2005). This was lower than densities found in Ethiopia (Dunbar, 1979; Dunbar and Dunbar, 1974), but the herbaceous layer in the kopjes was less developed in MNP than in the Ethiopian Highlands which may account for this.

A negative trend in population estimates was detected for klipspringer in MNP between 2002 and 2008 (Fig. 2.14), and since spoor encounter rate along strip transects also declined in this

period (Fig. 2.15), this probably indicated a real decline in density. Reasons for the decline may have included emigration or death of individuals from sampled strip transects (and therefore shifts in latrine sites), or competition with other ungulates such as hyraxes.

In the MNP study area, klipspringer showed preference for medium- to dense- woodland along the sides and at the bases of hills, *viz.* kopje, slope side and *Pterocarpus* spp. communities, but they also descended into valley communities especially during the dry season or following burns (Table 2.1). Their spatial distribution strongly overlapped with common duiker and kudu, and to a lesser extent with bushbuck (Fig. 2.16). Spatial overlap with steenbok and reedbuck occurred in vleis. About 67% of strip transect plots containing klipspringer sign were exclusive to this species, but since prime klipspringer habitat was slightly undersampled, the exclusive use proportion was probably higher in reality.

Overall steenbok density in the MNP study site, based on dry-season dung-heap counts along strip transects, was generally low (3.5 ± 1.0 individuals.km^{-2}), but animals were locally abundant in preferred habitat (N. Lunt, unpubl. data). Highest densities occurred in open *Terminalia* spp. and *Combretum* spp. woodland and in medium-height grassland (Table 2.1), which were structurally similar to habitat types described in the literature (du Toit, 1993; du Toit and Yetman, 2005; Kingdon, 1982c). Very dense, hilly terrain was avoided (Table 2.1). Of all resident antelope species, steenbok had the smallest "exclusive" spatial distribution (35%) along long-term strip transects; their habitat choice coincided strongly with common duiker, reedbuck and kudu (Fig. 2.16). Estimated densities fluctuated annually, usually showing an opposite pattern to common duiker (Fig. 2.14). However, there was no significant correlation between steenbok density and recorded environmental factors (i.e. rainfall and fire) (Spearman's rank correlation, $p > 0.05$).

Bushbuck densities increased between 2002 and 2008; the only species to exhibit such a trend (Figs. 2.15). By 2008, bushbuck comprised more than 45% of the resident antelope biomass (from 10% in 2002). Since this species prefers dense woodland and thicket areas (Simpson, 1974b), bush encroachment which was evident in parts of the MNP study site during this period probably contributed to this increase.

Bushbuck showed strong preferences for medium- to dense vegetation types with diverse plant communities (e.g. *Burkea africana* and slope side communities; Table 2.1), but spoor

was not infrequently detected in more open areas (e.g. *Terminalia* spp. woodland) between dense habitats. Unsurprisingly, of the 41% of shared spatial habitat, the majority of overlap was with other thicket-selecting species such as common duiker and kudu (Fig. 2.16).

Kudu, being large and wide-ranging, did not achieve high densities in the MNP study area (Fig. 2.14), and averaged 2.2 ± 0.5 individuals.km^{-2} along strip transects, with fluctuations among years that mimicked the pattern exhibited by bushbuck. Late dry season (October) densities tended to be higher than those estimated in the late wet season (April), indicating some seasonal shifts in distribution. Kudu constituted 20 to 40% of the resident antelope biomass annually.

Preference was shown for medium density woodland communities (Table 2.1), although individuals were also sighted in vleis, especially in the dry season when forbs persisted in that community. The majority of the spatial overlap was with common duiker, but sign of this species was found in conjunction with all other resident antelope along strip transects (Fig. 2.16). Approximately 59% of plots containing kudu sign were exclusive to this species.

Reedbuck showed strong preference for open woodland with diverse herbaceous layers (e.g. *Combretum* spp. and *Burkea africana* communities) and grassland (Table 2.1), and sign was rarely detected far from drainage lines (pers. obs.). Densities and spoor encounter rates along strip transects declined sharply between 2002 and 2007 (Figs. 2.15, 2.16), dropping from about six individuals.km^{-2} to one individual per 4 km^2 in 2007 before rising again slightly in 2008. In the period between 2004 and 2008, several known individuals disappeared, so the apparent decline was probably a reflection of a real decline in the population. Reasons for the decline were not unequivocally determined during the study, but I suggest that it was due primarily to habitat change. From 2005, changes in the density and species complement of the herbaceous layer were noticed, following frequent fire, heavy grazing by domestic livestock and extensive thatching grass (*Hyparrhenia* spp. and *Andropogon gayanus*) harvesting in vlei areas (pers. obs.). Reedbuck are water dependent and early drying of vleis in dry years, combined with possible reduction in water retention properties in fire-prone, heavily grazed areas (Savadogo et al., 2007), may have encouraged dispersal of resident reedbuck or affected breeding and recruitment success. There was a significant negative correlation between reedbuck density and fire in the year preceding assessment (Spearman's rank correlation; $r = -0.859$, $p = 0.028$), which further suggests emigration or population

crashes. In addition, the reedbuck's sedentary habits and poor antipredator responses (Estes, 1991) make it vulnerable to poaching, especially if dogs are used.

Reedbuck were usually found closely associated with surface water in the study site, and were the only antelope that appeared to routinely utilise *Phragmites* reedbeds along river courses. Just under 50% of strip transect plots containing reedbuck sign were exclusive to this species, but a further 51% of plots were shared with common duiker, kudu, steenbok, or combinations thereof (Fig. 2.16). Faecal piles were frequently found in close proximity to steenbok latrine sites (pers. obs.).

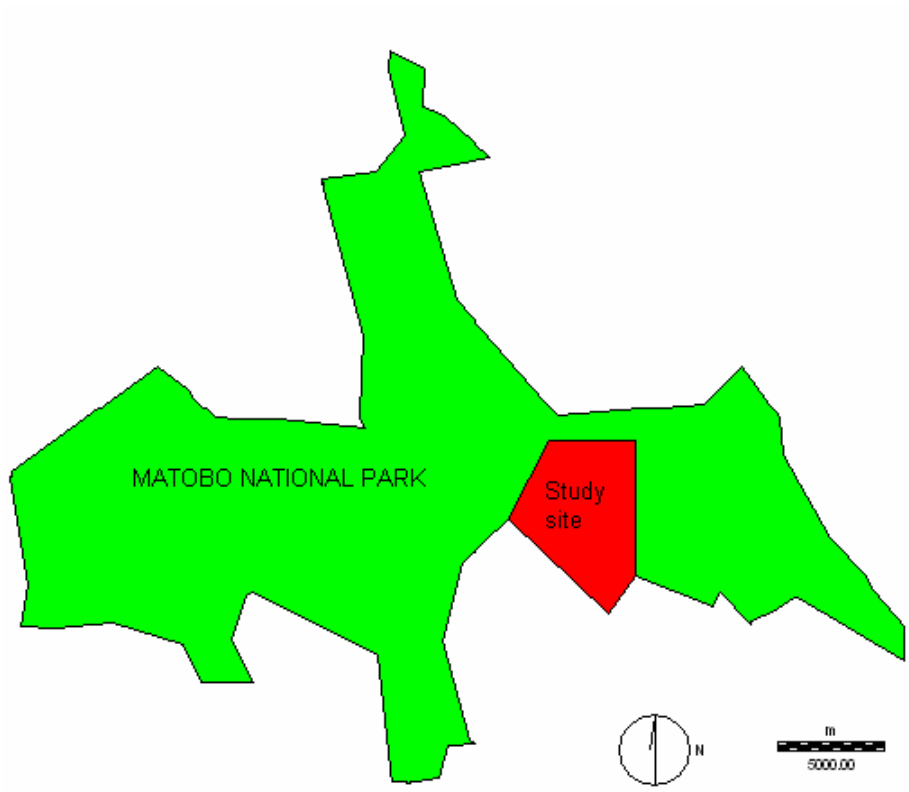
2.4. DEVELOPMENT OF THE STUDY

Results from this preliminary suite of investigations provided detailed background information about the study site, and led to the development of the specific hypotheses erected in Chapter 1. Identification of *Burkea africana* woodland as a habitat with a large diversity of palatable plants, and one utilised by most species of antelope enabled the selection of this community for exclusion plot experiments (Chapter 3). Vegetation assessments facilitated the selection of a range of palatable and unpalatable plants for shoot extension experiments (Chapter 3), while prior knowledge and familiarity with the study site were used to locate latrine sites for dung decomposition experiments (Chapter 4).

Table 2.1: Habitat preferences of resident antelope in the Matobo study site, as indicated by encounter rate (field signs/km of community sampled) and standardised selection indices (Kenney and Krebs, 2002). Indices > 0.1 (in boldface) indicate relative selection, < 0.1 indicate avoidance. Data from routes walked between April 2004 and May 2005.

Species		*Burkea*	Kopje	*Terminalia*	*Pterocarpus*	Vlei	Dwala	*Combretum*/ Miombo	Mixed woodland	Slope base	Bare ground
Steenbok	Encounter rate	0.15	0.02	0.30	0.09	0.21	0	0.38	0.14	0	0.07
	Selection index	**0.1093**	0.0158	**0.2181**	0.0637	**0.1516**	0	**0.2810**	**0.1056**	0	0.0549
Klipspringer	Encounter rate	0.11	0.41	0.18	0.41	0.21	0.27	0.19	0.18	0.93	0.04
	Selection index	0.0364	**0.1397**	0.0610	**0.1419**	0.0707	0.0928	0.0655	0.0606	**0.3183**	0.0128
Duiker	Encounter rate	1.27	0.65	1.42	0.85	1.11	0.27	1.40	1.03	0.72	1.08
	Selection index	**0.1299**	0.0667	**0.1452**	0.0863	**0.1128**	0.0276	**0.1429**	**0.1048**	0.0736	**0.1104**
Reedbuck	Encounter rate	0.51	0.03	0.39	0.11	0.34	0.27	0.83	0.28	0	0.19
	Selection index	**0.1738**	0.0110	**0.1315**	0.0361	**0.1151**	0.0923	**0.2824**	0.0942	0	0.0637
Bushbuck	Encounter rate	0.08	0.04	0.06	0.04	0.05	0	0	0.03	0.10	0
	Selection index	**0.2708**	**0.1049**	**0.1451**	0.0942	**0.1147**	0	0	0.0811	**0.2523**	0
Kudu	Encounter rate	0.49	0.26	0.50	0.38	0.27	0	0	0.33	0	0.15
	Selection index	**0.2045**	**0.1078**	**0.2112**	**0.1612**	**0.1139**	0	0	**0.1388**	0	0.0626

(a)



(b)

Figure 2.1: Location of (a) the Matobo National Park (MNP) and Dambari Field Station in Matabeleland South, Zimbabwe; and (b) the study site within the MNP boundary.

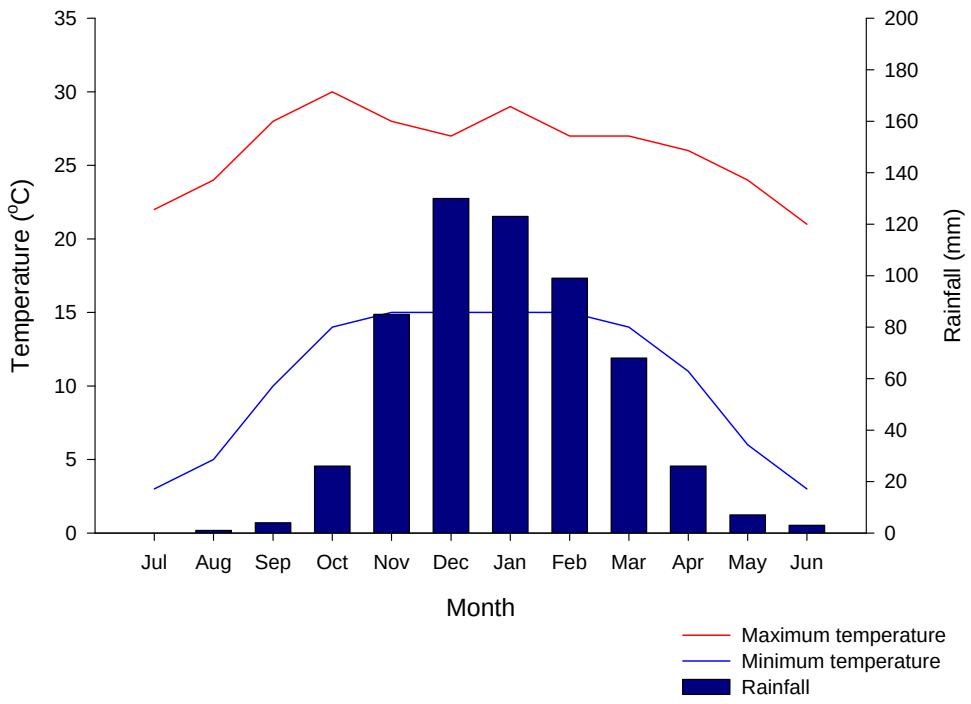


Figure 2.2: Mean monthly rainfall and temperature patterns for Matobo National Park (source: Zimbabwe Parks and Wildlife Management Authority).

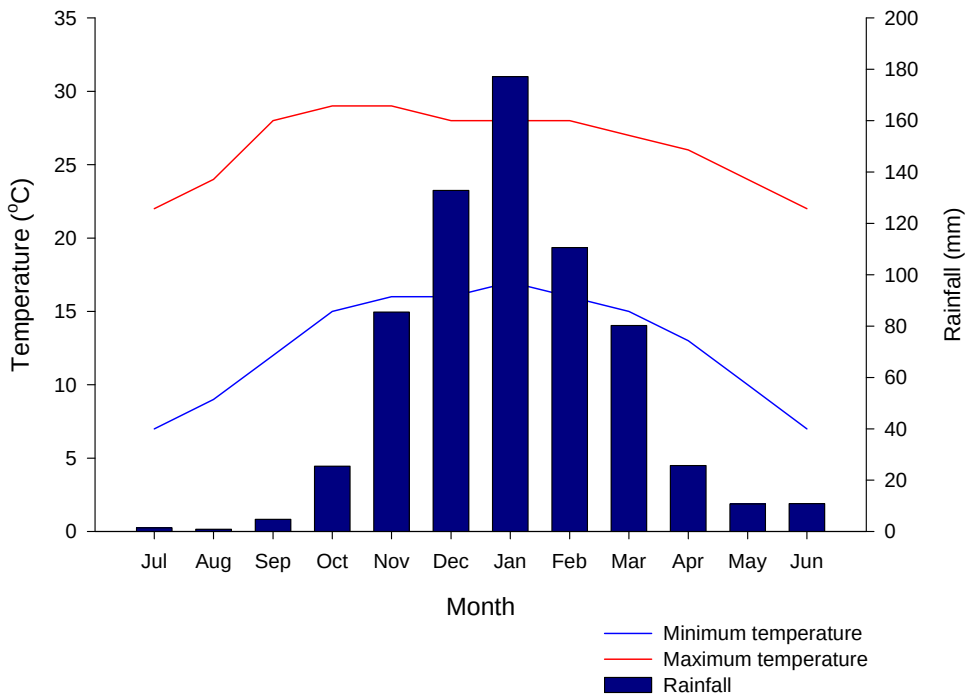


Figure 2.3: Mean monthly rainfall totals at Dambari Field Station between 1999 and 2009 (station records), and mean minimum and maximum temperatures for eastern Bulawayo (source: **www.weather.com**).

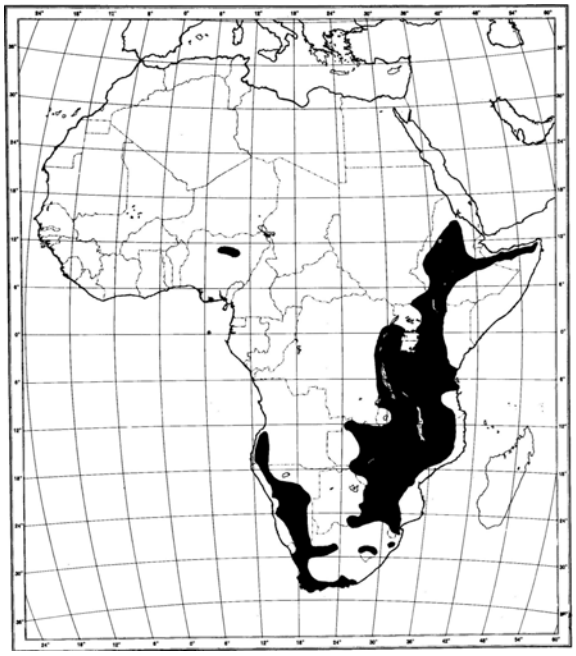


Figure 2.4: Distribution of klipspringer (*Oreotragus oreotragus*) in Africa (from Smithers, 1983).

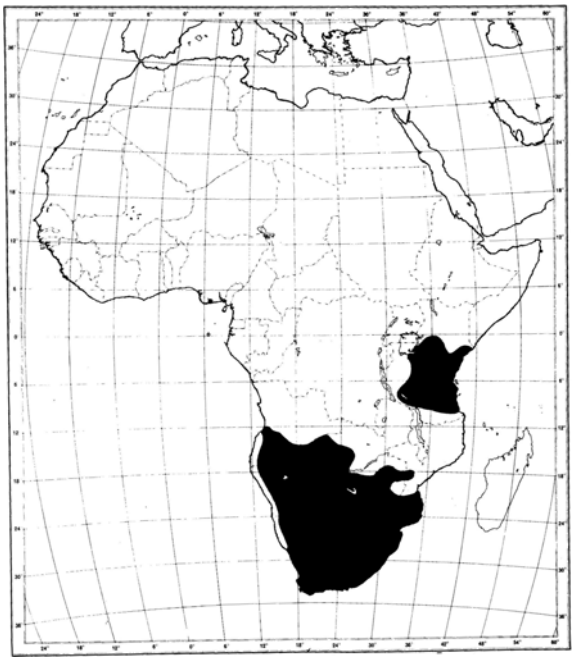


Figure 2.5: Distribution of steenbok (*Raphicerus campestris*) in Africa (from Smithers, 1983).

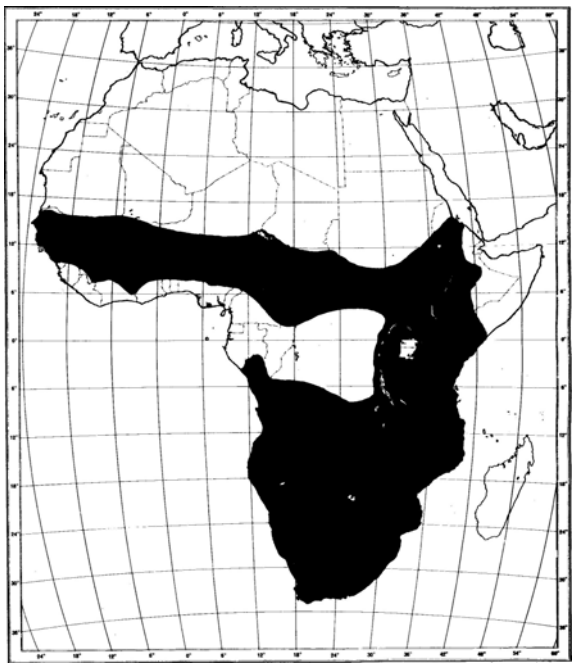


Figure 2.6: Distribution of common duiker (*Sylvicapra grimmia*) in Africa (from Smithers, 1983)

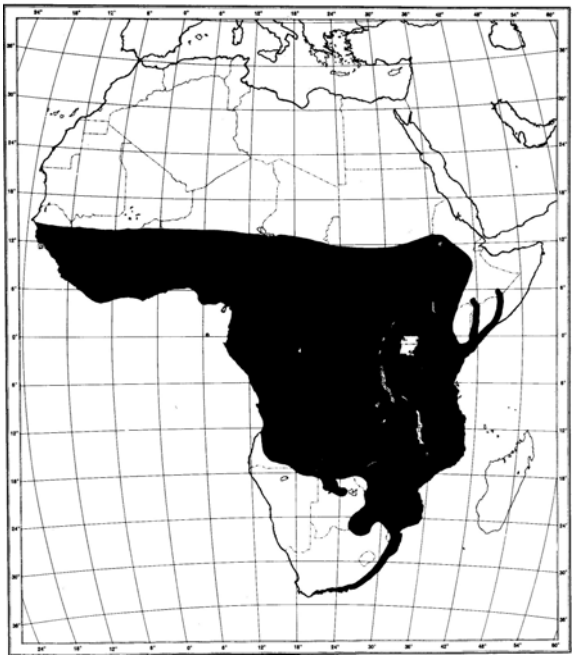


Figure 2.7: Distribution of bushbuck (*Tragelaphus scriptus*) in Africa (from Smithers, 1983)

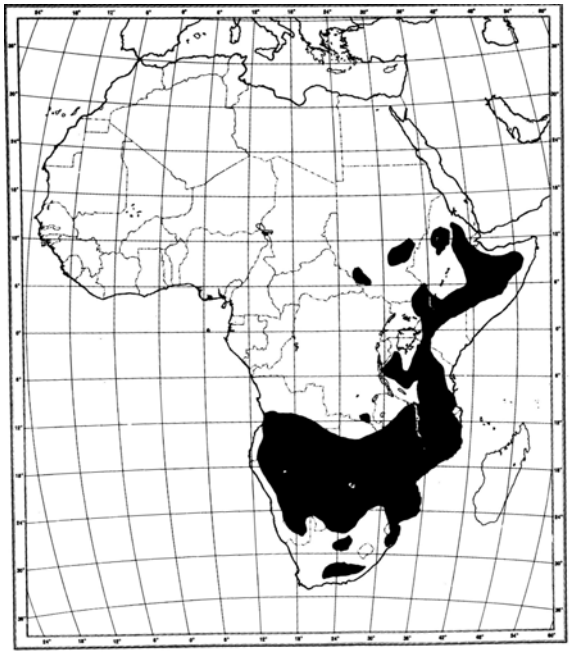


Figure 2.8: Distribution of greater kudu (*Tragelaphus strepsiceros*) in Africa (from Smithers, 1983)

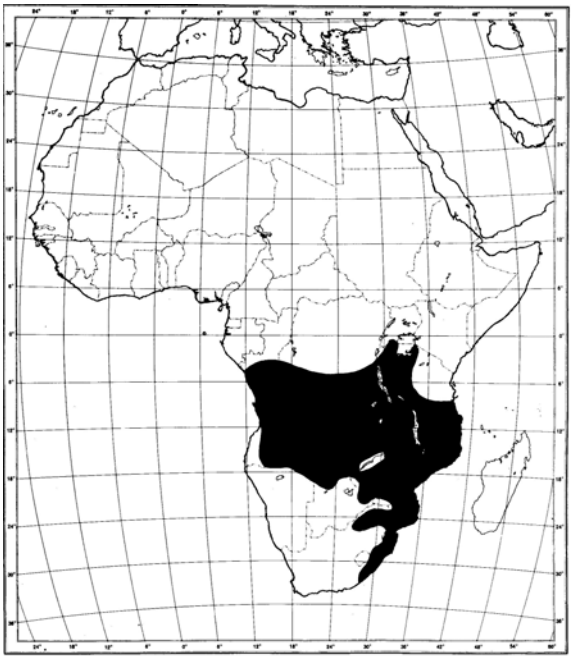


Figure 2.9: Distribution of common reedbuck (*Redunca arundinum*) in Africa (from Smithers, 1983)

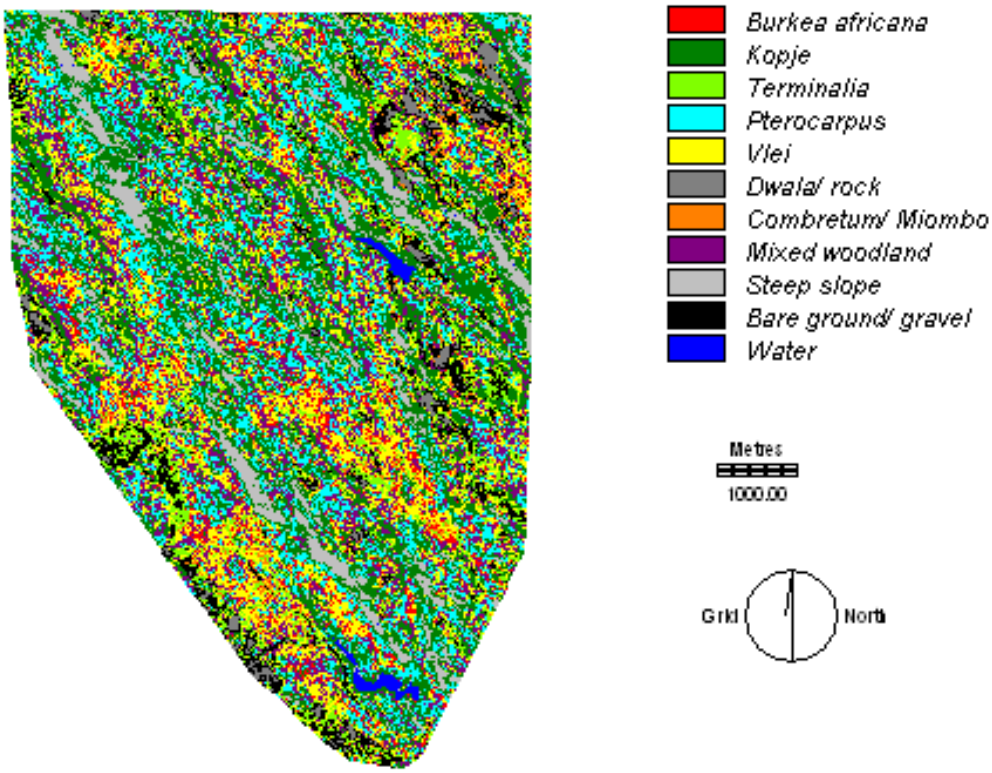


Figure 2.10: Vegetation map of the Togwe Wilderness Area study site. Miombo and *Combretum* woodland were combined in the map as it was not possible to separate them using LandSat images. Large water bodies are Toghwana Dam (in North) and Mtsheleli Dam (in South). Refer to Fig. 2.1(b) for location of the study site within the Matobo National Park.

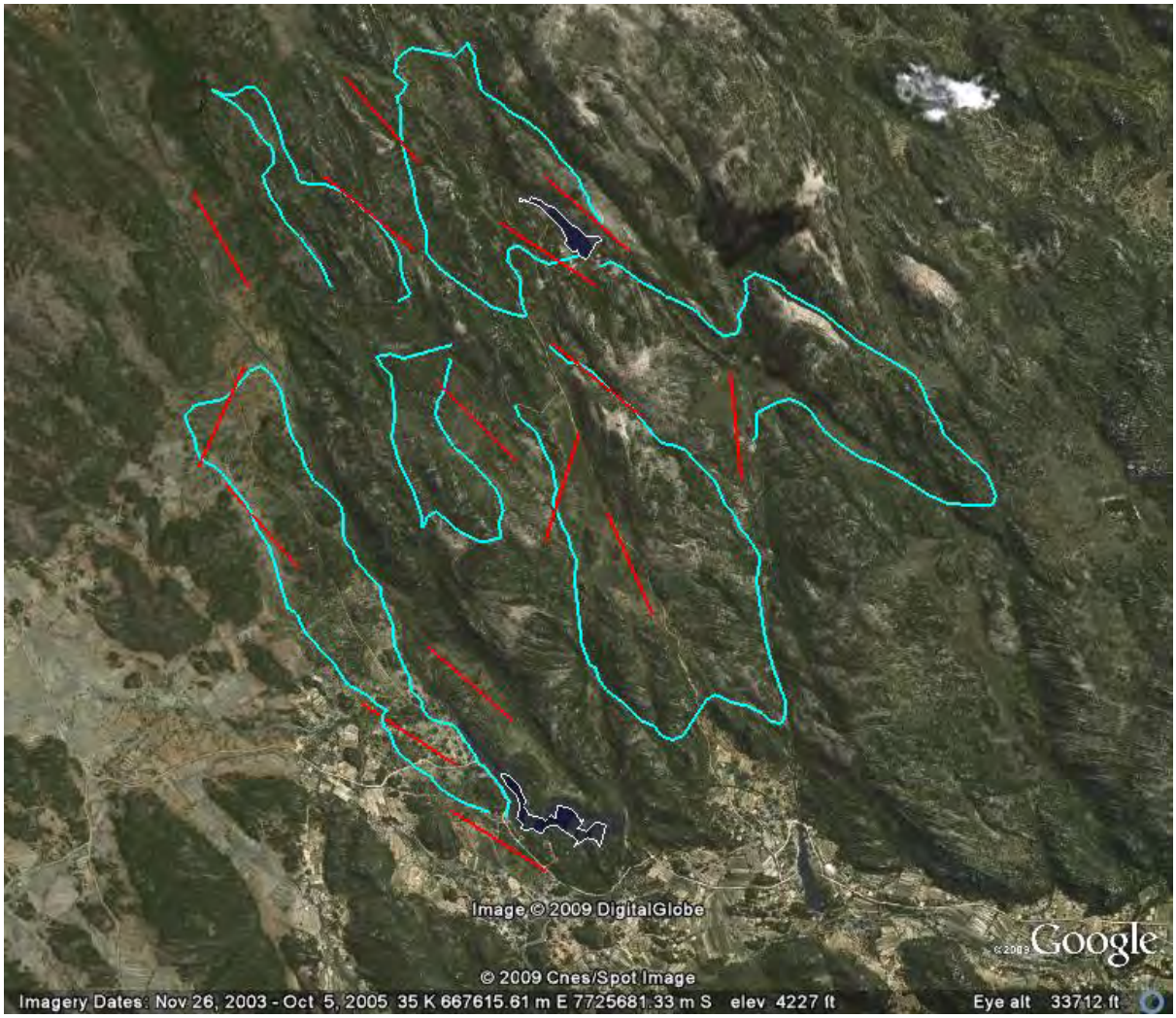


Figure 2.11: Distribution of antelope habitat assessment routes (light blue) walked monthly between April 2004 and May 2005, and 1 km long strip transects (red) assessed twice yearly between 2004 and 2008. Toghwana Dam (in North) and Mtsheleli Dam (in South) shown in dark blue with white borders.

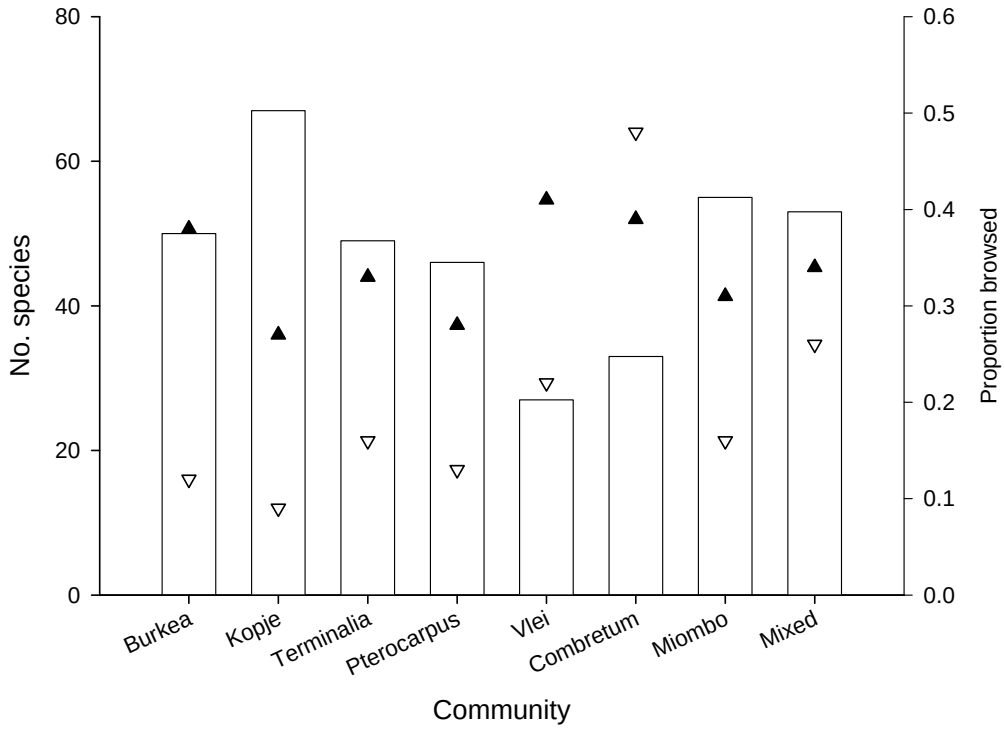


Figure 2.12: Number of woody plant species (bar) and proportion of species palatable (closed triangle) in each community. Proportion of heavily browsed species (more than 20% of assessed individuals browsed) denoted by open triangles.

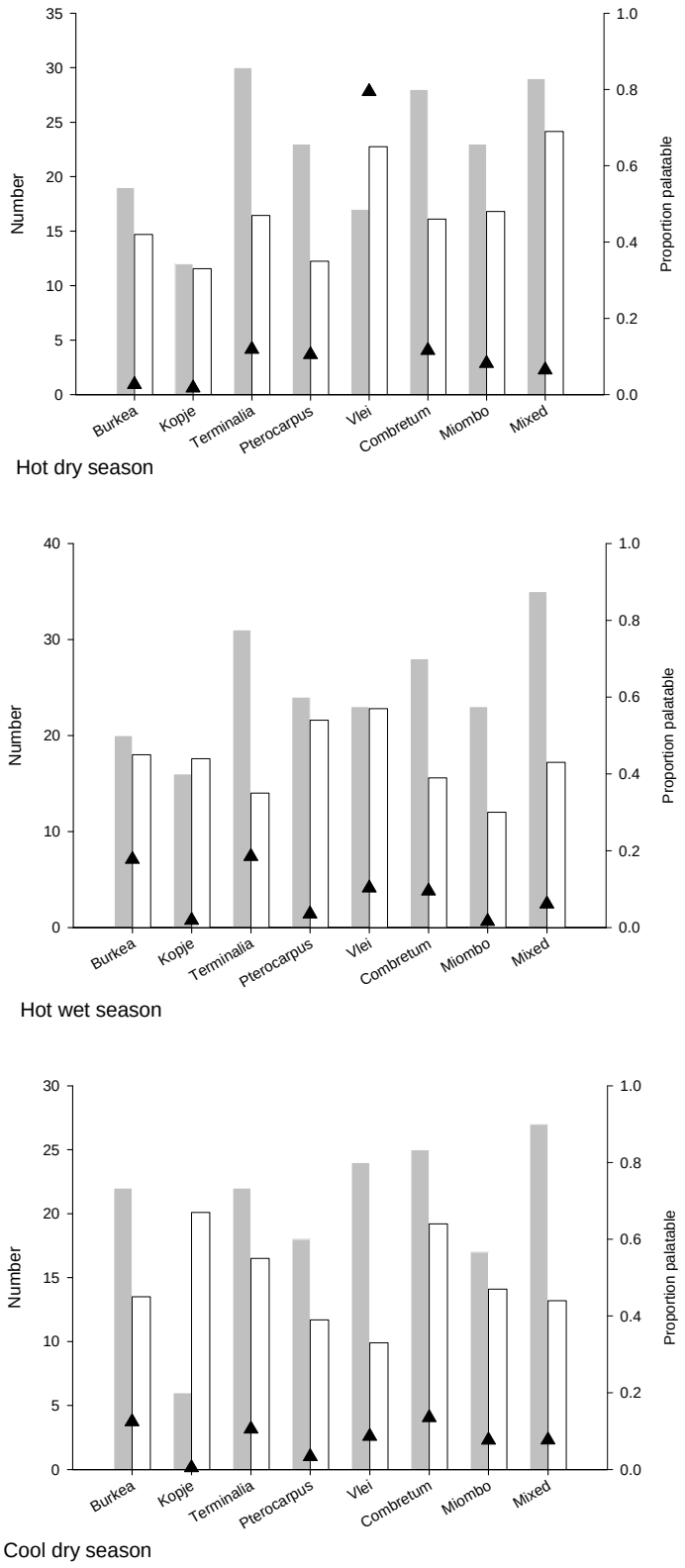


Figure 2.13: Mean seasonal variation in forb species richness (grey bar), proportion palatable (clear bar) and encounter rate of palatable forbs (black triangle) Encounter rate = individuals.m^{-2}.

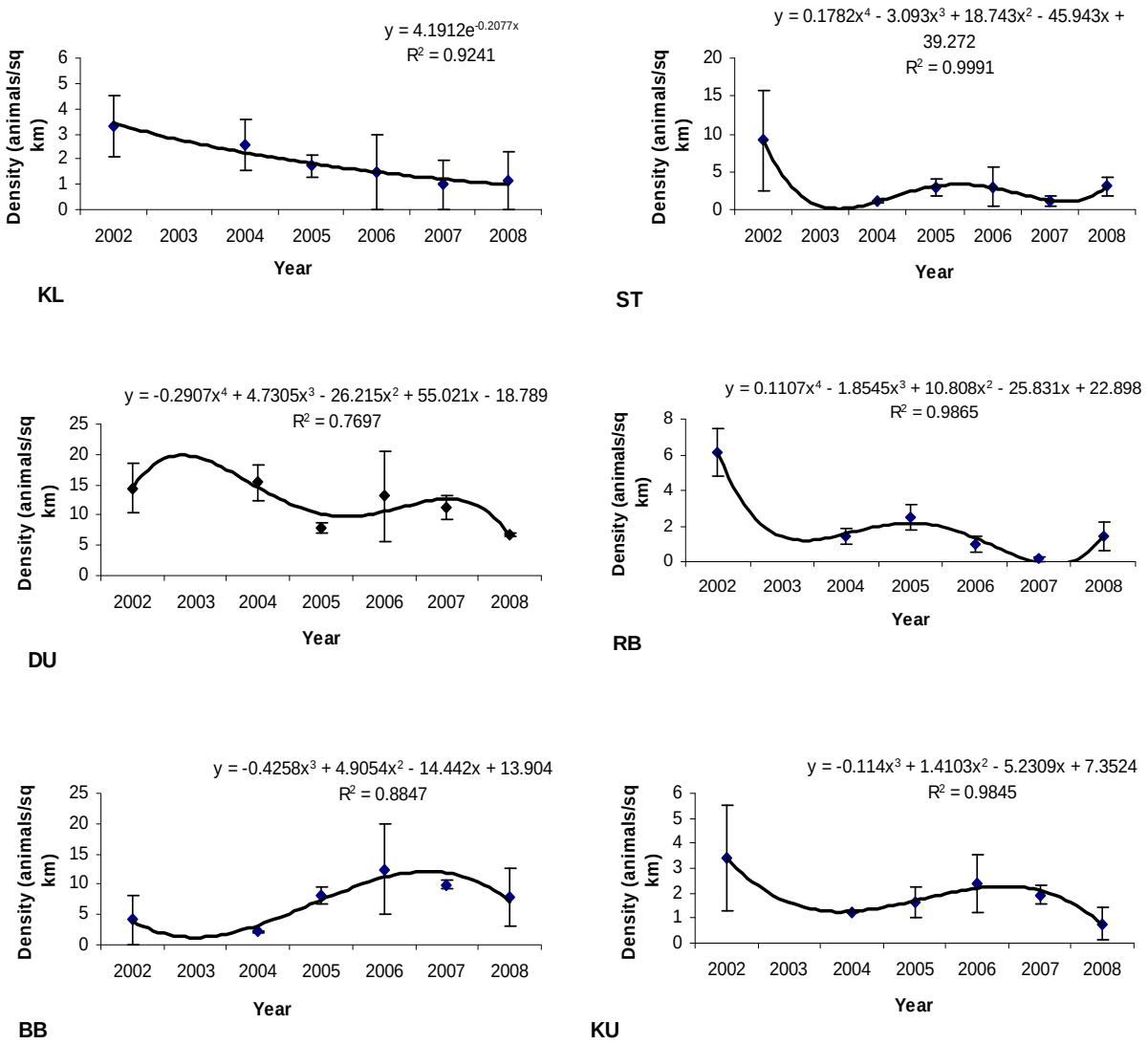


Figure 2.14: Trends in antelope density estimates (mean ± SE) in the Togwe Wilderness Area since 2002. Lines of best fit are included to describe trends as follows: fourth-order polynomial for common duiker, steenbok and reedbuck; third-order polynomial for kudu and bushbuck; exponential for klipspringer. Data from strip transects assessed in April and October each year, except 2003 when transects were not assessed. Species codes: DU = common duiker; ST = steenbok; KL = klipspringer; RB = reedbuck; KU = kudu; BB = bushbuck.

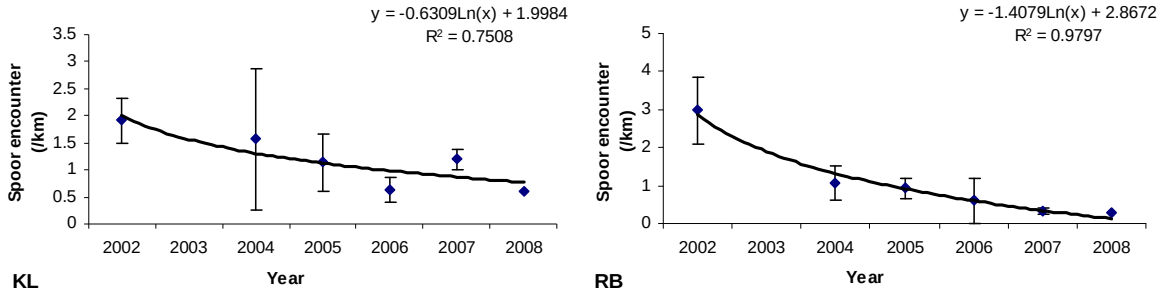


Figure 2.15: Spoor encounter rate (mean no. spoor per km ± SE) trends for two species (klipspringer: KL and reedbuck: RB), the numbers of which appeared to be in decline. Data from established strip transects assessed in April and October each year. No data were available for 2003. Logarithmic lines of best fit applied.

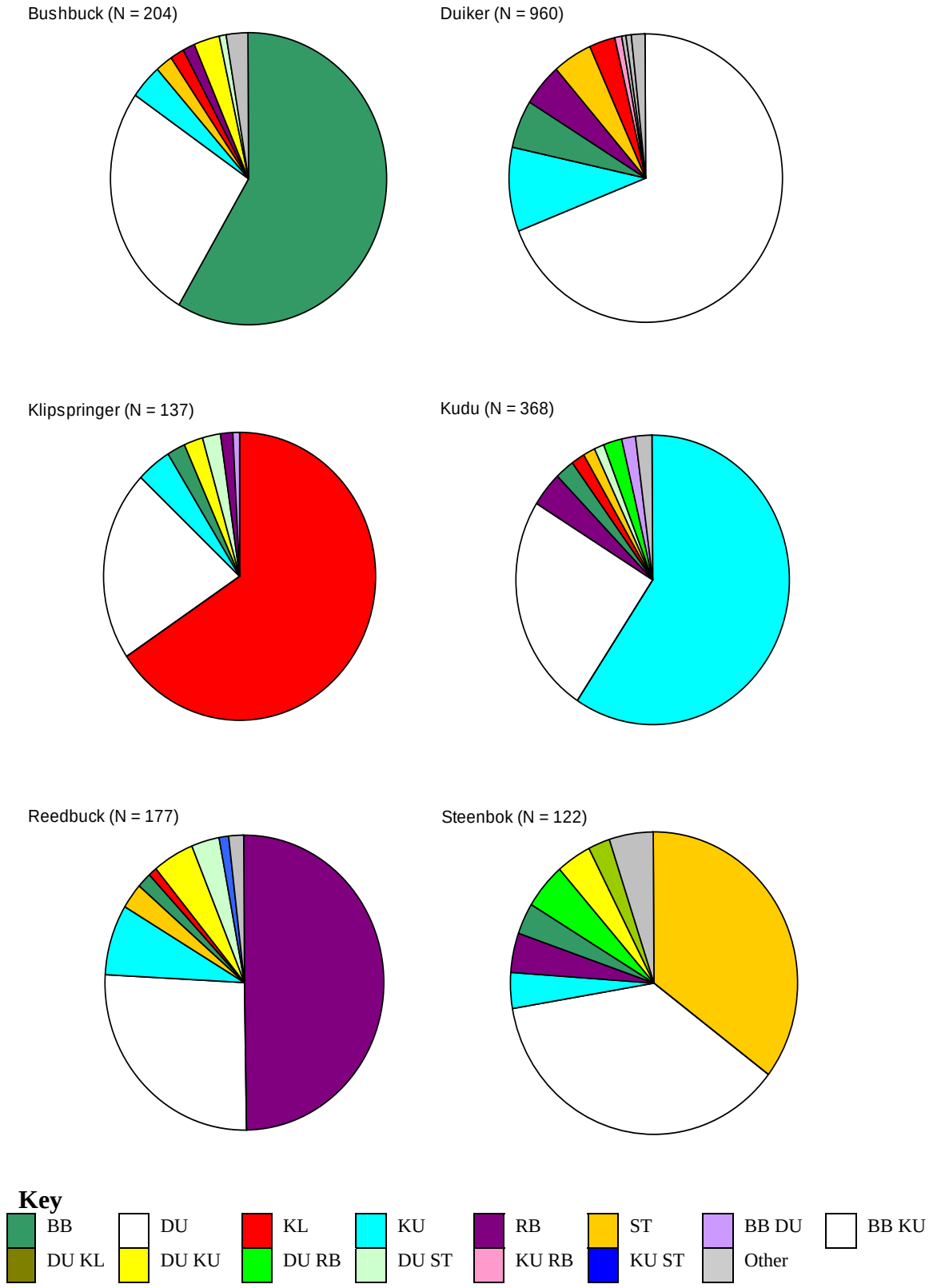


Figure 2.16: Proportion of 100 m^2 plots along strip transects containing sign of each species alone and in combination (overlap) with other species. Species codes: BB = bushbuck, DU = common duiker, KL = klipspringer, RB = reedbuck, ST = steenbok, KU = kudu. Combinations are in addition to base species. *N* refers to the number of plots containing sign of each species between 2004 and 2008.

3. EFFECTS OF ANTELOPE AND FIRE ON VEGETATION STRUCTURE

3.1. INTRODUCTION

Savannas are characterised by a well-developed continuous herbaceous layer that is intermingled with trees and shrubs (Skarpe, 1992). Whilst broad savanna structure varies with climate and soil type (Chapter 1, Sankaran *et al.*, 2005; Scholes, 1990), local conditions and disturbance regimes influence smaller-scale patterns and processes (Chidumayo, 2006; Cumming and Cumming, 2003; Govender *et al.*, 2006; Hulme, 1996; McNaughton *et al.*, 1988; Mills and Fey, 2005; Roques *et al.*, 2001; Sankaran *et al.*, 2005; Savadogo *et al.*, 2008; Sawadogo *et al.*, 2005; Scholes, 1990; Waldram *et al.*, 2008; Zida *et al.*, 2007) and maintain the spatiotemporal heterogeneity typical of this biome.

African savannas have been shaped by a long history of fire, herbivory and anthropogenic factors and changes in structure have been linked to shifts in wild herbivore abundance (McNaughton, 1992), changes in fire regimes (Ehrlich *et al.*, 1997; Eriksson *et al.*, 2003; Freckleton, 2004; Hudak *et al.*, 2004; King *et al.*, 1997; Savadogo *et al.*, 2008), pastoralism (du Toit and Cumming, 1999; Georgiadis *et al.*, 2007; Skarpe *et al.*, 2007) and climate change (Bobe and Behrensmeyer, 2004). Since savannas are heterogeneous, investigating the effects of any factor in isolation is virtually impossible under field conditions. Among-year variation in rainfall or fire, for example, can have a dramatic influence on seed germination and seedling recruitment, despite control of herbivore stocking rates (Danthu *et al.*, 2003; Gerhardt and Todd, 2009; Savadogo *et al.*, 2008). Despite the difficulties involved in teasing apart the effects of different factors on savanna structure, repeated patterns have resulted in scientists being able to draw broad conclusions about the role of disturbance on savanna dynamics.

Biotic influences on savanna dynamics are complex, with body size, feeding strategy and residence time being important considerations (Cumming and Cumming, 2003; Hulme, 1996; McNaughton *et al.*, 1988; Wassie *et al.*, 2009). Trampling and other mechanical pressures (e.g. twig breakage) are strongly linked to body size. Although pressure exerted is comparable across body sizes, larger ungulates have shorter relative stride lengths, larger foot size and generally cover larger distances than small ungulates and thus have a greater impact

over a wider area (Cumming and Cumming, 2003). As with any disturbance, moderate trampling can create gaps for seedling establishment and promote species and structural diversity (Bakker and Olff, 2003; Van Uytvanck *et al.*, 2008) whilst heavy trampling pressures can have detrimental effects on soil properties, especially in marginal environments (Boelhouwers and Scheepers, 2004; Savadogo *et al.*, 2007).

Herbivory has a range of effects on savanna vegetation at a variety of spatial and temporal scales, and these differences can be explained by the initial conditions, the type, timing, duration and intensity of herbivory, and interactions with other biotic and abiotic factors (e.g. climate, soil depth and fire). As a general rule, high grazer stocking rates, especially non-native species (livestock), in the absence of fire results in shrub encroachment (Roques *et al.*, 2001; Weber and Jeltsch, 2000). Exclusion of large browsers such as elephants (*Loxodonta africana*) may also result in an increase in woody cover as shrubs and trees are not removed (Jacobs and Naiman, 2008; Levick and Rogers, 2008), and woody plant architecture can be heavily influenced by browsing, depending on the size of browser and the plant parts selected (Archibald and Bond, 2003; Wilson and Kerley, 2003a,b). Herbivores are also important seed dispersers and seed predators (Barnes, 2001; Middleton and Mason, 1992; Miller, 1996; Milton and Dean, 2001; Slater and du Toit, 2002), and all animals contribute to nutrient cycling by depositing dung and urine which contain nutrients in forms that are more readily available to plants (de Mazancourt and Loreau, 2000b; Hobbs, 1996; McNaughton *et al.*, 1988).

Whilst herbivory at the individual plant scale may be apparently detrimental (Belsky, 1987), the long co-evolutionary history between large ungulates and savanna vegetation has resulted in plants developing resistance to defoliation through chemical defence (e.g. tannins), physical defence (e.g. spinescence, silica in leaves) and growth-form plasticity (e.g. tussock formation by grasses) (du Toit *et al.*, 1990; Freeland *et al.*, 1985; Hanley *et al.*, 2007; Ndhlala *et al.*, 2007; Sarmiento, 1992; Wilson and Kerley, 2003b). However, many anti-herbivore strategies are energetically expensive to maintain (de Mazancourt and Loreau, 2000b), and many plants adopt a strategy of tolerance: they are stimulated by low- to moderate defoliation which allows them to compensate for tissue removal or even supersede growth of undamaged parts (i.e. overcompensate) (Agrawal, 2000; du Toit *et al.*, 1990). Mammalian herbivore saliva stimulates leaf production in some species (Rooke, 2003). Adventitious and axillary budding are also strategies used to compensate for damage (Klimešová and Klimeš, 2007). It

has been suggested that by tolerating herbivory without negatively affecting herbivores, plants in local patches benefit because herbivores remain in the patch for longer, so dung and urine nutrients are retained locally (Augustine and McNaughton, 1998).

Fire usually has an attenuating effect on bush encroachment, by killing woody plant seedlings, even of species that are fire-tolerant when mature (Augustine and McNaughton, 2004; McNaughton *et al.*, 1988; Menaut *et al.*, 1990; Roques *et al.*, 2001; Sheuyange *et al.*, 2005; Skarpe, 1992; Zida *et al.*, 2007). Paradoxically, germination of seeds of some fire-adapted woody plant species is improved by heat-shock and smoke (Banda *et al.*, 2006; Danthu *et al.*, 2003; Dayamba *et al.*, 2008) which may ultimately favour shrub encroachment (Strang, 1973). In rangelands, fire can have a beneficial effect on productivity through accelerating mineralization of nutrients in moribund material (Aranibar *et al.*, 2003; Govender *et al.*, 2006; Savadogo *et al.*, 2009; Sheuyange *et al.*, 2005). However, fire can be exceptionally detrimental to soil properties and vegetation if the timing, intensity or frequency are not optimal (Kay *et al.*, 2008; Mills and Fey, 2004).

Historically, the factors influencing savanna vegetation dynamics have been investigated in areas with high herbivore biomass (usually grazers), and often at the landscape scale (Augustine and McNaughton, 2004; Jacobs and Naiman, 2008; McNaughton and Georgiadis, 1986; Skarpe, 1990,1992). The use of herbivore exclusion plots has allowed scientists to investigate the specific effects of herbivores on a range of vegetation characteristics (e.g. shrub/grass dynamics, seedling recruitment) in a number of systems (Focardi and Tinelli, 2005; Heske *et al.*, 1994; Jacobs and Naiman, 2008; Levick and Rogers, 2008; Smart *et al.*, 1985; Wassie *et al.*, 2009).

Since ungulate body size, through its influence on feeding selectivity, biomass removal and trampling, has been identified as an important driver of savanna dynamics (Augustine and McNaughton, 1998; Cumming and Cumming, 2003; Demment and van Soest, 1985), this study investigated the effects that herbivores of a range of sizes have on *Burkea africana* woodland at a local scale and over a short time period within the Matobo Hills. This was done through the use of a differentiated exclusion plot design. Unlike most other exclusion plot experiments (e.g. Jacobs and Naiman, 2008; Levick and Rogers, 2008; Smart *et al.*, 1985), herbivore biomass was low (Chapter 2), browser-dominated, and with the largest species being the greater kudu (*Tragelaphus strepsiceros*). During the experimental period,

an unplanned fire affected two sets of replicates, resulting in the inclusion of fire as an interactive factor in the study. Specific research questions were: (i) How do woody plants of different putative palatability respond to herbivory, ungulate exclusion and mechanical damage? (ii) Through which mechanisms are plant biomass, species richness and diversity affected by ungulates of different sizes? and (iii) How does fire interact with mammalian herbivores in structuring the *Burkea* community?

3.2. MATERIALS AND METHODS

3.2.1. Treatment design

In July 2006, four treatments were set up at each of three sites in *Burkea africana* woodland in a randomised complete block design (Fig. 3.1). Selection of this community was based on its utilisation by all resident antelope species (Chapter 2). Sites were selected based on five major criteria: (i) matched plant community, (ii) sites separated by a barrier (e.g. rocky outcrop) or distance of more than 2 km, (iii) similar altitude (1320 to 1360 m a.s.l.) and proximity (< 100 m) to rocky outcrops, (iv) relative inaccessibility to people and livestock to prevent tampering, and (v) evidence of the presence of antelope. None of the sites had been burnt within one year of the beginning of the experiment: Sites 1 and 2 had not been burnt since prior to March 2004, while Site 3 was burnt in February 2005. Apart from a brief period (less than one week in the wet season of 2007/08) when three cattle were allowed by National Parks rangers to graze at Site 1, livestock were not present at any of the exclusion sites, nor had any livestock had access to any of the sites for at least two years (pers. obs.).

Treatments consisted of 30 m by 30 m plots which were fenced from and to different heights to exclude different sized herbivores. Whilst the primary aim was to exclude antelope, the fence design impacted on other non-volant herbivores unable to fit through or climb over the mesh. Fence designs were:

1. Nil exclusion (E_0) – plot demarcated with wooden poles, but no fence erected. This design allowed free access to the plot by all animals, and is referred to in the text as an "accessible" treatment.
2. Large antelope exclusion (E_L) – plot fenced with 10 cm diamond mesh from 1 m to 2.1 m above ground level. This prevented access to larger antelope such as kudu, but smaller animals were unrestricted. Due to the high usage levels by small herbivores during the study, this design is termed a "relatively accessible" treatment.

3. Small antelope exclusion (E_S) – plot fenced with 10 cm diamond mesh from ground level to 1.5 m above the ground. This prevented access by small antelope (common duiker, klipspringer, steenbok) and other non-climbing terrestrial animals, while allowing access to large antelope such as kudu. No sign of antelope was found in this exclusion type during the study, so it is referred to as an "inaccessible" treatment.
4. Total exclusion (E_T) – plot fenced with 8 cm diamond mesh from ground level to 2.4 m above ground. This treatment excluded all herbivores that were unable to fit through the mesh or climb or fly over the top of the fence, and is thus termed "inaccessible".

Initially, all treatment plots had black metal corner posts and wooden droppers at 5 m intervals along each side. Where needed over the course of the study when fences or poles were damaged, additional droppers were erected at irregular intervals to support fencing material.

The original experimental plan was to monitor changes in vegetation over a single annual cycle from July/August 2006 to early September 2007. However, an accidental fire passed through Sites 1 and 2 (Fig. 3.1) in July 2007, which resulted in premature cessation of some experiments. Therefore, changes to the experimental setup were implemented to include the effects of fire (details below), and the study was continued until the beginning of the 2008/09 wet season. A further complication arose when fencing material was stolen from the E_L at Site 1 in April 2008. Since replacement materials were not available, the plot was abandoned, which reduced the replicates for that design. A timeline of experimental setup and assessments is given in Appendix 2.

3.2.2. Woody layer experiments

3.2.2.1. Woody plant shoot extension

In the dry season (July/August) of 2006, at the start of the exclosure experiment, ten woody plant species, including a range of species that exhibited different browsing pressure during pilot studies (Appendix 3), were selected for shoot extension trials (Table 3.1). All species were represented in at least two replicates of each plot type. Up to five individuals (depending on local abundance) of each species were randomly selected in each plot. On each individual, eight randomly-selected small, terminal, growing branches (for simplicity, termed "shoots" hereafter) within the adjudged browsing range of antelope (0 cm to 220 cm) were tagged with 3 cm by 2 cm plastic tags. A number of tagged shoots had small (<5 cm

length) subsidiary shoots branching from them at the beginning of the experiment. Species, individual and shoot number were recorded on each tag. Where plants were multi-stemmed, tags were affixed to shoots on the same stem. Random shoot selection resulted in some damaged/ browsed shoots being included in the sample. Basal circumference of the stem supporting tagged shoots was measured to the nearest 0.5 cm.

For each tagged shoot, the following measurements were made:

i. Height from the ground (to the nearest 0.5 cm).
ii. Shoot length "between pegs", from the internal shoot base to the tip of the shoot (to the nearest mm).
iii. Number of subsidiary shoots, categorised as secondary shoots or subordinate shoots.
iv. Signs of browsing were recorded, categorising browsing as "stem" or "leaf" removal. Shoot truncation that could not unequivocally be assigned to "browsing" was treated as mechanical damage.
v. Damage, through breakage (which may have included old browsing damage) or insect damage (e.g. Coreidae: Hemiptera damage to shoot tips) was recorded.

An interim assessment was carried out in the wet season (January/February) of 2007. Some loss of tags as a result of heavy winds and rain had occurred in the intervening months, reducing sample sizes (Table 3.1). For identifiable shoots, measurements were repeated and mortality was recorded.

It was intended that a final assessment would be done at the end of the dry season in August/ September 2007. However, the fire destroyed tags and caused extensive shoot mortality, so the experiment was discontinued.

Analysis and assumptions

Effect of browsing and mechanical damage on shoot growth

Shoots were categorised as browsed, damaged or intact. At experimental setup, it was impossible to predict which shoots would be browsed or damaged, and at the final assessment it was impossible to determine when the event occurred or what quantity (linear length) of shoot was removed. For this reason, it was assumed that within a species, mean tissue removal (both quantity and timing) from shoots was similar among individuals and that

recovery from tissue loss could be averaged across measured shoots of an individual; the base unit for analysis was therefore the individual plant. This assumption is intuitively supported, given the similarity of herbivores present among sites (i.e. comparable bite sizes), and the selective nature of browser feeding (i.e. similar plant parts and quantities from each individual removed). For each individual plant, the mean change in shoot length (hereafter termed "extension rate") in $mm.day^{-1}$ over the growing season was calculated for each category. Browsing and mechanical damage were treated separately as preliminary analyses indicated that these factors resulted in different plant effects.

Species that had suffered browsing or mechanical damage were later categorised as compensators, over-compensators or sensitive, as follows. If the mean shoot extension rate was statistically similar between damaged and intact shoots (i.e. growth rate was accelerated for damaged shoots to "make up" for the damage), the species was defined as a compensator. If mean shoot extension rate of damaged shoots exceeded that of intact shoots (i.e. growth rate was greatly accelerated, such that damaged shoots attained a greater length than intact shoots), the species was an over-compensator. When mean shoot extension rate was significantly shorter than intact shoots (i.e. growth rate did not accelerate sufficiently to replace lost tissues), plants were categorised as sensitive to damage.

Effect of browsing and damage on shoot bushiness

The difference in the number of subsidiary shoots (secondary and subsidiary shoots combined) per mm primary shoot was calculated for each primary shoot. To compensate for slight differences in the time lapse between first and second measurements, the difference was converted to a rate (change in number of side $shoots.mm^{-1}$ primary $stem.day^{-1}$). Mean rates of change were calculated for browsed and damaged shoots, and intact stems. Preliminary analyses indicated that browsing and mechanical damage resulted in different plant responses (data distributions had different shapes), so these effects were treated separately.

For each species individually, ANOVA assumptions of normality and variance homogeneity were tested using Kolmogorov-Smirnov and Levene's tests, respectively, with treatment and browse/ intact or damage/ intact as factors and $\alpha = 0.05$. Most data were right-tailed, and included both positive and negative values so cube-root transformations were applied to non-normal data. After transformation, data that met assumptions were analysed using general

linear model (GLM) ANOVAs with treatment (four levels) and damage (binary) or browse (binary) as factors, and $\alpha = 0.05$. Tukey's HSD tests were used to determine sources of variation in significant tests.

Due to small sample sizes of browsed shoots, only treatment (E_0, E_S, E_L and E_T) effects were investigated for *Burkea africana, Grewia monticola, Gymnosporia senegalensis, Lannea discolor, Terminalia brachystemma* and *Ziziphus mucronata*. Some species had few individuals with one or other category or unbalanced designs. In these cases, factors were tested separately.

Comparison of rate of shoot extension with height above ground

Height of shoots above ground level was divided into two classes (< 110 cm and > 110 cm), based on maximum browse height of the largest small antelope (the grey duiker, *Sylvicapra grimmia*) present in the study area (see Chapter 4).

Intact and mechanically damaged and/or browsed shoots of each species were treated separately in analyses. Mean shoot extension rate (either intact or browsed/ damaged) per individual plant in each height class was calculated as described above. For individuals that had shoots in both height classes, rates of extension were compared between height classes using paired *t*-tests at $\alpha = 0.05$.

Proportion of shoots in each height class damaged/ intact

The arcsine-transformed proportion of tagged shoots in each height class and status category (i.e. height classes < 110 cm and > 110 cm; shoot status intact or damaged/browsed) was calculated for each plant.

Considering intact and damaged/browsed shoots separately, the arcsine-transformed proportion of shoots in each height class were compared using 1-way ANOVA, with accessibility included as a covariate and $\alpha = 0.05$. E_0 was coded as accessible (2), E_L and E_S as intermediate (1) and E_T as inaccessible (0). Tukeys' HSD tests were used to determine sources of variation in significant tests.

3.2.2.2. Woody layer basal area

Pipe model theory states that the above-ground biomass of woody plants may be calculated from the basal cross-sectional stem area, if the specific gravity of the wood is known (Chiba, 1998). Wood specific gravity measurements were not available for the majority of the 61 species of woody plant in the exclosure plots, and destructive sampling would have been necessary to estimate it. Therefore, cross-sectional stem basal area was used as a proxy for biomass, and changes were used to determine the effects of exclusion on woody vegetation.

The basal circumference of all live woody stems was measured to the nearest 0.5 cm in August/September 2006, January 2008 and November 2008. Wet season measurements facilitated species identification, especially of congeners such as *Rhus* spp. that were difficult to differentiate when leafless.

Analysis

For each stem of each species, basal area was calculated assuming stems were circular. Rate of change was calculated by subtracting the initial measurements from subsequent measurements, and dividing by the number of days between measurements. The change in the number of stems was calculated similarly: dividing the difference between consecutive measurements by the number of intervening days. Since N = 1 or 2 for the unburnt and burnt sites respectively, descriptive statistics were used to illustrate the effects of exclusion plot type and fire on woody plant biomass.

Stem size distribution was heavily right-skewed, so median stem circumference of (a) all species combined, and (b) a selection of ten common species that were represented in more than three plot types, was compared among years in each plot using Mood's Median Tests. Overall trends (decrease, no change or increase) in median stem circumference was calculated for the burnt sites, unburnt site, and for all sites combined to determine whether species responded to fire, exclusion or their interaction.

3.2.3. Herbaceous layer experiments

3.2.3.1. Herbaceous layer and woody plant seedlings

The herbaceous layer was defined as the vegetation stratum that contained forbs, grasses and sedges and woody plant seedlings. The latter were defined as individual plants that were less than 50 cm in height. Resprouts (stems growing from an established plant's root system) and

stunted individuals (e.g. through damage to the primary axis meristem) that fell into this height class were excluded.

Assessments were done seasonally over the experimental period: in September 2006 (HD06), January 2007 (HW07), May 2007 (CD07), March 2008 (HW08) and July 2008 (CD08). Codes refer to the season, with HD = hot, dry, HW = hot, wet and CD = cool, dry. The planned 2007 HD assessment was precluded by the fire that affected Sites 1 and 2, and the CD08 assessment was delayed from May to July by political violence in the area.

3.2.3.2. Herbaceous plant biomass

At seasonal intervals, above-ground herbaceous vegetation was collected from four 0.125 m^2 quadrats in each plot. Samples were cleaned of any residual soil and root matter, and were dried to constant mass at 80 °C. The mean dry mass was calculated for each plot, and converted to above-ground biomass in tonnes/ha.

3.2.3.3. Quadrat and sample size determination

Optimal quadrat sizes for herbaceous layer assessments (species richness determination) and woody plant seedling density measurements were determined in the wet season when plant species richness was highest (N. Lunt unpubl. data), using nested quadrats, with a minimum size of 0.25 m^2 and a maximum of 16 m^2. Assuming a linear increase in effort with size, and setting a cost of 1 to the smallest quadrat size, the Weigert method (Kenney and Krebs, 2002) generated an optimal quadrat size of 4 m^2 for forbs and grasses and woody plant seedlings.

Sample size was calculated using the "continuous variables – means" module of Ecological Methodology (Kenney and Krebs, 2002). Number of species (i.e. species richness) of forbs and woody plant seedlings for the wet season was determined from nested quadrats until no new species were encountered, and a 95% confidence interval was calculated. Sample size was estimated at 5.0.

3.2.3.4. Herbaceous layer sampling

At seasonal intervals, the following measurements were taken from each of the five 4 m^2 quadrats in each plot:

A. Overall measurements

i. Percent aerial cover of the herbaceous layer, estimated (per quadrat) as the proportion of the ground covered by grasses, sedges and forbs.

ii. Percent moribund load – the estimated percentage of standing herbaceous moribund matter in each quadrat.

B. Grass measurements

i. Number and identity of species. Species were identified using van Oudtshoorn (2002).

ii. Percent aerial cover of each species individually, estimated as for A(i).

iii. Percent moribund load of each species, estimated as for A(ii).

iv. Height of three individuals of each species (if sufficient individuals were available), measured to the nearest cm using measuring sticks.

v. Evidence of grazing, determined by signs of tissue removal. Obvious insect damage (e.g. partial leaf removal, holey leaves or leaf mining) was recorded separately.

C. Forb measurements

i. Number of species. Due to the difficulties involved in identifying species, each putative species was assigned a code that was used for the duration of the study.

ii. Number of individuals of each species, or for very abundant species, percent aerial cover.

iii. Height (H), longest diameter (LD) and diameter perpendicular to longest diameter (PD) of five individuals of each species (if sufficient individuals were available). Measurements were made to the nearest 0.5 cm. These measurements were converted to canopy area (LDxPD) and plant volume (HxLDxPD).

iv. Evidence of browsing, recorded as for B(v).

D. Woody seedling measurements

i. Species were identified where possible, using van Wyk and van Wyk (1997).

ii. Measurements (H, LD and PD) were made of all seedlings, as described for forbs, from the wet season of 2008.

iii. Any evidence of browsing was recorded as for B(v).

Analysis

For each treatment at each site on each sampling occasion, species richness of forbs and grasses separately were calculated by pooling species across replicates. Using Ecological Methodology (Kenney and Krebs, 2002), Simpson's diversity index was calculated in each assessment session for each plot at each site, for each category of herbaceous plant individually. Woody seedling and forb calculations used counts of individuals, whilst percentage aerial cover was used for grass and sedge calculations.

For each plant group individually (i.e. forbs, woody plant seedlings, grasses and sedges), multiple regression analysis was used to determine the environmental factors (Table 3.2) influencing the species richness, diversity and abundance (encounter rate in individuals/ ha for forbs and seedlings, above-ground volume in m^3/ha for grasses). Prior to regression analysis, scatterplots were used to determine possible linear relationships, and regression model assumptions were tested using Levene's test (homoscedasticity) and Kolmogorov-Smirnov (normality), with $\alpha = 0.05$. Grass volume (m^3/ha) was $\log_{10}$ transformed, and herbaceous biomass was Box-Cox transformed to improve linearity. Stepwise regression (forwards and backwards), with $\alpha = 0.1$ for inclusion or exclusion was used to determine significant predictors. Model adequacy was tested with lack-of-fit (data subsetting) and variance inflation factor (VIF) tests. No VIF values exceeded 4.

3.2.4. Soil seed bank

Five soil cores were collected from each exclusion plot in the wet seasons of 2007/08 and 2008/09. Cores were 5 cm in diameter, and 10 cm in depth. Samples were sieved through a 1.5 mm mesh, and seeds were collected, divided into growth form (grass/ sedge or dicotyledon) and, where possible, identified. Seed viability was determined by germination trials, in which seeds were placed on blotting paper, kept moist and monitored for signs of germination.

Analysis

Seed yield (seeds/ 1000 cm^3 soil) were compared (i) within years among plot and burn treatments and (ii) among years among plot and burn treatments with permutational GLM ANOVA using DISTLM (Anderson, 2004). For the latter test, time since experimental setup (in weeks) was included as a covariate.

3.2.5. Soil type

Five soil cores (5 cm diameter by 10 cm depth) were collected from each plot and mixed. A subsample of 240 ml soil was shaken with water and allowed to settle out. Proportions of coarse and fine sand, silt, clay and organic material were calculated for each sample, with class boundaries determined by eye. Proportions were arcsine transformed and compared across sites and treatments using two-way ANOVA. Ratios of soil components were calculated and included as predictors in regression analysis (Table 3.2); only clay+silt: sand (clay/silt: sand) and sand: clay ratios were extracted as useful predictors.

3.3. RESULTS

3.3.1. Woody plants

3.3.1.1. Shoot extension

Responses of shoots to browsing

Apparent palatability, which is inferred from the proportion of browsed shoots, differed among species (Table 3.1). No tagged *Burkea africana* or *Lannea discolor* shoots showed evidence of browsing, and fewer than three individuals of *Gymnosporia senegalensis*, *Terminalia brachystemma* and *Ziziphus mucronata* exhibited browsed shoots. However, it is possible that more *Z. mucronata* shoots – which had shoot apices with diameters less than 2 mm – were browsed, but the conservative approach to determining type of damage (see Methods) resulted in some truncated shoots being coded as "mechanical damage".

Growth responses to browsing varied among the remaining five species (Table 3.3; Fig. 3.2). *Flacourtia indica*, *Gymnosporia senegalensis* and *P. maprouneifolia* compensated for tissue removal, as evidenced by the insignificant difference in shoot extension rates between browsed and intact shoots (Table 3.3). *Gardenia resiniflua* was sensitive to browsing (Table 3.3), and *Lippia javanica* overcompensated for browsing damage, with browsed shoots attaining greater extension rates than intact shoots (Table 3.3; Fig. 3.2). Exclusion plot type was only important for *Lannea discolor* and *Gymnosporia senegalensis*, with shoot extension rate lower in more accessible (E_0 and E_L) plots (Table 3.3).

Subsidiary shoot density (change in subsidiary shoots/ mm primary shoot) was negatively affected by browsing in the two most heavily browsed species – *Flacourtia indica* and *Gardenia resiniflua* (Table 3.4) and leaf density was significantly lower on browsed *F. indica* shoots (Mood's median test; χ^2 = 23.73, d.f. = 1, p <0.001). None of the other species

showed significant changes in leaf density (Mood's median tests; $p > 0.05$) or subsidiary shoot density (Table 3.4) with browsing and/or herbivore accessibility. Fruit production by *Lippia javanica* was not significantly negatively affected by browsing (one-tailed *T*-test; $t = 0.28$, $p = 0.390$). The effects of browsing on fruit production of other species were not measured, due to ephemeral fruiting seasons that were not necessarily incorporated into assessment sessions.

Effects of mechanical damage and treatment on shoot growth

With the exception of *F. indica, L. discolor* and *P. maprouneifolia,* which apparently compensated for damage, mechanical damage significantly reduced shoot extension rate (Table 3.5; Fig. 3.3). Exclusion plot type did not have a significant effect for most species; however, significance was again linked to accessibility, with relatively accessible plots having lower extension rates (Table 3.5).

Subsidiary shoot density was negatively affected by damage in *L. discolor*, while in general, undamaged shoots of *G. resiniflua* in relatively inaccessible plots had higher subsidiary shoot densities (Table 3.6). Leaf density was significantly lower on damaged shoots for six species *viz. G. resiniflua, G. monticola, L. discolor, L. javanica, P. maprouneifolia* and *Z. mucronata* (one-tailed *t*-tests, $p < 0.05$).

Effect of height and damage on shoot growth

Small sample sizes and unbalanced designs precluded statistical tests being applied to browsing effects on shoot extension rate in the two height classes (<110 cm and >110 cm). However, patterns of growth varied substantially among species (Fig. 3.4).

Considering intact shoots only, paired *t*-tests indicated significantly faster growth in shoots higher than 110 cm from the ground for three of the four typically single-stemmed "tree" species, *B. africana, L. discolor* and *P. maprouneifolia* (Table 3.7), but increased shoot density in the upper height class was only recorded for *P. maprouneifolia* (Table 3.7). The multi-stemmed "shrub" species (remainder of species except *T. brachystemma*) exhibited insignificant differences in growth and shoot density with height.

Height class did not significantly affect shoot extension rate in the species with damaged shoots (Table 3.7), but subsidiary shoot density was greater in the upper height class for *F.*

indica (Table 3.7). The overall proportion of shoots that were damaged in the lower height class was significantly higher than expected (based on available shoots in each category) for *G. resiniflua* and *G. monticola* (Chi-square tests; *G. resiniflua*: $\chi^2 = 14.40$, $p < 0.001$; *G. monticola*: $\chi^2 = 4.09$, $p = 0.043$). No other species exhibited damage out of proportion to the relative abundance of shoot height distribution.

3.3.1.2. Woody plant cover and growth

Effects of fire and exclusion on stem circumference, stem density, basal area and species richness of woody species

Over the two years of the exclusion experiment, pooled median stem circumference decreased significantly in all plot types (Mood's median test, $p < 0.001$ for all tests). However, trends differed between the burnt and unburnt sites. At the burnt sites, circumferences decreased significantly, whilst circumference in the unburnt E_0 and E_S plots changed insignificantly, decreased in the E_L and increased in the E_T. Changes in circumference were the result of stem mortality and stem recruitment (seedlings and resprouts). The overall trend was complicated by differential responses to exclusion and fire by individual woody plant species (Tables 3.8, 3.9, 3.10), and in general, the effects of fire overwhelmed the recovery in the following year (Table 3.12).

In the first assessment (2006), which was carried out prior to the fires, all plots except the E_S and E_T at Site 3 ("unburnt"; Fig. 3.5.3, 3.5.4) exhibited a bimodal stem-size distribution with peaks in the 4 to 5 cm classes and the greater than 15 cm class (Fig. 3.5.1 – 3.5.4). Although still bimodal as a result of the pooling of stems larger than 15 cm, the stem size distribution in the unburnt E_S and E_T approached an inverse-J shape, with high recruitment in the 2 to 4 cm size class (Fig. 3.5.3, 3.5.4). Over the first year of the experiment, there was a decline in total basal area in all plots at the burnt sites (Fig. 3.6a) due to high mortality rates of stems smaller than approximately 14 cm (Fig. 3.5.1 – 3.5.4). However, high recruitment rates in burnt plots resulted in an increase in the number of stems during the same period (Fig. 3.5.1 – 3.5.4; 3.6d). Slight increases (E_0, E_T and E_S) and a decrease (E_L) in stem number at the unburnt site (Fig. 3.6d) were evident, with net increases in basal area in the inaccessible plots and declines in basal area in the accessible plots (Fig. 3.6a).

Between 2007 and 2008, all burnt plots except the E_T showed an increase in basal area (Fig. 3.6b) and stem recruitment continued in all plots (Fig. 3.6e). At the unburnt site, positive

changes in stem basal area occurred in the E_0 and E_S, but losses were recorded in the E_L and E_T (Fig. 3.6b). Stem recruitment was positive in all plots (Fig. 3.6e).

Overall, the effects of exclusion were clear at the unburnt site, with increases in stem basal area in the inaccessible plots and declines in the accessible plots, although the change was small at the E_0 (Fig 3.6c). Stem number declined in the E_0, E_S and E_T and increased in the E_L. By contrast, at the burnt site, all exclusion plots, except the E_0, recorded a reduction in stem basal area while the E_0 showed a slight increase (Fig. 3.6c), and all burnt plots exhibited stem recruitment, with the greatest increases evident in the E_S and E_T (Fig. 3.6f).

Species richness changed slightly over the period of the experiment, with increases in the number of species at the burnt sites, loss of species in the accessible plots, and an increase in species in the inaccessible unburnt plots (Fig. 3.7). Of the species that were either gained or lost over the experimental period (Table 3.8), four species were apparently sensitive to fire and/ or the absence of medium and large fauna. Several species were stimulated by fire, and six palatable species appeared in inaccessible plots over the experimental period. Since most of these six species were relatively uncommon in the study site, I was unable to test the hypothesis of fire/ herbivore exclusion affecting the establishment of putatively palatable species.

3.3.1.3. Effect of fire and exclusion on selected species

The effects of exclusion and fire on ten species represented in all plot types was investigated through a combination of stem density, changes in median stem circumference, and changes in the total stem basal area in each plot type. Changes in stem density (i.e. the number of stems per plot) were due to recruitment and mortality. Recruitment was illustrated by an increase in the number or proportion of smaller stems (< 5 cm circumference), whilst a reduction in the number of stems in given size classes indicated either mortality or growth. Growth was indicated by an increase in the number of stems in larger size classes among years (e.g. burnt site, Fig. 3.22), whilst mortality was indicated by stem loss in given size classes among years (e.g. burnt site, Fig. 3.18).

Mortality could be a result of fire (usually small and medium sized stems), self-thinning (intra-stem competition among medium-sized stems) or senescence (large stems). Thus, interpretation of the cause of mortality was plot (burnt/ unburnt) and stem-size dependent.

Increases in stem density did not necessarily translate into increased basal area if mortality in the medium- to large-stem ranges (> 7 cm) was counteracted by heavy recruitment of smaller stems. For example, *Flacourtia indica* in the burnt E_L exhibited a significant reduction in stem circumference and increase in stem density (Table 3.12), loss of many stems > 7 cm circumference and recruitment of smaller stems (Fig. 3.13) and an overall reduction in stem basal area (Fig. 3.48).

Burkea africana

Exclusion alone had no significant effect on median stem size between consecutive years (i.e. 2006 to 2007 and 2007 to 2008) (Tables 3.10, 3.11), but there were higher stem recruitment rates in exclusion plots (E_L, E_S and E_T) compared with E_0 over the experimental period (Table 3.12; Fig. 3.8-3.11). Loss of basal area in all but the E_T indicated density-dependent mortality of intermediate stems (Fig. 3.48). Substantial recruitment (illustrated by increased stem density) and growth ensured an increase in basal area in the E_T (Table 3.12; Fig. 3.48).

At the burnt sites, fire and exclusion interacted. In general, fire caused mortality, especially of stems smaller than 15 cm circumference (burnt sites, Fig. 3.8-3.11), but this was partially masked by resprouting in the following (2007/08) wet season. In the burnt E_0, high mortality of small and medium-sized stems following the burn (Table 3.11) and limited recruitment between 2006 and 2007 (Table 3.10; Fig. 3.8) resulted in an insignificant increase in median stem circumference and a 25% reduction in stem density over the experimental period (Table 3.12). Loss of intermediate sized stems in the fire (burnt plots, Fig. 3.9 – 3.11) resulted in net losses in stem basal area in the burnt E_L, E_S and E_T (Fig. 3.48), despite recruitment of new stems between 2007 and 2008 (Table 3.11). This was associated with an insignificant reduction in median stem circumference (Table 3.12).

In summary, fire destroyed small and intermediate-sized stems of *B. africana* but encouraged recruitment in subsequent years. High recruitment in all unburnt plots compensated for mortality in the mid-size ranges, and resulted in an overall reduction in median stem circumference.

Flacourtia indica

The number of stems remained relatively constant in all plots at the unburnt site over the two-year experimental period (Table 3.12; Fig. 3.12-3.15), except for the E_S, where the 90%

increase in the number of stems between 2007 and 2008 (= recruitment) resulted in a significant reduction in median stem circumference (Table 3.12; Fig. 3.14). Substantial growth of established stems was evident in the inaccessible plots (Fig. 3.15, 3.16) which offset the effects of high recruitment in the second year and resulted in an overall increase in basal area (Fig. 3.48). In the accessible plots (E_0 and E_L), mortality in the intermediate size ranges was only partially compensated for by recruitment (unburnt plots; Fig. 3.12, 3.13), resulting in an overall reduction in stem basal area over the study (Fig. 3.48).

Fire caused high mortality of stems with circumferences <6 cm (Fig. 3.12-3.15), but post-fire recruitment was high, especially in the inaccessible (E_S and E_T) plots (Table 3.11), which resulted in stem density more than doubling in the E_0, E_S and E_T over the study period (Table 3.12). As a result of high recruitment, median stem circumference was significantly lower in 2008 than prior to the fire (Table 3.12). As a result of the variability in stem mortality and recruitment, no clear trends in stem basal area with plot type occurred at the burnt sites (Fig. 3.48).

In summary, *F. indica* exhibited a clear exclusion effect; in the absence of the larger antelope fauna (bushbuck and larger), basal area increased, but at a slow rate (< 1 cm^2/day) (Fig. 3.48). Fire masked the exclusion effect, primarily due to recruitment, mortality and growth of established stems varying among plot types (Fig. 3.48).

Gardenia resiniflua

High recruitment was measured during the study in the E_L, E_S and E_T (Table 3.12; Fig. 3.17-3.20). This was coupled with growth of established stems (Fig. 3.17-3.20) and resulted in an increase in total basal area in these plots. However, high recruitment only significantly reduced median stem circumference in the E_L (Table 3.12). In contrast, high mortality of intermediate and large stems in the E_0 in the first year (Table 3.10; unburnt site Fig. 3.16) resulted in both an overall reduction in stem density (Table 3.12) and a loss of total basal area (Fig. 3.48).

At the burnt site, by the first assessment after the fire, the number of stems had at least doubled in the E_0, E_S and E_T (Table 3.10). Median stem circumference decreased significantly in the E_0 and E_T between 2006 and 2007, due to recruitment (E_0: Fig. 3.16) or a combination of high recruitment and mortality of intermediate sized stems (E_T: Fig. 3.19). Some self-thinning was evident in the E_L (Fig. 3.17), as illustrated by the loss of some stems

in the mid-size ranges in 2007 (Fig. 3.17), but there was no significant change in median stem circumference (Table 3.10). Between 2007 and 2008, there was a reduction in stem density in all burnt plots (Table 3.11) and evidence of self-thinning and loss of small stems in all but the E_L (Fig. 3.16-3.20). The net effect over the study period was an increase in basal area in the accessible plots despite a reduction in median stem circumference (E_0 and E_L: Table 3.12; Fig. 3.48), and a slight decline in basal area in the E_S and E_T resulting from loss of larger stems early in the study (Table 3.12; Fig. 3.48).

In summary, exclusion favoured initial recruitment (Table 3.12) and resulted in an increase in basal area (Fig. 3.48). However, *Gardenia resiniflua* showed sensitivity to fire in that basal area loss through fire and density-dependent mortality was not compensated for in the burnt inaccessible plots (i.e. E_S and E_T: Fig. 3.48).

Grewia monticola

At the unburnt site, mortality among small- and intermediate-sized stems was observed in the E_0, E_L and E_S in all years (Table 3.10-3.12; Fig. 3.20-3.22), resulting in insignificant changes in median stem circumference (Table 3.12) but declines in stem density over the study period. Recruitment between 2007 and 2008 in the E_T resulted in an increase in stem density (Table 3.12; Fig. 3.23), but this did not entirely compensate for initial stem loss so there was an overall loss of basal area (Fig. 3.48). There was no clear trend in basal area with exclusion (Fig. 3.48). Only the E_L registered a nett gain in basal area, as a result of growth of stems between 2006 and 2007 (Table 3.10; Fig. 3.21) and mortality primarily affecting small stems (< 5cm circumference) (Fig. 3.21).

Fire caused mortality of intermediate and larger stems, especially in the more accessible E_0 and E_L (Fig. 3.20, 3.22), which suggests that *G. monticola* was sensitive to fire in the presence of additional disturbance. This mortality resulted in declines in median stem circumference (Table 3.10), at a significant level in the E_L. Less marked mortality was evident in the E_S and E_T (Table 3.10; Fig. 3.22, 3.23). Recruitment following fire was evident in the E_0 and E_S (Fig. 3.20, 3.21) and to a lesser extent in the E_T (Fig. 3.23). In the accessible plots (E_0 and E_L), the combination of mortality of larger stems and subsequent recruitment resulted in significant reductions in median stem circumference (Table 3.12). However, the initial loss of stems caused a reduction in basal area in the E_0 and E_T (Fig. 3.48).

To summarise, although exclusion level had no consistent effect on stem basal area (Fig. 3.48), additional disturbance in the form of fire and fauna presence resulted in greater loss of basal area in the E_0 (Fig. 3.48) due to recruitment being slower than stem loss (Table 3.12).

Gymnosporia senegalensis

Recruitment of new stems was evident in the unburnt E_0 throughout the study period (Fig. 3.24), resulting in increased stem density (Table 3.12) and a significant reduction in median circumference (Table 3.12). Coupled with the growth of established stems, an overall increase in total basal area was evident (Fig. 3.48). In the other three unburnt plot types, mortality in the intermediate size ranges (Fig. 3.25-3.27) was compensated for by recruitment, but resulted in a reduction in basal area over the study (Fig. 3.48). The E_T exhibited a recruiting pattern of stem size distribution, with the bulk of stems being 4 cm or less in circumference (Fig. 3.27).

At the burnt sites, fire-associated mortality occurred across the small- and intermediate (< 15 cm) size ranges in all plots. However, subsequent recruiting patterns were evident in the E_0 (Fig. 3.24), E_S (Fig. 3.26) and E_T (Fig. 3.27) in 2007 and in the E_L in 2008 (Fig. 3.25). Continual mortality in the intermediate size ranges, although partially compensated for by recruitment (Fig. 3.24-3.27), resulted in minor changes in stem density over the study period (Table 3.12) and a loss of total basal area (Fig. 3.48). Median stem circumference declined in all burnt plots (Table 3.12), but the change was only statistically significant in the E_0 and the E_T.

In summary, it was apparent that *Gymnosporia senegalensis* was stimulated by low levels of disturbance (either presence of antelope and other larger fauna, or fire), but was sensitive to the combined effects of fire and faunal disturbance (Fig. 3.48). In the absence of large animals such as antelope, recruiting patterns of growth were exhibited (Fig. 3.26, 3.27), but competition among intermediate-sized stems reduced the basal coverage of this species.

Lannea discolor

At the unburnt site, recruitment counteracted mortality of medium and large stems in the E_0 and E_L in 2007 (Fig. 3.28, 3.29), while the inaccessible plots had relatively high recruitment rates and low mortality (Table 3.10; Fig. 3.30, 3.31). Between 2007 and 2008, all plots

recorded an increase in the number of stems, but the greatest increases were in the inaccessible plots and there was a significant decrease in median stem circumference in the E_T due to seedling recruitment (Table 3.11). Despite high recruitment, initial low numbers of stems and/or mortality in the intermediate size ranges resulted in declines in basal area in all but E_S (Fig. 3.49), with the greatest losses occurring in the accessible plots (E_0 and E_L: Fig. 3.49).

At the burnt sites, mortality of intermediate stems was evident, especially in the accessible plots in 2007 (Fig. 3.28, 3.29). However, in the E_S, high recruitment in following the fire (Table 3.10; Fig. 3.30) and subsequent growth of those stems (with little mortality) between 2007 and 2008 resulted in both a significant increase in median stem circumference (Table 3.11) and an overall increase in basal area over the study (Fig. 3.49). Between 2007 and 2008, the E_0 and E_T had a nett increase in stems (Table 3.11) due primarily to recruitment (Fig. 3.28, 3.31). As seen at the unburnt site, basal area declined in the E_0, E_S and E_T (Fig. 3.49); however, the magnitude of change in the E_T was probably because stem number was low (<10) even after recruitment (Fig. 3.31).

In summary, *Lannea discolor* did not show clear trends in basal area changes with exclusion or fire (Fig. 3.49), but sample-size effects probably influenced the apparent magnitude of response (e.g. burnt E_T; Fig. 3.31). However, recruitment of new stems was recorded in all plot types at both sites, with the most substantial recruitment occurring in inaccessible plots (burnt E_S and unburnt E_T: Table 3.12).

Pseudolachnostylis maprouneifolia

High mortality of small stems in the E_0 and E_T at the unburnt site between 2006 and 2007 resulted in significant increases in median stem circumference in these plots and declines in stem density (Table 3.10, Fig. 3.32, 3.35). In the E_L and E_S, recruitment of new stems and growth of larger stems balanced out the effects of mortality in the medium size range (Fig. 3.33, 3.34), resulting in insignificant changes to median stem circumference and only small changes in stem density (Table 3.10). Between 2007 and 2008, continual self-thinning (loss of intermediate size stems) in the E_S and E_T, and recruitment in the E_T resulted in significant reductions in median stem circumference (Table 3.12; Fig. 3.34, 3.35). In the accessible plots, initial small-stem mortality in the E_0 (Table 3.10), followed by continual self-thinning and recruitment (Fig. 3.32) led to an insignificant increase in median stem circumference in

this plot (Table 3.12). Despite fluctuations in stem size distribution among years (Fig. 3.32-3.35), little change in basal area was recorded relative to the burnt plots (Fig. 3.49).

Mortality of small and intermediate size stems was evident at the burnt sites (Fig. 3.32-3.35), but this was compensated for by high recruitment in the exclusion plots over the following two wet seasons (Fig. 3.34, 3.35). The result in the E_S and E_T was nett decreases in stem circumference in the (Table 3.12) and little overall change in stem basal area (Fig. 3.49). By contrast, continual mortality in the small to intermediate size ranges in the E_0 and E_L was not compensated for by recruitment (Table 3.12; Fig. 3.32, 3.33), resulting in dramatic reductions in stem basal area in accessible plots (Fig. 3.49).

In summary, *Pseudolachnostylis maprouneifolia* did not appear to be affected by the presence or absence of antelope and other large mammals. Stem mortality (self-thinning) was compensated for by recruitment of new stems and growth of existing larger stems, resulting in little change to total basal area (Fig. 3.49). However, accessibility to fauna following fire prevented recovery of stem basal area: intermediate-sized stems continued to be lost, especially in the E_0 (Fig. 3.32) and basal area declined substantially in both the E_0 and E_L over the experimental period (Fig. 3.49).

Pterocarpus rotundifolius

At the unburnt site, stem density declined in the E_L, E_S and E_T but was unchanged in the E_0 over the experimental period (Table 3.12). Declines were caused by mortality in the small- to intermediate size ranges (Fig. 3.37-3.39), with no detectable recruitment occurring. Growth of established stems in the E_T resulted in an increase in median stem circumference (Table 3.12), but only a small change to basal area was recorded (Fig. 3.49). Basal area at the E_L and E_S declined slightly (Fig. 3.49) due to initial stem mortality, while growth of established stems at the E_0 resulted in an increase in basal area (Fig. 3.49).

Fire stimulated recruitment in all plot types (Fig. 3.36-3.39), especially in the short term (Table 3.10). Self-thinning (loss of intermediate-sized stems) in the E_0, E_S and E_T was evident between 2007 and 2008, but growth of larger stems and continual recruitment resulted in increases in basal stem area in all burnt plots (Fig. 3.49).

In summary, fire stimulated recruitment and growth of *P. rotundifolius*, with the greatest increase in basal area occurring in accessible plots (E_0 and E_L: Fig. 3.49). Mortality of small and intermediate sized stems in the E_S (Fig. 3.38) and E_T (Fig. 3.39) was more obvious than in the E_L (Fig. 3.37) and E_T (Fig. 3.36) in both burnt and unburnt plots, indicating that high levels of disturbance favour the expansion of this species.

Terminalia spp.

At the unburnt site, relatively few *Terminalia* stems were encountered in accessible plots (E_0: Fig. 3.41, E_L: 3.42), and initial losses of medium-sized stems between 2006 and 2007 (Table 3.10) was only partially compensated for in the E_L by 2008 (Table 3.12; Fig. 3.41). Growth of larger stems compensated for loss of intermediate sized stems, resulting in virtually unchanged basal area in the accessible plots (Fig. 3.49). Despite evidence of self-thinning (loss of intermediate sized stems) in the inaccessible E_S (Fig. 3.42) and E_T (Fig. 3.43), growth of larger stems ensured an increase in basal area (Fig. 3.49).

Fire had a detrimental effect on basal area in the E_0, E_S and E_T (Fig. 3.49), due in part to loss of small- to intermediate sized stems between 2006 and 2007 (Fig. 3.40, 3.42, 3.43). High recruitment was measured in these three plots, which reduced the median stem circumference over the study period (Table 3.12). In addition, several larger trees of *Terminalia* spp. in E_S at Site One senesced and died during the study, which explains the greater loss in basal area and stem density in the burnt E_S (Table 3.12; Fig. 3.49). No significant change in stem circumference was measured in the burnt E_L (Table 3.12), and the combination of stem growth and recruitment (Fig. 3.41) ensured an increase in basal area in this plot type (Fig. 3.49).

In summary, *Terminalia* spp. showed sensitivity to fire, with self-thinning (mid size range) exceeding gains from recruitment (Fig. 3.40-3.43). In the absence of fire, faunal exclusion promoted stem growth but had little effect on stem density (E_S and E_T: Table 3.12).

Ziziphus mucronata

The number of *Z. mucronata* stems in all plot types was low ($N < 20$), which may have influenced the observation of slight changes in basal area (1 to 2 cm^2/day; Fig. 3.49) and insignificant changes in median stem circumference (Table 3.12) over the experimental period. Recruitment was only apparent in the burnt plots, most especially in the burnt E_S and

E_T (Table 3.12). Mortality of mid- and large-sized stems was recorded in most plots (Fig. 3.44-3.47), and this loss accounted for basal area reductions in the burnt E_L (Fig. 3.45) and the burnt and unburnt E_T (Fig. 3.47). Growth of some established stems (unburnt E_0: Fig. 3.44; unburnt E_S: Fig. 3.46) and high recruitment (burnt E_S: Fig. 3.46) resulted in an increase in basal area (Fig. 3.49).

In summary, there was no clear exclusion or fire effect on *Z. mucronata* development. Observed patterns may have been exaggerated by sample size effects.

3.3.1.4. Woody plant seedlings

Seedling density was not significantly correlated with any of the predictor variables described in Table 3.2 (Stepwise regression: no factors selected or removed when α for inclusion/removal = 0.15). The E_0 and E_L typically had higher densities of seedlings than the E_T (Fig. 3.50) but this was significant only in the HW07 (Permutation ANOVA: $F_{1,58} = 0.871$, $p = 0.015$) and CD08 (Permutation ANOVA with "burn" included as a covariate: $F_{1,52} = 5.854$, $p = 0.011$) and no other consistent trends were noticeable (Fig. 3.50). Since seedling densities were generally low and very variable among quadrats, statistical investigation of exclusion and fire effects were not possible at the species level. However, trends were evident for 15 species, and seemed to be loosely linked with seed size (Table 3.9). Of the eight large-seeded species, five were stimulated by fire or a combination of fire and exclusion. Two species, both with large, soft seeds, were apparently sensitive to fire and the eighth species increased in exclusion plots. Five of seven small-seeded species were sensitive to fire and/or fauna presence, and only two species were apparently stimulated by fire and/or fauna presence (Table 3.9).

3.3.2. Herbaceous layer

The majority of variation in measured herbaceous layer variables was related to seasonal changes, with fire also playing a role in species richness and diversity.

3.3.2.1. Trends in variables within seasons

The percent aerial cover of the herbaceous layer was marginally higher in the wet season than in the dry season (Table 3.13), especially in the 2008 wet season following higher rainfall. No plot effects or plot-burn interaction effects were significant in any season (Kruskal-Wallis; $p > 0.06$ for all tests). Although the inaccessible plots generally had higher above-

ground biomass (except for the E_T at the unburnt site in the dry season of 2008), exclusion type and burning had no statistically significant effect in any season (Kruskal-Wallis; $p > 0.06$ for all tests), and biomass was similar among plots initially (HD06; Table 3.14).

The moribund load was initially lower in the E_S and higher in the E_T than in other plot types (Kruskal-Wallis: HD06: H = 17.27, d.f. = 3, $p = 0.001$; HW07: H = 11.34, d.f. = 3, $p = 0.008$), but this plot effect had disappeared by the CD07 (Kruskal-Wallis: H = 1.84, d.f. = 3, $p = 0.582$; Table 3.15). Following the fire, burnt plots had significantly lower moribund loads (Kruskal-Wallis; HW08: H = 34.35, d.f. = 7, $p < 0.001$; CD08: H = 29.37, d.f. = 7, $p < 0.001$).

The number of grass and sedge species was comparable among plots and differed only slightly among seasons (Table 3.16) until the CD08, when fewer species were found in the unburnt E_L and E_T compared with all other treatment types (Kruskal-Wallis; H = 19.52, d.f. = 7, $p = 0.006$). Grass diversity was similar among seasons for most plots (Table 3.17), and there was no detectable trend in diversity among treatments.

Forb species richness (Table 3.18) and diversity (Table 3.19) were generally highest in the wet season, but clear trends in diversity with exclusion and burning were not evident (Table 3.19). Species richness was substantially higher in disturbed (burnt and/or accessible) plots than in inaccessible plots at the unburnt site in the CD08 (Kruskal-Wallis; H = 19.52 d.f. = 7, $p = 0.006$). Forb encounter rate was lower in unburnt inaccessible plots in 2008 (Kruskal-Wallis; $p < 0.020$ for HW08 and CD08), but this was possibly related to initial conditions in the plots and may not be an effect of exclusion *per se* (Table 3.20). After burning, accessible plots recorded higher forb densities than burnt inaccessible plots, but values were still lower than observed in the unburnt accessible plots (Table 3.20).

3.3.2.2. Effects of physical variables on the herbaceous layer

Herbaceous cover was a function of grass and forb diversity, biomass and grass volume, with no significant season or exclusion effect (Table 3.21). The moribund load (Table 3.22) was heavily associated with seasonal influences, such as temperature and rainfall, while increasing time since rain, diversity of grasses and grass volume contributed positively to the moribund load. Rainfall, exclusion and increasing grass diversity increased herbaceous layer biomass, but fire and increasing time since experimental setup reduced biomass (Table 3.23).

The total number of herbaceous species (grasses and forbs combined) was influenced by seven factors, five of which were significant at $\alpha = 0.05$ (Table 3.24). Positive relationships were evident for ranked season wetness, silt/clay: sand ratio and ranked season temperature, whilst species richness was negatively related to months since burn, woody base area, exclusion and grass volume (Table 3.24).

Grass species richness regressions were significant, although only 34% of variation was accounted for by the significant predictors (Table 3.25). Species richness was negatively affected by increasing time since burn, woody plant basal area, grass volume and exclusion. Forb species richness was strongly positively affected by season, with ranked wetness and temperature both being included in the regression model (Table 3.26). Silt/clay: sand ratio was a positive determinant of forb richness, but the opposite was true of herbivore exclusion, increasing time since burn and increasing woody plant basal area (Table 3.26). Encounter rate of forbs was negatively affected by increasing time since burn, time since rain and a high ratio of sand to clay in the soil (Table 3.27).

3.3.3. Soil seed bank

Seed yields were generally low (171 seeds in 2007, 34 in 2008/09), and the second sample collected (2008/09 wet season) had lower seed yields than the 2007 sample (Permutation ANOVA; pseudo-F = 4.20, d.f. = 2, 111, $p = 0.013$), probably because the rains commenced before the samples could be collected and appreciable numbers of seeds may already have germinated. The majority of seeds were grass seeds (71% in 2007; 76% in 2008).

In the 2007 sample, 12% of dicotyledonous and 5% of grass seeds were obviously non-viable through damage. Although the proportion of damaged grass seeds was similar in 2008 (4%), unviable dicot seeds comprised 75% of the sample. Few seeds (of those possibly viable) germinated under laboratory conditions. Although the preparation method (placing seeds on wet blotting paper) has been used successfully by other authors (e.g. Campos and Ojeda, 1997), it was unsuccessful in this study, as a number of seeds (especially dicotyledonous seeds) developed fungal infections and rotted.

The samples collected within two months of the fire in 2007 exhibited a significant treatment (plot and burn) effect (Permutation ANOVA; pseudo-F = 19.59, d.f. = 2, 57, $p = 0.001$), with

much higher yields in unburnt plots compared to burnt plots, and in inaccessible plots compared to accessible plots (Fig. 3.51). Burn and exclusion treatment did not have a significant effect on yield in the second sample (Permutation ANOVA; pseudo-F = 1.46, d.f. = 2, 52, p = 0.088), but burnt plots had slightly higher yields than the unburnt plots (Fig. 3.51).

3.3.4. Soil structure

Soils were of a sandy-loam type (Fig. 3.52). The proportion of clay was significantly lower at Site 1 (ANOVA: F = 5.34, d.f. = 2, p = 0.047), and Site 2 soils had a lower silt content (ANOVA: F = 15.81, d.f. = 2, p = 0.004). No other soil fractions were significantly different among sites or plots (ANOVA: $p > 0.05$ for all tests).

3.4. DISCUSSION

Savanna ecosystems are viewed as being relatively stable at a large scale, with a continuum of states from closed woodland to open grassland (Dublin *et al.*, 1990; Sankaran *et al.*, 2005; Skarpe, 1992), which is largely mediated through woody plant-grass competition for water (Sankaran et al., 2005). Disturbance, i.e. a factor applied to a system that causes a temporary directional change in the structure or functioning of the system (Skarpe, 1992), is responsible for maintaining savanna heterogeneity. The temporal and spatial distribution of disturbance results in a heterogeneous landscape as different patches respond asynchronously to environmental variables. Africa is a geologically ancient continent, and the historical sequence of disturbances at a variety of scales has resulted in a highly heterogeneous savanna ecosystem both spatially and temporally.

Skarpe (1992) argues that a disturbance can only be regarded as such for as long as it results in a directional change in the system. Thus, for systems that have reached an equilibrium point, what may initially have been a disturbance may simply have become a determinant or constraint. In this study, therefore, herbivore exclusion could be viewed as a disturbance due to it potentially altering the equilibrium of the *Burkea* community in the study site. However, to prevent confusion with the published literature, browsing, trampling and other animal-induced effects, along with fire, will be termed “disturbance”.

Given the long coevolution of savanna vegetation and indigenous ungulates, and the adaptation by plants to frequent fires, monitoring the effects of accessibility to large animals

and fire on a selection of plant species of differing palatability, growth form and response to disturbance should facilitate the detection of the range of resistance and tolerance strategies used by savanna plants. Physical and biological factors interacted strongly to shape the plant community in this study. Although fire complicated the patterns, some combined effects of fire and exclusion were evident during the recovery period. Vegetation did not react to herbivore exclusion alone, but rather to an interaction of exclusion and other biological and physical factors. Effects varied with growth form, species and season and fire had a dramatic effect on most measured variables.

3.4.1. Effects of herbivory and mechanical damage on woody vegetation

As a measure of utilisation (referred to as "apparent palatability), I categorised species *a posteriori* according to mammalian browsing pressure. Some species that were rarely browsed in the MNP study site are known to be utilised by mammalian herbivores elsewhere (e.g. *Burkea africana* in Hwange National Park, pers. obs.), but browser selectivity resulted in minor utilisation of these species in MNP. Since chemical defences were not quantified, the reasons for the reduced selection cannot be clearly elucidated beyond assuming the presence of anti-feedants and toxins in species known to contain them (Watson and Dallwitz, 1992 onwards). Three broad utilisation groups can therefore be recognised: (i) apparently unpalatable woody plants with < 1% shoots browsed, (ii) moderately palatable species with 1 to 10% of shoots browsed, and (iii) highly palatable species with > 10% shoots browsed. A range of avoidance, resistance and tolerance mechanisms were exhibited by the ten target species in this study, and several species potentially utilised multiple strategies to limit defoliation.

At least seven of the chosen species belong to families or genera known to produce alkaloids (*Burkea africana, Gardenia resiniflua, Grewia monticola, Lannea discolor, Pseudolachnostylis maprouneifolia*), tannins (*Burkea africana, Terminalia brachystemma*) and phenols (*Flacourtia indica*), which can be detrimental to browsers (Watson and Dallwitz, 1992 onwards). Browsing pressure, even on the most sought-after species under study, was relatively low (<30%). This may have been due to moderate levels of chemical and physical defence in plants, but is more likely an effect of the high diversity and abundance of woody species and low browser biomass at the exclusion sites. Occasional tissue removal from a single individual and shifting between individuals and species would be expected to limit defence responses in plants, as intraspecific pheromonal communication among plants is

usually in response to intense pressure (Hooimeijer et al., 2005). Furthermore, the experiment was run over the wet (growing) season, when tissue loss could potentially be readily replaced by plants. Chemical defences tend to increase when environmental conditions challenge plants, or under very high herbivory pressure (Hooimeijer et al., 2005).

The apparently unpalatable species in this chemical-defence group were *B. africana, L. discolor* and *T. brachystemma*, all of which are primarily single-stemmed trees (van Wyk and van Wyk, 1997), although resprouts (except *Lannea discolor*) and occasional twinning were noticed in this study (pers. obs.). All three species are relatively fast-growing, and with the exception of *T. brachystemma*, shoots higher on the plant grew more rapidly. Whilst this disparity in growth rate may be partly due to self-shading, the canopies of younger trees are not sufficiently dense to fully support this hypothesis (pers. obs.). I suggest that these trees use a combination of resistance (chemical defence) and avoidance (rapid vertical growth and a reduction in shoot production lower on the plant) to provide protection from herbivory and fire (Archibald and Bond, 2003; Renaud *et al.*, 2003).

The fourth (usually) single-stemmed tree is *Pseudolachnostylis maprouneifolia*, a member of the Euphorbiaceae (van Wyk and van Wyk, 1997), which produces coppice-type shoots low on the stem in response to fire (Coates-Palgrave, 1996). This species is browsed by game (pers. obs.), and fell in apparent palatability group ii. (moderately palatable). Tolerance of browsing was demonstrated by compensatory regrowth (Table 3.3) and it is probable that excessive defoliation was limited by chemical means (Watson and Dallwitz, 1992 onwards). Further avoidance of browsing damage would be conferred by rapid vertical growth, and the prioritisation of shoot development (both length and subsidiary shoot density) above the browsing height of small antelope (Table 3.7). The branching arrangement of individual shoots was observed to be in a zigzag pattern with no dominant central (primary) shoot. Thus, browsing damage did not appear to affect shoot development to any great extent (pers. obs.), which may also be a compensation adaptation.

The shorter, shrubby species – *Gardenia resiniflua, Grewia monticola* and *Flacourtia indica*. *Grewia* spp. are utilised by antelope and other browsers despite possessing chemical defences (Hooimeijer *et al.*, 2005; Maloiy and Clemens, 1999; Muya and Oguge, 2000), but it is possible that in the MNP study site *Grewia monticola* was utilised less intensively due to the

abundance of species that were relatively more palatable. Alternatively, due to large leaf size, it is possible that removal of individual leaves was undetected.

Gardenia resiniflua was heavily browsed, particularly by kudu (pers. obs.), and was the only species of the ten studied that was apparently sensitive to browsing at both the individual and population levels. Compensatory regrowth of browsed shoots was not evident, nor was there any indication of growth promotion higher on the plant. However, given the height to which kudu reach, concentrating resources at greater heights would confer little advantage to the plant until it was well beyond browsing range. While the lack of compensation may simply suggest that resources were shunted to unaffected tissues (Agrawal, 2000), in the presence of all herbivores (E_0), the mean stem circumference, stem density and basal area declined significantly over the study period (but increased in the partial and total exclusion plots), which suggests sensitivity to browsing and regulation by ungulates. This effect may have been a result of variable rainfall patterns (654 mm in 2006/07 *c.f.* 905 mm in 2007/08) or, more likely, competitive inferiority in the presence of herbivores with increasing time after fire. Stem number increased substantially in the burnt plots within a year of fire, but the low density of mature plants indicates that either density-dependent factors (e.g. self-thinning, Wiegand et al., 2008) prevail, or that herbivores regulate this species. In accessible plots, mature *Gardenia* persisted as a result of "associational resistance" (Smit *et al.*, 2006), i.e. in refuges, surrounded by other less palatable species (e.g. *Rhus leptodictya* and *Euclea* spp.; pers. obs.), so I suggest that regulation by herbivores is the more likely scenario. Without quantifying chemical responses to browsing, it is impossible to determine whether *Gardenia* reduced chemical production under browsing pressure (e.g. du Toit et al., 1990; Scogings, 2005), or responded too slowly, or herbivores were not substantially deterred by the concentrations of anti-feedants present in the tissues.

Ziziphus mucronata, *Flacourtia indica* and *Gymnosporia senegalensis* are spinescent (van Wyk and van Wyk, 1997), and the mature leaves of the latter are stiff and waxy (pers. obs.). Physical defences typically act to reduce bite size rather than preventing browsing (Wilson and Kerley, 2003a,b). Unsurprisingly, all three showed evidence of browsing, especially of new growth with pliable spines (pers. obs.). The majority of individuals were multi-stemmed, and few exceeded 2.5 m in height, which meant that the majority of tissue was within browsing range. Over the growing season, these species compensated for loss, resulting in insignificant differences in shoot length compared with unaffected shoots. Whilst

only a small proportion of *Z. mucronata* and *G. senegalensis* shoots were affected, one fifth of *F. indica* shoots were browsed, indicating that this species is highly palatable. *Flacourtia indica* also produces phenols (Watson and Dallwitz, 1992 onwards), but levels were not investigated in this study.

Lippia javanica, a multi-stemmed shrub that rarely exceeded 1.2 m in height in the study area, was only moderately browsed (1% of shoots browsed), although there was evidence of insect damage. Given its accessibility to herbivores of all sizes, it would be expected that *Lippia* would either have very strong defences, or show tolerance. In fact, *Lippia* was the only species investigated that showed evidence of overcompensation – browsed shoots grew faster and therefore attained greater extension rates than unaffected shoots, and there was no apparent negative effect on fruit production. Tolerance and overcompensation as a strategy would be expected to be employed by species that cannot escape herbivory, or that have a long history of co-evolution with herbivores but it does not necessarily imply a mutualistic association (sensu Agrawal, 2000).

No species exhibited increased subsidiary shoot density with browsing or damage of primary shoots, which is a recognised response to the removal of apical meristem dominance (Archibald and Bond, 2003; Joys *et al.*, 2004; Klimešová and Klimeš, 2007; Makhabu *et al.*, 2006; Pollock *et al.*, 2005; Skarpe *et al.*, 2007). In fact, the two most palatable species (*Flacourtia* and *Gardenia*) exhibited higher subsidiary shoot densities on undamaged shoots, and for species exhibiting significant differences in leaf density, there was a reduction in leaf density on damaged shoots. Similar effects were found in *Acacia* spp. browsed by dik-dik (*Madoqua kirkii*) in Kenya (Augustine and McNaughton, 2004). Bushy growth forms are utilised more heavily by herbivores (Makhabu *et al.*, 2006; Pollock *et al.*, 2005), so limited branching and reduced leafiness – especially following damage – may in fact be an avoidance strategy in a browser-dominated environment. This does not imply, however, that shoot density did not increase elsewhere on the plant. For example, subsidiary shoot density was greater at higher elevations in *P. maprouneifolia* and *F. indica* which may be an indication of disturbance avoidance in a vertical plane (Klimešová and Klimeš, 2007).

3.4.1.1. Responses of woody plants to mechanical damage

Inevitably, some browsing damage was included in the “mechanical damage” category, since the source of some damage was ambiguous. Differential shoot extension rates between

damaged and undamaged shoots of three species (*F. indica*, *P. maprouneifolia* and *L. discolor*) was insignificant, which implies compensatory regrowth, but the other seven species investigated were apparently sensitive to mechanical damage. Of the five palatable species that were sensitive, four had shown signs of compensatory regrowth following herbivory. Furthermore, two species (*G. monticola* and *G. resiniflua*) exhibited a higher-than-expected proportion of damage below 1 m, indicating susceptibility to mechanical pressures.

There are multiple explanations for the differences in response to browsing and mechanical damage. Firstly, mechanical damage tended to be "greenstick" breaks rather than clean cuts which may have affected the healing response, or increased the opportunity for microbial damage (Carline and Bardgett, 2005). Secondly, mechanical breakage usually removed a larger section of shoot than browsing damage, and at recorded growth rates, complete compensation was unlikely to occur. Finally, compensation for damage without the application of potential growth promoters found in herbivore saliva, may have been limited (Rooke, 2003).

3.4.2. Effects of fire and exclusion of large fauna on woody plants

Previous authors have suggested that short-term effects of herbivore exclusion on plant communities – especially the woody component – are not detectable (e.g. Levick and Rogers, 2008), although Augustine and McNaughton (2004) demonstrated significant browsing effects within three years of herbivore exclusion. Whilst it is probable that the end-point had not been reached by the end of the experimental period of this study, measurable changes were evident, and the fine scale of measurement facilitated the identification of possible mechanisms for change. This study is unusual in that it was carried out in a selective browser-dominated system, with relatively low animal densities (c.f. Focardi and Tinelli, 2005; Jacobs and Naiman, 2008; Levick and Rogers, 2008; McNaughton *et al.*, 1988; Smart *et al.*, 1985; Wassie *et al.*, 2009), and was designed to explore the effects of different sized animals on vegetation. Thus changes are less likely to be attributable to the quantity of plant biomass removed, but rather to the focus of herbivore pressure. That low densities of animals can have marked effects on vegetation over such a short period is testament to the regulatory role of indigenous mammals in the environment.

3.4.2.1. Community-level patterns

In this study, at least in the short term, vegetation changes (basal area, stem density and stem size distributions) appeared to be affected by changes in herbivory pattern and animal access, and the direct effects of and subsequent recovery from fire. Importantly, fire caused mortality or arrested the development of most woody plant seedlings, so stem recruitment at the end of 2007 in burnt plots was primarily vegetative resprouts from subterranean buds, with recruitment of only a small number of fast-growing seedlings. Unburnt plots contained a combination of resprouts and seedlings that entered the sapling cohort. Overall changes in basal area over the two years in the unburnt plots were positive for the relatively inaccessible treatments (E_S and E_T) and negligible (E_0) or negative (E_L) for the accessible treatments. Fire caused high mortality and loss of basal area initially in all plots. This loss was ultimately reversed in the E_0, but partial and total exclusion plots did not compensate for the loss. Although herbivore density was not continually measured during the study, there was no evidence of animals leaving the burnt sites following the fire. In fact, herbivore pressure probably increased for a short time when new herbaceous growth and woody resprouts were produced, but this was a short-term effect. I suggest that the mechanisms driving differences among plot types involve the vertical level (height) at which animal (and fire) pressure occurred or was released, as described below.

In the first assessment, before the fire, all plots except the E_T at Site 3 exhibited similar stem size distribution patterns characterised by peaks at 4 to 6 cm and in the large (>15 cm) circumference classes. This distribution shape is typical of a mature community, with the majority of stems in small-intermediate and large size classes (Wiegand et al., 2008). Site 3's E_T, and to a lesser extent the same site's E_S, had a recruiting "inverse-J" pattern with the vast majority of stems falling into the small-intermediate size class (Wiegand et al., 2008), which may have been a rapid response to exclusion or an artefact of recovery from the February 2005 fire at that site. Given the contrasting distributions in the E_L and E_0 at the same site, the former is the preferred explanation. Interestingly, the initial stem distribution patterns in this study are in contrast to Levick's and Rogers' (2008) thirteen-year exclusion experiment in Kruger National Park, where they recorded a recruiting pattern (inverse-J shaped distribution) in the sites accessible to herbivores, and stable (bimodal) distribution of stem sizes in exclusion plots. This demonstrates three things. Firstly, the vegetation in the Matobo site was in a mature state at the beginning of the study. Secondly, high browser biomass (especially elephant) prevents the establishment of a classically stable plant community with

a predominance of mature trees. Thirdly, in the Matobo *Burkea* community, exclusion of herbivores in the short term acted as a disturbance (sensu Skarpe, 1992).

Unfenced control plots (E_0) were subject to herbivory and mechanical pressure from ground level to the canopy. In the unburnt E_0, stem size distribution remained similar throughout the experimental period and there were negligible changes in stem density and basal area beyond minor inter-annual fluctuations (Fig. 3.6). This apparent stability suggests that the community was in a self-regulatory stable state, as has been found in other austral savannas (Prior *et al.*, 2009). By contrast, the 2007 fire caused substantial mortality of fire-prone small and intermediate sized (<15 cm circumference) stems (Fig. 3.5; 3.6). Loss was partially compensated for within the following growing season as plants with underground reserves resprouted (Chidumayo, 2006; Klimešová and Klimeš, 2007) and new stems took advantage of the gaps created by the fire and the influx of nutrients. Stem recruitment slowed between 2007 and 2008 as stem competition among smaller stems increased (Yu et al., 2009), continual herbivory and mechanical pressures were applied, and gap availability decreased with the re-establishment of the herbaceous layer. Herbivory was uninterrupted once recovery was initiated, and the predominance of selective browsers acting to a height of 2 m or more (i.e. maximum browse height of kudu, Hooimeijer et al., 2005) limited apical dominance, at least of palatable shrubs. This reduced inter-shoot competition in the vertical plane, and maintained gaps in the lower levels that facilitated continual stem development. These effects, coupled with the fertilising effects of animal excrement, promoted overall basal area expansion and stem density increases (Fig. 3.5): the original “stable state” had been overshot. With time, it would be expected that stem size distribution would return to the original (2006) pattern instead of the actively recruiting pattern (Fig. 3.5,Wiegand et al., 2008), but possibly with an elevated woody basal area and stem density due to the injection of nutrients and loss of surface litter (Eriksson *et al.*, 2003; Glasgow and Matlack, 2007; Pastor and Cohen, 1997). Given that the unburnt site had been subjected to a fire in early 2005 and was close to a stable state by late 2006, indications are that *Burkea* woodland in this environment recovers to a pre-fire (stable) state within two years.

At the other extreme, the total exclusion (E_T) treatment removed both the positive and negative effects of medium- and large animals, while insect, bird and small rodent accessibility was probably unhindered. In the unburnt treatment, high competition among intermediate-sized stems and growth of larger stems (Fig. 3.5) resulted in a negative trend in

stem density and increase in basal area, despite continual stem recruitment (Fig. 3.6 b, e). Stem competition may have been exacerbated by a reduction in mechanical and browsing pressure, which is important for limiting growth within the lower strata of the vegetation, combined with an interruption of the "fast" animal-mediated nutrient cycle, i.e. deposition of animal excrement and trampling of litter into the soil (McNaughton et al., 1988). With the release from damage and a reduction in nutrient supply, established plants prioritised nutrient supply to the shoots in the crown, which promoted growth of larger stems but further disadvantaged intermediate-sized stems. Therefore, as demonstrated in other studies, exclusion of the bulk of the faunal biomass resulted in an increase in woody cover (e.g. Augustine and McNaughton, 2004; Levick and Rogers, 2008), but at the expense of woody stem density.

Vegetation in the unburnt small animal exclusion plot (E_S) responded in a similar fashion to the unburnt E_T, with the notable exceptions that stem loss (density) was lower and basal area expansion was much greater. Unlike the E_T, the E_S was accessible to large animals (but admittedly, only used rarely, if at all, by antelope such as kudu) and baboons and vervet monkeys capable of climbing over the relatively low fence. Thus, mechanical pressure was applied in the canopy, possibly accompanied by some removal of new shoots, reproductive shoots and fruits (Skinner and Smithers, 1990). Mechanical pressure also occurred at ground level, with probable selective removal (by primates) of underground plant reserves (e.g. roots and tubers) and new woody growth, rather than browsing on leaves *per se* (Skinner and Smithers, 1990). As a result, although shoot dominance in the canopy was probably restricted due to mechanical damage, recruitment was also limited. Pressure in the canopy reduced shading, while low recruitment and reduced intra-unit competition for resources allowed stems and shoots at lower levels to become established and grow (du Toit et al., 1990), especially in the second year (Fig. 3.6). Frictional effects facilitated gap creation at ground level, and removal of subterranean reserves of herbaceous as well as woody plants acted to further ease competition for nutrients. The overall effect was an initial increase in stems (Fig. 3.5d) followed by intense stem competition (Fig. 3.5e), combined with rapid growth of established stems especially in the second year. This situation is akin to clearing woody vegetation and stocking with grazers in rangelands, where woody cover recovers to a level higher than pre-clearing (Smit, 2004; Strang, 1973).

Burning of the E_T and E_S promoted resprouting and adventitious bud development (Klimešová and Klimeš, 2007), but fire-induced mortality of intermediate and small stems produced a negative trend in basal area. In the year following fire, stem competition and limited recruitment (due to space constraints following redevelopment of the herbaceous layer) further decreased the stem basal area in the E_T. However, partial recovery of basal area occurred in the E_S, probably through the mechanisms described for the unburnt E_S. Nonetheless, this plot type also showed an overall negative basal area trend. The high recruitment rate in both plot types would probably result in an increase in woody cover over time as growth occurs (Smit, 2004; Strang, 1973).

Vegetation responses in the unburnt E_L were most similar to the E_0, but were of a greater magnitude. This plot type lost basal area and increased in stem density at a relatively stable rate throughout the experimental period (Fig. 3.5). Being accessible only to smaller animals able to fit under the fence, the majority of pressure was applied to lower strata (below 1.5 m), although some primate and hyrax activity in the canopy is likely. Continual friction and herbivory acted to reduce the competitive ability of small- and intermediate sized stems, while dominance of shoots above browsing height was relatively unchecked (Augustine and McNaughton, 2004). However, herbivore saliva stimulates compensatory regrowth of browsed shoots in some savanna species (Rooke, 2003), and apical dominance may have been restricted by nutrients being shunted to replace tissues rather than to produce new growth and increase biomass. Gaps created by stem loss (through friction and herbivory-induced mortality of small stems) were colonised by new stems (primarily resprouts) which did not gain biomass rapidly due to inter-stem competition for nutrients and continual herbivore pressure.

When burnt, the E_L initially exhibited a dramatic decline in basal area, primarily through loss of fire-prone intermediate and small sized stems (Fig. 3.5, 3.6 a, d). Continual herbivore pressure in the lower stratum reduced the competitive ability of the intermediate sized stems, which led to mortality of that size class, but allowed further stem recruitment. Minimal herbivore pressure in higher strata encouraged upper shoot dominance (Klimešová and Klimeš, 2007), but growth of larger stems and high stem recruitment rates did not counteract the effects of biomass loss within the experimental period.

The trends and proposed mechanisms described above illustrate some important points and highlight the importance of interactions between herbivory and fire. Firstly, the effects of infrequent fire are of limited duration, and recovery by woody vegetation is dependent on the ability to resprout and the intensity of herbivore and mechanical pressure in a vertical plane. Following fire, and in the absence of medium and/or large animals, woody cover was reduced (at least in the short term), primarily through the loss of intermediate sized stems. This supports Smit's (2004) suggestion that the combined removal of smaller stems and conservation of large savanna trees, which suppress the development of new growth, limit bush-encroachment in rangelands. However, as found by Strang (1973), fire, in the presence of large animals, promoted woody cover development, despite low grazing pressure which was predicted to limit shrub development (Roques et al., 2001).

Secondly, in the absence of fire, total exclusion of medium and large animals encourages woody cover expansion as found in other studies (Augustine and McNaughton, 2004; Roques *et al.*, 2001; Strang, 1973), but further expansion is ultimately limited by competition for resources. It is apparent that a diverse herbivore community is important for maintaining a stable woody component. Removal of smaller herbivores promotes stem recruitment and woody growth, while accessibility to small herbivores results in a loss of woody cover through increased inter-stem competition in the mid size ranges, and high herbivory pressure in lower strata. This latter effect supports Strang's (1973) contention that woody plant development is limited most effectively by smaller mammalian browsers such as goats (*Capra hircus*), and mirrors Augustine and McNaughton's (2004) observations of the effects of dik-dik.

3.4.2.2. Species responses

A broad range of responses to fire and exclusion were evident and provide insight into the factors regulating species dynamics. What is immediately apparent is that uniformity in growth form or palatability and coexistence in areas subject to the same disturbance regimes, do not necessarily translate into uniform responses. This demonstrates that disturbance, biotic and abiotic factors interact, which is why community heterogeneity is retained (de Mazancourt and Loreau, 2000b). For example, *Burkea africana* and *Pterocarpus rotundifolius*, wind-dispersed unpalatable trees that grow to similar heights, both lost biomass in the absence of herbivores, but exhibited opposite regeneration patterns following fire. *Burkea africana* only proliferated in exclusion plots while *P. rotundifolius* increased most

dramatically in the presence of large fauna. A similar response to *P. rotundifolius* has been recorded for its congener *P. angolensis*, which is fire-induced, both due to enhancement of germination (Banda et al., 2006) and competitive release resulting from improved access to light (Caro et al., 2005).

Three species (*Flacourtia indica*, *Gardenia resiniflua* and *Terminalia brachystemma*) increased in exclosures, suggesting regulation by herbivores (Augustine and McNaughton, 2004) under natural circumstances. This result is unsurprising for *Flacourtia indica* and *Gardenia resiniflua* which were highly palatable, but *Terminalia brachystemma* fell in the apparently unpalatable group. It is possible that *Terminalia* spp. seedling recruitment was limited by herbivory (which would not have been detected by this study), but an alternative explanation is that it outcompeted other unpalatable species (such as *B. africana*) that seemed to be reliant on the presence of herbivores. It was in the presence of herbivores following fire that *G. resiniflua* increased, which may have been the result of endozoochory or local nutrient cycling, or possibly a reduction in palatability given that plants tend to increase chemical defences in times of stress (Hooimeijer et al., 2005; Scogings, 2005).

Herbivory alone had little effect on the tolerant *Pseudolachnostylis maprouneifolia*, but the combination of fire intolerance and herbivory led to loss of biomass in this species, indicating herbivory intolerance following damage (Hooimeijer *et al.*, 2005; Thompson Hobbs, 1996). A similar interactive effect was evident for *Gymnosporia senegalensis*, despite its reliance on faunal presence for expansion in the absence of fire.

3.4.2.3. Seedling development and recruitment

The emergence of seedlings and their subsequent recruitment into the mature population are reliant on a number of factors. Ultimately, seeds need to be available in the seed bank, so the location of parent plants, dispersal traits of plants, activities of seed dispersers and seed predators, resistance to microbial and fungal attack and seed persistence times are critical determinants of germination potential (Argaw *et al.*, 1999; Barnes, 2001; Bonfil, 1998; Calviño-Cancela, 2004; Ezoe, 1998; Muller-Landau *et al.*, 2008; Schafer and Kotanen, 2003). When appropriate moisture and temperature conditions occur, seed dormancy needs to be broken and the seed coat must be porous to water to allow germination to occur. Emergence from the soil and subsequent growth are reliant on available gaps and nutrients, adequate water, and protection from disturbance. The seedling stage is the most vulnerable to damage:

seedlings are less tolerant of herbivory, trampling and fire and are more susceptible to drought and frost than mature plants (Augustine and McNaughton, 1998; Gerhardt and Todd, 2009; Smit *et al.*, 2006; Van Uytvanck *et al.*, 2008). As a result of the necessity for the interaction of multiple factors at appropriate times, seedling distributions and densities tend to be sparse and patchy (Muller-Landau et al., 2008), as was found in this study.

Immediately following the fire and prior to suitable germination conditions, significantly fewer seeds were found in burnt and accessible plots compared with unburnt and inaccessible plots, suggesting high seed mortality due to fire and seed predation by larger herbivores. In contrast to this, seedling density increased and persisted following fire, but the responses of individual species varied and there was no significant exclusion effect. The 2007 fire occurred late in the dry season, and burn intensity was high; thus, there were few refugia for seedlings and consequently high mortality rates (Plate 3.1; pers. obs.). The vast majority of seedlings encountered after the fire at Sites 1 and 2 were therefore new growth, which allowed predictions to be made about the interactive effects of fire and exclusion on several species. Responses of seeds to heat-shock and fire damage vary widely, depending on the timing and intensity of fire, the position of seeds (buried, or on the soil surface), seed size and evolutionary history with fire (Banda *et al.*, 2006; Buhk and Hensen, 2006; Crosti *et al.*, 2006; Danthu *et al.*, 2003; Mouissie *et al.*, 2005b).

The majority of seedling species that increased in abundance following fire had large seeds with tough seed coats, or seeds protected by woody stones (Coates-Palgrave, 1996). Large seeds have greater energy reserves and may be more persistent in the seed bank as a result (Brown *et al.*, 2003), and many large-seeded species in the study area were animal-dispersed, ensuring a broad spatial and temporal germination potential. Fire is known to have a direct, positive effect on the water imbibition potential of hard-coated seeds through scarifying the seed coat of seeds near the soil surface, heating the soil and breaking seed dormancy, or producing smoke containing germination-enhancing chemicals (Banda *et al.*, 2006; Crosti *et al.*, 2006; Danthu *et al.*, 2003; Dayamba *et al.*, 2008; Gómez-González *et al.*, 2008; Kulkarni *et al.*, 2007; Luna *et al.*, 2007). Indirect effects of fire include creating gaps, accelerating the return of nutrients to the soil, and negatively affecting below-ground biomass of competing individuals (Hoffmann, 2000; Hudak *et al.*, 2004; McNaughton *et al.*, 1988; Roques *et al.*, 2001; Snyman, 2004). These indirect effects may account for the increase in abundance of smaller-seeded, bird-dispersed species such as *Lippia javanica* and *Euclea* spp.. Five species,

three of which were small-seeded, declined in abundance following fire. This infers that seedlings were killed by fire and then not replaced, due to fire-induced seed mortality, few viable seeds in the seed-bank, or rarity of mature individuals in the community contributing seeds to the seed bank. Apart from *Bridelia mollis*, the species that declined were uncommon, which suggests that available seeds were rare or post-germination growth was constrained by other factors such as herbivory (Augustine and McNaughton, 1998).

Like fire, the actions of animals may be positive or negative. Dispersal of propagules some distance from parent plants is often beneficial, and deposition within manure can accelerate growth rates after germination (Argaw *et al.*, 1999; Eycott *et al.*, 2007; Feer, 1995; Mouissie *et al.*, 2005b; Myers *et al.*, 2004; Suarez and Malo, 1998). However, not all seeds survive ingestion and mastication (Feer, 1995), and not all seedlings will mature due to density-dependent effects, drought, frost and herbivory (Duncan *et al.*, 2009; Turnbull *et al.*, 2008; Yu *et al.*, 2009). Furthermore, for palatable species with edible fruits, seed dispersal and germination may be enhanced by herbivores, but seedling development may be arrested if tolerance of herbivory low (Augustine and McNaughton, 2004; Bonfil, 1998; Moe *et al.*, 2009). Of the species with detectable trends in this study, all seedlings that increased in abundance with exclusion were palatable, and 75% were smaller-seeded plants, a trait that confers little tolerance to herbivory as seedlings (Bonfil, 1998).

During the study period, a total of 13 species became established (> 50 cm height) and two species were lost from plots, with gains and losses varying among exclusion and burn treatments. Fire appeared to have the most measurable effect, with gains of eleven species. Given that the majority of seedlings were destroyed by the fire in 2007, the presence of saplings a year later suggests that germination was enhanced and/or that growth of seedlings was rapid.

Studies suggest that palatable plants and early-successional species are faster-growing than unpalatable and late-successional species: less energy is invested in defence (Cebrian and Duarte, 1994) in an attempt to escape beyond browsing height and reproduce as quickly as possible (Augustine and McNaughton, 2004; Davidson, 1993; Dörgeloh, 2001; Sanon *et al.*, 2007). Slower-growing palatable species would be expected to be constrained by herbivory (Augustine and McNaughton, 1998). Support for these predictions was found in this study: (i) half of the palatable species that became established during the study period did so in the

absence of large fauna, and (ii) five of six palatable species increased in inaccessible plots following fire.

Despite two unpalatable species increasing in the presence of herbivores, there was little evidence that unpalatable plants would come to dominate the community (Augustine and McNaughton, 1998; de Mazancourt and Loreau, 2000b). In fact, two palatable species were also sensitive to exclusion, but whether because of being outcompeted by other species or because of reliance on herbivore presence (e.g. soil enrichment) (de Mazancourt and Loreau, 2000b) cannot be determined from the data. Furthermore, establishment of highly palatable plants continued in accessible plots (e.g. *Flacourtia indica*, Fig. 3.48) and refuges were present amongst unpalatable (e.g. *Euclea*) and defended plants (e.g. *Ziziphus, Gymnosporia*) (pers. obs., Queenborough *et al.*, 2007; Smit *et al.*, 2006; Yang *et al.*, 2009).

3.4.3. Effects of biotic and abiotic factors on herbaceous vegetation

The structure and development of the herbaceous layer were influenced by the interaction of a range of biotic and abiotic factors. Seasonal effects were marked in this study, especially when considering the synergistic effects of temperature and water availability. Temperature is an important factor, especially in frost-prone regions such as MNP where ground-frosts commonly occur in the cool, dry season: by late July, a large proportion of forbs and tree seedlings exhibit frost damage (pers. obs.). Soil composition (silt and clay content), the timing of significant rainfall, soil and ambient temperature and the presence of plant roots affect moisture retention in the upper soil strata (Cipriotti et al., 2008; Simmons et al., 2008) where herbaceous plant roots are concentrated. In clayey soil, however, not all water is available to plants, as it complexes with clay particles forming insoluble compounds that plant roots cannot absorb. Additionally, the presence of air in interstitial spaces in soil is critical for the persistence of plants; many species are sensitive to waterlogging (Daleo and Iribarne, 2009). Biomass and species richness were positively associated with the hot wet season, although herbaceous biomass showed a lag effect with rain, and reached a maximum later in the wet season. Reproductive tissue development of grasses and sedges probably contributed to this pattern, as most species flowered and set seed late in the wet season and into the cool dry season. Forb abundance was highest soon after rainfall and in sandier soils, which suggests that available water and good drainage were significant determinants of forb development. Additionally, the lower water-retention properties of sandy soils limit

herbaceous cover development in drier months, ensuring the availability of gaps for colonisation following rain.

Woody cover negatively affected species richness of all herbaceous components, but in contrast to other studies (e.g. Simmons et al., 2008; Vandenberghe et al., 2008), it was not extracted as a significant determinant of herbaceous cover or biomass. Interactions between the woody and herbaceous components of vegetation vary with local circumstances and the scale of measurement. Facilitation tends to occur under conditions of environmental stress, where woody plants may moderate ambient and soil temperature fluctuations and retain water in the upper soil strata by hydraulic action, while competition tends to dominate under moderate conditions (Berger *et al.*, 2008; Holzapfel *et al.*, 2006; Isbell *et al.*, 2009; Veblen, 2008). Given the interactive effects of faunal exclusion and increasing woody biomass, and the confounding effects of seasonal changes, I suggest that the decline in species richness with increasing woody cover was a corollary of the limitation of disturbance and the *Burkea* community's progression towards a climax state, rather than a direct consequence of competition between growth forms.

Grazing/ browsing, frictional pressures (e.g. trampling) and fire are typical savanna disturbances that encourage heterogeneity at a variety of spatial and temporal scales, and promote species richness and diversity (Bakker and Olff, 2003; Cosyns *et al.*, 2006; Fuhlendorf and Engle, 2004; Hulme, 1996). I suggest that the removal of these disturbances in this study caused plant tissue (biomass) to accumulate, resulting in an increase in the moribund load and surface litter and an interruption of decomposition due to the absence of hoof action trampling plant matter back into the soil (Cumming and Cumming, 2003; Hudak *et al.*, 2004; Laterra and Solbrig, 2001; McNaughton *et al.*, 1988; Sheuyange *et al.*, 2005; Smart *et al.*, 1985; Van Uytvanck *et al.*, 2008). The herbaceous community thus approached a species-poor climax state as a result of shading out of smaller forbs and grasses by later successional species (Jacobs and Naiman, 2008; Lamb, 2008).

3.5. CONCLUSIONS

Temporal and spatial scales and intensity of disturbance are critical determinants of vegetation patterns, as they govern the size of patches, and influence which species are available for colonisation of gaps. Large-scale or frequent disturbances tend to result in homogenisation, whereas smaller-scale disturbances promote heterogeneity at the landscape

scale (Fuhlendorf and Engle, 2004; Sheuyange *et al.*, 2005). At a species level, tolerance of disturbance may vary widely, depending on evolutionary history and the timing and intensity of disturbance in relation to the species' phenology (Adler *et al.*, 2004; Sarmiento, 1992; Thompson Hobbs, 1996; Veblen, 2008). Individual responses depend on spatial position (e.g. exposed site or in a refuge), the capacity to tolerate or recover from damage (e.g. underground reserves), and the extent and type of continual pressures (Glasgow and Matlack, 2007; Klimešová and Klimeš, 2007; Yang *et al.*, 2009). Mosaic patterns in savannas therefore develop due to the stochasticity of disturbance in time and space and the range of possible responses by vegetation within the constraints of herbivory pressure, soil fertility and texture and rainfall (Sankaran *et al.*, 2005; Skarpe, 1992).

The fire that affected two sites in this study was a large spatial disturbance with a relatively short temporal effect. It caused death or die-back of woody plant seedlings and saplings and removed the bulk of above-ground herbaceous standing biomass and surface litter, but had a limited effect on larger woody species. Solid combusted materials were then available for return to the soil (McNaughton et al., 1988). The creation of space and enrichment of the soil facilitated regeneration of perennial plants with subterranean reserves (Glasgow and Matlack, 2007; Klimešová and Klimeš, 2007) and the establishment of new individuals from the seed bank (Buhk and Hensen, 2006; Neill *et al.*, 2007). The species available for regeneration were determined by the previous community composition, and the continued dominance of established plants ensured a minimal change in community structure. Recovery, especially during the following wet season, was relatively rapid, and biomass of the herbaceous and woody layers regained their pre-fire states within a year when subjected to "normal" pressures such as large mammal activities. However, the pattern of recovery was different in the absence of large fauna. Partial or complete exclusion of herbivores following fire resulted in an overall loss of woody basal area but an increase in stem density and species richness coupled with a large increase in the herbaceous biomass (especially in the wet season). This illustrates the importance of a balanced herbivore (browser) guild on maintaining the stability of mature woodlands, and hints at the important roles that larger mammalian herbivores play in woody plant seed dispersal.

The exclusion of terrestrial fauna (in the absence of fire) illustrated the impacts that different-sized herbivores have on vegetation. Importantly, the design of this study demonstrates that the focus of animal pressure has significant implications for woody vegetation, although such

effects have been inferred by previous experiments (Augustine and McNaughton, 2004; Strang, 1973). In addition, results indicate that mechanical or "frictional" pressures such as trampling and breakage have different effects to herbivory but are no less important in maintaining heterogeneity. As found in numerous other studies, the complete exclusion of large herbivores resulted in an increase in woody basal area and herbaceous biomass, and a decline in species richness of all plant growth forms (Augustine and McNaughton, 2004; Isbell *et al.*, 2009; Jacobs and Naiman, 2008; Levick and Rogers, 2008; Smart *et al.*, 1985; Wassie *et al.*, 2009). Such patterns are believed to be due to reduced disturbance, in the form of herbivory and trampling, allowing the development of a depauperate climax community (Davidson, 1993; McNaughton *et al.*, 1988). Continual pressure in the lower strata by smaller herbivores in isolation limits stem recruitment, especially of palatable species, and results in a net loss in woody cover. Finally, the concentration of herbivory effects above 1 m combined with slight frictional pressures in lower strata encourage woody growth through creating gaps for establishment of new stems at ground level (frictional pressure), while releasing apical dominance (herbivory) and allowing subterranean adventitious buds to develop (Klimešová and Klimeš, 2007).

The limited effect of exclusion on the herbaceous layer – beyond the increase in biomass and loss of species richness which were by-products of the removal of frictional pressures – is probably due primarily to the dominance of browsers in the study site. Grazer-dominated systems exhibit far greater herbaceous layer responses than recorded here (Jacobs and Naiman, 2008; Smart *et al.*, 1985).

Table 3.1: Summary of the number of shoots marked per species, and the proportion of primary (1°) and subsidiary (2°) shoots browsed or damaged. Damage refers to breakage, insect damage or unidentified damage at the growing tip.

Species	Growth form[1]; Response to fire	Plants tagged	N shoots tagged (Jul 2006)	N shoots remaining (Feb 2007)	% loss	% browsed		% damaged	
						1°	**2°**	**1°**	**2°**
Burkea africana	Tree; Resprout	59	472	443	6.1	0	0	3	0
Flacourtia indica	Shrub; Coppice	50	406	386	4.9	21	14	20	4
Gardenia resiniflua	Shrub; Sensitive	38	303	299	1.3	13	3	7	0
Grewia monticola	Shrub; Resprout	35	327	281	14.1	1	0	20	0
Gymnosporia senegalensis	Shrub; Resprout	56	448	431	3.8	2	1	30	1
Lannea discolor	Tree; Coppice	31	253	223	11.9	0	0	4	0
Lippia javanica	Shrub; Resprout	60	480	423	11.9	0	1	12	0
Pseudolachnostylis maprouneifolia	Tree; Coppice/ resprout	53	424	380	10.4	1	0	10	0
Terminalia brachystemma	Tree; Resprout	39	311	270	13.2	0.3	0	6	0
Ziziphus mucronata	Shrub/ Tree; Coppice	41	336	301	10.4	1	0	27	1
TOTAL			3760	3437					

[1]"Tree" = generally single-stemmed; height as mature plant greater than 3 m; "Shrub" = multi-stemmed; height as mature plant usually less than 2 m.

Table 3.2: Definitions and descriptions of predictor variables included in multiple regression analysis of the herbaceous layer.

Variable	Variable type	Coding
Season wetness	Discrete	Hot dry season = 1 Cool dry season = 2 Hot wet season = 3
Season temperature	Discrete	Cool dry season = 1 Hot wet season = 2 Hot dry season = 3
Soil fraction ratios i. Clay/silt: sand ii. Sand: clay	Continuous	
Months since burn	Continuous	
Woody plant basal area (m^2/ ha)	Continuous	
Number of weeks since last rainfall >5 mm	Continuous	
Exclusion	Discrete	No barrier (E_0) = 0 Partial barrier (E_L and E_S) = 0.5 Complete barrier (E_T) = 1
Log_{10} Grass volume (m^3/ha)	Continuous	
Number of weeks since exclusion plot setup	Continuous	
Mean percent aerial cover for plot	Continuous	
Mean percent moribund load for plot	Continuous	
Herbaceous biomass (tonnes/ha)	Continuous	

Table 3.3: GLM ANOVA results for the effects of browsing and exclusion treatment on shoot growth (mm.day^{-1}). Interaction effects between treatment (plot type) and browse damage were done only for species where the smallest *N* for any category >5. Browse effects were not tested for five species (*Burkea, Grewia, Lannea, Terminalia* and *Ziziphus*) as fewer than three individuals were browsed. Significant differences are in boldface, with the source of variation (using Tukey's HSD tests) given in the "Source" column.

Species	Effect (d.f.)	*F*	*p*	Source [a]
Burkea africana	Treatment (3, 50)	0.21	0.889	
Flacourtia indica	Treatment (3, 85)	0.70	0.553	
	Browse (1, 85)	0.75	0.390	
	Interaction (3, 85)	0.58	0.629	
Gardenia resiniflua	Treatment (3, 45)	0.97	0.413	
	Browse (1, 45)	**8.80**	**0.004**	$\mathbf{B_0 > B_1}$
	Interaction (3, 45)	0.10	0.961	
Grewia monticola	Treatment (3, 34)	1.26	0.305	
Gymnosporia senegalensis	**Treatment (3, 58)**	**2.92**	**0.041**	$\mathbf{E_0 < E_T}$
	Browse (1, 60)	0.02	0.888	
Lannea discolor	**Treatment (3, 26)**	**4.30**	**0.014**	$\mathbf{E_S < E_T}$
Lippia javanica	Treatment (3, 63)	0.37	0.773	
	Browse (1, 65)	**10.67**	**0.002**	$\mathbf{B_0 < B_1}$
Pseudolachnostylis maprouneifolia	Treatment (3, 53)	0.95	0.425	
	Browse (1, 55)	0.06	0.810	
Terminalia brachystemma	Treatment (3, 36)	0.64	0.591	
Ziziphus mucronata	Treatment (3, 39)	2.80	0.053	

[a] E_0 = nil exclusion, E_S = small antelope exclusion; E_L = large antelope exclusion; E_T = total exclusion. B_0 = non-browsed shoots, B_1 = browsed shoots

Table 3.4: GLM ANOVA results for the effects of browsing and exclusion treatment on subsidiary shoot density (shoots/mm primary stem/day). Interaction effects between treatment (plot type) and browse damage were done only for species where the smallest *N* for any category >5. Browse effects were not tested for five species (*Burkea, Grewia, Lannea, Terminalia* and *Ziziphus*) as fewer than three individuals were browsed. Significant differences are in boldface, with the source of variation (using Tukey's HSD tests) given in the "Source" column.

Species	Effect (d.f.)	*F*	*p*	Source [a]
Burkea africana	Treatment (3, 50)	1.08	0.365	
Flacourtia indica	Treatment (3, 78)	0.76	0.520	
	Browse (1, 78)	**6.34**	**0.014**	$\mathbf{B_0 > B_1}$
	Interaction (3, 78)	0.16	0.920	
Gardenia resiniflua	Treatment (3, 45)	1.21	0.316	
	Browse (1, 45)	**57.06**	**<0.001**	$\mathbf{B_0 > B_1}$
	Interaction (3, 45)	1.36	0.267	
Grewia monticola	Treatment (3, 34)	0.54	0.660	
Gymnosporia senegalensis	Treatment (3, 57)	0.68	0.567	
	Browse (1, 59)	2.77	0.101	
Lannea discolor	Treatment (3, 26)	2.00	0.138	
Lippia javanica	Treatment (3, 63)	0.45	0.718	
	Browse (1, 65)	0.569	0.450	
Pseudolachnostylis maprouneifolia	Treatment (3, 53)	1.96	0.132	
	Browse (1, 55)	2.15	0.140	
Terminalia brachystemma	Treatment (3, 36)	0.03	0.992	
Ziziphus mucronata	Treatment (3, 37)	1.65	0.194	

[a] E_0 = nil exclusion, E_S = small antelope exclusion; E_L = large antelope exclusion; E_T = total exclusion. B_0 = non-browsed shoots, B_1 = browsed shoots

Table 3.5: GLM ANOVA results for the effects of mechanical damage and exclusion treatment on shoot growth. Interaction effects between treatment and damage calculated for species where the smallest *N* for any category >5. Significant differences are in boldface, with the source of variation (using Tukey's HSD tests) given in the "Source" column.

Species	Effect (d.f.)	*F*	*p*	Source [a]
Burkea africana	Treatment (3, 66)	0.38	0.766	
	Damage (1, 66)	**61.75**	**<0.001**	**$D_0 > D_1$**
Flacourtia indica	Treatment (3, 90)	1.27	0.289	
	Damage (1, 90)	**10.92**	**0.001**	**$D_0 > D_1$**
	Interaction (3, 90)	0.38	0.769	
Gardenia resiniflua	Treatment (3, 45)	0.60	0.617	
	Damage (1, 45)	**26.99**	**<0.001**	**$D_0 > D_1$**
	Interaction (3, 45)	1.45	0.241	
Grewia monticola	Treatment (3, 60)	0.29	0.833	
	Damage (1, 60)	**72.54**	**<0.001**	**$D_0 > D_1$**
	Interaction (3, 60)	1.20	0.318	
Gymnosporia senegalensis	**Treatment (3, 105)**	**3.08**	**0.031**	**$E_L < E_T$**
	Damage (1, 105)	**3.96**	**0.049**	**$D_0 > D_1$**
	Interaction (3, 105)	0.43	0.732	
Lannea discolor	Treatment (3, 39)	2.53	0.073	
	Damage (1, 39)	0.40	0.531	
Lippia javanica	Treatment (3, 98)	3.98	0.419	
	Damage (1, 98)	**19.38**	**<0.001**	**$D_0 > D_1$**
	Interaction (3, 98)	0.82	0.487	
Pseudolachnostylis maprouneifolia	Treatment (3, 83)	0.10	0.962	
	Damage (1, 83)	3.10	0.082	
	Interaction (3, 83)	1.37	0.257	
Terminalia brachystemma	Treatment (3, 53)	0.59	0.623	
	Damage (1, 53)	**75.99**	**<0.001**	**$D_0 > D_1$**
	Interaction (3, 53)	2.41	0.079	
Ziziphus mucronata	**Treatment (3, 69)**	**4.22**	**0.002**	**$E_0 < E_S$**
	Damage (1, 69)	**53.27**	**<0.001**	**$D_0 > D_1$**
	Interaction (3, 69)	0.88	0.456	

[a] E_0 = nil exclusion, E_S = small antelope exclusion; E_L = large antelope exclusion; E_T = total exclusion. D_0 = intact shoots, D_1 = damaged shoots

Table 3.6: GLM ANOVA results for the effects of mechanical damage and exclusion treatment on subsidiary shoot density. Interaction effects between treatment and damage calculated for species where the smallest *N* for any category >5. Significant differences are in boldface, with the source of variation (using Tukey's HSD tests) given in the "Source" column.

Species	Effect (d.f.)	*F*	*p*	Source [a]
Burkea africana	Treatment (3, 66)	0.86	0.467	
	Damage (1, 66)	0.68	0.412	
Flacourtia indica	Treatment (3, 90)	0.50	0.686	
	Damage (1, 90)	0.01	0.930	
	Interaction (3, 90)	0.87	0.461	
Gardenia resiniflua	**Treatment (3, 54)**	**3.61**	**0.020**	**$E_L D_1 \neq E_T D_1$**
	Damage (1, 54)	**14.99**	**<0.001**	**$E_T D_1 \neq E_T D_0$**
	Interaction (3, 54)	**5.41**	**0.003**	**$E_L D_0 \neq E_T D_1$**
Grewia monticola	Treatment (3, 60)	0.53	0.664	
	Damage (1, 60)	2.95	0.092	
	Interaction (3, 60)	0.77	0.516	
Gymnosporia senegalensis	Treatment (3, 105)	1.27	0.288	
	Damage (1, 105)	0.73	0.394	
	Interaction (3, 105)	0.83	0.480	
Lannea discolor	Treatment (3, 39)	0.89	0.454	
	Damage (1, 39)	**5.38**	**0.026**	**$D_0 > D_1$**
Lippia javanica	Treatment (3, 98)	1.50	0.219	
	Damage (1, 98)	3.54	0.063	
	Interaction (3, 98)	1.13	0.341	
Pseudolachnostylis maprouneifolia	Treatment (3, 83)	0.53	0.666	
	Damage (1, 83)	1.22	0.274	
	Interaction (3, 83)	0.68	0.567	
Terminalia brachystemma	Treatment (3, 53)	0.87	0.462	
	Damage (1, 53)	0.13	0.722	
	Interaction (3, 53)	1.00	0.404	
Ziziphus mucronata	Treatment (3, 69)	2.03	0.119	
	Damage (1, 69)	0.08	0.782	
	Interaction (3, 69)	0.10	0.960	

[a] E_0 = nil exclusion, E_S = small antelope exclusion; E_L = large antelope exclusion; E_T = total exclusion. D_0 = intact shoots, D_1 = damaged shoots

Table 3.7: Paired *t*-tests investigating the effect of shoot height above ground (<110 cm and >110 cm; see text) on shoot growth (mm/day) and subsidiary shoot density (shoots/mm primary stem/day) for (a) intact shoots only and (b) damaged shoots only. Only plants which had shoots in each height class were included in the analysis, and tests were not run if N ≤ 5. Significant results (at α = 0.05) are in boldface.

Species	N	Shoot growth			Subsidiary shoot density		
		T	*P*	Effect[a]	*T*	*P*	Effect[a]
(a) Intact shoots							
Burkea africana	37	**-2.86**	**0.007**	**L < H**	0.54	0.594	L > H
Flacourtia indica	6	0.44	0.679	L > H	-0.81	0.454	L < H
Gardenia resiniflua	6	-1.82	0.129	L < H	-2.38	0.063	L < H
Grewia monticola	24	-1.45	0.160	L < H	-1.09	0.286	L < H
Gymnosporia senegalensis	29	-0.70	0.490	L < H	-1.45	0.159	L < H
Lannea discolor	12	**-2.90**	**0.015**	**L < H**	0.42	0.683	L > H
Lippia javanica	9	-0.60	0.563	L < H	-0.42	0.683	L < H
Pseudolachnostylis maprouneifolia	27	**-2.78**	**0.010**	**L < H**	**-3.66**	**0.001**	**L < H**
Terminalia brachystemma	22	-1.56	0.133	L < H	-0.22	0.825	L < H
Ziziphus mucronata	20	0.96	0.350	L > H	-0.46	0.649	L < H
(b) Damaged shoots							
Flacourtia indica	11	-0.50	0.630	L < H	**-2.24**	**0.049**	**L < H**
Grewia monticola	9	0.87	0.410	L > H	-0.76	0.469	L < H
Gymnosporia senegalensis	20	-1.06	0.304	L < H	-0.06	0.952	L < H
Ziziphus mucronata	9	1.21	0.261	L > H	1.27	0.241	L > H

[a] L = shoots below 110 cm from ground; H = shoots above 110 cm from ground

Table 3.8: Gains (+) and losses (-) of woody plant species in accessible (E_0 and E_L) and inaccessible (E_S and E_T) plots between 2006 and 2008. Gains refer to seedlings recruited into the mature height class (>50 cm) in exclusion plots in which that species was not previously recorded. Seeds (or stones) classified as "small" (< 0.5 cm diameter) or "large" (> 0.5 cm diameter).

	Putative categorisation	Species	Seed size	Accessible		Inaccessible	
				Burnt	Unburnt	Burnt	Unburnt
UNPALATABLE SPECIES	Stimulated by fire	*Cassia abbreviata*	Large	+		+	
		Strychnos spinosa	Large	+		+	
		Euclea divinorum	Small		-	+	
	Stimulated by fire & large fauna presence	*Peltophorum africanum*	Large	+			
		Commiphora mollis	Small	+			
	Unclear pattern	*Ptaeroxylon obliquum*				+/-	
PALATABLE SPECIES	Stimulated by fire	*Elaeodendron matebelicum*		+	-		
	Stimulated by fire and exclusion	*Flueggea virosa*	Small			+	
		Grewia monticola	Small			+	
		Lannea discolor	Small			+	
		Parinari sp.	Large			+	
	Stimulated by fire and/or exclusion	*Vangueria* spp.	Small	+		+	+
	Stimulated by exclusion	*Sclerocarya birrea*	Large			+	+
	Sensitive to exclusion	*Pappea capensis*					-
		Ximenia caffra	Large				-
	Unclear pattern	*Bridelia mollis*	Small		+	+	
		Combretum spp.	Small	+/-			
		Ficus spp.	Large		-	-	

Table 3.9: Gains (+) and losses (-) in density of woody plant seedlings in accessible (E_0 and E_L) and inaccessible (E_S and E_T) plots between 2006 and 2008. Seedlings were immature (not stunted) plants <50 cm in height. Seeds classified as "small" (<0.5 cm diameter) or "large" (>0.5 cm diameter). Seedling palatability was not determined.

Putative categorisation	Species	Seed characteristics	Accessible		Inaccessible	
			Burnt	Unburnt	Burnt	Unburnt
Stimulated by fire & exclusion	*Flacourtia indica*	Large	+	-	+	+
Stimulated by fire & fauna presence	*Lippia javanica*	Small	+	-	-	-
	Euclea divinorum	Small	+	-	+/-	+/-
Stimulated by fire	*Dichrostachys cinerea*	Large	+		+	
	Schrebera alata	Large	+		+	
	Strychnos sp.	Large	+		+	
	Ziziphus mucronata	Large	+	-/+	+	
Sensitive to fire and fauna presence	*Gymnosporia senegalensis*	Small	-	+	+	+
Stimulated by exclusion	*Rhus leptodictya*	Small	-		+	
	Vepris reflexa	Small	-		+	
Sensitive to fire	*Bridelia mollis*	Small	-		-	
	Cassia abbreviata	Large	-		-	
	Mimusops zeyheri	Large			-	+
	Ozoroa insignis	Small	-		-	
	Solanum sp.	Small	-	+	-	

Table 3.10: Trends in changes in median circumference (Mood's Median tests, p-values reported) and number of stems (% of 2006) among plot and fire treatments between 2006 and 2007. Key: ↓ = decrease, ≈ = minimal change (<0.5 cm circumference or <5% number), ↑ = increase. Non-significant results denoted by "n.s." and * indicates N<6. Plot codes as per text.

Species	**Plot**	**Δ Circumference (median tests; p-values)**						**Δ Number (%)**					
		Burnt			Unburnt			Burnt			Unburnt		
		↓	≈	↑	↓	≈	↑	↓	≈	↑	↓	≈	↑
B. africana	E_0			**0.002**	n.s.			-58				-4	
	E_L	n.s.					n.s.		5				27
	E_S			n.s.		n.s.		-24					14
	E_T	n.s.				n.s.				11			7
F. indica	E_0	n.s.			n.s.					22		-1	
	E_L	n.s.				n.s.			-8			-8	
	E_S	n.s.			n.s.			-18				5	
	E_T	n.s.				n.s.				14		9	
G. resiniflua	E_0	**<0.001**			**0.011**					108	-47		
	E_L			n.s.	**0.013**				3				67
	E_S		*			n.s.				100			71
	E_T	**<0.001**			n.s.					255			95
G. monticola	E_0	n.s.					n.s.	-22			-15		
	E_L	**0.002**					**0.025**		5		-15		
	E_S			n.s.	n.s.					13		-4	
	E_T		*		n.s.				0		-9		
G. senegalensis	E_0	**<0.001**				n.s.				10			44
	E_L	n.s.			n.s.				5		-11		
	E_S	n.s.			n.s.				-8			5	
	E_T	**<0.001**				n.s.		-18			-23		
L. discolor	E_0	n.s.	.		n.s.					13		0	
	E_L			n.s.	*				8		-17		
	E_S		*				n.s.			375			26
	E_T	n.s.			n.s.					14			47

Continued overleaf

Species	Plot	Δ Circumference (median tests; p-values)						Δ Number (%)					
		Burnt			Unburnt			Burnt			Unburnt		
		↓	≈	↑	↓	≈	↑	↓	≈	↑	↓	≈	↑
P. maprouneifolia	E_0			n.s.			**0.001**	-23			-53		
	E_L	n.s.				n.s.				29		-7	
	E_S	**<0.001**				*				80			120
	E_T			n.s.			**0.011**			40	-33		
P. rotundifolius	E_0	**<0.001**					n.s.			54		0	
	E_L	**<0.001**					n.s.			33	-52		
	E_S			n.s.			n.s.			57	-50		
	E_T	**0.032**					n.s.			49	-30		
Terminalia spp.	E_0	**<0.001**					n.s.			44		-9	
	E_L	n.s.					*		6		-17		
	E_S	**0.015**					**0.018**	-48				-9	
	E_T	n.s.					**0.004**			35	-23		
Z. mucronata	E_0	n.s.				n.s.			-6			-7	
	E_L			n.s.	n.s.			-20				0	
	E_S	n.s.			n.s.					25			27
	E_T		*				n.s.			100		0	

Table 3.11: Trends in changes in median circumference (Mood's Median tests, p-values reported) and number of stems (% of 2007) among plot and fire treatments between 2007 and 2008. Key: ↓ = decrease, ≈ = minimal change (<0.5 cm circumference or <10% number), ↑ = increase. Non-significant results denoted by "n.s." and * indicates N<6. Plot codes as per text.

Species	**Plot**[1]	**Δ Circumference (median tests; p-values)**						**Δ Number (%)**					
		Burnt			Unburnt			Burnt			Unburnt		
		↓	≈	↑	↓	≈	↑	↓	≈	↑	↓	≈	↑
B. africana	E_0			**0.024**	n.s.					78			19
	E_L	n.s.			n.s.					71			38
	E_S	**0.007**			n.s.					47		3	
	E_T	n.s.			n.s.					13			30
F. indica	E_0			n.s.			n.s.			74		-8	
	E_L		n.s.			n.s.				25			26
	E_S	n.s.				n.s.				164			82
	E_T	n.s.				n.s.				100		8	
G. resiniflua	E_0			**<0.001**		n.s.			-1				46
	E_L			n.s.		n.s.		-17					93
	E_S		*		n.s.			-90					25
	E_T			n.s.	n.s.			-38				8	
G. monticola	E_0	n.s.				n.s.				24	-18		
	E_L	n.s.				n.s.				17	-12		
	E_S			n.s.			n.s.	-12				-4	
	E_T		*			n.s.				125			30
G. senegalensis	E_0		n.s.			n.s.			4			9	
	E_L		n.s.			n.s.			0			9	
	E_S	n.s.				n.s.			9			-7	
	E_T		n.s.			n.s.				49			17
L. discolor	E_0	n.s.				n.s.				53			21
	E_L		n.s.		*				-8				80
	E_S			**<0.001**	n.s.			-26					17
	E_T	n.s.			**0.035**					13			91

Continued overleaf

Species	Plot[1]	Δ Circumference (median tests; p-values)						Δ Number (%)					
		Burnt			Unburnt			Burnt			Unburnt		
		↓	≈	↑	↓	≈	↑	↓	≈	↑	↓	≈	↑
P. maprouneifolia	E_0	n.s.				n.s.			-3				22
	E_L			n.s.	n.s.			-21					64
	E_S			n.s.	n.s.			-21			-18		
	E_T	**0.027**			n.s.				-7			10	
P. rotundifolius	E_0		n.s.			n.s.		-27				0	
	E_L	n.s.			n.s.					50		-10	
	E_S			**<0.001**		n.s.			-8			8	
	E_T		n.s.			n.s.		-16				0	
Terminalia spp.	E_0			n.s.	n.s.			-15			-30		
	E_L	**0.010**					*			44			40
	E_S		n.s.			n.s.				27		-4	
	E_T	**0.019**					n.s.			64	-12		
Z. mucronata	E_0	n.s.				n.s.				24	-14		
	E_L	n.s.					n.s.		8			-8	
	E_S	n.s.				n.s.				70		-7	
	E_T		*		n.s.				0		-17		

[1] Burnt E_L used data from Site 2 only, as Site 1 E_L was destroyed in April 2008.

Table 3.12: Trends in changes in median circumference (Mood's Median tests, p-values reported) and number of stems (% of 2006) among plot and fire treatments between 2006 and 2008. Key: ↓ = decrease, ≈ = minimal change (<0.5 cm circumference or <10% number), ↑ = increase. Non-significant results denoted by "n.s." and * indicates N<6. Plot codes as per text.

Species	**Plot**[1]	**Δ Circumference (median tests; p-values)**						**Δ Number (%)**					
		Burnt			Unburnt			Burnt[1]			Unburnt		
		↓	≈	↑	↓	≈	↑	↓	≈	↑	↓	≈	↑
B. africana	E_0			n.s.	n.s.			-25					14
	E_L	n.s.			n.s.					16			75
	E_S	n.s.			n.s.					12			17
	E_T	n.s.			n.s.					25			39
F. indica	E_0	**<0.001**					n.s.			113		-9	
	E_L	**0.019**					n.s.			15			16
	E_S	**<0.001**			**0.002**					118			90
	E_T	**<0.001**				n.s.				129			18
G. resiniflua	E_0	**<0.001**			**<0.001**			-5			-22		
	E_L		*		**0.011**			-47					222
	E_S			n.s.		n.s.		-80					114
	E_T	**<0.001**			n.s.					118			111
G. monticola	E_0	**0.022**				n.s.			-3		-30		
	E_L	**0.001**					n.s.			180	-25		
	E_S			n.s.		n.s.			0			-8	
	E_T		*		n.s.					125			18
G. senegalensis	E_0	**<0.001**				n.s.				15			58
	E_L	n.s.			n.s.			-28				-3	
	E_S	n.s.			n.s.				0			-3	
	E_T	**<0.001**				n.s.				23		-10	
L. discolor	E_0	**0.008**				n.s.				73			21
	E_L			n.s.	n.s.				9				50
	E_S			*	n.s.					250			47
	E_T	n.s.			**0.012**					29			180

Continued overleaf

Species	**Plot**[1]	**Δ Circumference (median tests; p-values)**						**Δ Number (%)**					
		Burnt			Unburnt			Burnt[1]			Unburnt		
		↓	≈	↑	↓	≈	↑	↓	≈	↑	↓	≈	↑
P. maprouneifolia	E_0			n.s.			**0.002**	-26			-43		
	E_L		n.s.		n.s.				5				52
	E_S	**0.011**			*					43			80
	E_T	**0.021**					n.s.			30	-27		
P. rotundifolius	E_0	**<0.001**				n.s.				13		0	
	E_L	n.s.			n.s.					125	-57		
	E_S	**<0.001**					**0.047**			44	-46		
	E_T	**0.038**					n.s.			24	-30		
Terminalia spp.	E_0	**<0.001**			n.s.					22	-36		
	E_L	n.s.					n.s.			63			17
	E_S	**0.001**					**0.017**	-34			-12		
	E_T	**<0.001**					**<0.001**			120	-32		
Z. mucronata	E_0	n.s.				n.s.				17	-20		
	E_L	n.s.					n.s.	-13				-8	
	E_S	n.s.			n.s.					113			18
	E_T		*				n.s.			100	-17		

[1] Burnt E_L used data from Site 2 only, as Site 1 E_L was destroyed in April 2008.

Table 3.13: Percentage herbaceous aerial cover per treatment seasonally. Data are mean ± SE.

Treatment	Burn status	HOT DRY	HOT WET		COOL DRY	
		2006	2007	2008	2007	2008
E_0	Unburnt	63.0 ± 5.2	64.8 ± 3.9	60.0 ± 2.2	61.7 ± 2.9	68.0 ± 3.0
	Burnt			50.5 ± 6.3		54.0 ± 5.7
E_L	Unburnt	49.7 ± 3.0	60.5 ± 3.9	72.0 ± 2.0	65.3 ± 2.1	58.0 ± 6.6
	Burnt			53.0 ± 5.0		51.0 ± 7.3
E_S	Unburnt	58.0 ± 5.5	63.7 ± 5.9	71.6 ± 7.8	61.3 ± 3.5	52.0 ± 7.4
	Burnt			50.0 ± 5.4		57.0 ± 4.7
E_T	Unburnt	57.3 ± 4.8	72.5 ± 4.1	65.0 ± 5.2	61.7 ± 2.8	68.0 ± 8.5
	Burnt			60.0 ± 3.5		59.0 ± 4.2

Table 3.14: Above-ground herbaceous biomass (tonne/ha) per treatment seasonally. Data are mean ± SE.

Treatment	Burn status	HOT DRY	HOT WET		COOL DRY	
		2006	2007	2008	2007	2008
E_0	Unburnt	1.46 ± 0.55	1.43 ± 0.49	0.86 ± 0.24	0.61 ± 0.26	0.42 ± 0.38
	Burnt			0.60 ± 0.32		1.44 ± 0.45
E_L	Unburnt	1.11 ± 0.26	1.93 ± 0.51	0.77 ± 0.37	0.69 ± 0.23	3.05 ± 1.58
	Burnt			1.51 ± 0.95		0.43 ± 0.38
E_S	Unburnt	1.44 ± 0.66	4.42 ± 1.45	0.67 ± 0.25	0.94 ± 0.28	2.94 ± 1.33
	Burnt			1.22 ± 0.49		1.24 ± 0.68
E_T	Unburnt	1.35 ± 0.38	5.13 ± 1.55	4.65 ± 1.38	1.77 ± 0.80	0.20 ± 0.13
	Burnt			1.01 ± 0.44		2.03 ± 0.63

Table 3.15: Percentage herbaceous moribund load per treatment seasonally. Data are mean ± SE.

Treatment	Burn status	HOT DRY	HOT WET		COOL DRY	
		2006	2007	2008	2007	2008
E_0	Unburnt	42.3 ± 5.6	9.0 ± 2.3	15.0 ± 1.6	14.3 ± 2.9	87.0 ± 1.2
	Burnt			2.5 ± 0.4		77.5 ± 1.7
E_L	Unburnt	34.7 ± 3.3	8.4 ± 1.5	11.0 ± 3.6	15.9 ± 5.5	84.0 ± 1.0
	Burnt			2.5 ± 0.3		66.0 ± 4.0
E_S	Unburnt	22.7 ± 3.2	3.9 ± 1.2	12.0 ± 2.6	10.0 ± 1.8	87.0 ± 1.2
	Burnt			2.5 ± 0.4		79.0 ± 1.8
E_T	Unburnt	54.3 ± 5.9	9.3 ± 2.1	11.0 ± 2.6	10.1 ± 1.3	87.0 ± 2.0
	Burnt			2.3 ± 0.3		81.5 ± 1.8

[a] No SE calculated for unburnt site (N = 1). [b] No SE calculated for burnt large antelope exclusion (N = 1).

Table 3.16: Grass species richness (# species encountered) per treatment seasonally. Data are mean ± SE.

Treatment	Burn status	HOT DRY	HOT WET		COOL DRY	
		2006	2007	2008[a]	2007	2008[b]
E_0	Unburnt	11.3 ± 1.3	11.7 ± 2.2	12.0	10.0 ± 2.3	14.0
	Burnt			12.5 ± 1.5		10.0 ± 1.0
E_L	Unburnt	11.3 ± 1.3	10.7 ± 0.7	10.0	10.3 ± 0.9	8.0
	Burnt			13.0 ± 0.0		12.0
E_S	Unburnt	10.0 ± 0.6	11.3 ± 1.2	13.0	9.7 ± 1.5	10.0
	Burnt			13.0 ± 1.0		11.5 ± 2.5
E_T	Unburnt	11.7 ± 1.3	8.0 ± 1.5	11.0	9.7 ± 1.2	6.0
	Burnt			12.5 ± 1.5		13 ± 1.0

[a] No SE calculated for unburnt site (N = 1). [b] No SE calculated for burnt large antelope exclusion (N = 1).

Table 3.17: Simpson's Diversity Indices for grasses in each plot type each season. Data (mean ± SE) from percent aerial cover.

Treatment	Burn status	HOT DRY	HOT WET		COOL DRY	
		2006	2007	2008[a]	2007	2008[b]
E_0	Unburnt	0.713 ± 0.111	0.795 ± 0.010	0.892	0.704 ± 0.123	0.861
	Burnt			0.853 ± 0.003		0.801 ± 0.067
E_L	Unburnt	0.813 ± 0.034	0.798 ± 0.020	0.842	0.781 ± 0.026	0.813
	Burnt			0.869 ± 0.004		0.804
E_S	Unburnt	0.642 ± 0.063	0.744 ± 0.063	0.796	0.778 ± 0.012	0.812
	Burnt			0.844 ± 0.011		0.857 ± 0.053
E_T	Unburnt	0.779 ± 0.023	0.739 ± 0.040	0.813	0.772 ± 0.038	0.636
	Burnt			0.858 ± 0.002		0.834 ± 0.021

[a] No SE calculated for unburnt site (N = 1). [b] No SE calculated for burnt large antelope exclusion (N = 1).

Table 3.18: Number of species of forb encountered per treatment seasonally. Data are mean ± SE.

Treatment	Burn status	HOT DRY	HOT WET		COOL DRY	
		2006	2007	2008[a]	2007	2008[b]
E_0	Unburnt	12.33 ± 2.60	22.33 ± 3.48	28.00	17.00 ± 3.21	26.00
	Burnt			26.00 ± 1.00		15.00 ± 1.00
E_L	Unburnt	14.67 ± 2.33	19.00 ± 1.00	25.00	18.00 ± 0.58	20.00
	Burnt			21.50 + 1.50		18.00
E_S	Unburnt	15.00 ± 2.08	20.00 ± 2.08	27.00	13.00 ± 1.53	10.00
	Burnt			23.50 ± 5.50		20.00 ± 1.00
E_T	Unburnt	16.67 ± 0.67	20.00 ± 3.21	24.00	16.33 ± 3.84	9.00
	Burnt			22.50 ± 2.50		17.50 ± 1.50

[a] No SE calculated for unburnt site (N = 1). [b] No SE calculated for burnt large antelope exclusion (N = 1).

Table 3.19: Forb diversity (Simpson's Diversity Index) for each plot type each season. Data (mean ± SE) derived from count of individuals.

Treatment	Burn status	HOT DRY	HOT WET		COOL DRY	
		2006	2007	2008[a]	2007	2008[b]
E_0	Unburnt	0.666 ± 0.098	0.806 ± 0.082	0.839	0.750 ± 0.104	0.770
	Burnt			0.896 ± 0.004		0.852 ± 0.031
E_L	Unburnt	0.819 ± 0.035	0.847 ± 0.013	0.835	0.759 ± 0.108	0.612
	Burnt			0.879 ± 0.018		0.892
E_S	Unburnt	0.826 ± 0.045	0.868 ± 0.011	0.898	0.777 ± 0.026	0.692
	Burnt			0.901 ± 0.005		0.869 ± 0.013
E_T	Unburnt	0.823 ± 0.030	0.792 ± 0.029	0.898	0.826 ± 0.037	0.521
	Burnt			0.854 ± 0.069		0.857 ± 0.051

[a] No SE calculated for unburnt site (N = 1). [b] No SE calculated for burnt large antelope exclusion (N = 1).

Table 3.20: Forb encounter rate (individuals.m^{-2}) per treatment seasonally. Data are mean ± SE.

Treatment	Burn status	HOT DRY	HOT WET		COOL DRY	
		2006	2007	2008[a]	2007	2008[b]
E_0	Unburnt	10.92 ± 5.27	18.30 ± 9.85	22.85	8.42 ± 3.65	11.50
	Burnt			15.23 ± 3.88		4.65 ± 0.40
E_L	Unburnt	14.38 ± 8.36	17.50 ± 7.56	22.60	11.25 ± 6.45	22.2
	Burnt			16.20 ± 2.65		9.25
E_S	Unburnt	7.30 ± 1.68	11.47 ± 0.56	4.35	5.10 ± 0.70	5.25
	Burnt			18.55 ± 7.35		7.43 ± 0.58
E_T	Unburnt	8.30 ± 0.79	13.37 ± 0.79	9.20	7.45 ± 0.88	2.55
	Burnt			20.60 ± 7.70		9.40 ± 1.25

[a] No SE calculated for unburnt site (N = 1). [b] No SE calculated for burnt large antelope exclusion (N = 1).

Table 3.21: Multiple regression analysis result for herbaceous cover (%). R^2 = 0.490. Lack-of-fit tests not significant at α = 0.1.

REGRESSION				
Predictor	Co-efficient	SE Co-efficient	T	*p*
Constant	-8.59	12.44	-0.69	0.493
Log_{10} grass volume (m^3/ha)	39.34	6.24	6.3	**<0.001**
Herbaceous biomass (tonne/ha)	1.15	0.54	2.12	**0.039**
Forb encounter rate (/m^2)	0.32	0.11	2.79	**0.007**
Grass diversity	19.59	10.09	1.94	0.058

ANOVA					
Source	D.F.	SS	MS	F	*p*
Regression	5	2262.35	452.47	12.15	<0.001
Residual error	53	19.74.25	37.25		
Total	58	4236.60			

Table 3.22: Multiple regression analysis result for herbaceous moribund load (%). R^2 = 0.934. Lack-of-fit tests not significant at α = 0.1.

REGRESSION				
Predictor	Co-efficient	SE Co-efficient	T	*p*
Constant	-147.55	20.26	-7.28	**<0.001**
Weeks since rain	5.65	0.27	21.27	**<0.001**
Season wetness	21.92	2.70	8.11	**<0.001**
Months since burn	0.36	0.06	6.26	**<0.001**
Grass diversity	47.31	13.06	3.62	**0.001**
Log_{10} grass volume (m^3/ha)	24.86	9.96	3.12	**0.003**
Season temperature	4.86	1.70	2.86	**0.006**

ANOVA					
Source	D.F.	SS	MS	F	*p*
Regression	6	47871.3	7978.6	137.68	<0.001
Residual error	52	3013.5	58.0		
Total	58	50884.8			

Table 3.23: Multiple regression analysis result for herbaceous biomass (Box-Cox transformed; tonnes/ha). $R^2 = 0.319$. Lack-of-fit tests not significant at $\alpha = 0.1$.

REGRESSION				
Predictor	Co-efficient	SE Co-efficient	T	*p*
Constant	-3.71	1.25	-2.96	**0.005**
Exclusion	0.78	0.27	2.94	**0.005**
Season moisture	1.33	0.34	3.94	**<0.001**
Weeks since setup	-0.02	0.01	-4.32	**<0.001**
Weeks since rain	0.11	0.03	3.19	**0.002**
Months since burn	-0.01	0.01	-1.67	0.100
Grass diversity	1.70	1.16	1.47	0.149

ANOVA					
Source	D.F.	SS	MS	F	*p*
Regression	6	17.64	2.9398	5.53	<0.001
Residual error	52	27.66	0.5319		
Total	58	45.30			

Table 3.24: Multiple regression analysis result for herbaceous plant (forbs, grasses and sedges combined) species richness. $R^2 = 0.625$; Lack-of-fit tests not significant at $\alpha = 0.1$.

REGRESSION				
Predictor	Co-efficient	SE Co-efficient	T	*p*
Constant	39.68	2.61	6.00	**<0.001**
Season wetness	3.96	0.81	4.92	**<0.001**
Months since burn	-0.09	0.03	-3.28	**0.002**
Clay/silt: sand ratio	28.88	9.05	3.19	**0.002**
Woody base area (/ha)	-0.74	0.17	-4.42	**<0.001**
Exclusion	-6.39	2.37	-2.69	**0.010**
Log_{10} grass volume (m^3/ha)	-8.41	4.46	-1.88	0.065
Season temperature	1.53	0.80	1.92	0.061

ANOVA					
Source	D.F.	SS	MS	F	*p*
Regression	7	1514.41	216.34	10.85	<0.001
Residual error	51	1016.78	19.94		
Total	58	2531.19			

Table 3.25: Multiple regression analysis results for grass species richness. $R^2 = 0.340$; Lack-of-fit tests not significant at $\alpha = 0.1$.

REGRESSION					
Predictor	Co-efficient	SE Co-efficient	T	*p*	
Constant	22.78	2.55	8.94	**<0.001**	
Months since burn	-0.03	0.01	-3.00	**0.004**	
Log_{10} grass volume (m^3/ha)	-3.75	1.80	-2.95	**0.042**	
Woody base area (/ha)	-0.30	0.07	-4.16	**<0.001**	
Exclusion	-3.41	0.97	-3.51	**0.001**	
ANOVA					
Source	D.F.	SS	MS	F	*p*
Regression	4	118.93	29.73	8.47	<0.001
Residual error	54	189.65	3.51		
Total	58	308.58			

Table 3.26: Multiple regression analysis result for forb species richness. $R^2 = 0.559$; Lack-of-fit tests not significant at $\alpha = 0.1$.

REGRESSION					
Predictor	Co-efficient	SE Co-efficient	T	*p*	
Constant	15.25	4.02	3.79	**<0.001**	
Season wetness	3.69	0.63	5.82	**<0.001**	
Clay/silt: sand ratio	20.19	6.71	3.01	**0.004**	
Months since burn	-0.06	0.02	-2.78	**0.008**	
Woody base area (/ha)	-0.43	0.13	-3.23	**0.002**	
Exclusion	-3.92	1.83	-2.14	**0.037**	
Season temperature	1.15	0.62	1.85	0.070	
ANOVA					
Source	D.F.	SS	MS	F	*p*
Regression	6	923.82	153.97	13.27	<0.001
Residual error	52	603.41	11.60		
Total	58	1527.22			

Table 3.27: Multiple regression analysis result for forb encounter rate (individuals.m^{-2}). R^2 = 0.318; Lack-of-fit tests not significant at α = 0.1.

REGRESSION					
Predictor	Co-efficient	SE Co-efficient	T	*p*	
Constant	144.68	59.43	2.43	**0.018**	
Months since burn	-0.16	0.05	-3.97	**<0.001**	
Weeks since rain	-0.41	0.12	-3.37	**0.001**	
Sand: clay ratio	-128.72	61.72	-2.09	**0.042**	
ANOVA					
Source	D.F.	SS	MS	F	*p*
Regression	3	1318.98	439.66	10.02	<0.001
Residual error	55	2413.83	43.89		
Total	58				

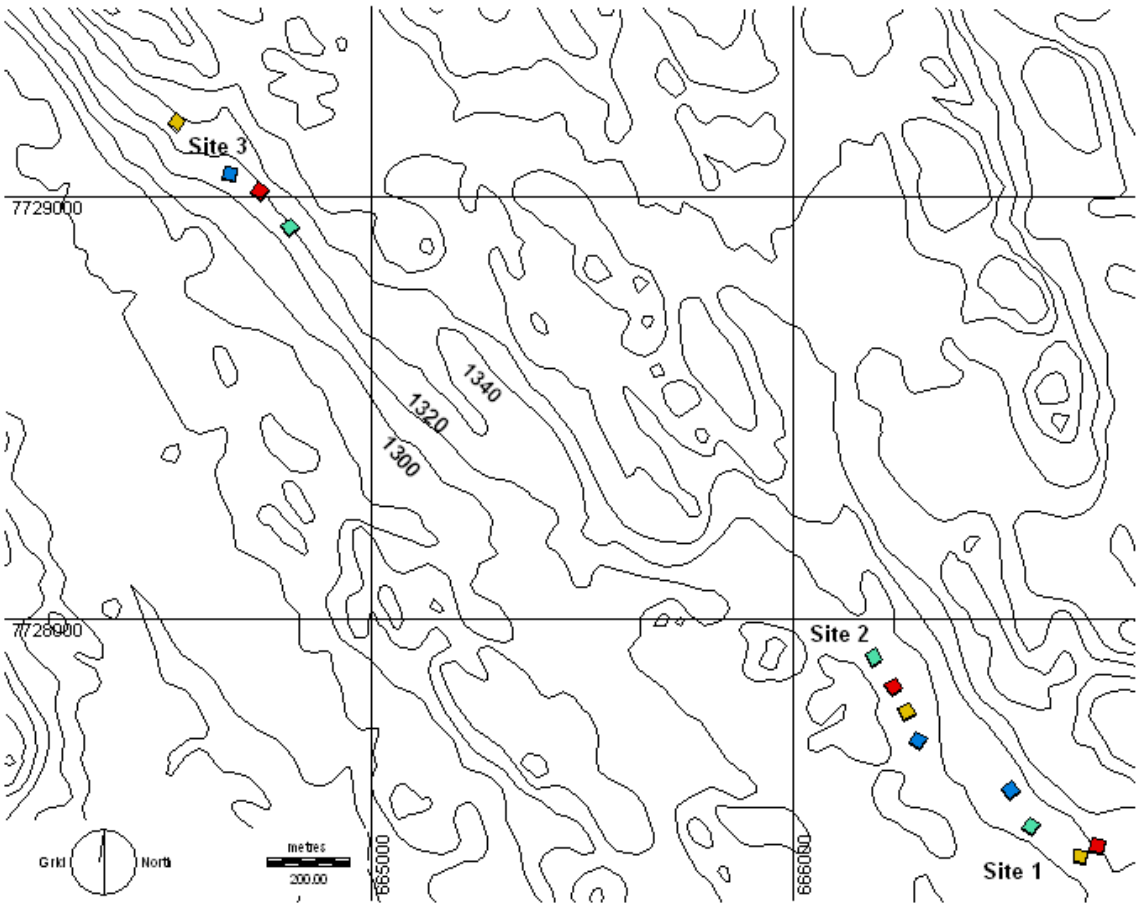


Figure 3.1: Spatial arrangement and topography of the three exclusion plot sites. Sites 1 and 2 were separated by a steep rocky outcrop not evident from contour lines. Plot types are: green = E_0; blue = E_S; yellow = E_L; red = E_T (see text for plot codes). Descriptions of fence designs are given in the text. Map datum is UTM based on modified Arc 1950.

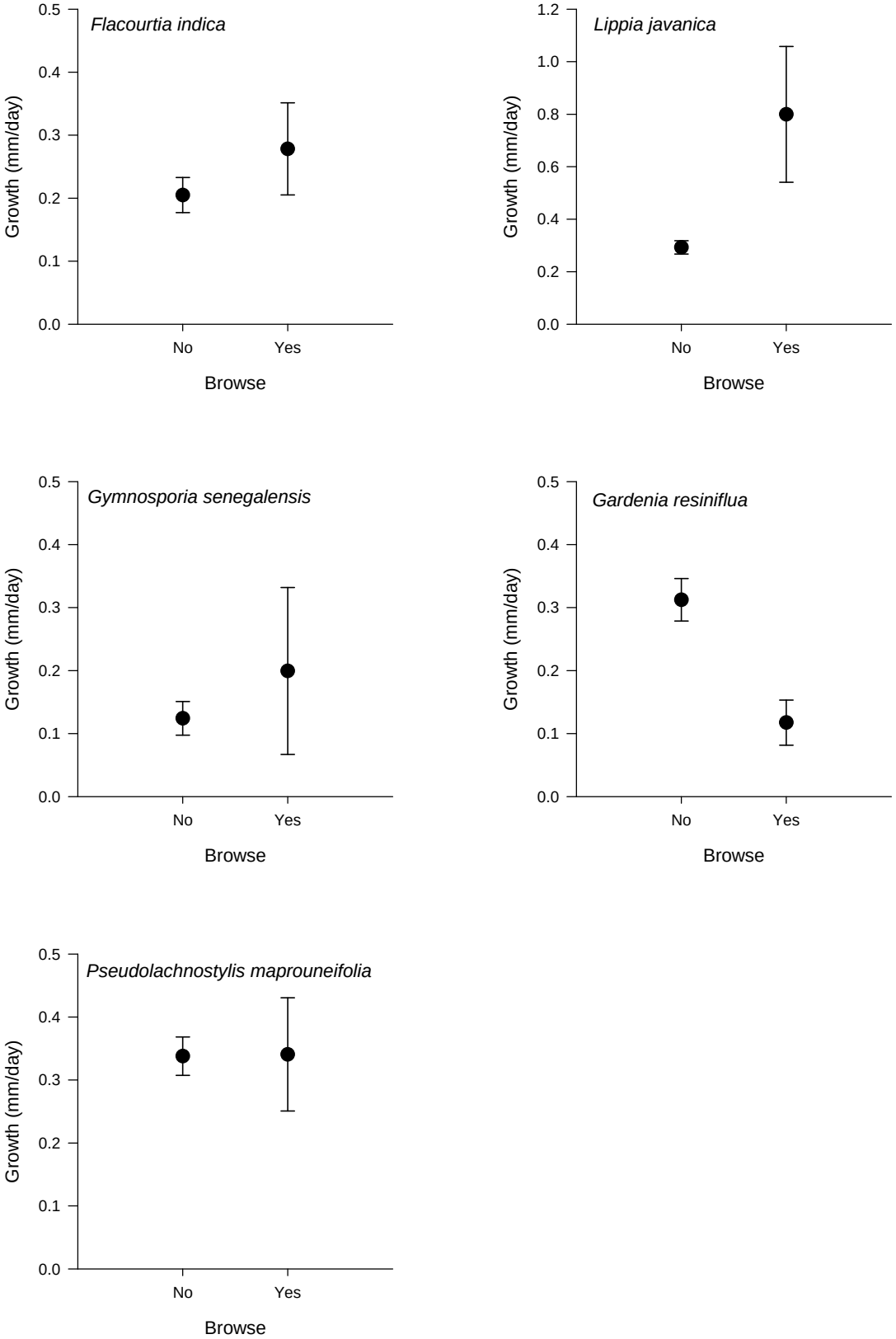


Figure 3.2: Mean growth rates (± SE) of shoots of five species of woody plant categorised by browse damage. Data from all plots pooled.

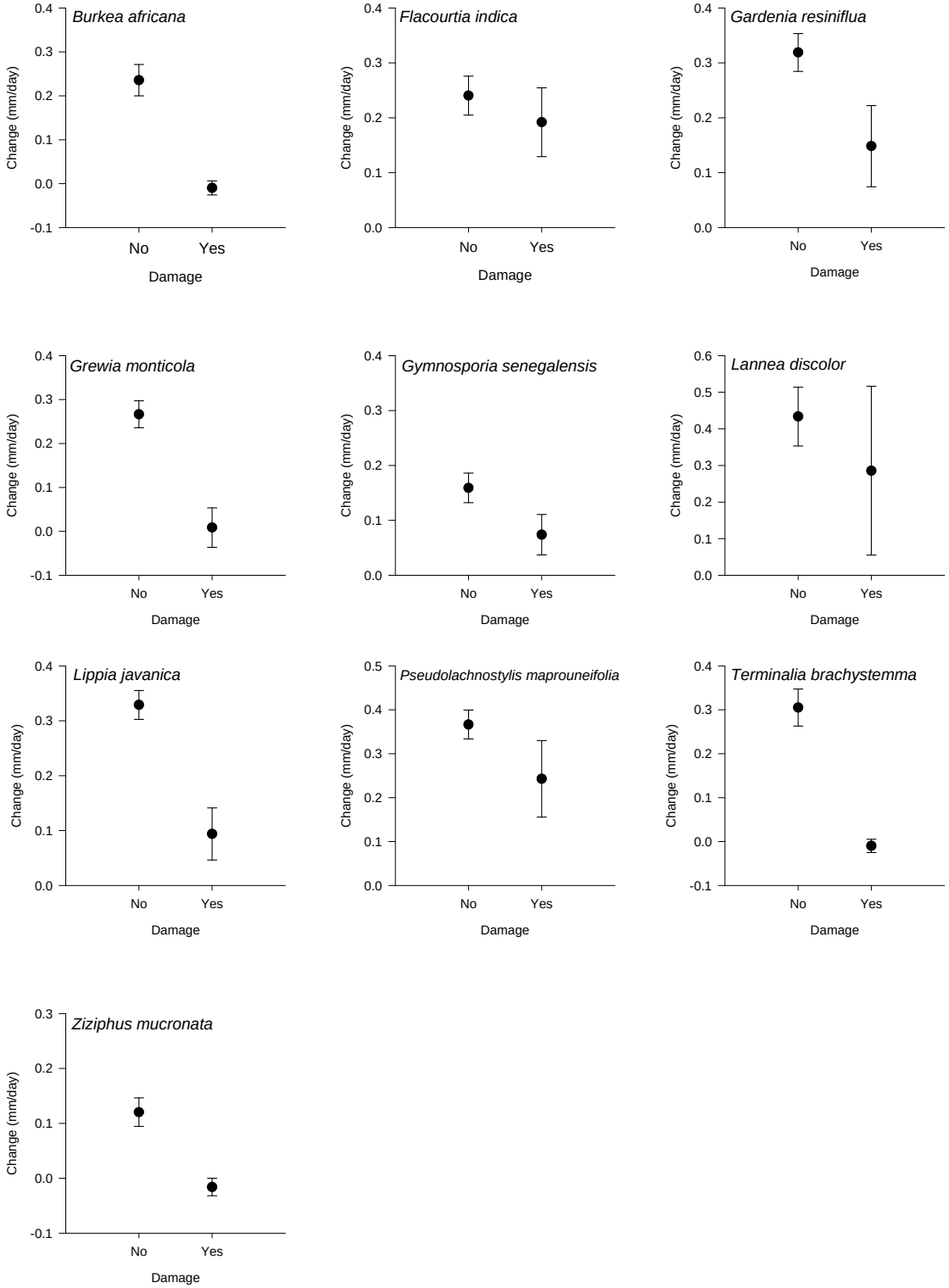


Figure 3.3: Mean (± SE) change in shoot length of selected species categorised by mechanical damage. Data from all plots pooled.

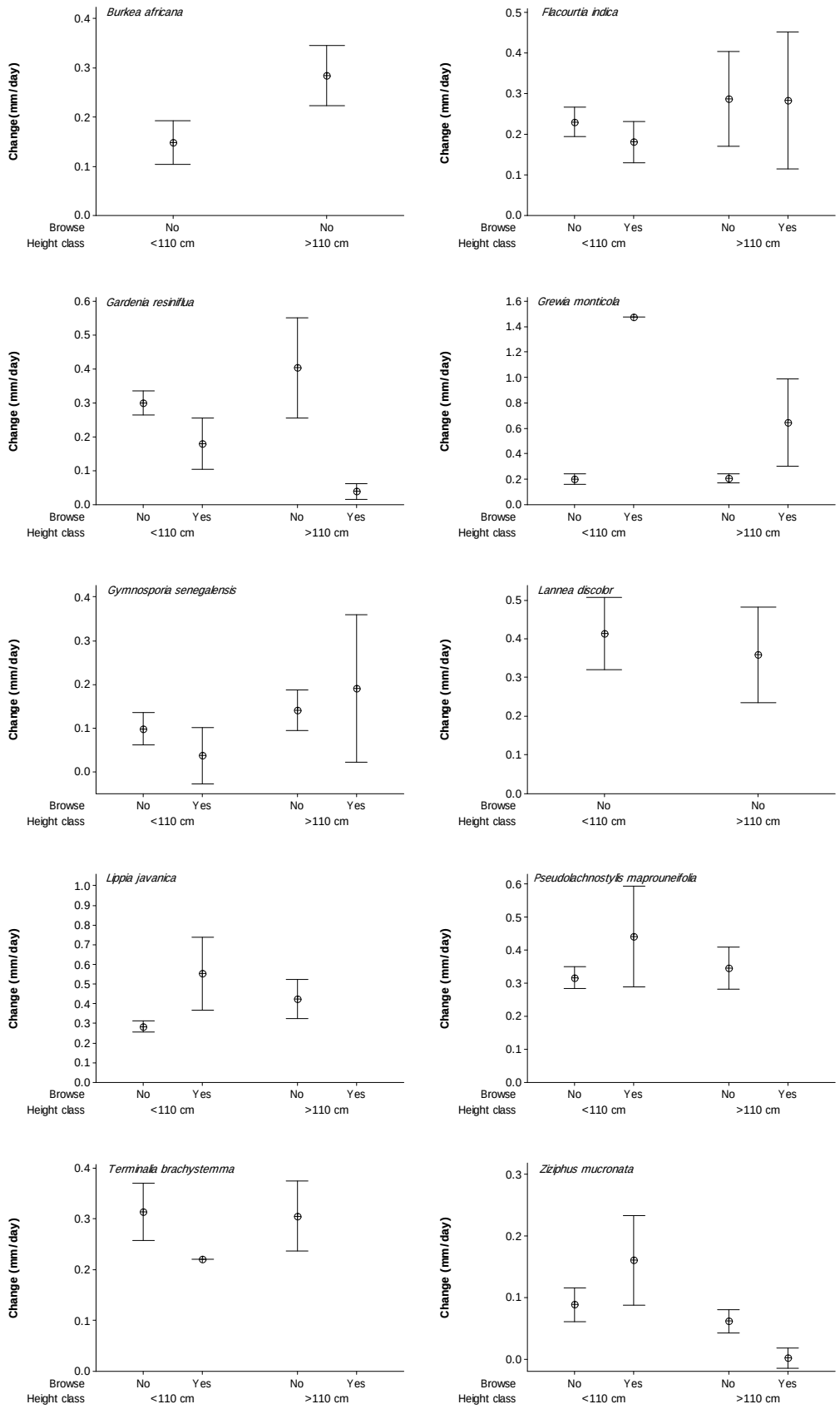
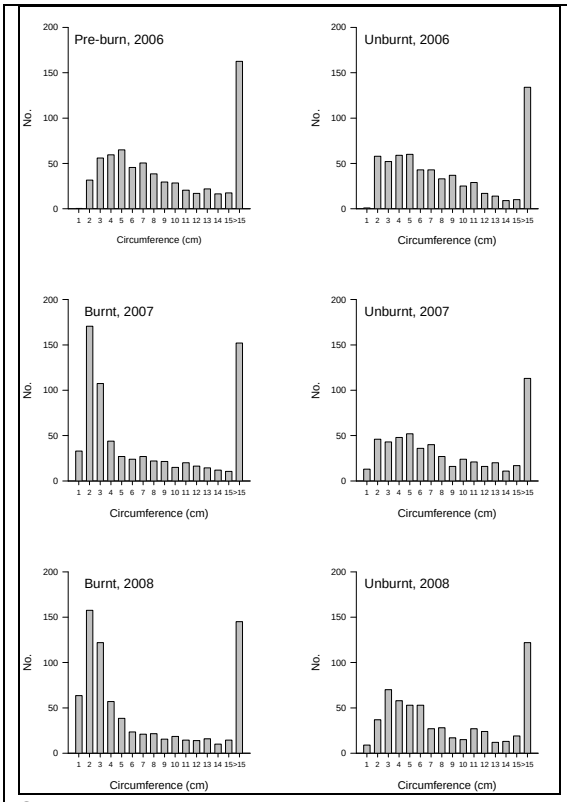
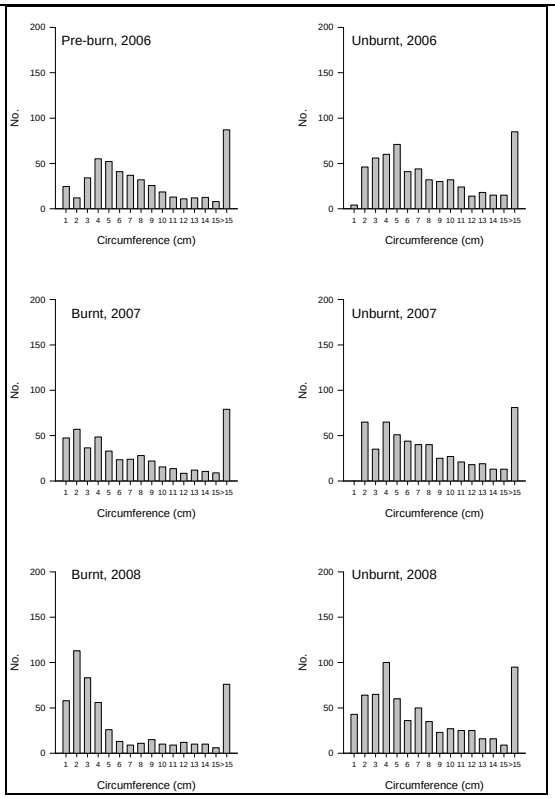


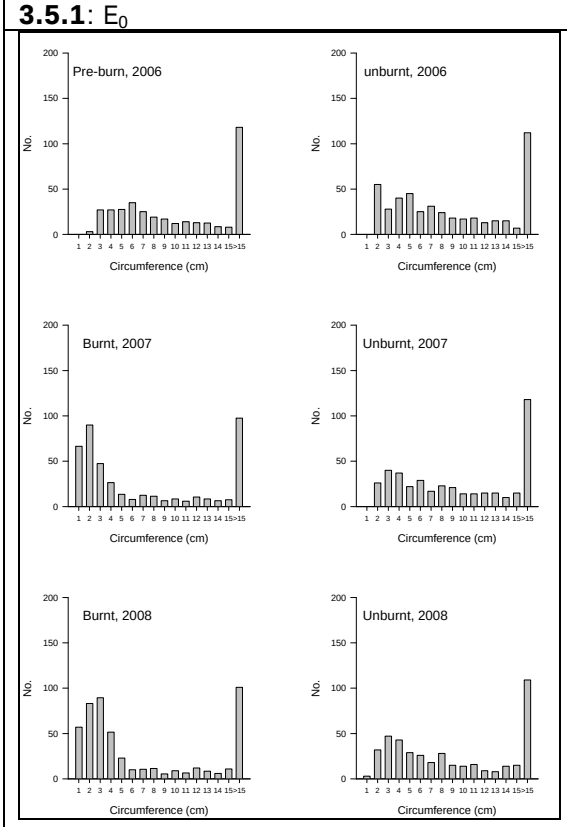
Figure 3.4: Mean growth rates (± SE) of browsed and intact woody plant shoots within the browsing range of all antelope (<110 cm) and large antelope only (>110 cm).



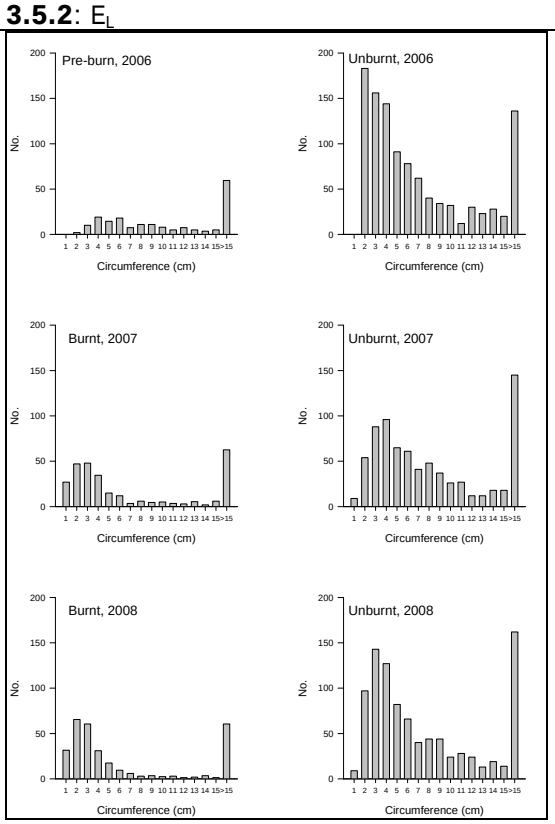
3.5.1: E_0



3.5.2: E_L



3.5.3: E_S



3.5.4: E_T

Figure 3.5: Woody plant stem size distributions in exclusion plots in consecutive years. See text for plot codes.

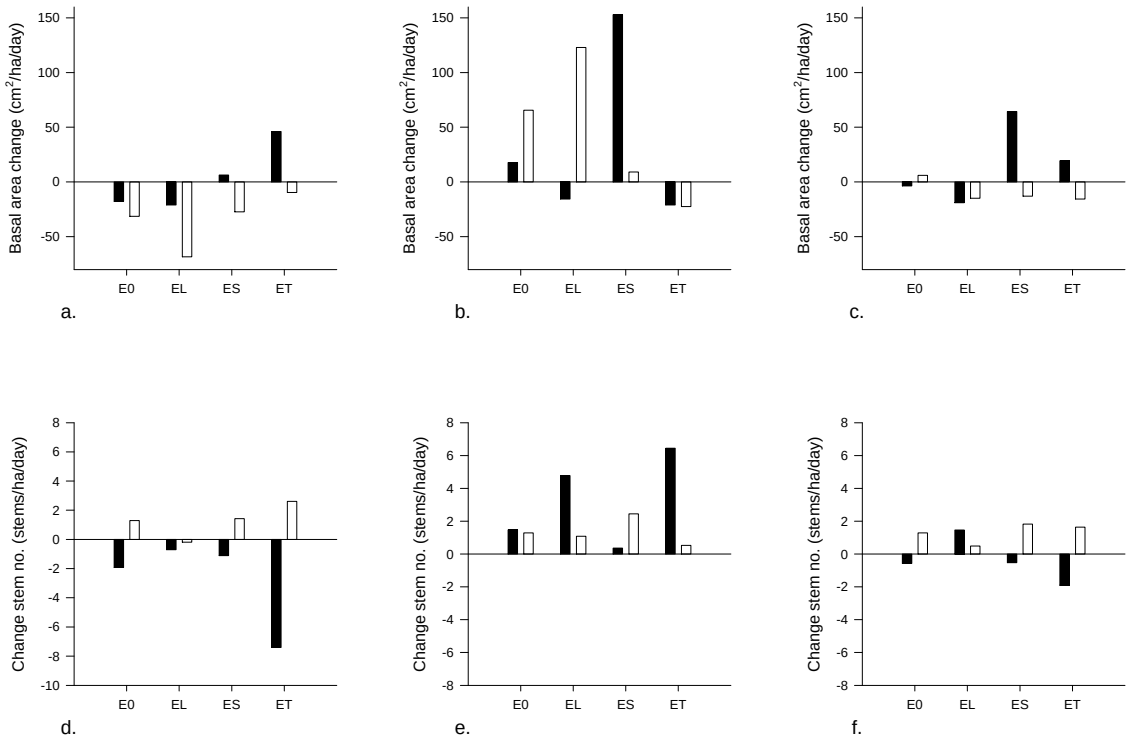


Figure 3.6: Rate of change in basal stem area (cm^2/ha/day; graphs a. to c.) and stem density (stems/ha/day; graphs d. to f.) for all woody plant species between 2006 and 2007 (a., d.), 2007 and 2008 (b., e.) and 2006 and 2008 (c., f.) in burnt (white bars) and unburnt (black bars) plots.

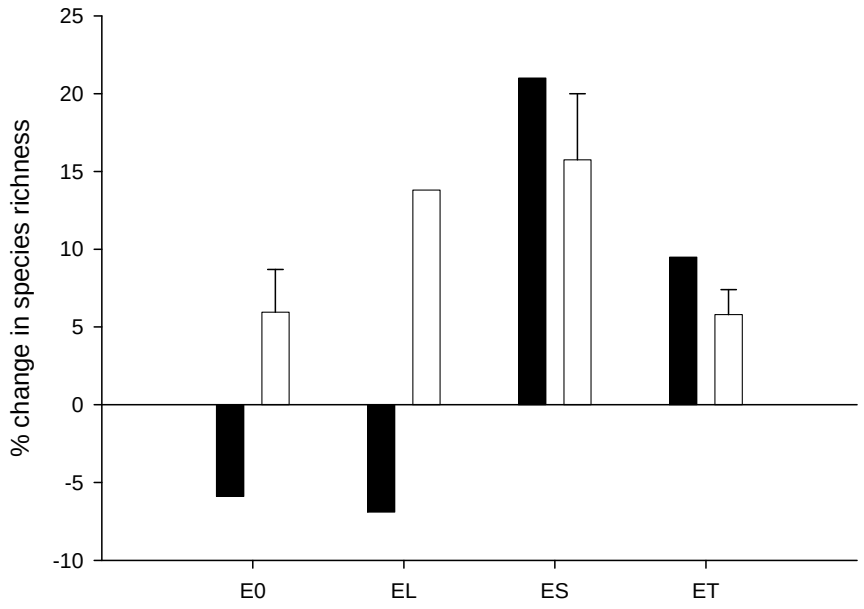


Figure 3.7: Percentage change in woody species richness between 2006 and 2008 in burnt (clear bar) and unburnt (black bar) plots. Burnt plot data are mean ± SE.

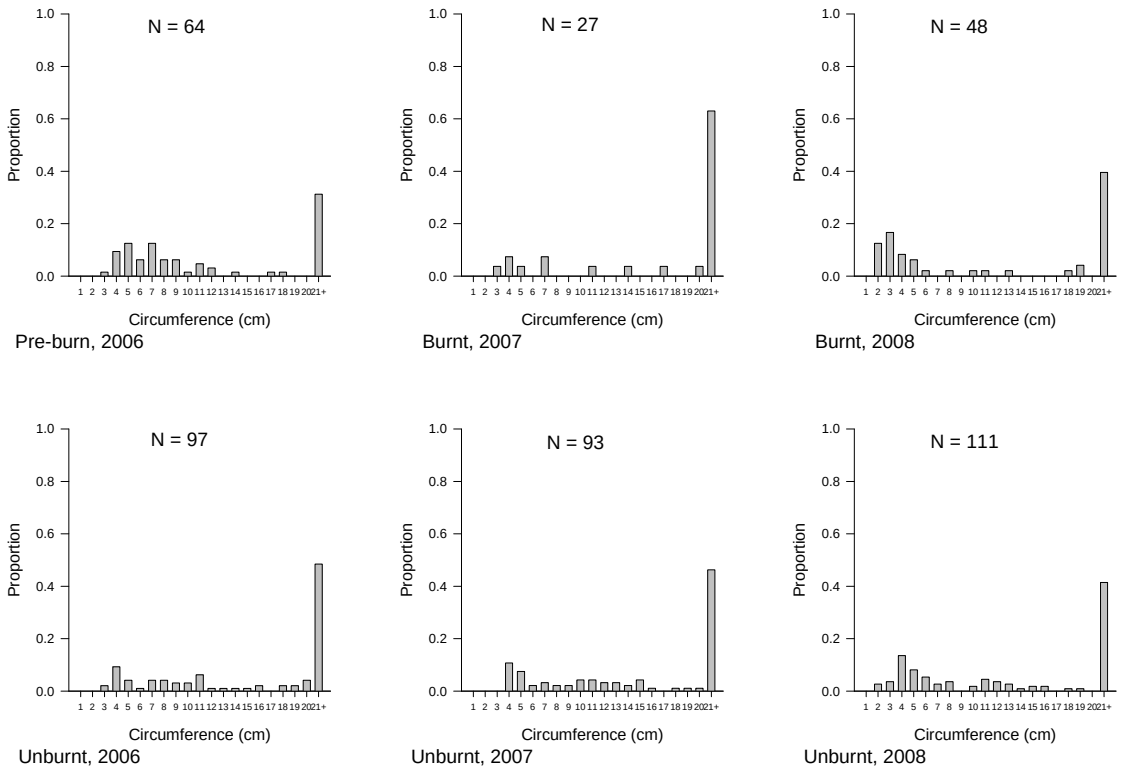


Figure 3.8: Stem size distribution of *Burkea africana* in E_0 plots in consecutive years. Sites 1 and 2 combined ("Burnt" plots), Site 3 ("Unburnt") treated separately.

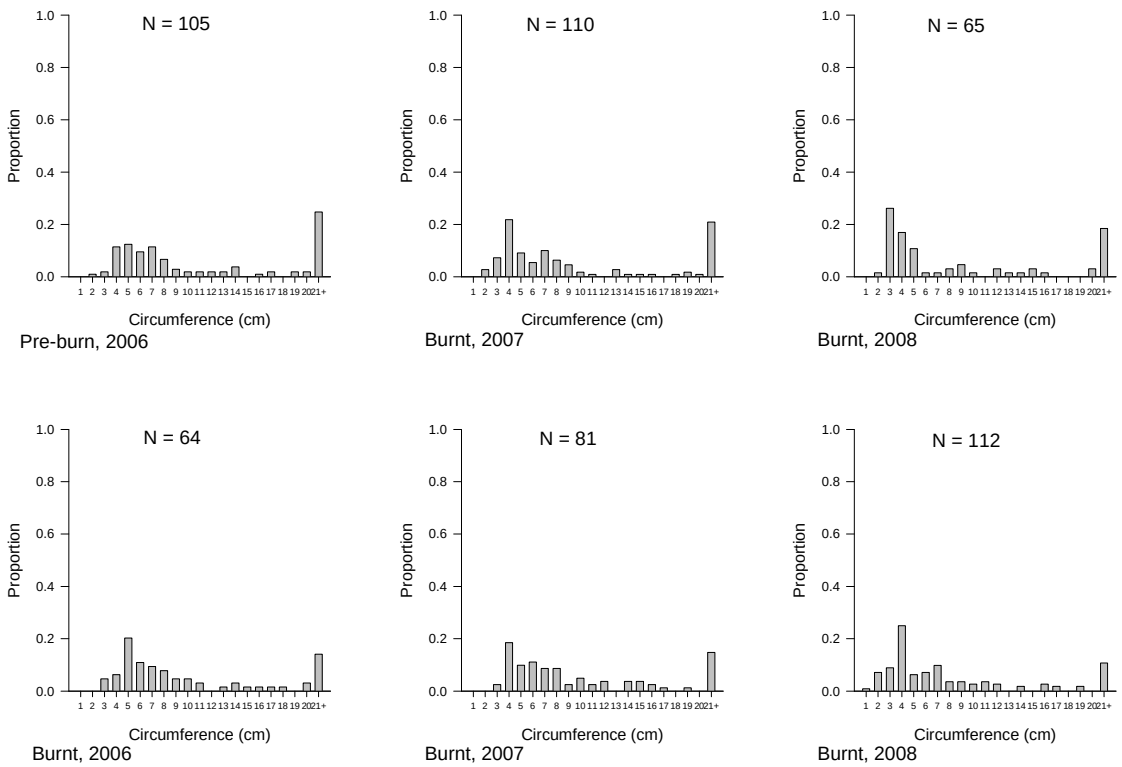


Figure 3.9: Stem size distribution of *Burkea africana* in E_L plots in consecutive years. Sites 1 and 2 combined ("Burnt" plots) except in 2008 when S1 E_L was destroyed, Site 3 ("Unburnt") treated separately.

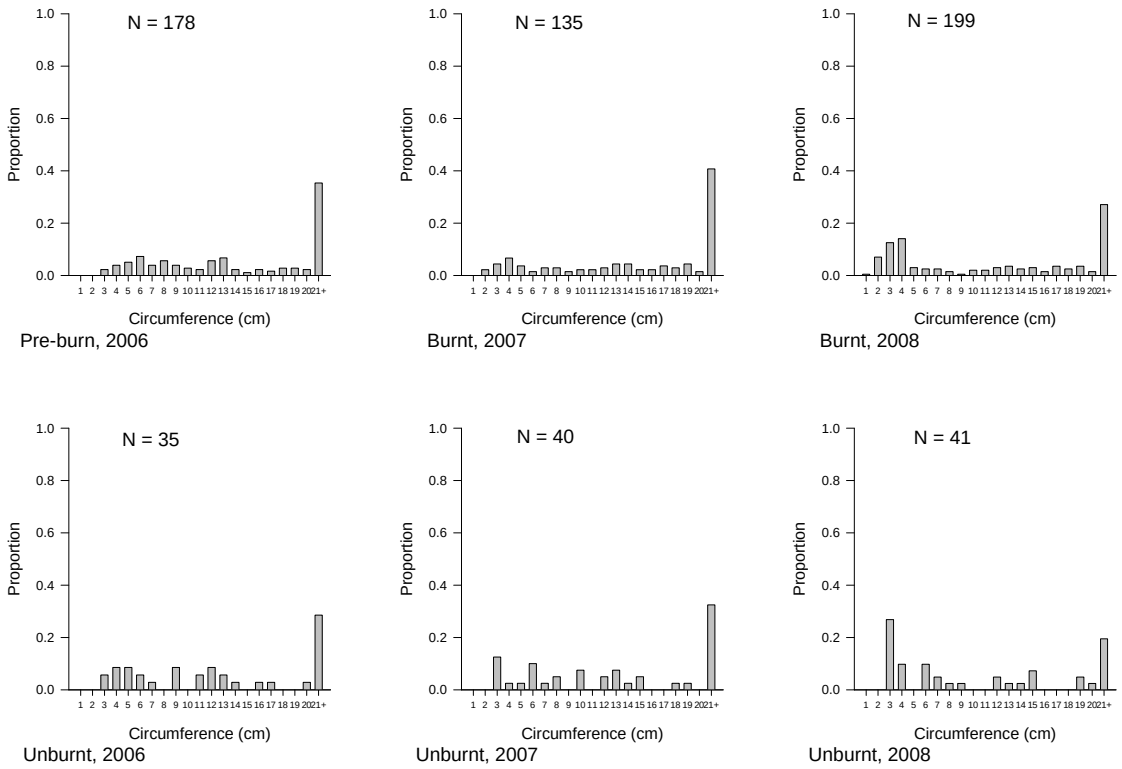


Figure 3.10: Stem size distribution of *Burkea africana* in E_S plots in consecutive years. Sites 1 and 2 combined ("Burnt" plots), Site 3 ("Unburnt") treated separately.

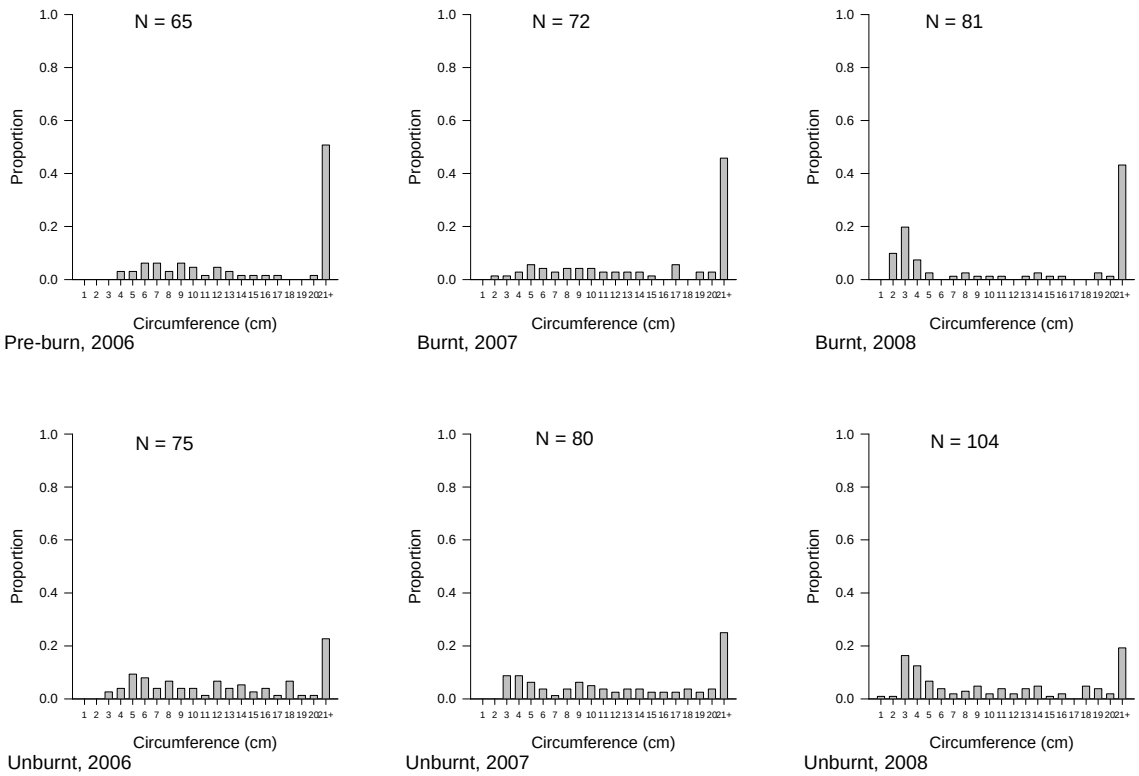


Figure 3.11: Stem size distribution of *Burkea africana* in E_T plots in consecutive years. Sites 1 and 2 combined ("Burnt" plots), Site 3 ("Unburnt") treated separately.

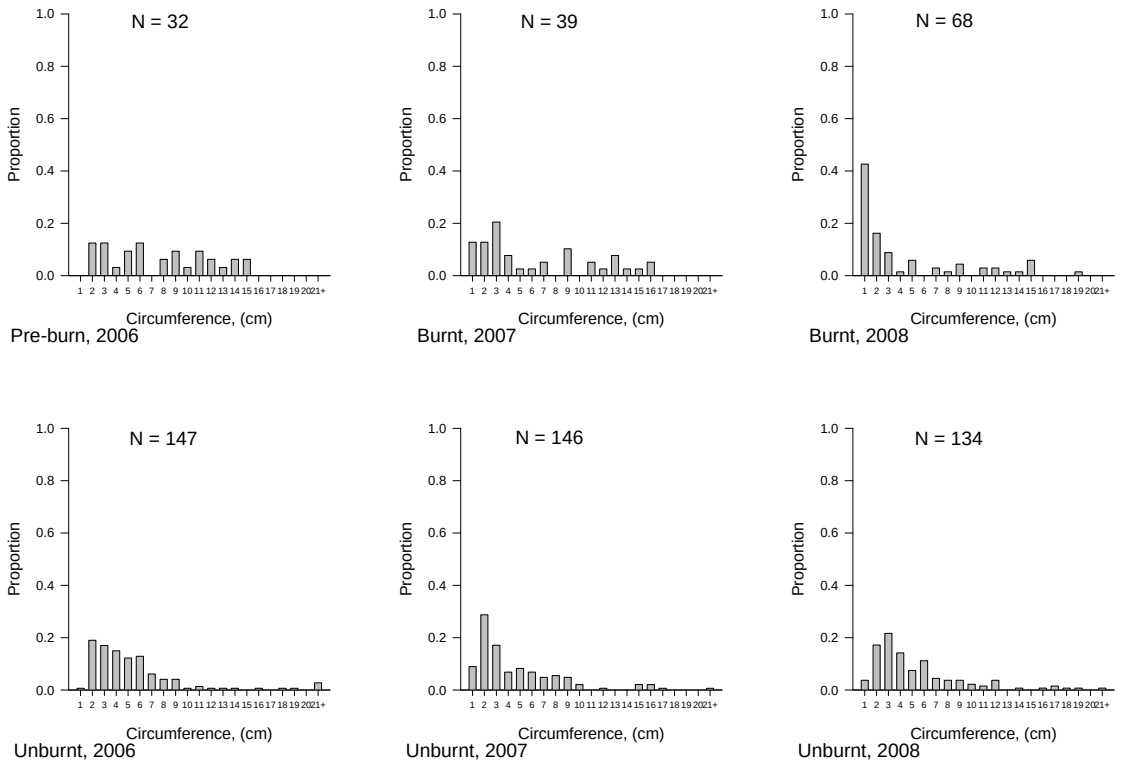


Figure 3.12: Stem size distribution of *Flacourtia indica* in E_0 plots in consecutive years. Sites 1 and 2 combined ("Burnt" plots), Site 3 ("Unburnt") treated separately.

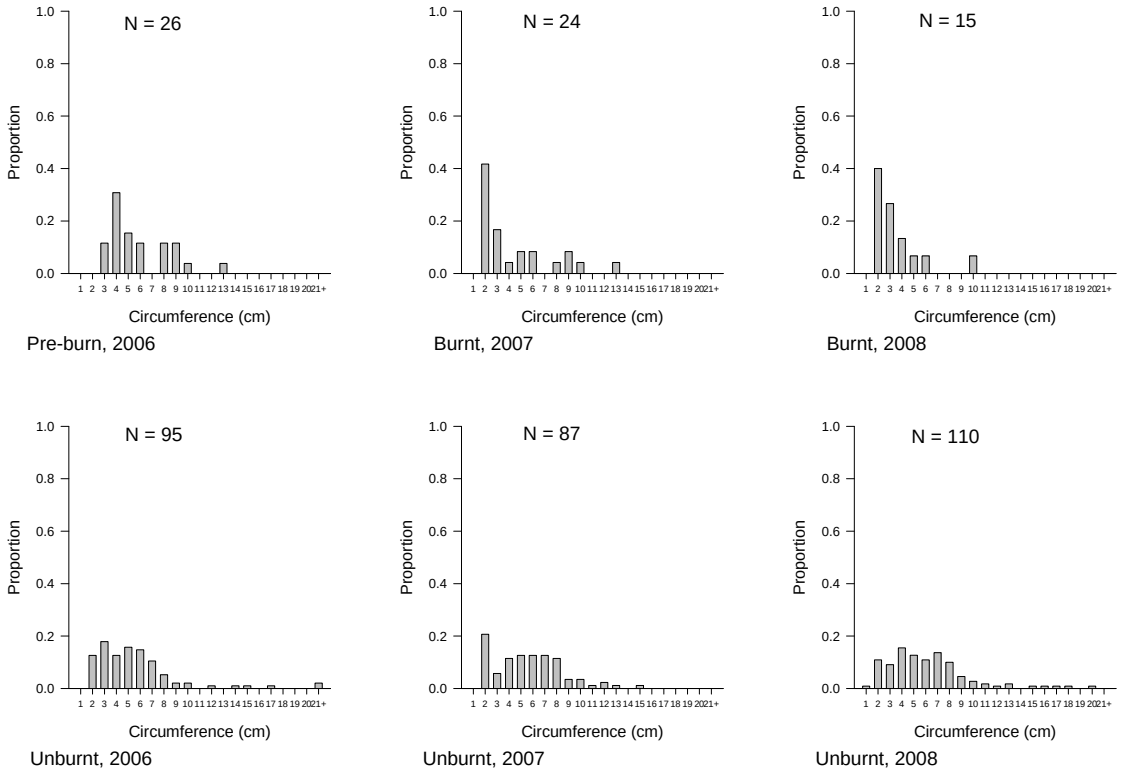


Figure 3.13: Stem size distribution of *Flacourtia indica* in E_L plots in consecutive years. Sites 1 and 2 combined ("Burnt" plots) except in 2008 when S1 E_L was destroyed, Site 3 ("Unburnt") treated separately.

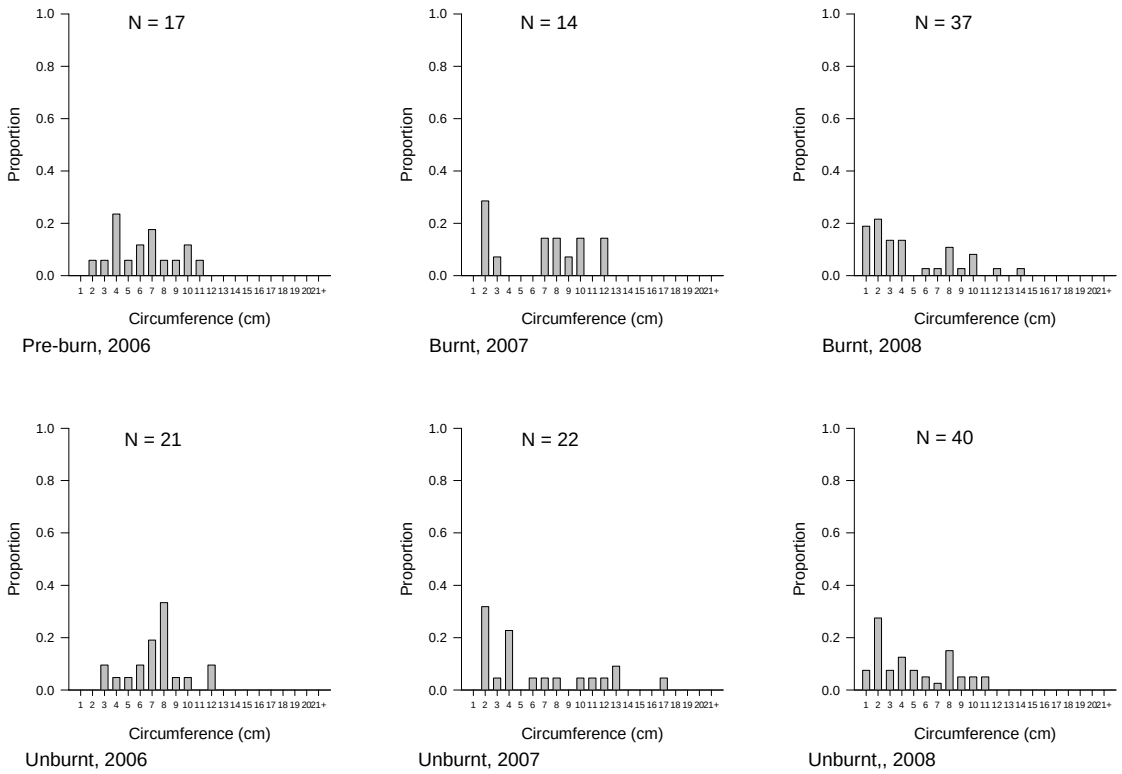


Figure 3.14: Stem size distribution of *Flacourtia indica* in E_S plots in consecutive years. Sites 1 and 2 combined ("Burnt" plots), Site 3 ("Unburnt") treated separately.

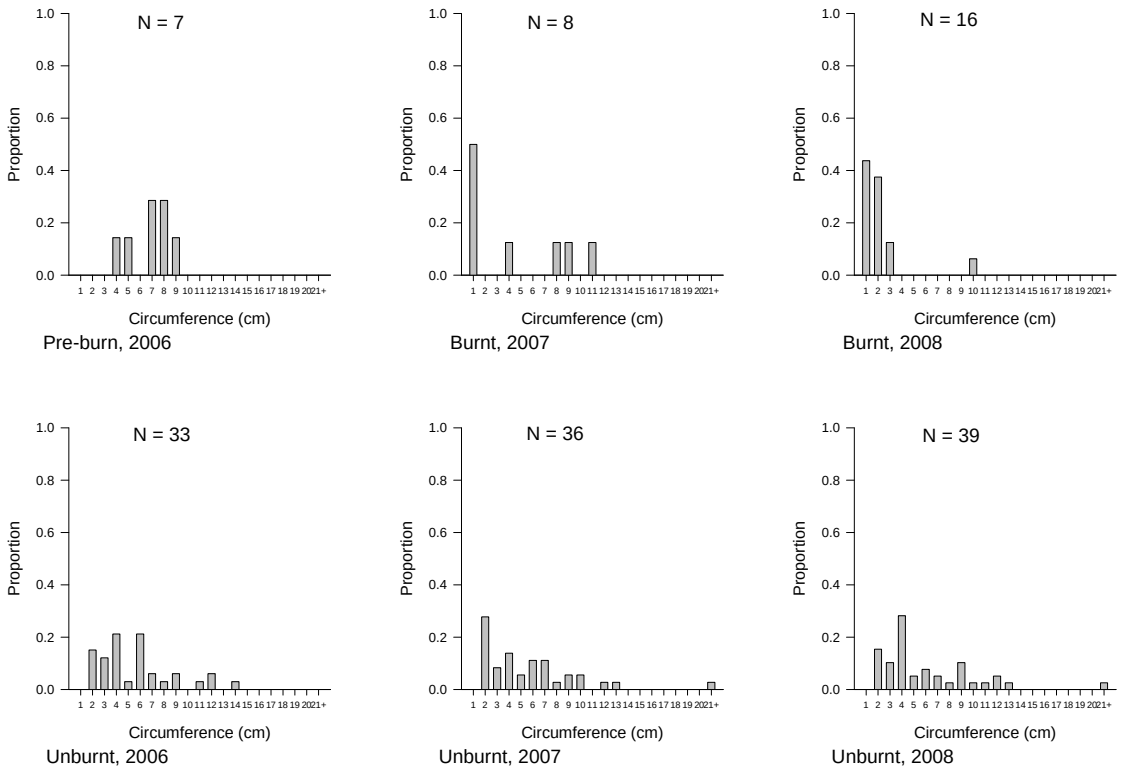


Figure 3.15: Stem size distribution of *Flacourtia indica* in E_T plots in consecutive years. Sites 1 and 2 combined ("Burnt" plots), Site 3 ("Unburnt") treated separately.

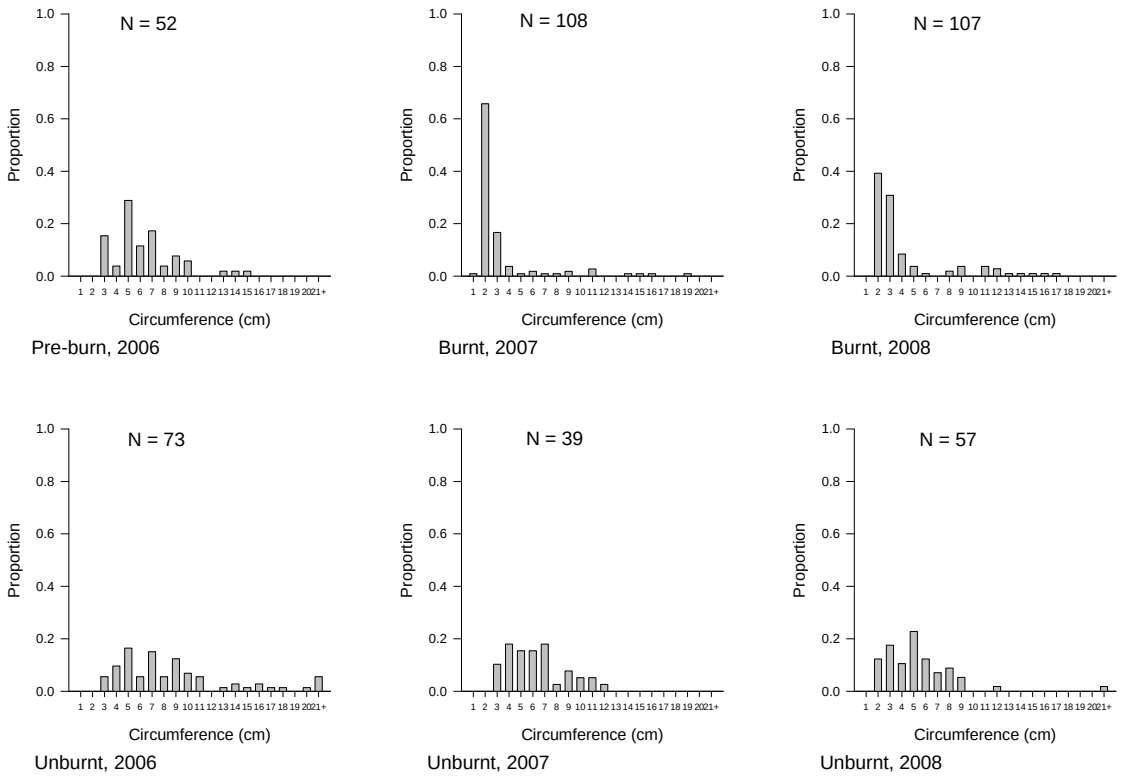


Figure 3.16: Stem size distribution of *Gardenia resiniflua* in E_0 plots in consecutive years. Sites 1 and 2 combined ("Burnt" plots), Site 3 ("Unburnt") treated separately.

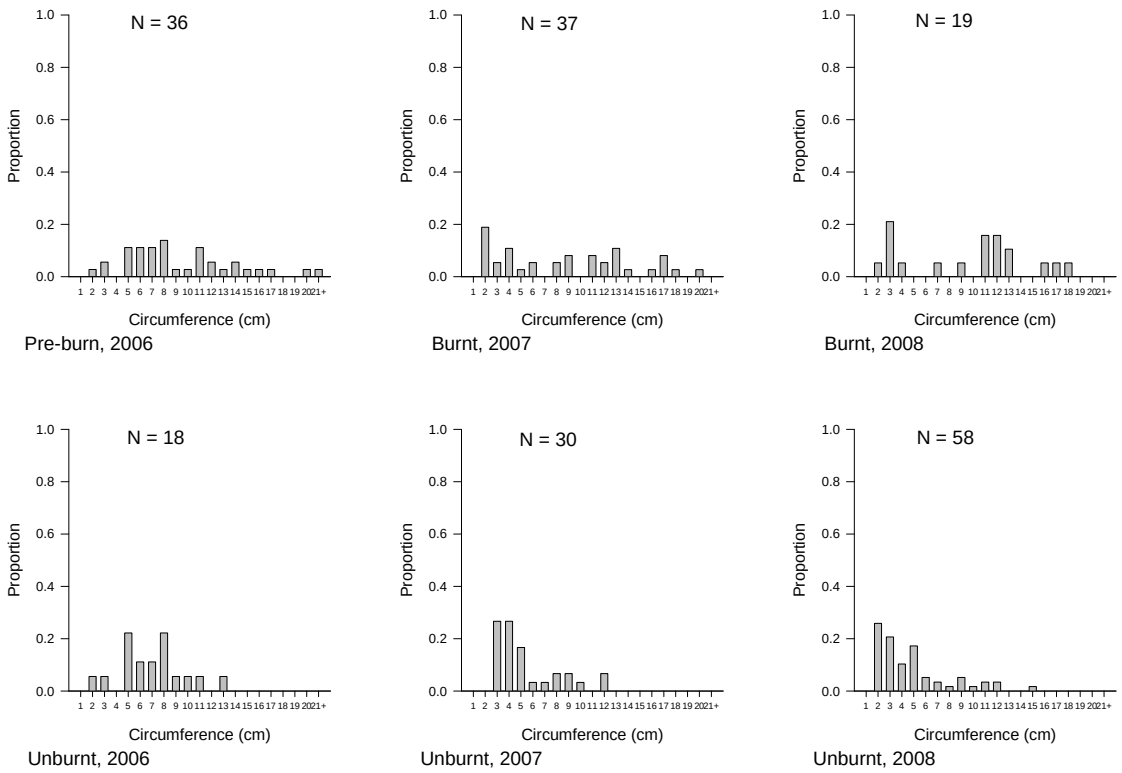


Figure 3.17: Stem size distribution of *Gardenia resiniflua* in E_L plots in consecutive years. Sites 1 and 2 combined ("Burnt" plots) except in 2008 when S1 E_L was destroyed, Site 3 ("Unburnt") treated separately.

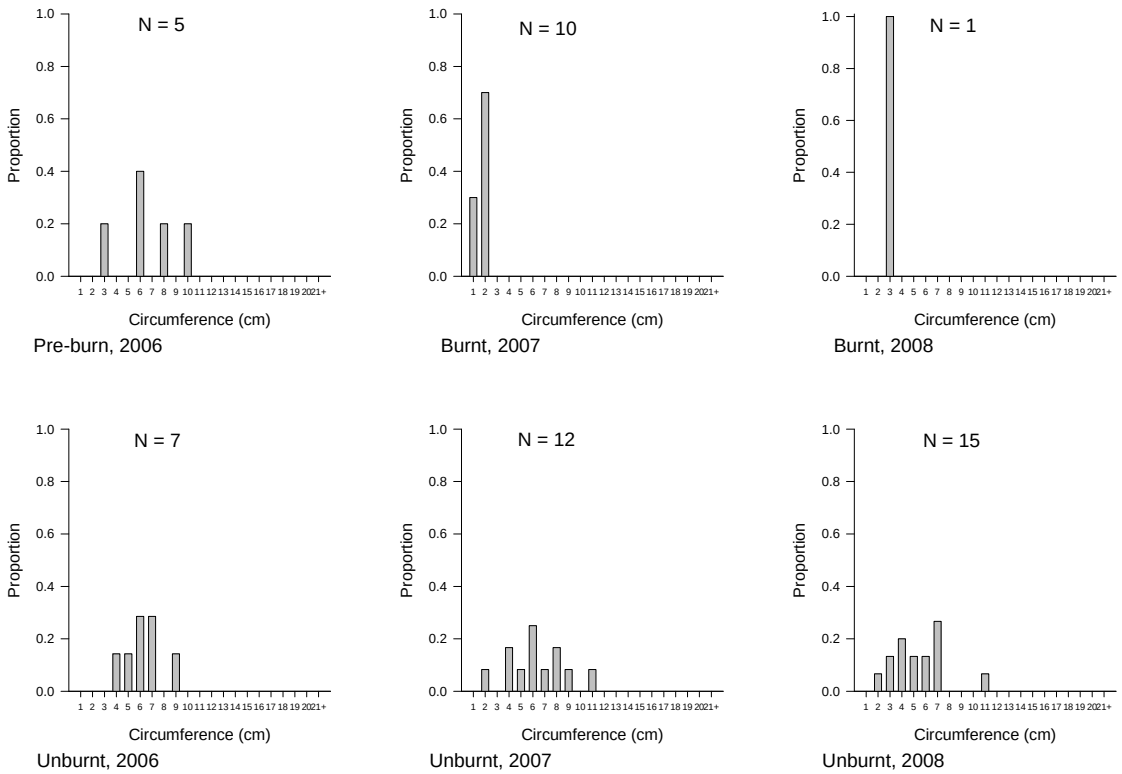


Figure 3.18: Stem size distribution of *Gardenia resiniflua* in E_S plots in consecutive years. Sites 1 and 2 combined ("Burnt" plots), Site 3 ("Unburnt") treated separately.

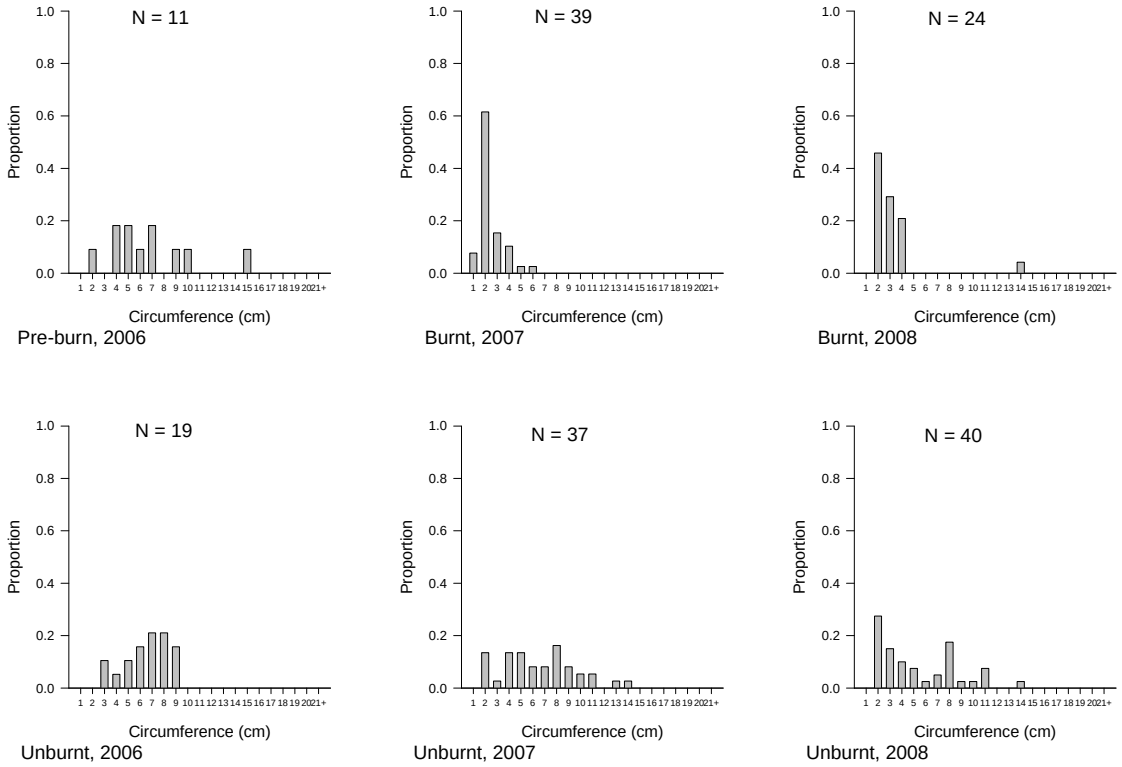


Figure 3.19: Stem size distribution of *Gardenia resiniflua* in E_T plots in consecutive years. Sites 1 and 2 combined ("Burnt" plots), Site 3 ("Unburnt") treated separately.

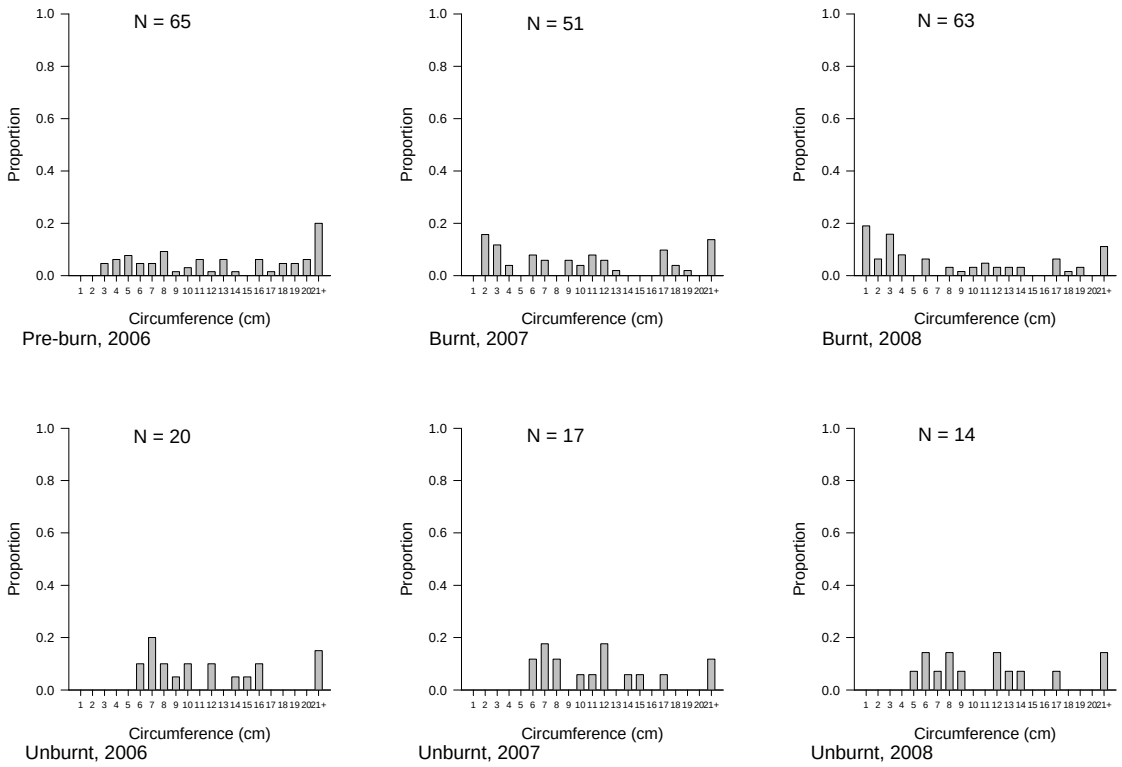


Figure 3.20: Stem size distribution of *Grewia monticola* in E_0 plots in consecutive years. Sites 1 and 2 combined ("Burnt" plots), Site 3 ("Unburnt") treated separately.

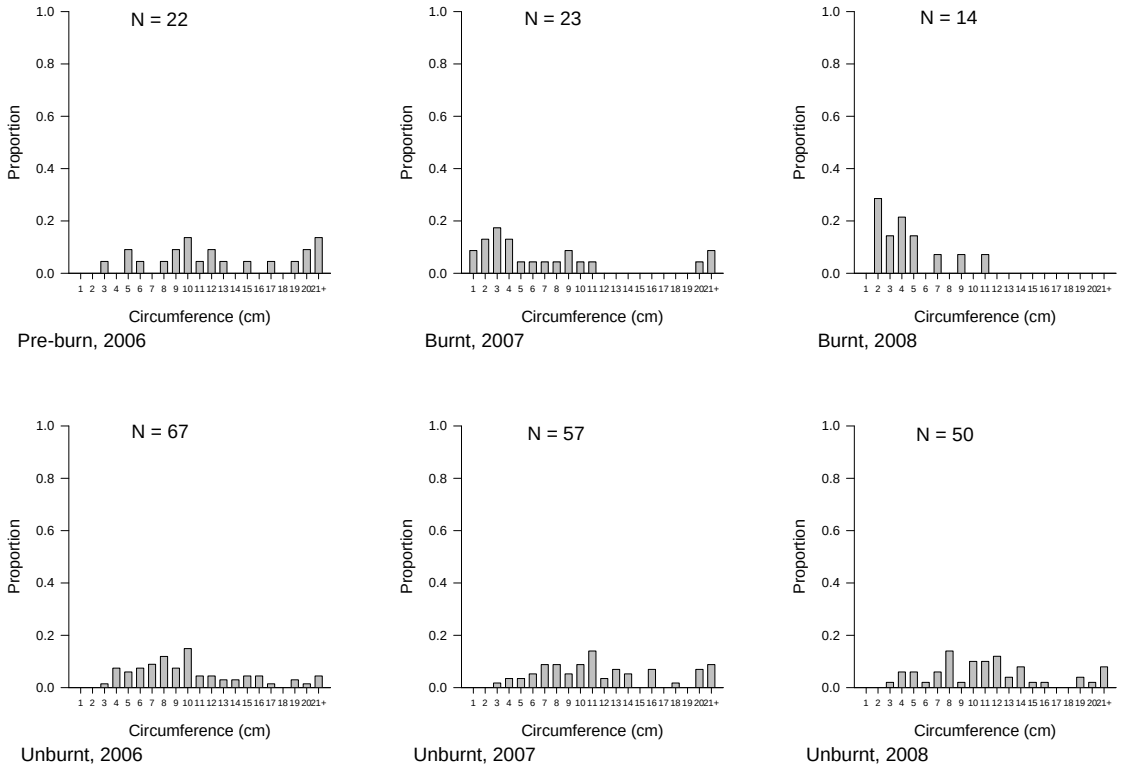


Figure 3.21: Stem size distribution of *Grewia monticola* in E_L plots in consecutive years. Sites 1 and 2 combined ("Burnt" plots) except in 2008 when S1 E_L was destroyed, Site 3 ("Unburnt") treated separately.

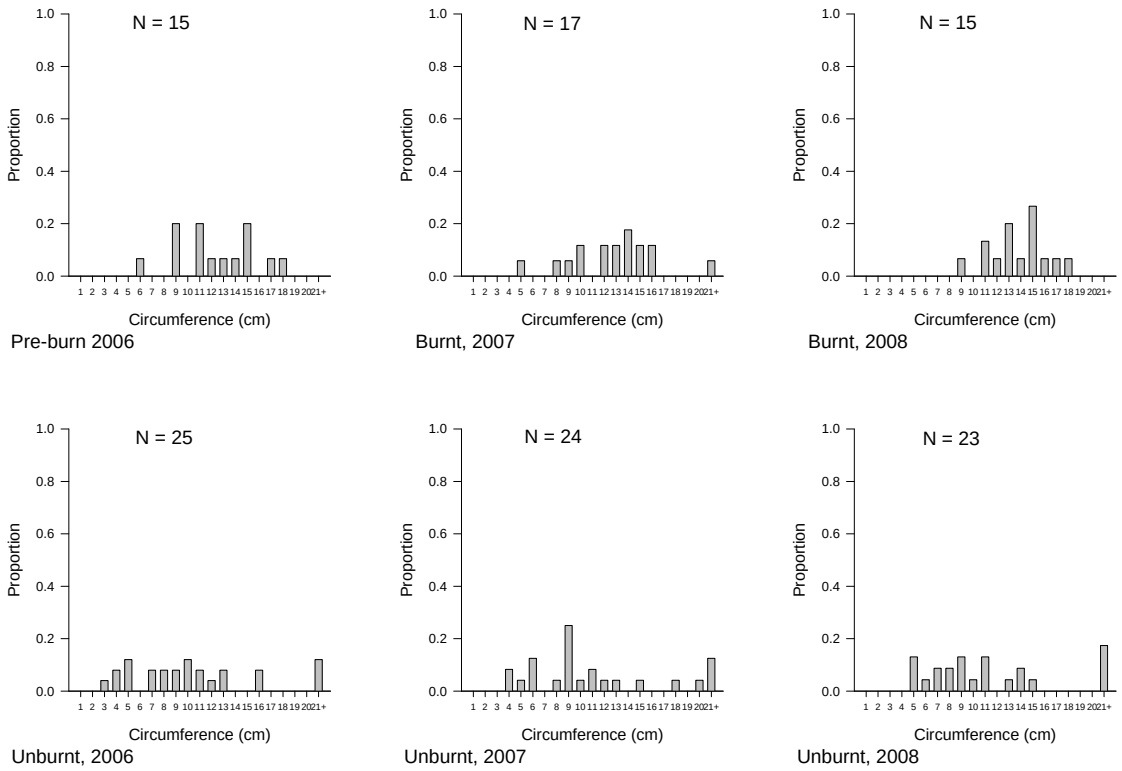


Figure 3.22: Stem size distribution of *Grewia monticola* in E_S plots in consecutive years. Sites 1 and 2 combined ("Burnt" plots), Site 3 ("Unburnt") treated separately.

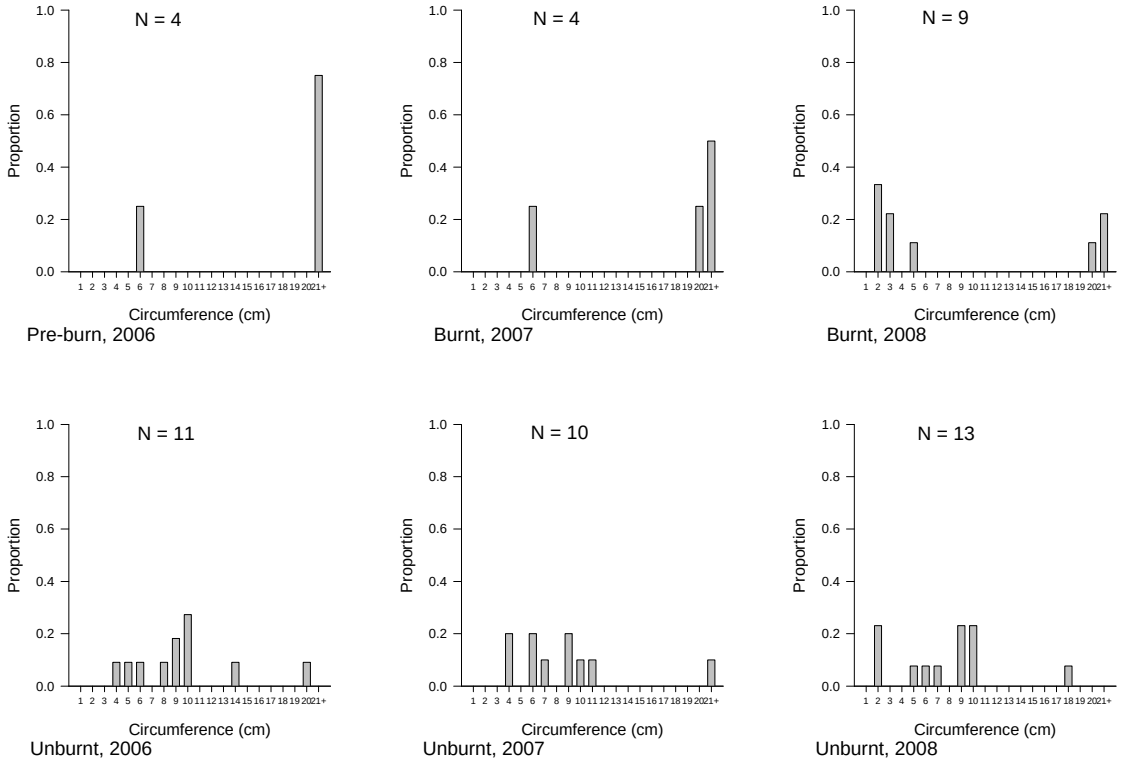


Figure 3.23: Stem size distribution of *Grewia monticola* in E_T plots in consecutive years. Sites 1 and 2 combined ("Burnt" plots), Site 3 ("Unburnt") treated separately.

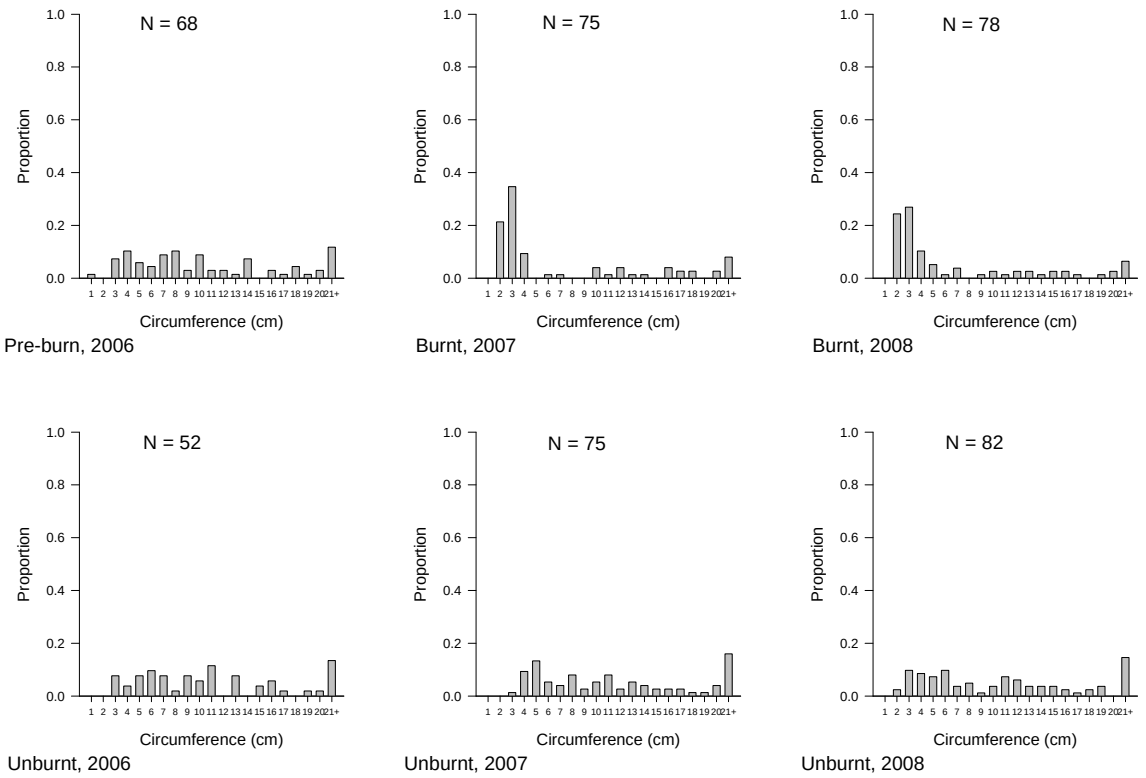


Figure 3.24: Stem size distribution of *Gymnosporia senegalensis* in E_0 plots in consecutive years. Sites 1 and 2 combined ("Burnt" plots), Site 3 ("Unburnt") treated separately.

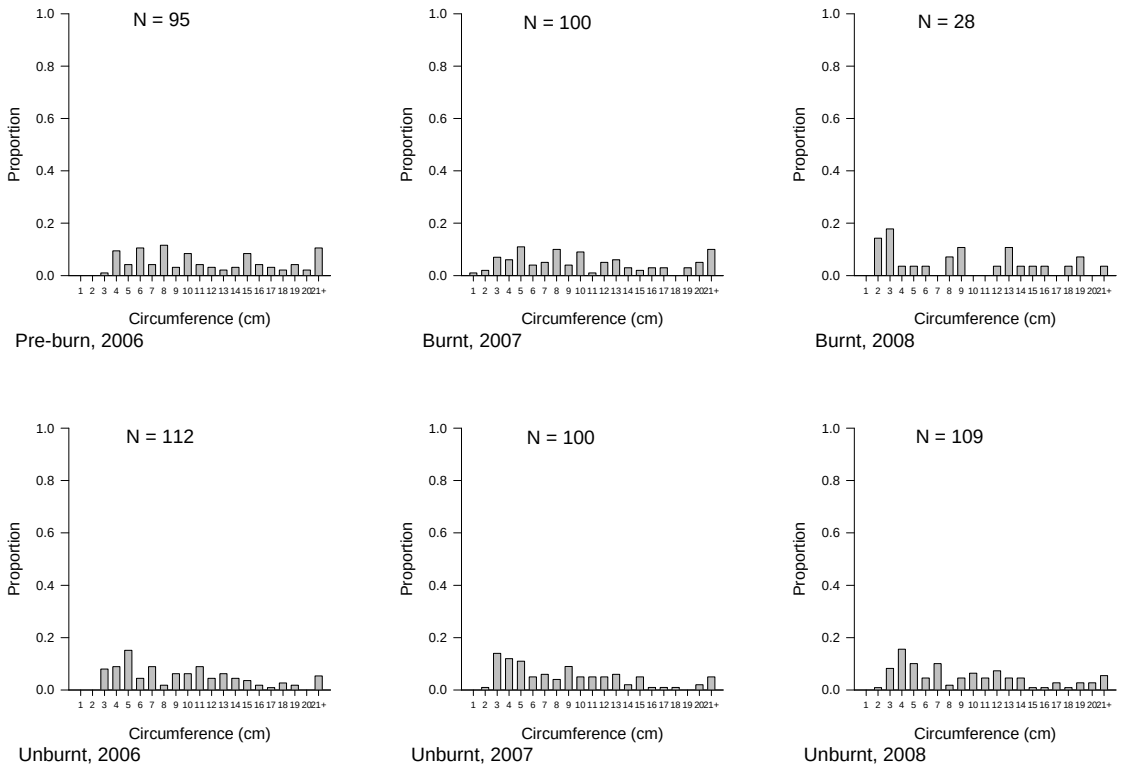


Figure 3.25: Stem size distribution of *Gymnosporia senegalensis* in E_L plots in consecutive years. Sites 1 and 2 combined ("Burnt" plots) except in 2008 when S1 E_L was destroyed, Site 3 ("Unburnt") treated separately.

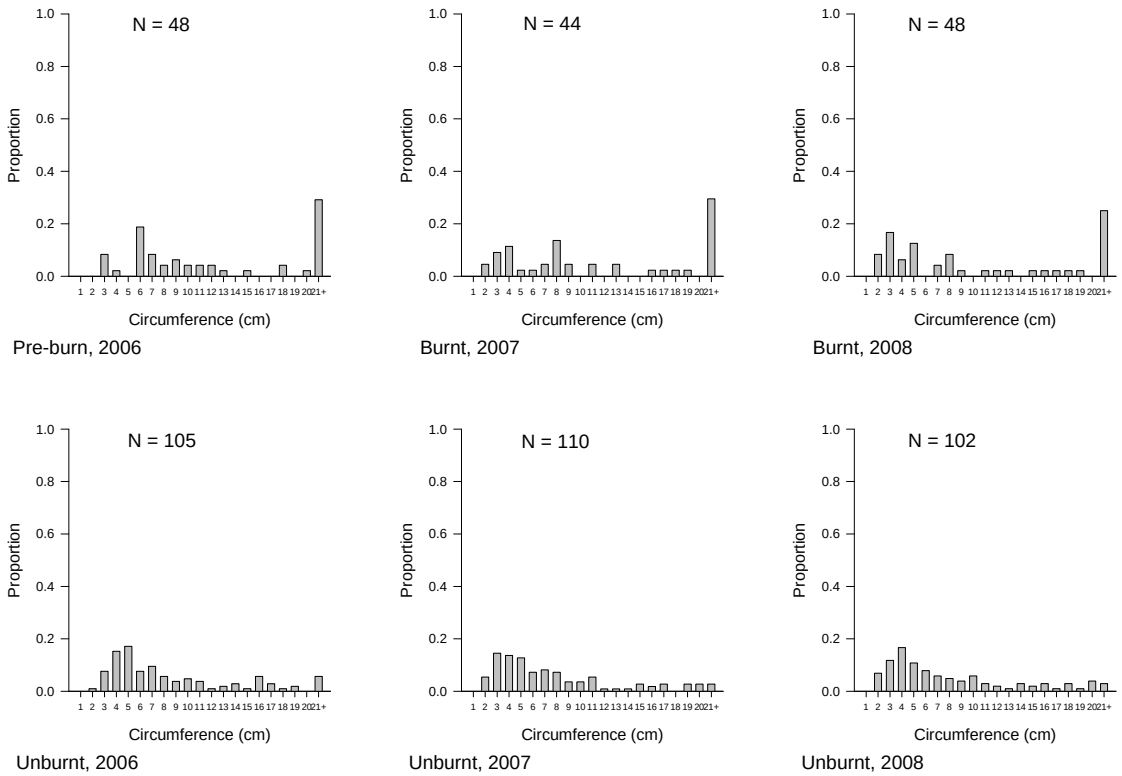


Figure 3.26: Stem size distribution of *Gymnosporia senegalensis* in E_S plots in consecutive years. Sites 1 and 2 combined ("Burnt" plots), Site 3 ("Unburnt") treated separately.

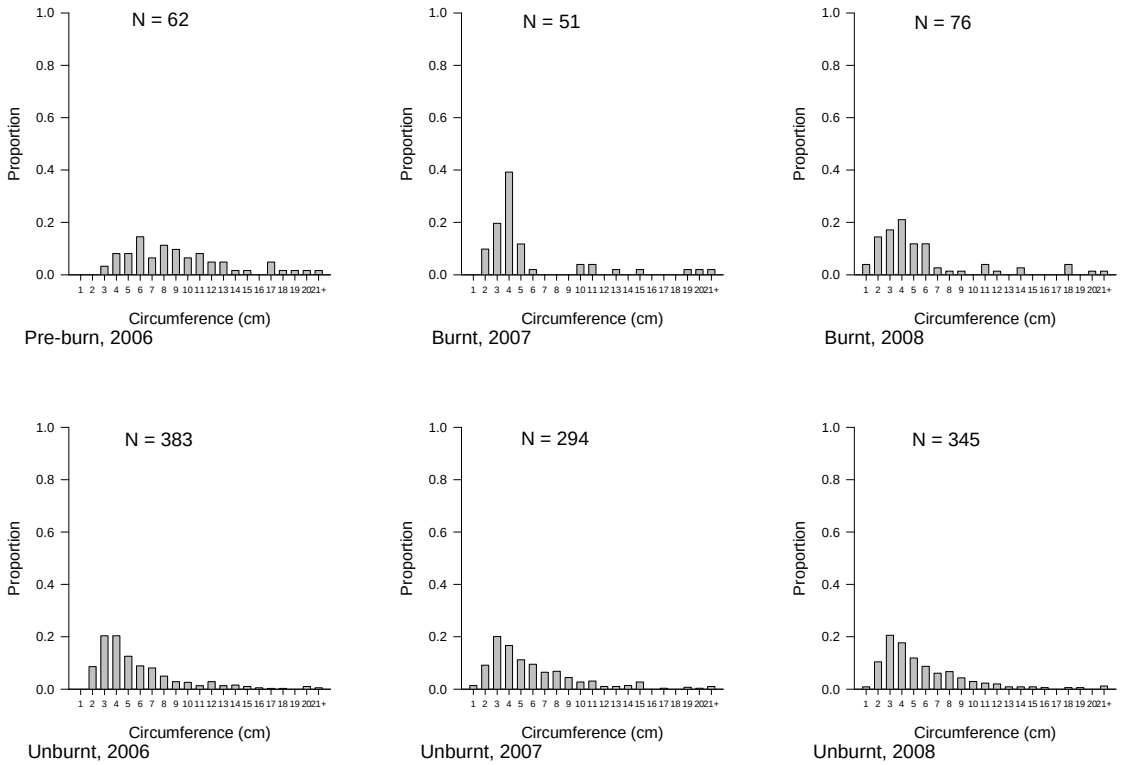


Figure 3.27: Stem size distribution of *Gymnosporia senegalensis* in E_T plots in consecutive years. Sites 1 and 2 combined ("Burnt" plots), Site 3 ("Unburnt") treated separately.

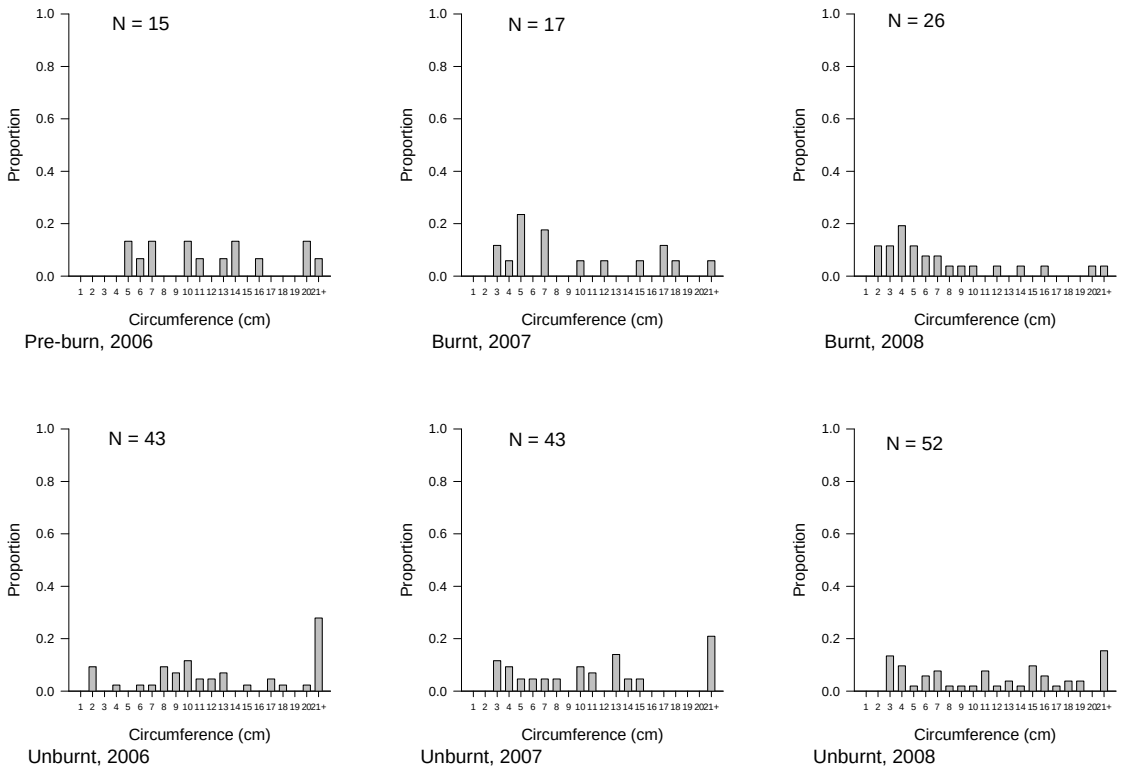


Figure 3.28: Stem size distribution of *Lannea discolor* in E_0 plots in consecutive years. Sites 1 and 2 combined ("Burnt" plots), Site 3 ("Unburnt") treated separately.

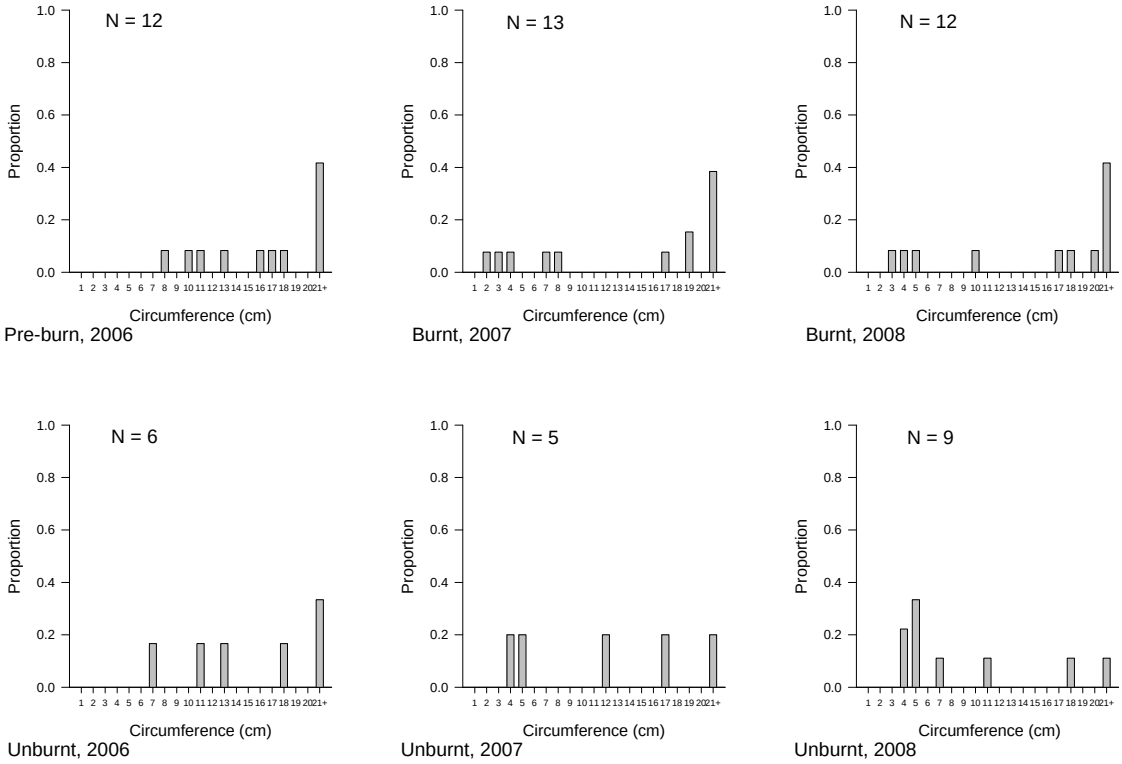


Figure 3.29: Stem size distribution of *Lannea discolor* in E_L plots in consecutive years. Sites 1 and 2 combined ("Burnt" plots) except in 2008 when S1 E_L was destroyed, Site 3 ("Unburnt") treated separately.

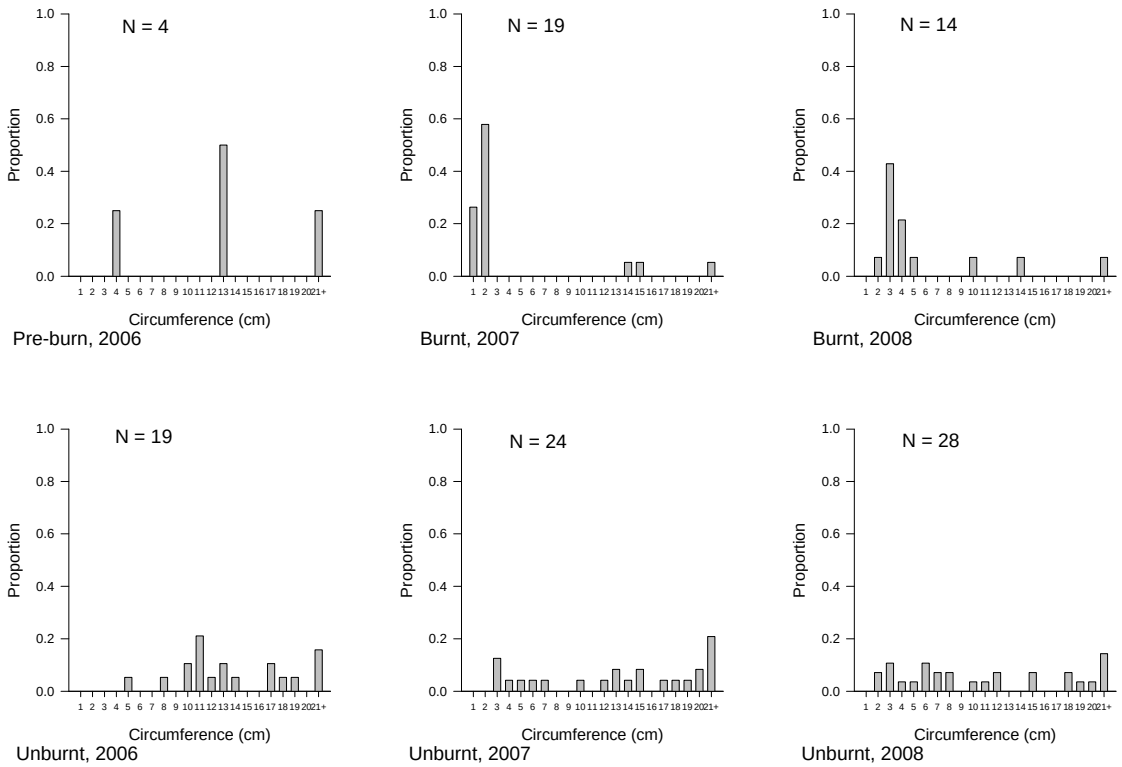


Figure 3.30: Stem size distribution of *Lannea discolor* in E_S plots in consecutive years. Sites 1 and 2 combined ("Burnt" plots), Site 3 ("Unburnt") treated separately.

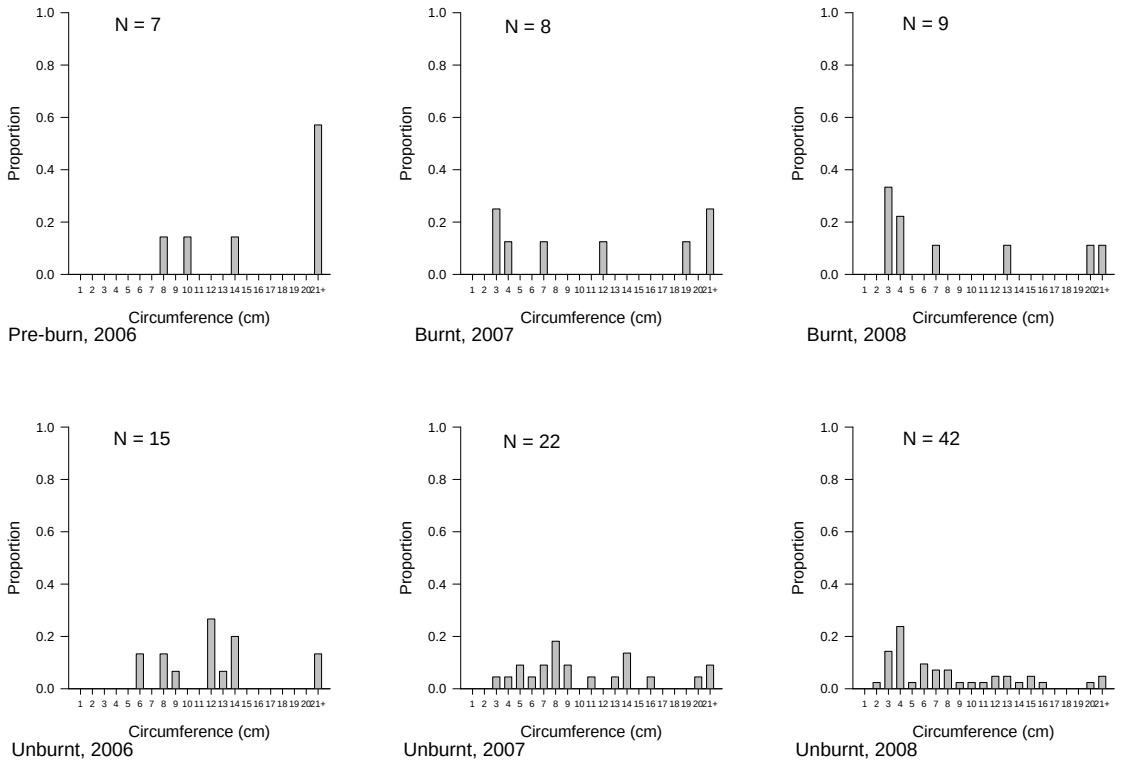


Figure 3.31: Stem size distribution of *Lannea discolor* in E_T plots in consecutive years. Sites 1 and 2 combined ("Burnt" plots), Site 3 ("Unburnt") treated separately.

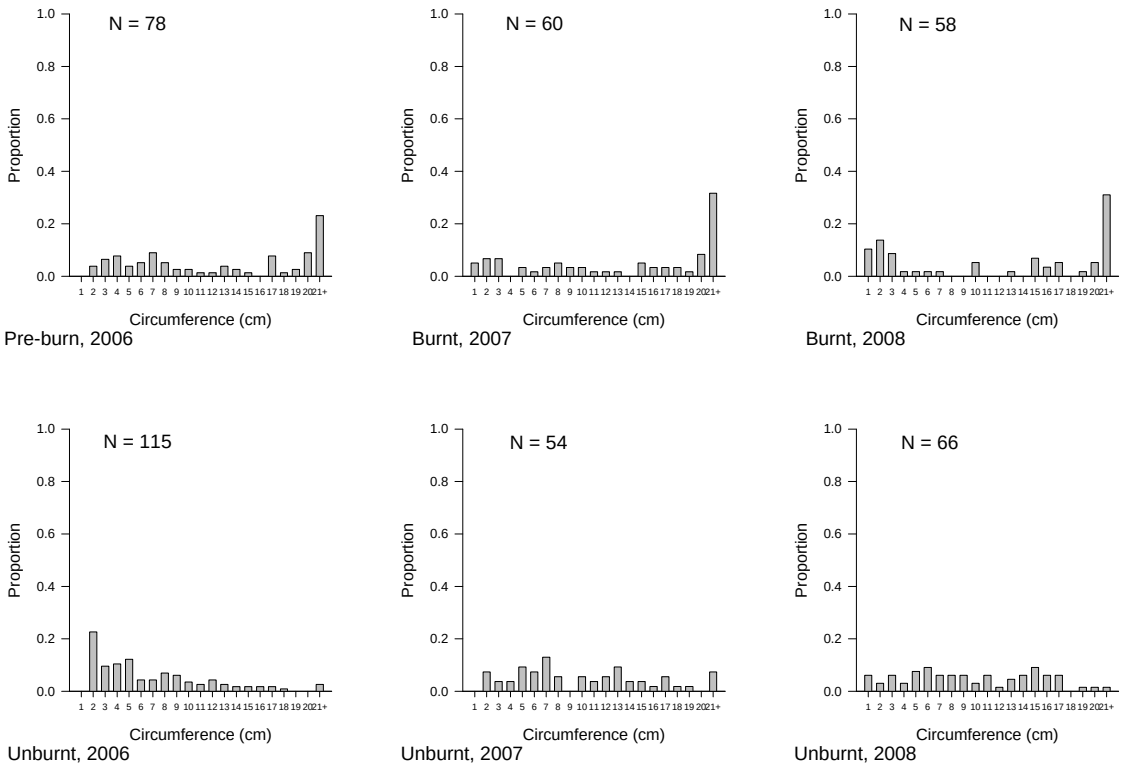


Figure 3.32: Stem size distribution of *Pseudolachnostylis maprouneifolia* in E_0 plots in consecutive years. Sites 1 and 2 combined ("Burnt" plots), Site 3 ("Unburnt") treated separately.

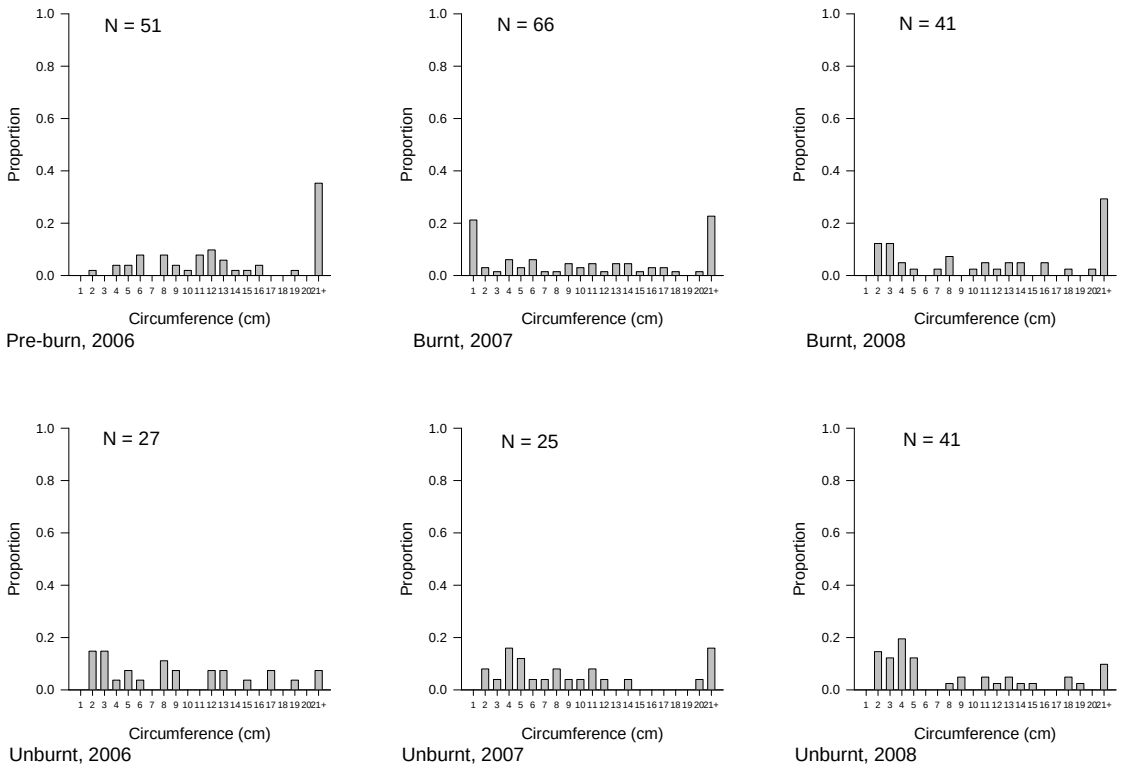


Figure 3.33: Stem size distribution of *Pseudolachnostylis maprouneifolia* in E_L plots in consecutive years. Sites 1 and 2 combined ("Burnt" plots) except in 2008 when S1 E_L was destroyed, Site 3 ("Unburnt") treated separately.

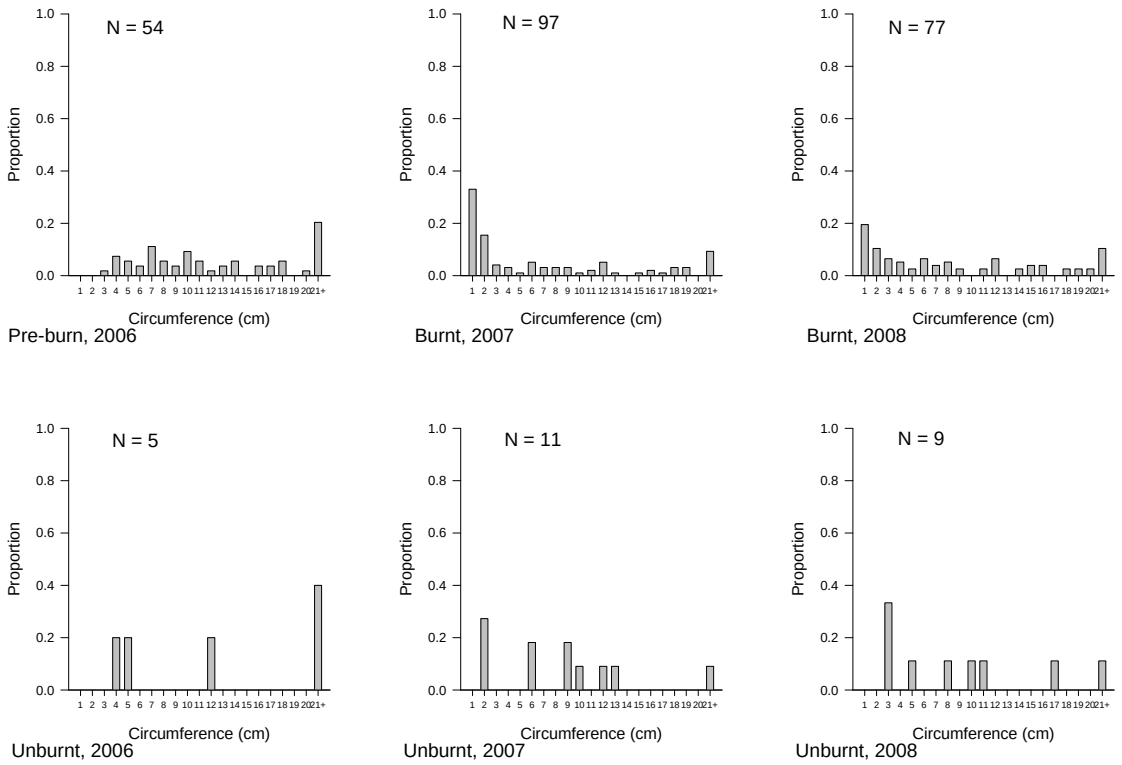


Figure 3.34: Stem size distribution of *Pseudolachnostylis maprouneifolia* in E_S plots in consecutive years. Sites 1 and 2 combined ("Burnt" plots), Site 3 ("Unburnt") treated separately.

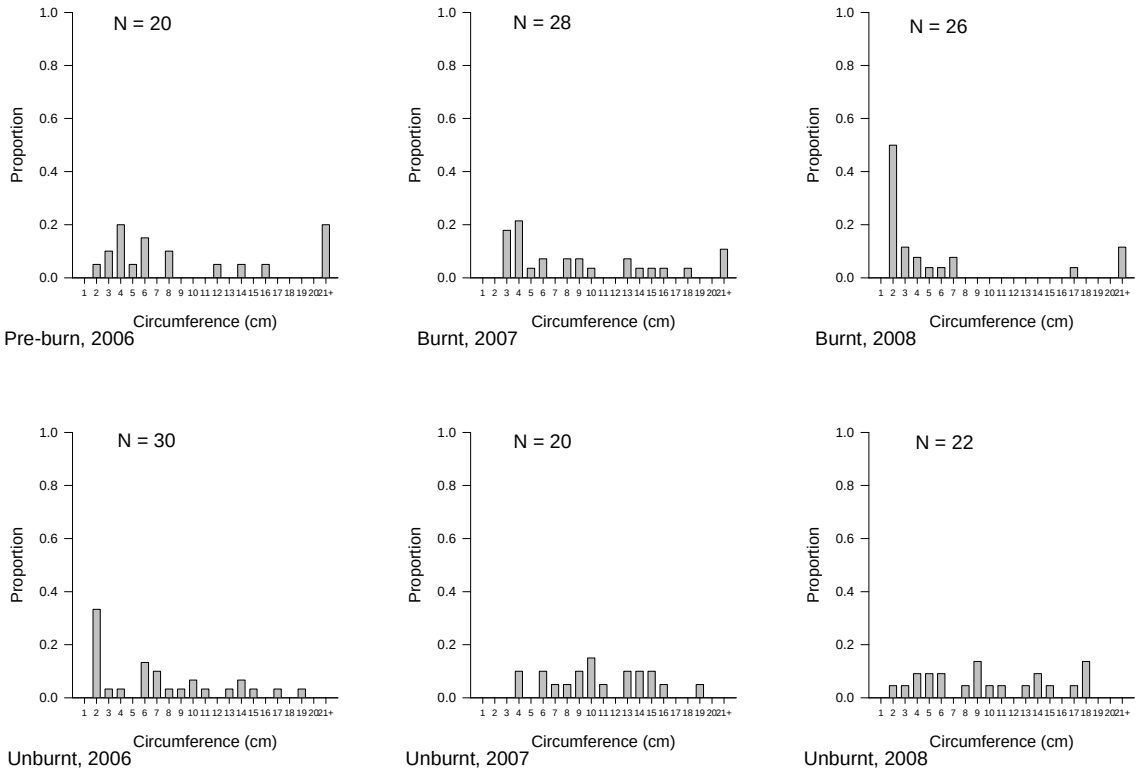


Figure 3.35: Stem size distribution of *Pseudolachnostylis maprouneifolia* in E_T plots in consecutive years. Sites 1 and 2 combined ("Burnt" plots), Site 3 ("Unburnt") treated separately.

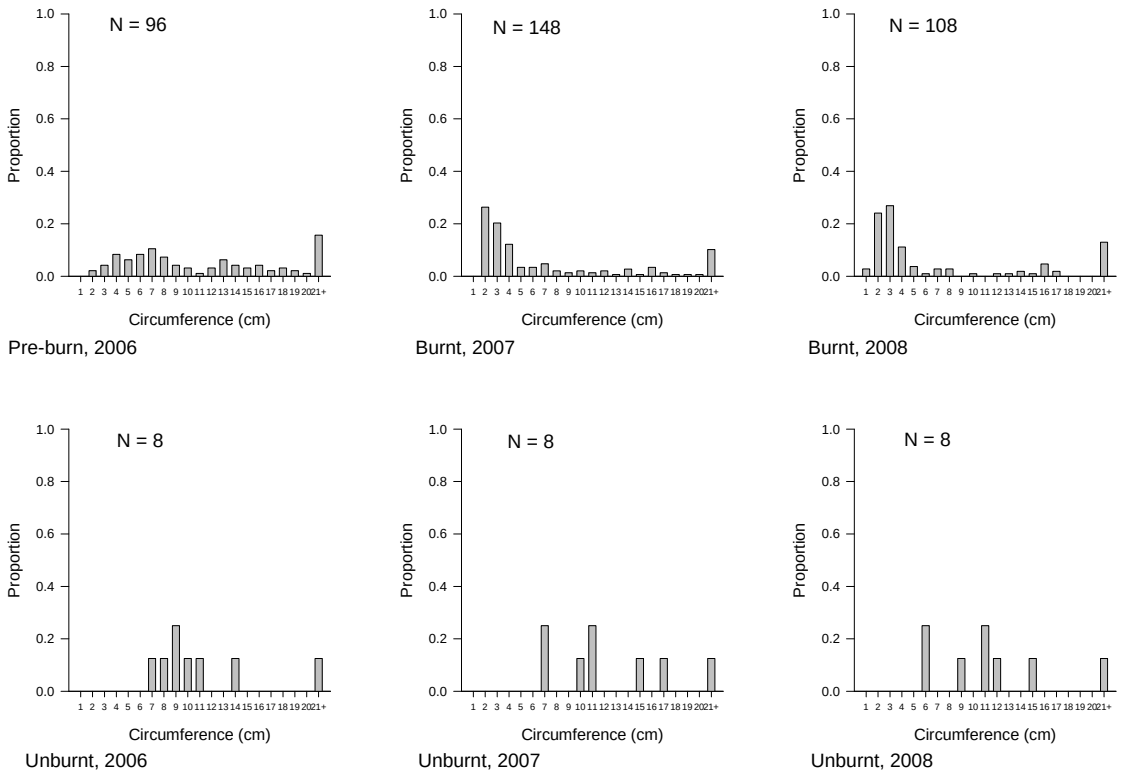


Figure 3.36: Stem size distribution of *Pterocarpus rotundifolius* in E_0 plots in consecutive years. Sites 1 and 2 combined ("Burnt" plots), Site 3 ("Unburnt") treated separately.

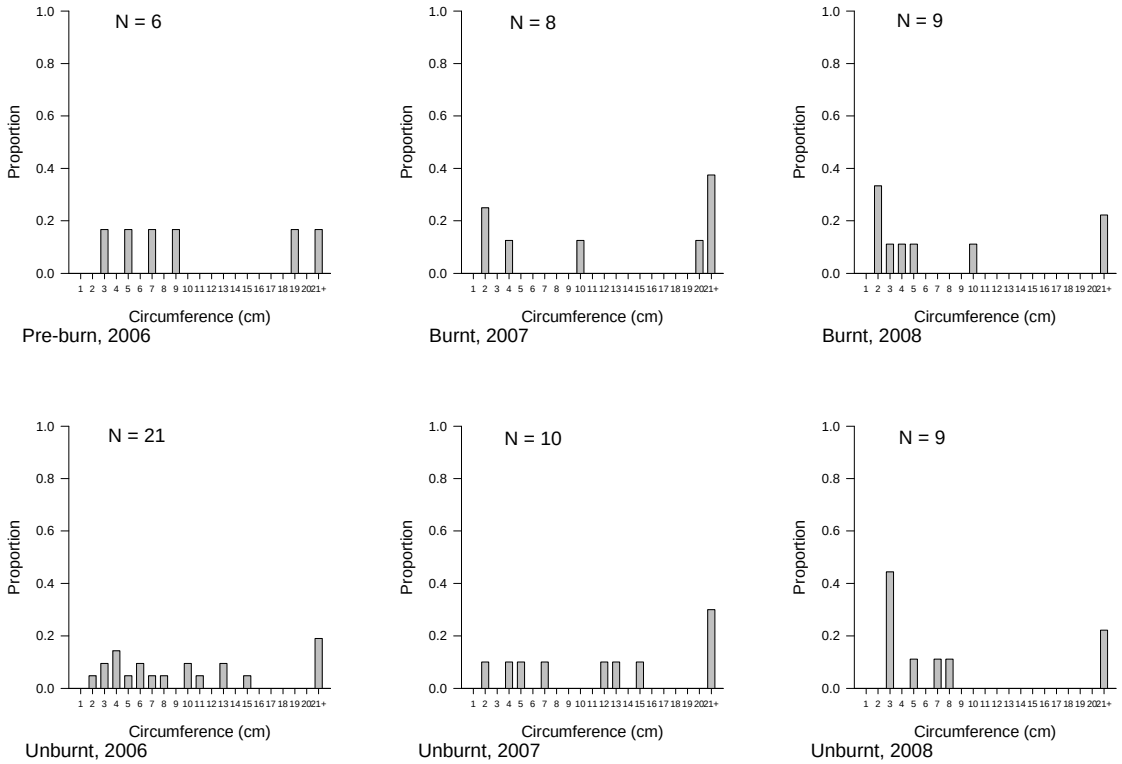


Figure 3.37: Stem size distribution of *Pterocarpus rotundifolius* in E_L plots in consecutive years. Sites 1 and 2 combined ("Burnt" plots) except in 2008 when S1 E_L was destroyed, Site 3 ("Unburnt") treated separately.

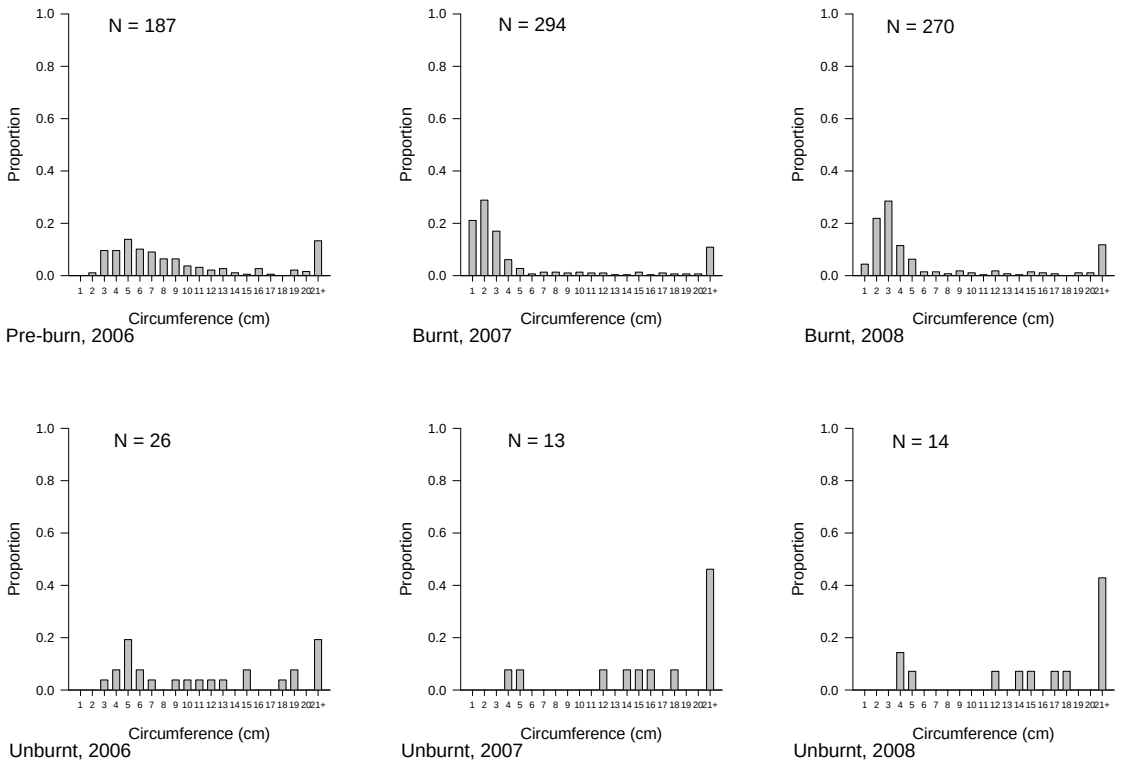


Figure 3.38: Stem size distribution of *Pterocarpus rotundifolius* in E_S plots in consecutive years. Sites 1 and 2 combined ("Burnt" plots), Site 3 ("Unburnt") treated separately.

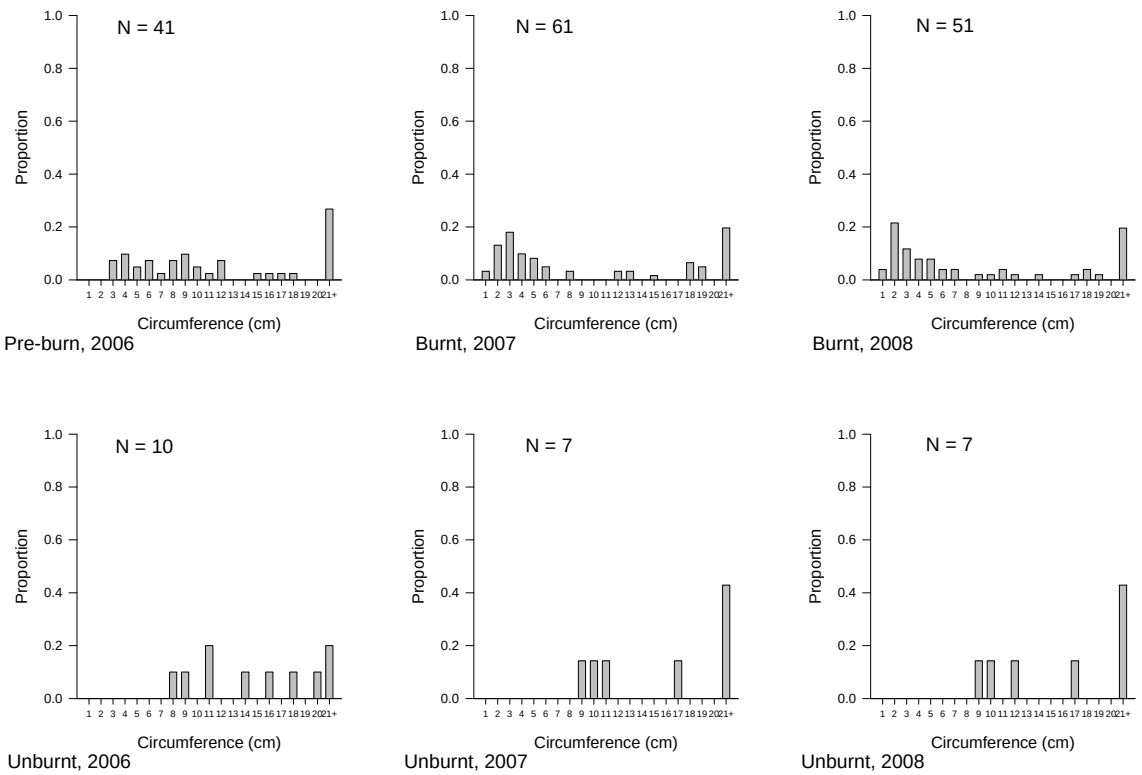


Figure 3.39: Stem size distribution of *Pterocarpus rotundifolius* in E_T plots in consecutive years. Sites 1 and 2 combined ("Burnt" plots), Site 3 ("Unburnt") treated separately.

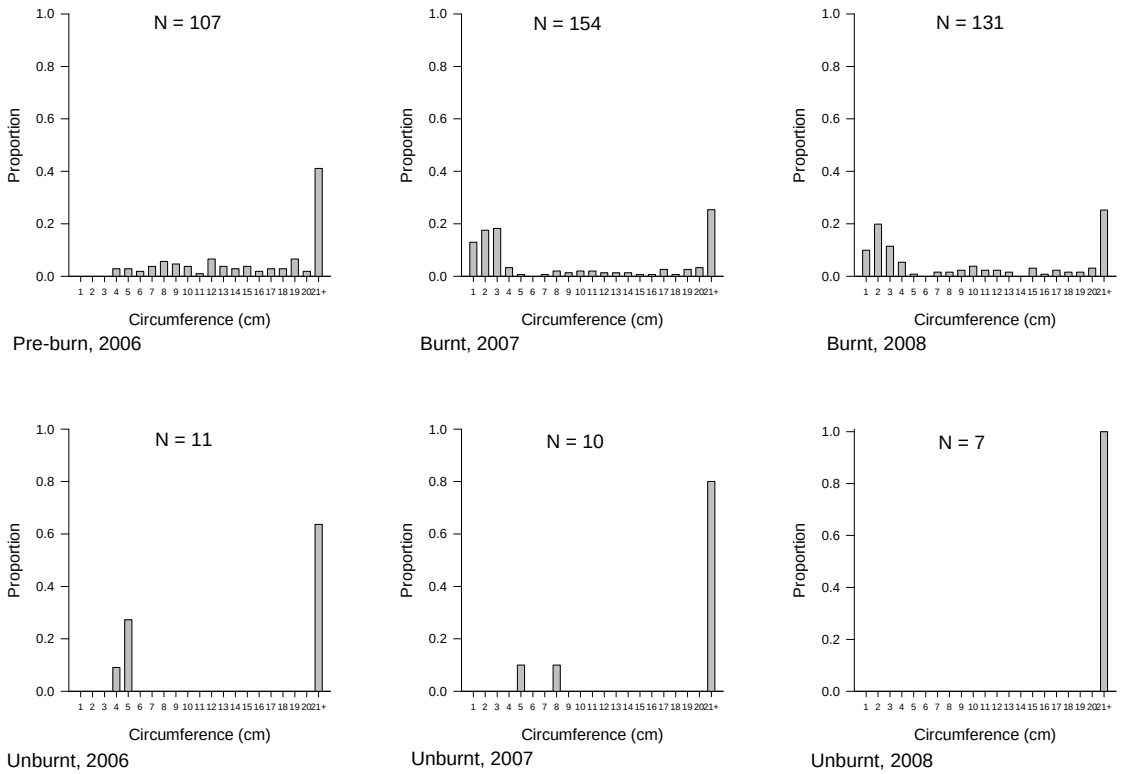


Figure 3.40: Stem size distribution of *Terminalia* spp. in E_0 plots in consecutive years. Sites 1 and 2 combined ("Burnt" plots), Site 3 ("Unburnt") treated separately.

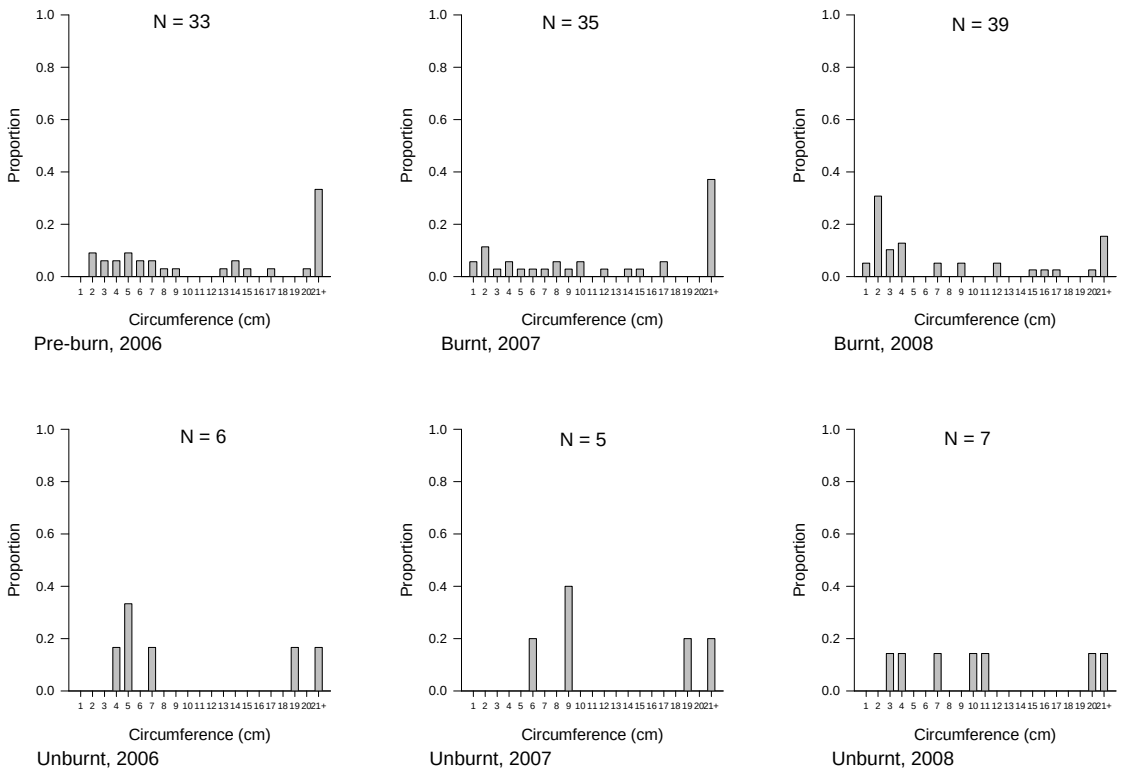


Figure 3.41: Stem size distribution of *Terminalia* spp. in E_L plots in consecutive years. Sites 1 and 2 combined ("Burnt" plots) except in 2008 when S1 E_L was destroyed, Site 3 ("Unburnt") treated separately.

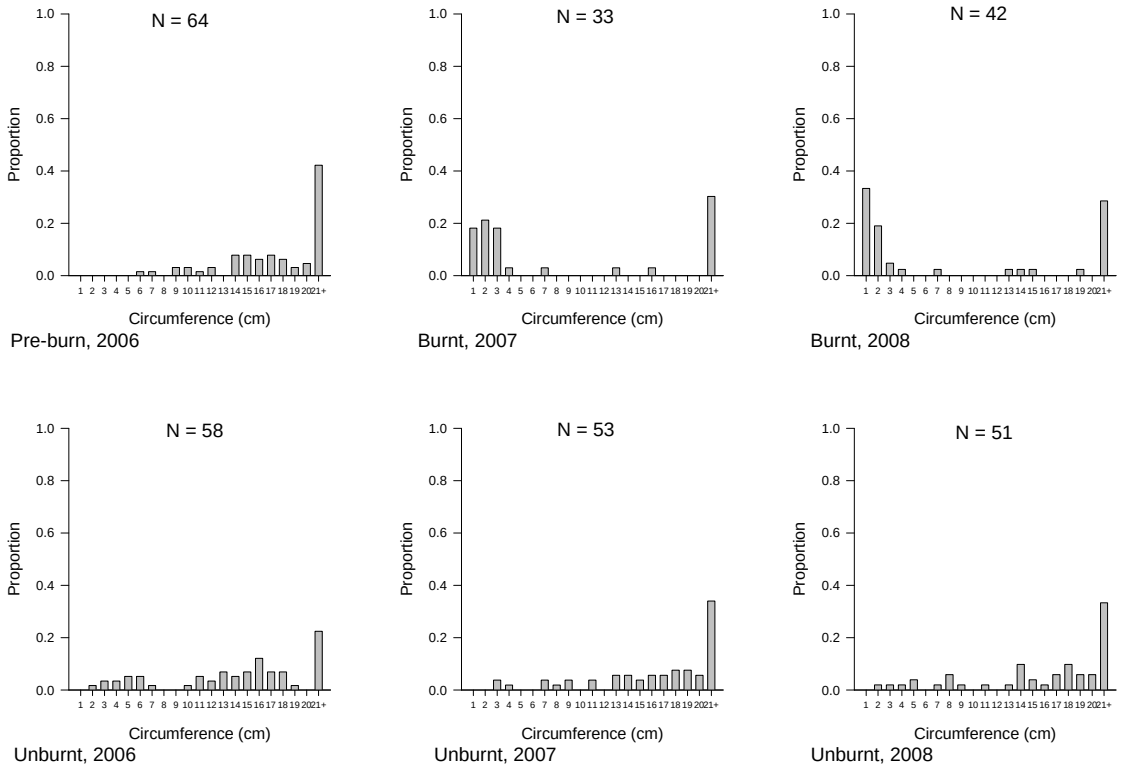


Figure 3.42: Stem size distribution of *Terminalia* spp. in E_S plots in consecutive years. Sites 1 and 2 combined ("Burnt" plots), Site 3 ("Unburnt") treated separately.

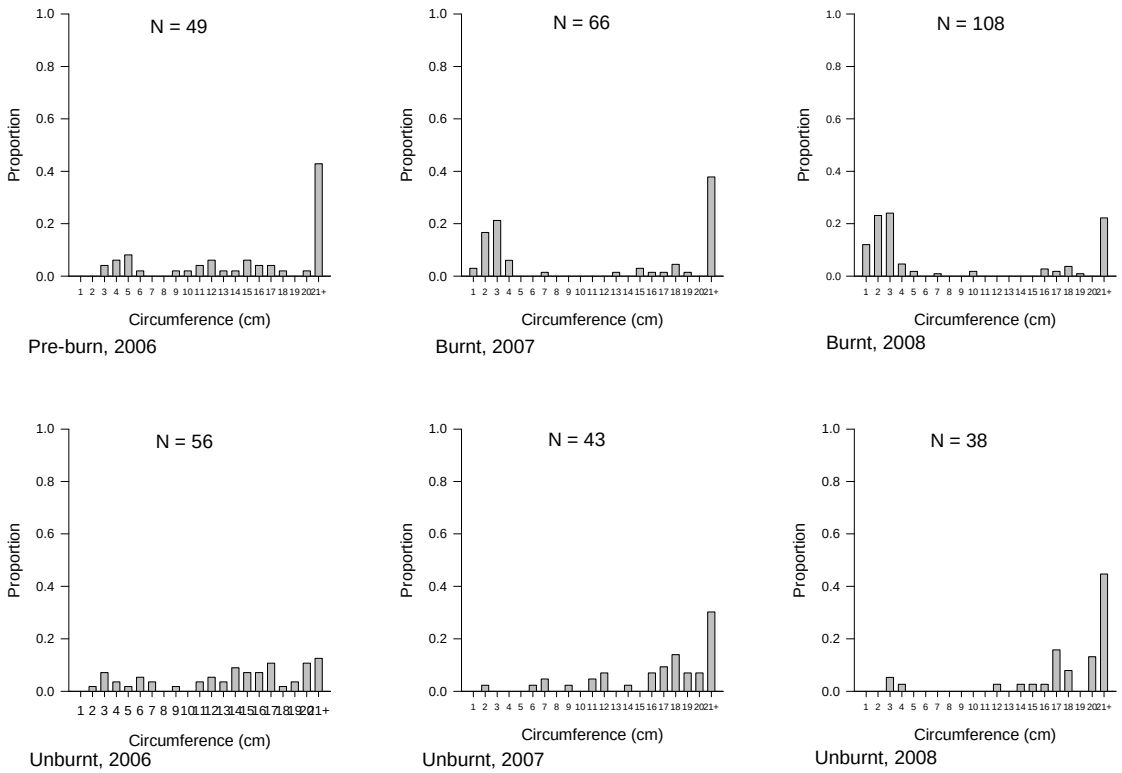


Figure 3.43: Stem size distribution of *Terminalia* spp. in E_T plots in consecutive years. Sites 1 and 2 combined ("Burnt" plots), Site 3 ("Unburnt") treated separately.

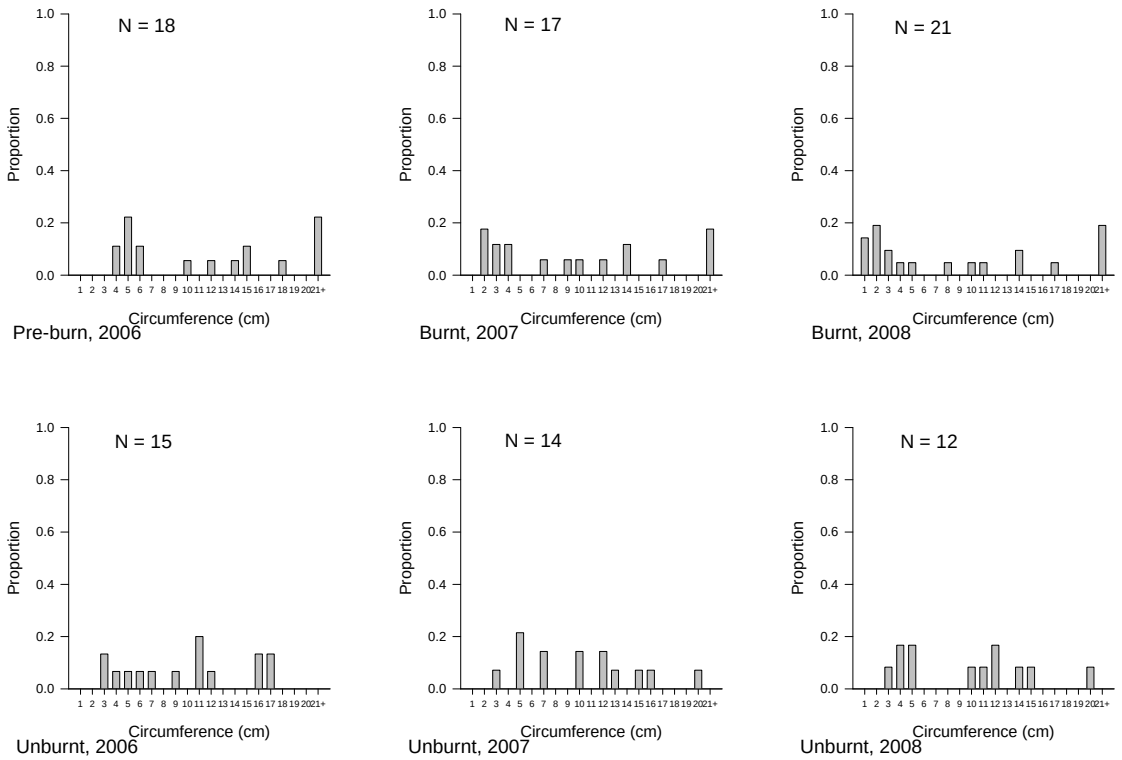


Figure 3.44: Stem size distribution of *Ziziphus mucronata* in E_0 plots in consecutive years. Sites 1 and 2 combined ("Burnt" plots), Site 3 ("Unburnt") treated separately.

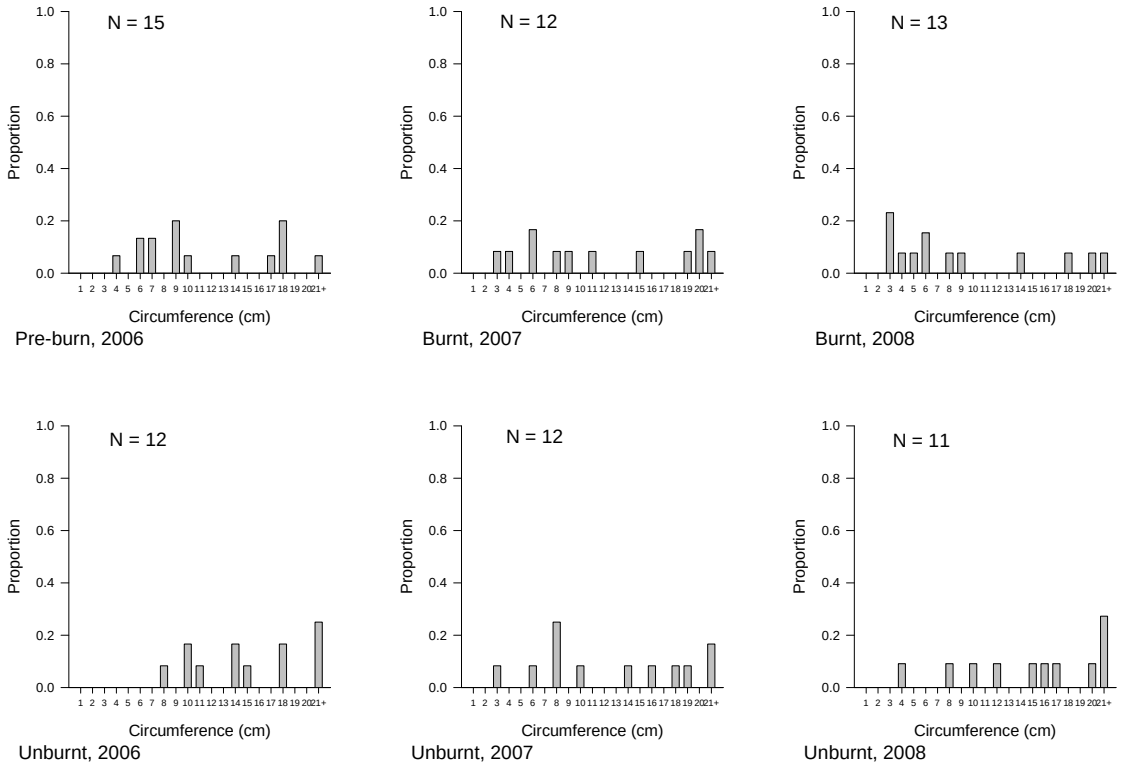


Figure 3.45: Stem size distribution of *Ziziphus mucronata* in E_L plots in consecutive years. Sites 1 and 2 combined ("Burnt" plots) except in 2008 when S1 E_L was destroyed, Site 3 ("Unburnt") treated separately.

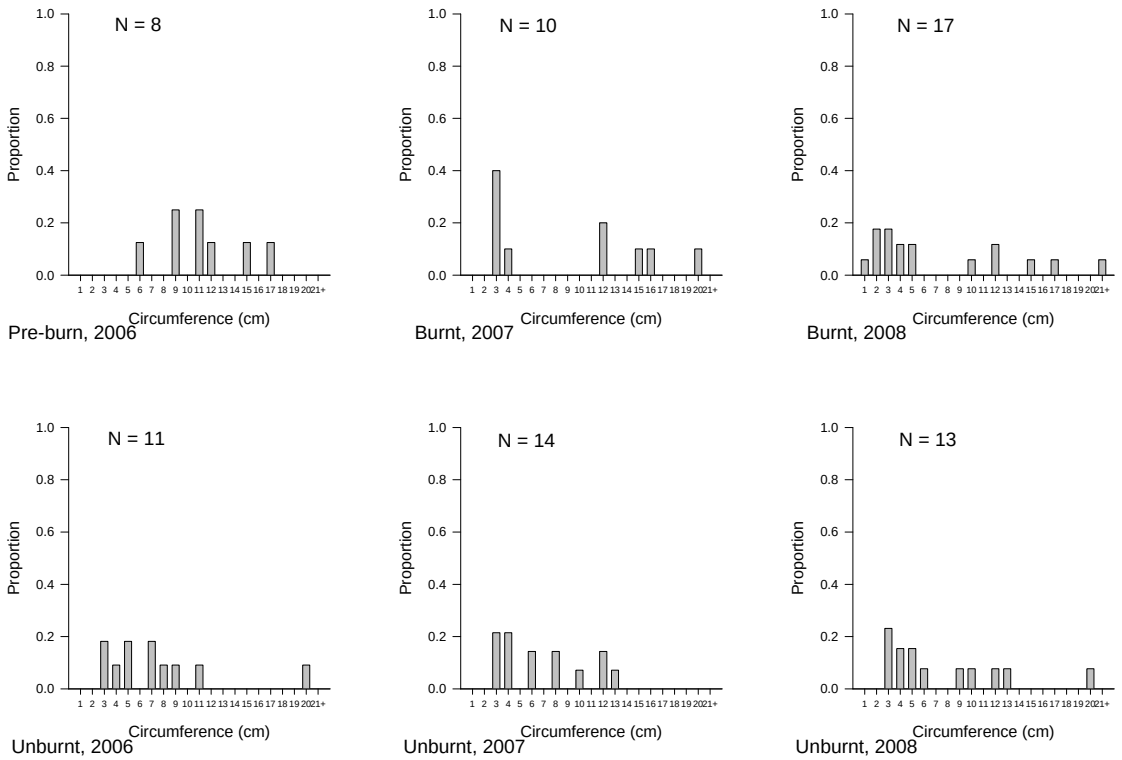


Figure 3.46: Stem size distribution of *Ziziphus mucronata* in E_S plots in consecutive years. Sites 1 and 2 combined ("Burnt" plots), Site 3 ("Unburnt") treated separately.

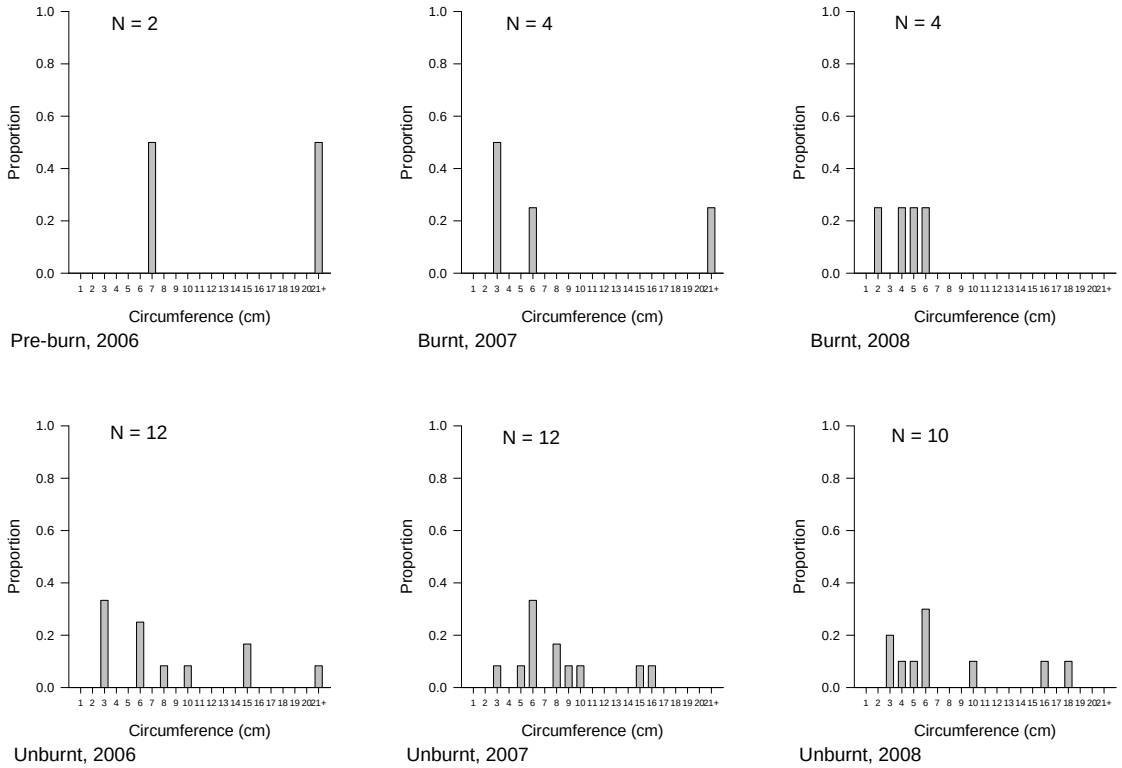


Figure 3.47: Stem size distribution of *Ziziphus mucronata* in E_T plots in consecutive years. Sites 1 and 2 combined ("Burnt" plots), Site 3 ("Unburnt") treated separately.

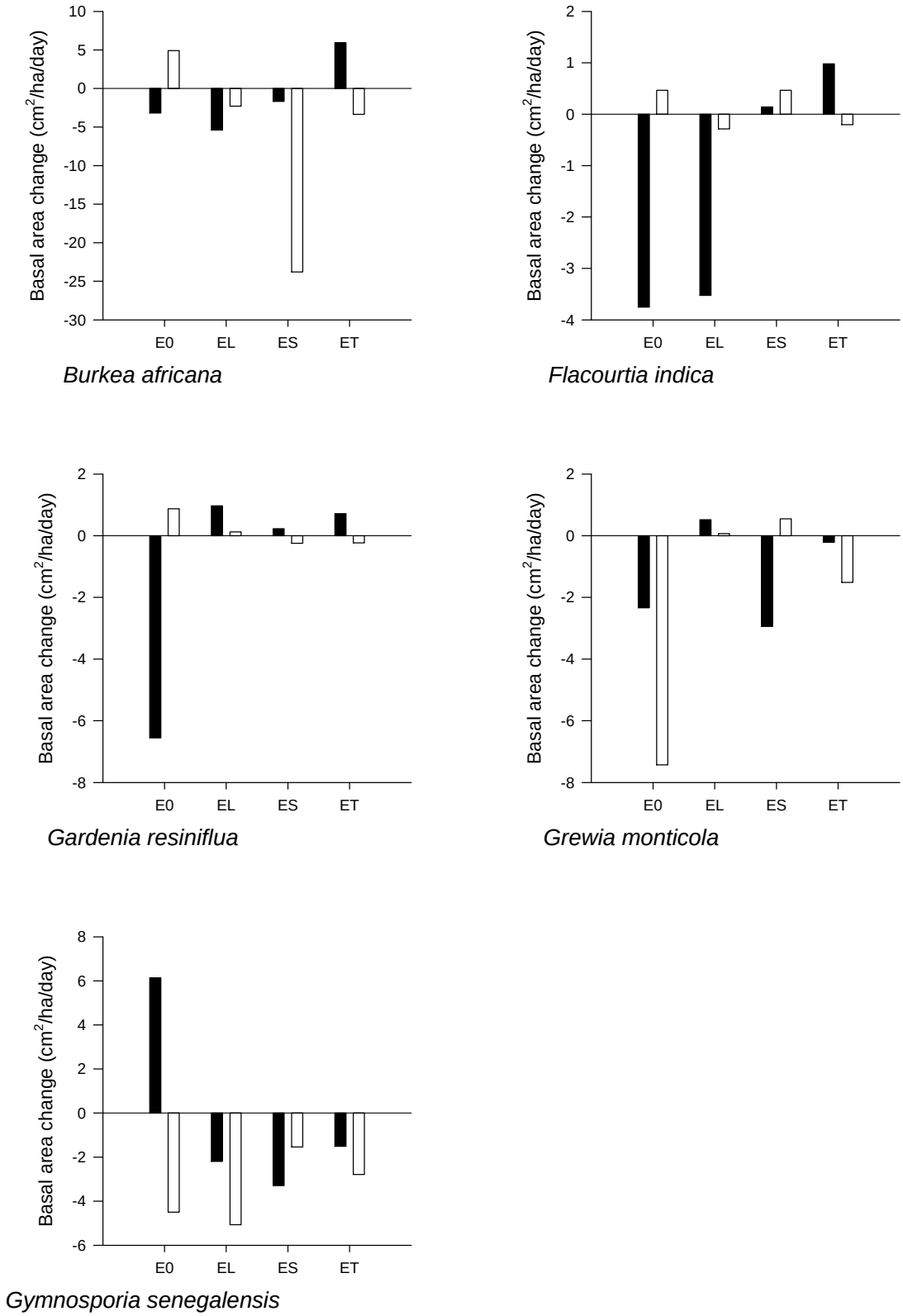


Figure 3.48: Per diem changes in basal stem areas of selected woody plants over the experimental period (2006 to 2008) in unburnt (black bars) and burnt (white bars) plots.

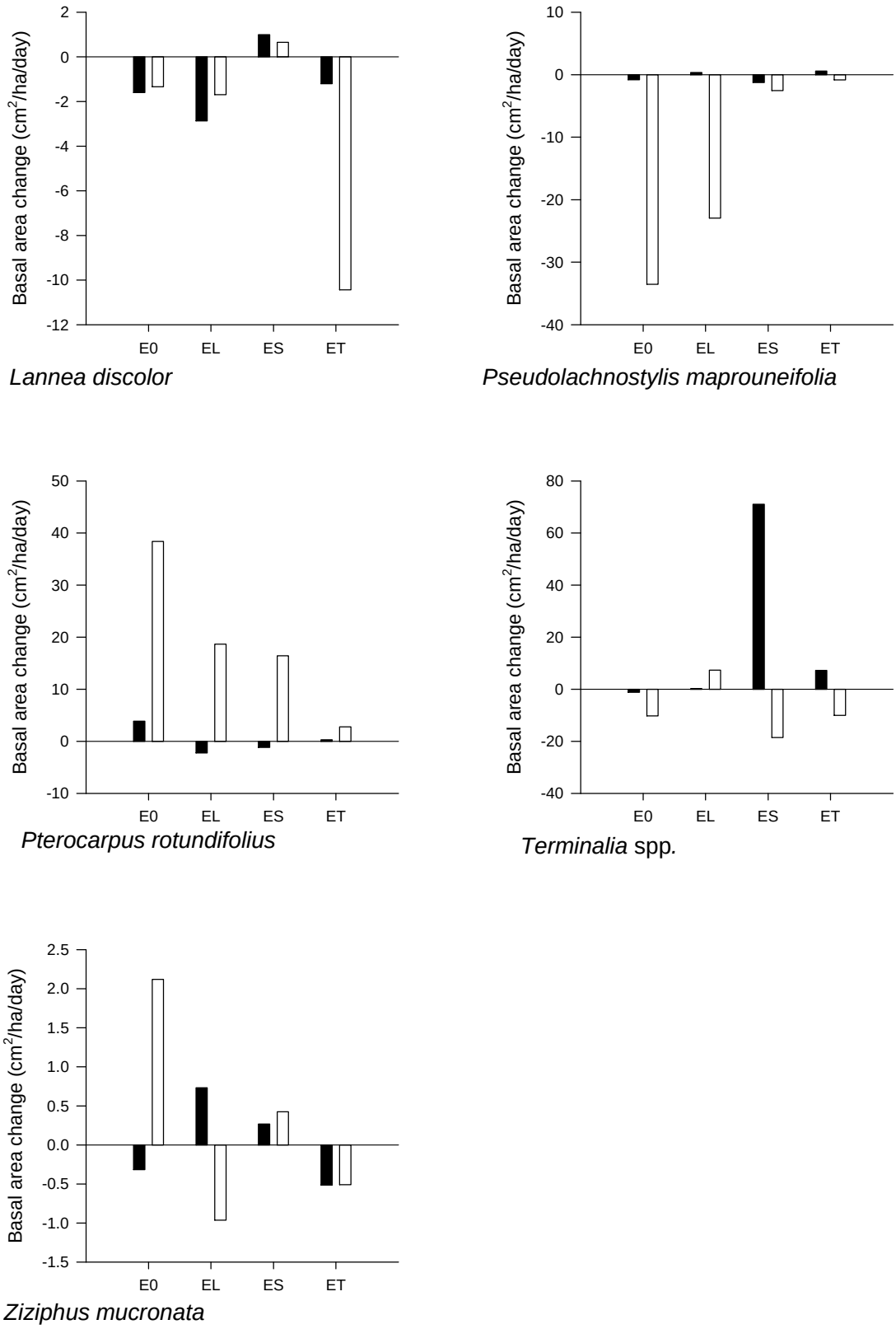


Figure 3.49: Per diem changes in basal stem areas of selected woody plants over the experimental period (2006 to 2008) in unburnt (black bars) and burnt (white bars) plots.

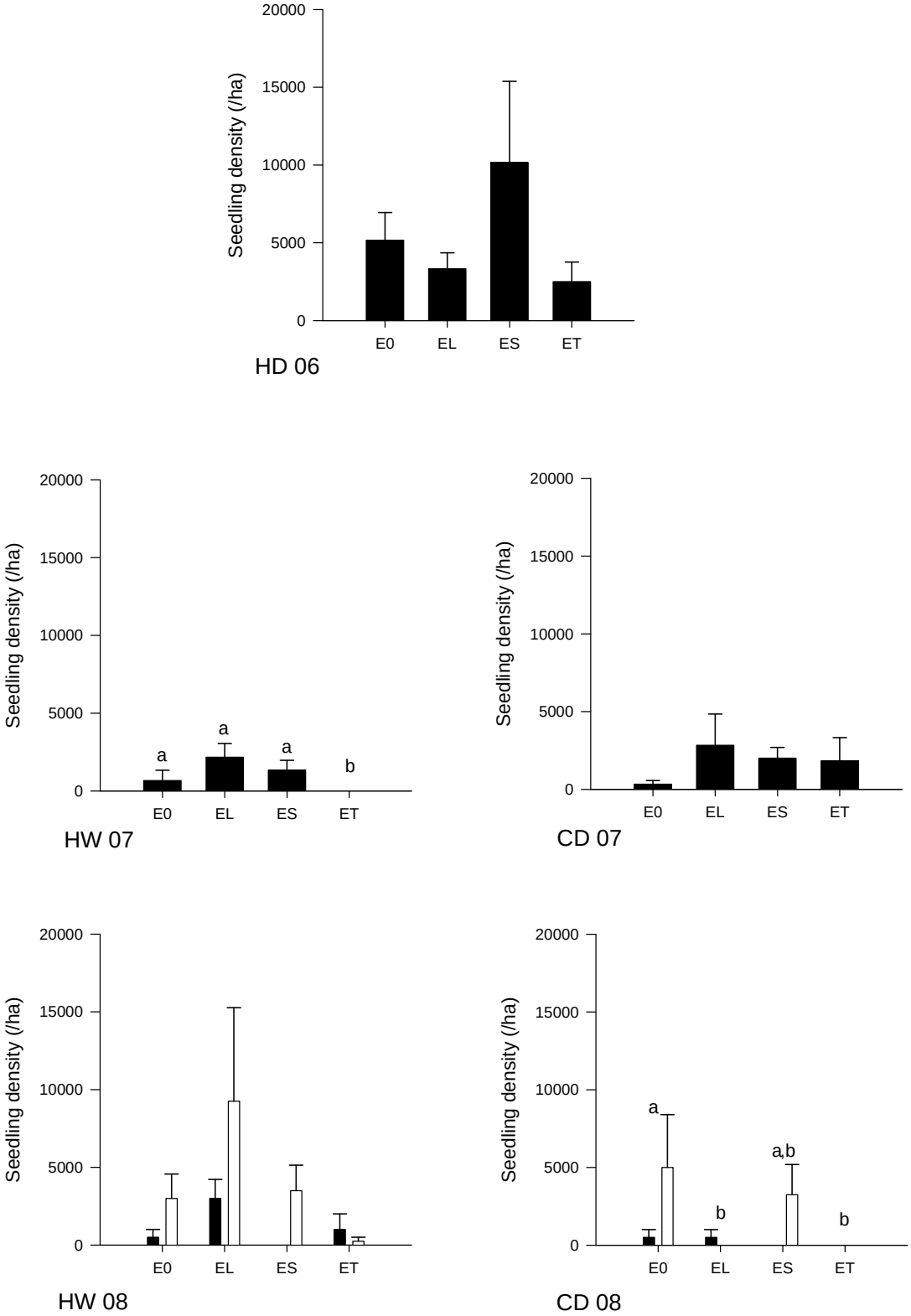


Figure 3.50: Woody plant seedling densities (mean ± SE) in each season in exclusion plots. 2008 data separated into burnt (white bars) and unburnt (black bars) categories. Letters above error bars indicate sources of variability in significant permutation ANOVA tests. Plot and season codes are given in the text.

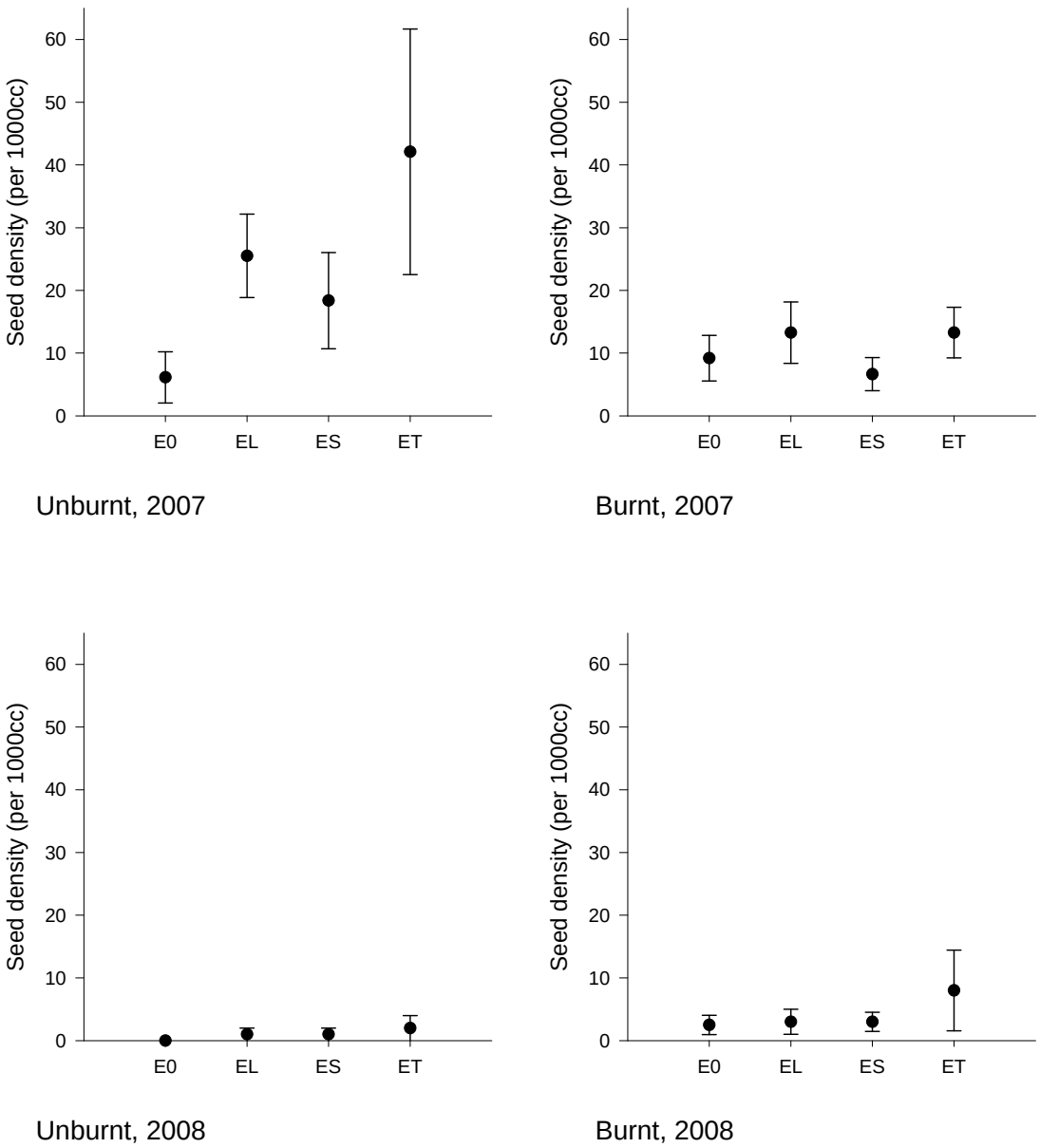


Figure 3.51: Seed yields (seeds/ litre of soil) from soil cores collected soon after the fire in 2007, and in the wet season of 2008 in each plot type. Burnt (Sites 1 and 2) and unburnt (Site 3) samples treated separately.

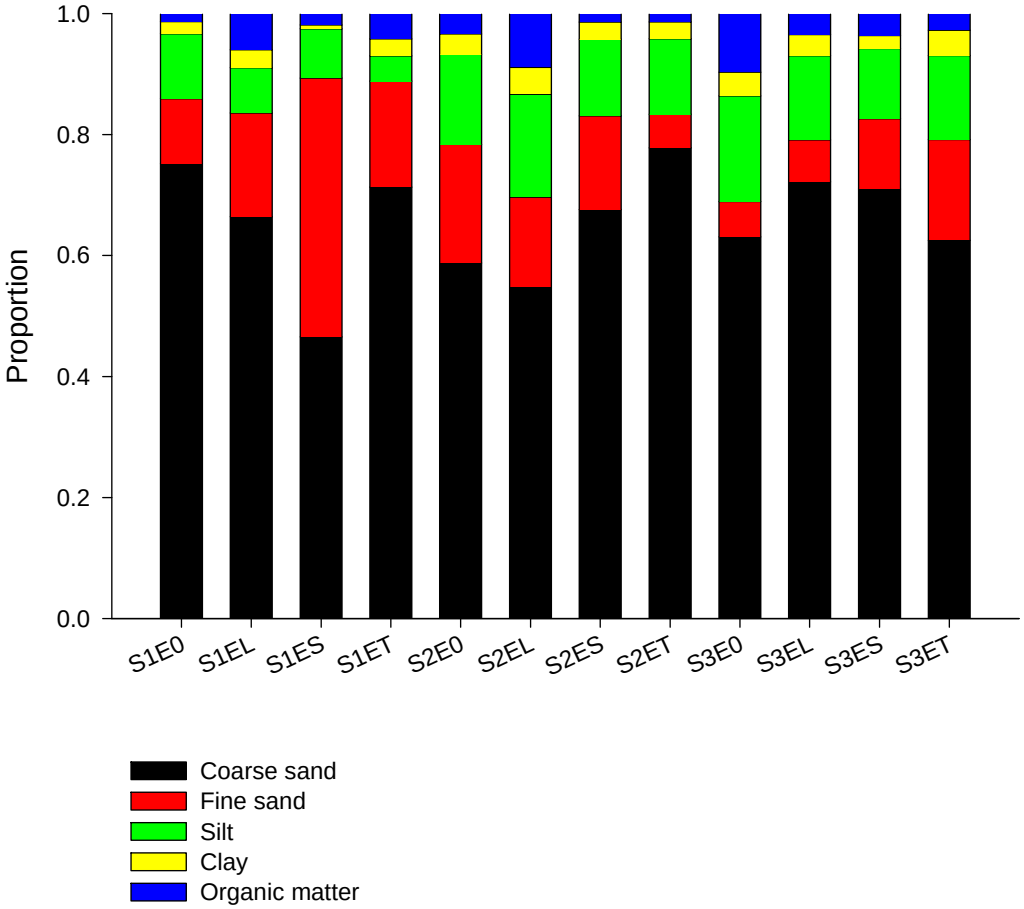


Figure 3.52: Soil fractions of the top 10 cm of soil in each plot. *X*-axis codes are site number (S1 to 3) followed by the exclusion code (E_0, E_L, E_S and E_T).

4. INDIRECT EFFECTS OF SMALL ANTELOPE ON VEGETATION AND ECOSYSTEM FUNCTIONING: BROWSING HEIGHT, SEED VIABILITY AND ANTELOPE DEFECATION BEHAVIOUR

4.1. INTRODUCTION

Mammalian herbivores have the potential to significantly affect their environment. The most obvious impact is the removal of plant tissue by herbivory (Augustine and McNaughton, 2004; Hulme, 1996; Skarpe, 1990), but there is a suite of direct and indirect effects that animals have on vegetation. These effects may be positive or negative, and often the perception of the value of faunal-induced habitat alteration depends on management goals (Moe et al., 2009). For example, in livestock rangelands, shrub encroachment is seen as being negative because of the reduction in grass production (Smit, 2004; Strang, 1973; Weber and Jeltsch, 2000), whilst woody removal in sensitive woodland systems has caused concern (Dharani *et al.*, 2008; O'Connor *et al.*, 2007).

Ungulates carry out crucial ecosystem services, including accelerating the return of mineralised nutrients to the soil in faeces and urine (Hulme, 1996; McNaughton *et al.*, 1988) and endo- and epizoochorous seed dispersal of a range of plant species (Feer, 1995; Heinken *et al.*, 2006a; Janzen, 1984; Myers *et al.*, 2004). However, in some environments, herbivores can inhibit soil microbial activity and cause land degradation, especially under conditions of frequent or intense disturbance such as fire or drought (Boelhouwers and Scheepers, 2004; Kay *et al.*, 2008). Their physical impacts on plants and the environment have important implications for the structure of community, in terms of species composition and richness and prevalent growth-forms (Augustine and McNaughton, 1998; Jacobs and Naiman, 2008; Manier and Hobbs, 2007; Navarro *et al.*, 2006; Painter *et al.*, 1993; Savadogo *et al.*, 2008).

Despite several studies alluding to the importance of smaller indigenous browsing ungulates (< 50 kg, feeding below 1.5 m above ground) in structuring vegetation (e.g. Augustine and McNaughton, 2004; Belsky, 1984; Moe *et al.*, 2009; Prins and van der Jeugd, 1993), the majority of African savanna plant-herbivore studies have focused on larger native herbivores and livestock that, by dint of their greater biomass and stocking rates, have conspicuous effects (Birkett and Stevens-Wood, 2005; Chira and Kinyamario, 2009; Levick and Rogers,

2008; Makhabu *et al.*, 2006; O'Connor *et al.*, 2007; Pellew, 1983; Skarpe *et al.*, 2007; Strang, 1973; Stuth and Kamau, 1990). However, several characteristics of small antelope suggest that their impacts may be more extensive than previously reported.

Feeding selectivity and the position of antelope along the grazing-browsing continuum have been linked to body size and evolutionary history (Codron *et al.*, 2007b; Spencer, 1995). Smaller species (e.g. cephalophines and neotragines) have high basal metabolic rates but low absolute energetic requirements and small gut capacities so they tend to be selective feeders, removing high-quality, sparsely distributed forage from the environment (Demment and van Soest, 1985; Jarman, 1974). With few exceptions, smaller species are predominantly browsers (sensu feeding on dicots, Spencer, 1995) and frugivores although some are mixed-feeders (e.g. oribi *Ourebia ourebi*) and most species include new grass growth in their diets in the early growing season or following fire (Codron *et al.*, 2007a; du Toit, 1993).

By concentrating their foraging in the lower vegetation strata, medium- and long-term plant community structure can be significantly affected by small antelope if woody plants are browsed early in their development (Augustine and McNaughton, 2004), and species richness of herbaceous plants can be expected to also be influenced. Furthermore, it could be predicted that because of the selection of high-protein plant parts and the relatively low digestive efficiency of small antelope (Augustine and McNaughton, 1998), the nutrient content of faecal material would be higher than for larger, less selective species such as tragelaphines. This, coupled with the use of latrine sites and favoured rumination and feeding sites within small home ranges (Kingdon, 1997; Lunt *et al.*, 2007; Roberts and Lowen, 1997), implies that enrichment of soil and nutrient cycling by small antelope potentially has a significant effect on vegetation at a localised scale. Such effects could be compounded over time, as antelope may live for several years. For example, in captivity in Zimbabwe, the mean age at death of independent common duiker was 4.8 years ± 1.0 SE, and a common duiker collared in Matobo National Park as an adult survived for at least three years following collaring (N. Lunt unpubl. data).

Given that savanna-dwelling small antelope are facultative frugivores (Kingdon, 1997; Wilson, 1966), endozoochorous seed dispersal and viability following ingestion are important considerations for seedling and sapling establishment . Although few studies have been undertaken in savanna systems, forest-dwelling duiker (Cephalophinae) are important seed

dispersers (Feer, 1995). Provided that ingestion does not render seeds unviable, chemical and mechanical scarification of the seed coat or stone often enhances germination, although trends are by no means universal and are subject to a wide range of extrinsic variables (Traveset, 1998). Germination of some fleshy-fruited species is inhibited by the presence of the fruit pulp (Griffiths and Lawes, 2006), which suggests reliance on ingestion for germination.

This study sought to determine the roles of antelope in several aspects of ecosystem functioning and to predict how antelope affect plant community structure. Experiments were designed to investigate (i) post-ingestion seed viability of four species of large-, medium-and small-seeded savanna trees; (ii) feeding heights of small antelope, to predict browsing pressure in field conditions; and (iii) potential nutrient cyling rates, through determining effects of diet quality on defecation rates, and monitoring dung decomposition.

4.2. METHODS

Both *in situ* and *ex situ* experiments were carried out, at Dambari Field Station and Matobo National Park (MNP) respectively (see Chapter 2 for details). *In situ* experiments were carried out only on common duiker, as no other captive antelope species present in the Matobo Hills were available at Dambari Field Station.

4.2.1. Seed viability trials

Four species of fruiting plant were selected for seed viability trials. All four species have multiple seeds encased in stones (van Wyk and van Wyk, 1997). One large-fruited species (marula – *Sclerocarya birrea*; mean stone length 21.5 mm), one medium-fruited species (duikerberry – *Pseudolachnostylis maprouneifolia*; mean stone length 12.0 mm) and two small-fruited species (raisinberry – *Grewia monticola* and bluebush – *Euclea divinorum*; mean stone lengths *c*. 5.0 mm) were used, with the aim to determine if seed viability following ingestion by antelope differed with seed size.

Experiments were run during tree fruiting periods: marula experiments in February/March 2007, and March/April 2009, duikerberry experiments in August/September 2007 and the other two species' experiments in June/July 2008. Repeats of marula and duikerberry experiments were planned for 2008, but trees fruited late and had low yields consisting of small fruits, probably as a result of the poor 2006/07 rainy season (Dunham, 1990). A

previous study indicated that late fruit production negatively influenced germination rate in the savanna tree *Lannea edulis* (Chidumayo, 2006; Dunham, 1990), so the use of fruits not comparable with the first year's sample was deemed spurious.

At least sixty ripe fruits that had no external signs of damage were collected from individual plants, with two or three replicate plants per species depending on availability. Fruits from each plant were randomly assigned to one of three treatments as follows:

i. Intact control (IC) (N = 20) – fruits planted intact.
ii. Depulped control (DC) (N = 10) – fruit pulp removed manually, taking care not to scarify the stone or seed coat. Stones were measured (length and width) to the nearest mm using Vernier callipers. In the 2009 marula experiments, this treatment was excluded due to nil germination of previous replicates, and a shortage of suitable fruits.
iii. Antelope ingested treatment (AI) (Total N = 50) – eight common duiker (4 male and 4 female) were selected for trials. However, some individuals refused to take provided fruits, and it was necessary to compromise a balanced experimental design to increase the number of animals included in the trials. Since it could be expected that tooth wear and digestive efficiency would influence seed-coat porosity and therefore germination, recipient animals were divided into two age classes based on tooth wear. Tooth wear of Dambari common duiker is positively correlated with age (Spearman's rank correlation; $R_s = 0.903$, $p < 0.001$, $n = 33$), with clear differentiation between mild and heavy wear occurring at approximately 7.8 yr, which corresponds with published records (Wilson *et al.*, 1984). Each antelope was provided with at least ten fruits of each species on different occasions, at their usual feeding time (15h30). Fruits from different plants were provided at intervals greater than one week, to ensure that replicates were collected separately. Seeds were searched for from the following morning until four days after the provision of the fruits. Large- and medium-fruited species were egested during rumination, so were found scattered around enclosures, while small-seeded species were egested in the faeces. The time interval between ingestion and recovery of seeds was recorded. Retrieved seeds or stones were measured (length and width) to the nearest 0.5 mm using Vernier callipers.

Stones or fruits were planted in soil in labelled containers at a depth of 2 cm (2007, 2008) or lightly pressed into the soil but not buried (2009), watered regularly, and kept in a shadehouse for the duration of the experiments. Antelope-ingested stones were planted in individually-labelled plastic cups. *Pseudolachnostylis maprouneifolia* seeds that had been ejected from the stone between retrieval and germination preparation (n = 6) were placed on wet blotting paper and monitored for water imbibation. When germination occurred, the time interval between planting and germination was recorded. Planted seeds were monitored for 250 days, by which time germination rates had slowed.

Analysis

Permutational ANOVA using PERMANOVA (Anderson, 2005) was employed to compare germination times and stone size of germinated vs. ungerminated seeds among treatments and replicates. Proportional germination of control and antelope-ingested fruits were compared using the Fisher Exact Test.

4.2.2. Browse height preference of common duiker

Six adult common duiker (four females, two males held singly) and a highly palatable tree species (wild rubber, *Diplorhynchus condylocarpon*) were used to determine preferred browse heights. Five replicates were carried out for each antelope. Additional animals were initially included in the experiment, but refused to feed on the browse when it was attached to the fence horizontally.

Samples of wild rubber terminal branches of approximately the same size, with similar distribution of stem diameters and a mass of 25 to 30 g, were weighed (fresh mass) to the nearest 0.1 g on an electronic microbalance, and randomly assigned to one of eight height classes. Samples were affixed to enclosure fences at 20 cm intervals from ground level to 140 cm above ground. Due to the flexibility of wild rubber shoots, height classes span the 20 cm up to the height given (e.g. height class 40 cm had leaves available from 20 cm to 40 cm above ground). A control sample was placed outside each enclosure at an intermediate height above ground, to determine mass loss due to evapotranspiration.

The following morning, all samples were collected and re-weighed. Samples from within each enclosure were corrected for moisture loss using the proportional mass lost by the

external control. The remaining mass difference in excess of 0.2 g (or the mass of one leaf) was assumed to be due to antelope feeding.

Each sample was inspected for signs of browsing, and the diameters of browsed twigs were measured to the nearest 0.5 mm using Vernier callipers. Bite type (i.e. by incisors or molars) was recorded where possible. Incisor bites and molar bites were distinguishable on wider diameter twigs: the former were clean cuts whilst twigs bitten by cheek teeth had frayed ends.

To compensate for the small sample size of the controlled experiments described above, additional measurements were made on an *ad hoc* basis. As part of standard daily feeding procedures, larger branches of palatable browse species were hung vertically from enclosure fences (i.e. with leaves hanging down) at usual feeding times (15h30 to 16h30). Typical heights were between 10 and 90 cm above ground level. On the following morning, the heights and diameters of cropped twigs were measured to the nearest cm and nearest 0.5 mm, respectively. Where possible, cropping was assigned to cheek or incisor bites (see above). The heights of intact twigs and the stem diameter at the base of leaf petioles were measured to provide a range of available twig heights.

Analysis

For the controlled experiments, the proportion of the total tissue removal (by mass) was calculated for each height class for each antelope, pooled across replicates. Data for all antelope were combined, and preference for height class was tested using the χ^2 test of homogeneity.

4.2.3. Dung decomposition rate

In situ dung decomposition rates were investigated for the three small antelope species (common duiker, steenbok and klipspringer) in the Matobo study site.

Dung piles were searched for between 06h00 and 09h00 throughout the study area during the hot, dry season (September/ October) and the hot, wet season (January to March). Fresh piles estimated to be less than 12 hours old (i.e. consisting of pellets that were soft and moist) were identified, and labelled wooden marker pegs were placed adjacent to piles. The estimated number of pellets was recorded along with microhabitat details (substrate type, shading, and plant community). Since steenbok dung piles were fully or partially buried, care was taken to

minimise disturbance that may affect decomposition rate. Faecal piles were monitored at approximately fortnightly intervals until the pellets had completely disappeared. On each assessment occasion, the condition of the pellets was described.

Analysis

Only piles marked in the dry season (September/ October) were included in analyses. Initially, seasonal variation in decomposition rates was to be investigated. However, in the wet season, low detection rates (Lunt et al., 2007) and loss (through rain washing dung piles away) resulted in very small final sample sizes. Therefore, although data for this season are reported, they are excluded from analyses. Pair-wise comparisons between species were made using Kruskal-Wallis tests.

4.2.4. Defecation rates of common duiker

Ten semi-captive adult common duiker (five males and five females) of in two age classes based on tooth wear (see 4.2.1 above), were selected for defecation rate trials on two different diets.

Diets

Experiments took place in October (dry season) and were repeated in January (wet season). In the latter season, one female was excluded from the trials due to injury and since another female of similar age was not available, the female sample size was reduced to four. In each season, two experimental diets were provided, separated by a transitional phase. All animals were fed the same diet simultaneously to prevent factors such as changes in browse quality from affecting results. All provided feed was weighed (fresh mass) to the nearest gram on an electronic microbalance, and provided at the usual feeding time (15h30).

For the first ten experimental days in each season, the standard Dambari maintenance diet (termed the low fibre diet or LFD) was provided, consisting of 250 g of domestic vegetables (equal fresh masses of butternut, carrot and green banana), 450 g of game nuts (National Foods, Harare, Zimbabwe) and excess fresh indigenous browse (small, leafy branches of *Ficus sur*, *Ficus thonningi*, *Faurea saligna* and *Lannea discolor*) (Plowman, 2002). This was followed by an eight-day transitional phase, during which the diet was gradually shifted to a high fibre diet (HFD) consisting entirely of the same four species of indigenous browse. After

a two-day acclimation period on this diet, data collection resumed for a further ten days. Animals were gradually returned to the standard LFD at the end of each experimental period.

Throughout the study, individuals had continual access to vegetation growing naturally in their enclosures, and no changes in animal condition were noticed. It was assumed that intake of vegetation was constant across seasons and diets and that additional, unmeasured intake did not significantly alter calculated fibre content of ingested food.

Fibre analysis

Samples of each dietary component – vegetables, leaves and twigs of browse species – in both seasons were dried to constant mass, and analysed separately for neutral detergent fibre (NDF) and acid detergent fibre (ADF) at a commercial laboratory (Matopos Research Station, Zimbabwe). Fibre fractions of game nuts were obtained from the manufacturer.

Intake trials and fibre content of ingested feed

On five randomly selected days in each experimental period, dry mass intake of all animals was measured. A separate sample of each food item was weighed (fresh mass) when feed was prepared and oven-dried to constant mass to determine moisture content.

The dry mass (DM) of food provided to each animal was estimated by correcting the fresh mass provided by the moisture content. On the following morning, uneaten feed was removed from enclosures and dried to constant mass. Intake of each component was calculated as the difference between the DM provided and the DM of remains.

Fibre consumption was calculated for each component, by multiplying the DM ingested by the fibre fraction (ADF and NDF). Fibre intake per intake-trial day was the sum of the fibre of each component. Apparent digestibility was calculated as the mass of faecal matter as a proportion of total DM intake.

Defecation rate and faecal output determination

All faecal piles were counted and collected from each enclosure daily between 06h00 and 08h00, and were individually dried to constant mass.

Analysis

Mean defecation rates, daily intake, mass per pile and total daily output, were calculated for each individual on each diet in each season. DISTLM v.5 (Anderson, 2004) was used to run randomisation tests with 999 iterations, Euclidean distances and no transformation, to investigate the influence of four factors – diet (LFD/ HFD), season (wet/ dry) and sex (male/ female) – on each variable. Age class was used as a covariable in all tests (Table 4.1). Median tests were used for overall diet comparisons. Log_{10} mean faecal pile mass was regressed against Log_{10} mean defecation to explore relationships between faecal output and defecation rate.

4.3. RESULTS

4.3.1. Seed germination trials

Sclerocarya birrea (Marula)

Retrieval rates of AI stones were low (Table 4.2), and younger captive animals refused to eat the fruits. Retrieved AI marula stones were significantly larger than the DC stones (permutational ANOVA; pseudo-$F_{1,35}$ = 1.034, p = 0.040; Table 4.2), despite fruits being randomly assigned to treatments. Since retrieval rate of AI stones was low, it is possible that smaller stones were less likely to be found. Alternatively, duiker may have selected larger fruits. However, since rejected fruits were not measured, it was not possible to test this.

Germination only began when ambient temperatures rose after the cool, dry season. Significantly more AI seeds germinated than IC seeds (Fisher exact test, Z = 3.15, p = 0.011) and no DC stones germinated (Table 4.2). Forty-eight percent of retrieved AI stones germinated 200.8 ± 9.2 days after ingestion, with the 2009 replicate germinating insignificantly faster than the 2007 replicates (permutation ANOVA; pseudo-$F_{1,11}$ = 0.317, p = 0.078) and germination rates were higher in 2009 (55 %) than in 2007 (44 %). AI stones whose seeds germinated were insignificantly smaller than those that did not germinate (Table 4.2) (permutation ANOVA, pseudo-$F_{1,25}$ = 0.720, p = 0.223). Antelope age class may have had an effect on germination rate, but small sample sizes precluded meaningful statistics from being applied (Table 4.2).

Pseudolachnostylis maprouneifolia, *Euclea divinorum* and *Grewia monticola*

Antelope did not readily take the small-fruited species (*Euclea* and *Grewia*), resulting in small sample sizes. Retrieval rates of ingested seeds for all three species were below 50 %, and all *Euclea* seeds that passed through the gut were crushed and unviable.

No germination occurred for any species or any treatment, despite planted seeds being monitored for more than six months through the hot season.

4.3.2. Browse height preferences

All individuals exhibited similar browse height preferences, although the proportion of material removed from each height class varied among individuals and replicates. A trimodal height selection pattern was evident at 0 to 20 cm, 60 to 80 cm and 100 to 120 cm above ground level (Fig. 4.1). The 20 to 40 cm height class was avoided, and removal of tissue above 120 cm was limited (Chi-square; $\chi^2 = 36.82$, $p < 0.001$).

Browsed twig diameter averaged 1.31 ± 0.09 mm, with the majority of bites being incisor bites. Incisor-bites were restricted to diameters less than 3 mm and to removal of terminal leaves. Cheek teeth were used to crop thicker twigs.

4.3.3. Dung decomposition

4.3.3.1. Defecation behaviour and selection of defecation sites

Common duiker tended to defecate in fairly exposed sites, generally on very sandy soil. Forty-seven percent of dung piles were deposited in full sun, with the remainder being partially shaded for part of the day. All dung piles were located at latrine sites (i.e. areas with multiple piles deposited within a radius of five metres). Signs of urination at latrine sites were not encountered. The estimated mean number of pellets per pile was 74.3 ± 10.2.

Klipspringer dung piles were restricted to rocky outcrops, with faeces being deposited on rock (71 %) or at the base of rocks (29 %). Most piles (56 %) were deposited in part-shade. All deposits were at latrine sites, and faeces were often deposited on top of previous faecal piles. Latrine sites were used for both urination and defecation; thus, faecal pellets often smelled strongly of urine. Estimated pellets per pile averaged 58.6 ± 6.8.

Steenbok faecal piles were located in sandy areas, usually in bare patches in open woodland and often in loose sand close to aardvark (*Orycteropus afer*) excavations. Most deposits were fully (45 %) or partially (40 %) buried, but the remainder were not covered. However, exposed steenbok faecal piles were readily distinguished from similar common duiker piles firstly by their location within established latrine sites, and secondly by the smell of urine: steenbok urinate and defecate simultaneously. Spoor and evidence of scraping nearby were also good indicators. The vast majority of dung piles (99 %) were located in full sun. Estimated pellets per pile averaged 43.5 ± 5.1; however, pellet counts were possibly underestimates due to burial.

4.3.3.2. Decomposition patterns and rates

For all species, fresh faecal pellets were moist, soft, shiny and mucus-covered. With time, pellets hardened, the outer coating cracked, and the pellets gradually became lacklustre. Klipspringer pellets whitened within a few weeks, and both steenbok and klipspringer pellets usually developed fungal growth. Pellet size decreased over time, until only small, dark remnants remained. Duiker pellets often hollowed out, leaving the hardened outer coat that took several more months to break down completely.

Twenty-six percent of all marked piles – mostly common duiker deposits – were lost during the experiments. Sources of loss included theft of marker pegs, rain washing faecal piles away, piles being covered by fresh deposits, and fire.

In the dry season, steenbok and klipspringer pellets decomposed at similar rates (Table 4.3), but duiker pellets decomposed significantly slower (Kruskal-Wallis tests; duiker/ steenbok: $H = 13.36$, d.f. = 1, $p < 0.001$; duiker/ klipspringer: $H = 13.00$, d.f. = 1, $p < 0.001$; klipspringer/ steenbok: $H = 0.04$, d.f. = 1,$p = 0.845$). Wet season decomposition rates seemed to be reversed, but this may be an artefact of small sample sizes. However, casual observation over time suggests that duiker faeces decomposition rates are greatly accelerated in the wet season (pers. obs.); statistical investigation was precluded by inadequate sample sizes.

4.3.4. Common duiker defecation rates

4.3.4.1. Intake quantities and fibre fractions

The HFD had a significantly higher (approximately five times) fibre content than the LFD in both seasons (Median test; $\chi^2 = 20.0$, d.f. = 1, $p < 0.001$) (Table 4.4). Males and females of

both age classes exhibited comparable intake quantities on the same diet, both in terms of total dry mass and fibre, but intake was significantly higher on the LFD than the HFD in both seasons and intake on the HFD was higher in the wet season than the dry season (Tables 4.1, 4.4). Apparent digestibility was significantly higher on the LFD than the HFD (Median test, $\chi^2 = 7.20$, d.f. = 1, p = 0.007).

4.3.4.2. Defecation rate and faecal production

Total daily faecal production was similar between sexes, seasons and diets (Table 4.4), but young animals of both sexes produced more faeces than old animals (Table 4.4). Male duiker defecated significantly more frequently than females (Table 4.4), but since both sexes egested similar quantities of faecal matter, males' faecal deposits were significantly smaller than females' (Tables 4.1, 4.4). No other factors significantly affected deposit mass (Table 4.1). Strong relationships ($R^2 > 0.775$) between faecal pile mass and defecation rate were detected for both diets in the dry season, but the scatter in the wet season was greater (Fig. 4.2). There was some delineation between males and females in regression plots, but the pattern became obscured in the wet season and when diets were combined for analysis (Fig. 4.2).

4.4. DISCUSSION

In this section, I will comment on the trends shown in the results, before discussing the interaction of these effects and their likely impacts on plant communities and ecosystem functions. By necessity, discussion will be focused primarily on common duiker, with extrapolation to other antelope species made where appropriate.

4.4.1. Common duiker as seed dispersers

Seed viability trials were of limited success, with germination only occurring in one of the four species investigated. Reasons for the low germination rates were difficult to elucidate as multiple germination preparation techniques were not investigated, and the low number of replicates (source trees and years) precluded further investigation. However, several explanations are possible.

Primary dispersal of the small-seeded species (*Euclea* and *Grewia*) is probably by birds and small mammals (Tews *et al.*, 2006; Traveset, 1998), so the mismatching of disperser and fruit may have reduced germination success of these species (Traveset et al., 2008). *Euclea* has a soft seed coat (pers. obs.), which could withstand neither mastication nor digestive fluids

since seeds were destroyed following ingestion by common duiker. Typical mammal-dispersed seeds have hard seed coats or are contained in stones, which provide some protection from lethal damage (Feer, 1995; Janzen, 1984). While incidental ingestion of small fruits by large herbivores does occur (Dudley, 2000; Janzen, 1984), post-ingestion germination and establishment do not necessarily occur (Traveset, 1998).

For the larger-seeded species (*Pseudolachnostylis maprouneifolia* and *Sclerocarya birrea*), I suggest that burial of seeds in the 2007/08 experiments contributed to the low success: germination of *S. birrea* was higher when stones were not completely buried. *Pseudolachnostylis maprouneifolia* stones dry and dehisce above-ground in natural systems, expelling seeds some distance (pers. obs.), and immediate burial may have inhibited this response rather than accelerating germination, as was the aim. However, placing dehisced seeds on moist blotting paper in 2007 was similarly unsuccessful, which suggests that another germination cue was missing.

It is also possible that among-year or individual variation in seed viability was responsible for the low germination success (Traveset, 1998), and the difference in germination success of marulas between 2007 (44 %) and 2009 (55 %) suggests that this may have been a factor. Marulas have episodic recruitment (Emanuel *et al.*, 2005), which indicates that germination success among years also varies. Dunham (1990) reported that fruit production of *Acacia albida* was positively correlated with rainfall in the preceding two years. In this study the 2004/05 wet season was 68 % of normal (N. Lunt, pers. rec.) which may have negatively affected seed viability. In contrast, subsequent years received 82 to 148 % of normal rainfall (N. Lunt, pers. rec.). The timing of fruit production in relation to rainfall is also important. Chidumayo (2006) found that early fruits of *Lannea edulis*, which fruits during the early wet season, had higher germination rates than late fruits. In this study, early marula fruits (March) had lower germination rates than late-maturing fruits (April/May). Since germination occurred in the following hot season (September onwards), it is possible that the longer dormancy period negatively affected seed viability (Valleriani and Tielborger, 2006).

Despite variable germination success among replicates, ingestion by antelope clearly promoted germination in *S. birrea* relative to the control group. Direct scarification of the seed testa was unlikely as a woody stone protected the seeds (Glew et al., 2004), but mechanical stress during mastication and chemical treatment in the rumen probably improved

the porosity of the stone thereby facilitating water uptake by the seed (Traveset, 1998), and it is possible that fruit pulp of the intact control (IC) inhibited germination (Griffiths and Lawes, 2006). Stones were too large to pass into the lower alimentary canal of duiker and were egested during rumination, usually within 12 hours of ingestion.

Larger stones would be expected to have greater seed reserves for germination, but, as was found by Xiao *et al.* (2004) for *Quercus* nuts, germination of seeds in smaller stones was higher. Although not measured in this study, larger stones probably had thicker walls, and short gut retention time may have been insufficient to adequately affect large stone porosity. Interestingly, when marulas were fed to the larger yellow-backed duiker (*Cephalophus silvicultor*, mass 80 kg), greater germination success was recorded (80 % *c.f.* 55 % for common duiker), and smaller stones had a lower germination success (germinated stones: 9033 ± 509 SE mm^3; ungerminated stones 7419 ± 453 SE mm^3; *c.f.* Table 4.2) (N. Lunt, unpubl. data). Sample sizes are too small to draw firm conclusions at this time, but it is possible that the variation in stone size is an adaptation to variability of chemical composition and gut retention time by a broad spectrum of dispersers; marula fruits are palatable to a large number of species (Aganga and Mosase, 2001; Emanuel *et al.*, 2005; Gadd, 2002). Longer retention or heavy scarification, for example by elephants (Dudley, 2000), may favour larger stones but be lethal to smaller stones, while short retention (e.g. by small antelope) may favour smaller stones but be insufficient to stimulate germination of large stones.

4.4.2. Feeding height preferences

The height at which ungulates feed is influenced by four major factors: (i) the diet (browser/ grazer) and forage selectivity, which are determined by body size and evolutionary history, (ii) the size of the animal and therefore its reach, (iii) morphology, especially of the vertebral column and the braincase angle, and (iv) behaviour such as predator vigilance (Bell, 1971; du Toit, 1990; Spencer, 1995; Waldram *et al.*, 2008; Wilmshurst *et al.*, 1999).

Given the position of the thoracic “hump” (thoracic vertebra 2) (Spencer, 1995), the height of the shoulder (approximately 60 cm) and head (80 cm) and its vulnerability to a wide range of predators, the common duiker would be expected to feed at or near ground level (below the knee) and at shoulder or head height (Spencer, 1995). Feeding at full neck stretch increases the risk of predation (du Toit, 1990). Furthermore, since the feeding level of common duiker

is shared by a range of other species (du Toit, 1990; Spencer, 1995), increased feeding height would confer little benefit unless major competitors were smaller species (Prins et al., 2006).

These predictions were partially borne out by the data, although low-level feeding was less prevalent than expected and substantial feeding near full neck-stretch was evident. It is possible that, due to the reduced risk of predation, captive duiker fed at full neck stretch more readily than would wild conspecifics, as anti-predator behaviour has been shown to vary with predation risk in other antelope species (Goldspink et al., 2002; Lian et al., 2007). The avoidance of feeding at intermediate heights (40 to 60 cm and 80 to 100 cm) was probably a mechanical limitation imposed by the structure of the spinal column and the attachment angle of the spine to the skull (Spencer, 1995).

It should be noted that measurements were made of the quantity of tissue removed rather than the time spent feeding at each level. If bite size varies with height, e.g. cropping with the narrow incisor row close to the ground resulting in small quantities per bite compared with a larger mouthful obtained from cropping with molariform teeth, then animals may spend less time feeding at higher levels but obtain more tissue. This suggests that handling time and potential bite size may be important determinants of feeding level when forage is vertically homogeneous in quality or quantity (Searle et al., 2005). However, natural systems are heterogeneous and the distribution of food items in several dimensions is a more critical determinant of selection. In savanna systems, many of the high-quality forage items available to and selected by medium sized antelope such as common duiker are in the lower vegetation strata although they tend to be widely dispersed spatially: seedlings, resprouts of established plants, fallen fruits and flowers, and herbaceous dicotyledons (Prins *et al.*, 2006; Wilson, 1966). The duiker's narrow premaxilla enables the animal to obtain high-quality items from within patches of mixed-quality resources (Spencer, 1995).

4.4.3. Small antelope defecation behaviour, defecation site selection and faecal decomposition rate

The high fibre diet (HFD) provided in this experiment was probably higher in fibre than a natural common duiker diet, given that duiker are concentrate selectors (Prins *et al.*, 2006; Skinner and Smithers, 1990; Wilson, 1966,2005), whilst the LFD was either comparable with or lower in fibre, than natural diets. Assuming that the two diets therefore encompassed the

range of natural diets, several conclusions can be drawn about common duiker defecation behaviour and the potential effects on plant communities.

Intake is constrained by gut capacity and processing time and it has been suggested that duiker have relatively rapid throughput rates and efficient digestion as a result of rumen and omasum adaptations and improved hindgut fermentation (Conklin-Brittain and Dierenfeld, 1996; Faurie and Perrin, 1995). Fibre content has been used in this study as a proxy for diet quality, assuming that less digestible dietary components (e.g. cell walls) reduce the proportion of ingesta absorbed, and/or affect passage rate. Since there is little sexual size dimorphism in common duiker (Skinner and Smithers, 1990), intake is scaled with body size (Shipley et al., 1994) and no sex-specific digestive adaptations have been identified in cephalophines, male and female duiker would be expected to exhibit similar ingestion and egestion rates.

Therefore, it can be predicted that on a high-fibre diet (i) intake would be constrained because of increased processing time (Searle et al., 2005) and low digestibility of fibrous material, and (ii) low digestibility would increase the quantity of faecal matter produced. The effect of diet quality on defecation rate is equivocal in the literature: some authors cite diet as a possible determinant of defecation rate (Bowland and Perrin, 1994), but Rollins *et al.* (1984) found that defecation rate of a range of ruminants was not consistently linked with changes in cell-wall fraction and crude protein.

Prediction (i) was supported by the data: intake quantity and apparent digestibility were approximately five times higher on the LFD than on the HFD. Although prediction (ii) was also supported, (relatively more faecal matter was produced on the HFD), the absolute quantity of faeces was comparable to faecal output on the LFD and there was no significant change in defecation rate (Tables 4.3; 4.4). Animals did not apparently lose condition on the HFD, and although the experimental period on this diet was short (10 days), this suggests that common duiker were able to obtain sufficient energy from a low-quality diet, which may explain this species' adaptability to highly variable environments (Kingdon, 1997). Previous studies have shown that cephalophine digestive adaptations improve digestive efficiency (Wenninger and Shipley, 2000) which may account for this tolerance.

As expected, intake, apparent digestibility and dry matter output did not differ significantly between sexes, although variability among individuals was apparent. Defecation rate, however, was strongly linked with animal sex (Fig. 4.2), and to a lesser extent with animal age (Table 4.1). I suggest that young (prime) males controlled defecation volume to maximise scent-mark distribution within their territories. If scent deposited with faeces confer information about animal condition, age and sex (Gosling and Roberts, 2000) and are used as territorial markers as has been suggested (Lunt et al., 2007), then it would be expected that territorial animals and those in prime condition would readily advertise their presence by depositing a large number of scent marks (Roberts and Dunbar, 2000). Post-prime animals would not be expected to "advertise" in this way, and non-territorial individuals would not necessarily benefit from faecal control. Since faecal matter is a finite resource, optimisation of scent distribution can only be effected by the parsimonious deposition of scent marks (Roberts and Gosling, 2001). Such behaviour has been demonstrated in oribi, where territorial males produced more (but smaller) faecal deposits than females and subordinate or immature males (Brashares and Arcese, 1999).

Thus, the variation in defecation rate among age and sex classes can be attributed to differences in territoriality. Male common duiker are actively territorial, rigorously overmark intruder scent – especially if deposited by a prime male – and do not tolerate same-sex conspecifics in their territories (Dunbar and Dunbar, 1979; Lunt *et al.*, 2007, pers. obs.). Older males, probably because of relatively lower fitness, were less actively territorial. Females carry out little territorial behaviour: they tolerate range overlap with other females and rarely scent-mark (Dunbar and Dunbar, 1979; Lunt *et al.*, 2007).

The selection of defecation sites by small antelope was clearly non-random. All three species used latrine sites, and indications are that for klipspringer and common duiker, faecal deposits are used as territorial markers (Roberts and Lowen, 1997, B. Msimanga & N. Lunt, in prep.), and it is likely to hold true for steenbok as well.

Since steenbok, klipspringer and common duiker pellets are of similar dimensions and moisture content (Woodall *et al.*, 1999, pers. obs.), I suggest that the striking among-species variation in dung decomposition was due to differential desiccation rates as a result of defecation behaviour and site selection, and the availability of microbes. In the dry season, steenbok faeces decomposed most rapidly, but not significantly faster than klipspringer

faeces. Both species urinate and defecate simultaneously, often in very close proximity to previous deposits (Skinner and Smithers, 1990, pers. obs.), where a well-developed microbial and insect community would be established. The application of moisture softened the pellets and encouraged decomposition by the associated decomposers. Dung beetles (Coleoptera: Scarabaeidae) and fungal cultures were commonly encountered at klipspringer latrines in the late wet and early dry season (pers. obs.). The steenbok's tendency to bury dung further slowed desiccation. Despite the duiker's use of latrine sites (Lunt et al., 2007), the selection of exposed sites and the dryness of pellets encouraged rapid desiccation and inhibited microbial attack, and faecal removal was carried out almost exclusively by insects such as termites (Isoptera). In the wet season, rainfall may have negatively affected soil microbes through waterlogging or leaching, resulting in slower decomposition rates of buried steenbok dung. However, exposed duiker dung was kept moist by rain, and the wet-season insect community took advantage of the readily available resource. Wet season decomposition of exposed dung tends to be more rapid than in the dry season (Ellis and Bernard, 2005; Plumptre and Harris, 1995). Reasons for the substantial slowing of klipspringer dung decomposition in the wet season are more difficult to determine. It is possible that water pooling in deposit sites on rocks affected microbial cultures, and certainly a number of deposits were completely dispersed by rain.

4.4.4. Potential impacts of small antelope on vegetation

The diet selectivity, long residence time in relatively small home ranges, and continual use of latrine sites and resting/ rumination sites (pers. obs.) of the three small antelope species included in this study have important implications for plant community structure. Whilst few of the following hypotheses were tested in this study, published reports and my field observations lend some support.

Mammalian scent-marking (e.g. latrine) sites tend to be distributed for optimal detection and located near defended resources such as resting sites, mates and food supplies (Gosling and Roberts, 2000; Jordan *et al.*, 2007; Roberts and Gosling, 2001; Roberts and Lowen, 1997). Scent-marks serve not only to advertise territory occupancy, but allow occupants to orientate themselves in their environment (Benhamou, 1989). The establishment of palatable plants, or plants with palatable fruits, would be expected at latrine sites for four reasons.

Firstly, faeces and urine enrich soil in the immediate vicinity of deposition. Nutrient cycling through herbivores is typically faster than through decomposition of moribund plant matter (Augustine and McNaughton, 1998; Hulme, 1996; Manier and Hobbs, 2007) and deposition sites are usually some distance from the source of the material. Based on known animal density (*c*. 12.7 km^{-2}), mean latrine site density (413 km^{-2}) and mean latrine area (25 m^2) (Lunt et al., 2007, N. Lunt, unpubl. data), common duiker in the MNP study site deposit in the region of 3100 kg (dry mass) of faecal material per square kilometre per year. Since faecal distribution is not uniform spatially, within each square kilometre, approximately one hectare of ground is enriched at a rate of 0.3 kg dry matter.m^{-2}. However, some of this deposit is lost or spread by the action of rain or coprophages prior to inclusion into the soil. Although dry matter intake and output would be lower for klipspringer and steenbok because of smaller body size (Shipley et al., 1994), the 60 (klipspringer) to 88 (steenbok) latrines sites per square kilometre (N. Lunt, unpubl. data) would also be expected to provide substantial local enrichment.

Secondly, continual disturbance by hoof action (Cumming and Cumming, 2003) reduces competition for resources (e.g. light) and opens gaps for new growth as well as trampling nutrients back into the top soil (McNaughton et al., 1988). Many colonisers are fast-growing and invest little energy into anti-herbivore defences (Augustine and McNaughton, 1998; Cebrian and Duarte, 1994), which would potentially have a feed-forward effect encouraging antelope to continue to frequent and defend the site. Thirdly, the proximity of preferred forage plants (at least at some latrine sites) ensures that propagules of palatable plants are available to colonise gaps. Finally, the enhanced germinability of some plant species following gut passage ensures the dispersal of viable seeds away from the parent plant, and seeds are deposited at open microsites. Furthermore, deposition within dung may accelerate germination (Barnes, 2001).

However, these same factors are also likely to have an attenuating effect on plant recruitment and limit woody development. Continual disturbance and trampling may kill small individuals and compact the soil, inhibiting the emergence of seedlings (Cumming and Cumming, 2003), although the small hoof size of small antelope will produce limited effects on a large spatial scale. The presence of browsers in a temperate region was shown to have negative effects on mineralization of nitrogen and carbon when browser density was low and dung deposition was patchy (Harrison and Bardgett, 2004), but such an effect would be

unlikely in an African savanna (McNaughton et al., 1988). For abundant seeds dispersed in dung that do germinate and emerge, high densities increase inter-stem competition (especially of conspecifics) and result in high mortality rates (Queenborough et al., 2007). As a result of continual use of the area, palatable seedlings may not escape browsing pressure, which may have lethal effects or alter the growth form of the individuals.

Seed dispersal distance varies with seed size, disperser size, gut retention time, and disperser behaviour (e.g. caching *vs.* immediate ingestion) (Diefenbach *et al.*, 2008; Ezoe, 1998; Mouissie *et al.*, 2005a; Xiao *et al.*, 2005). Both small seeds that pass through the digestive tract and large seeds that are egested during rumination or depulped orally and egested (i.e. "spit dispersal", Bodmer, 1991), benefit from being removed from the zone of influence of the parent plant (Smit, 2004). The relatively short retention time of spit-dispersed seeds may improve the probability of seeds being deposited in suitable habitats (Baythavong et al., 2009). For ruminant dispersers, habitual use of rest/ rumination sites results in the deposition of multiple spit-dispersed seeds in sheltered areas over a period of time (pers. obs.), for germination to occur when conditions are suitable (Hampe et al., 2008).

Given the arguments above, it would be expected that temporal release of antelope pressure would favour plant recruitment. Multiple latrine sites are typically used, and not all latrines are refreshed regularly (Lunt et al., 2007, pers. obs.). Latrine positions also shift with changes in the core area used by small antelope (pers. obs.), usually on a seasonal basis. Additionally, antelope do not necessarily feed at marking sites (Roberts and Lowen, 1997), and the periodicity of defecation and feeding times may not coincide (N. Lunt, unpubl. data). Eventually, individual turnover (emigration or mortality) and the establishment of new latrines by immigrants will enable plant establishment at unused sites, provided that germination conditions are suitable and seeds are persistent (Higgins *et al.*, 2008).

Although it would be unusual for duiker to act in isolation, and other herbivores may have impacts in height zones where duiker are less active (du Toit, 1990; Prins et al., 2006), I will consider the potential effects of the observed common duiker feeding height preferences and known feeding selectivity (Prins *et al.*, 2006; Wilson, 1966) on vegetation structure. In order to produce a working hypothesis, it is important to understand foraging behaviour and feeding adaptations of antelope. Searle *et al.* (2005) demonstrated a “diminishing returns” system for selective browsers: the number and size of bites taken from a patch diminished as

the patch size diminished and residence time in a patch declined as spatial heterogeneity of forage quality increased. Thus, bites taken from large plants or densely arranged small plants were initially large, but diminished in size as edible tissues were removed. The time between bites also declined as time spent searching for palatable tissues increased, and at some threshold, the browser moved to the next patch. Another important consideration is the size of the plant relative to the size of the herbivore. Browsers with narrow premaxillae (e.g. common duiker) can be highly selective for tissues within larger plants, but small plants such as low single-stemmed herbs and seedlings may be completely defoliated with one bite, or have the primary axis severed (Spencer, 1995; Wilson and Kerley, 2003a).

Aggregations of small palatable dicots would therefore be expected to be more susceptible to lethal defoliation than sparsely-distributed plants because of the probability of a browser encountering a large patch rather than an individual. In addition to random spatial distributions, the establishment of palatable plants within a patch dominated by unpalatable plants would also confer an advantage, as browsers are less likely to enter a relatively unproductive patch. This “nurse plant” effect (Smit et al., 2006; Van Uytvanck et al., 2008) was evident in MNP, with highly palatable species such as *Gardenia resiniflua* persisting in thicket refuges among unpalatable species such as *Euclea* spp. (Chapter 3, this study).

For larger dicotyledonous individuals, lethal effects may not occur as browsers move to another plant before complete defoliation occurs (Searle et al., 2005), but the growth structure may be irreversibly altered and tissue loss may impact on the competitive ability of intermediate-sized plants (Chapter 3, this study). Release of apical dominance following the removal of the apical meristem (especially on the primary axis) typically results in a bushy growth form; plants grow outwards rather than upwards and remain within browsing range for longer (Smaillie and O'Connor, 2000; Styles and Skinner, 2000). The feeding height preferences of common duiker suggest that herbivory escape (at least by the primary apical meristem) may occur when plants reach heights of 20 to 40 cm and 80 to 100 cm, which may allow development into large mature trees.

In summary, the feeding height preference of common duiker has the potential to limit recruitment of palatable woody plants and to alter the abundance and density of palatable herbaceous plants. This in turn will affect the plant species richness and diversity. Larger plants (e.g. small saplings), while not likely to be killed by common duiker browsing, may be

structurally altered through apical dominance release (Renaud *et al.*, 2003; Sebata *et al.*, 2009).

4.5. CONCLUSIONS

This chapter has considered several indirect effects of small antelope on vegetation. Firstly, promotion of marula germination following ingestion suggests that common duikers are dispersers of this and other hard-seeded tree species under natural conditions. Secondly, the focus of browsing pressure below 1.2 m may alter the architecture of smaller plants (Sebata et al., 2009) and limit woody growth by altering competitive relationships among saplings and contributing to self-thinning (Augustine and McNaughton, 2004; Belsky, 1984, Chapter 3 this study). Thirdly, local enrichment of soil at latrine sites coupled with trampling effects, create space and nutrients for the establishment of seedlings. The distribution and density of latrine sites (Lunt et al., 2007) and the quantity of dung deposited (this study) ensure patchy enrichment of the soil. These effects in combination contribute to vegetation heterogeneity; a pattern synonymous with the savanna biome.

Table 4.1: Summary of statistical comparisons showing the influences of major factors on feed intake and faecal output of common duiker. Tests are permutational ANOVA, with 999 iterations, no transformation, and Euclidean distance measures. *P*-values in boldface are significant at α = 0.05.

Variable	Factor (covariable)		
	Sex (age, diet)	Season (age, diet)	Diet (season)
Intake (mass)	F = 0.0001 P = 0.988	F = 24.2 **P = 0.001**	F = 147.9 **P = 0.001**
Faecal output (mass)	F = 1.455 P = 0.249	F = 0.224 P = 0.657	F = 1.622 P = 0.224
Mass/pile	F = 12.9 **P = 0.001**	F = 0.373 P = 0.565	F = 0.317 P = 0.569
No. piles	F = 20.3 **P = 0.001**	F = 0.309 P = 0.573	F = 0.008 P = 0.924

Table 4.2: Summary of germination success and stone size (mean ± SE) of marulas. Data are means ± SE. Letter superscripts denote statistically significant differences (permutation ANOVA) at α = 0.05.

Treatment	Antelope age class	Retrieved %	Germination %	Time to seedling emergence (days)	Germinated stone volume (mm^3)	Ungerminated stone volume (mm^3)
Intact control (IC)		100 (N = 20)	10^a	191 ± 4.0 (N = 2)	-	-
Depulped control (DC)		100 (N = 10)	0	-	-	5722 ± 1037 (N = 10)
Antelope ingested (AI)	Young 4.9 ± 0.6 yr (N = 5)	44 (N = 22)	45^b	198.3 ± 10.1 (N = 10)	7042^c ± 558 (N = 10)	7846^c ± 457 (N = 12)
	Old 13.7 ± 1.5 yr (N = 3)	33 (N = 5)	60^b	209.0 ± 25.0 (N = 3)	7079^c ± 1104 (N = 3)	7401^c ± 213 (N = 2)

Table 4.3: Decomposition rates of small antelope faecal deposits. Data are means ± SE. Letter superscripts link statistically similar decomposition rates (Kruskal-Wallis tests). Statistics were not done on wet season data, due to small sample sizes.

Species	Season	N final sample (original sample)	Decomposition rate (days)
Common duiker	Dry	7 (13)	459.6 ± 29.8[a]
	Wet	5 (5)	187.4 ± 36.7
Klipspringer	Dry	13 (14)	145.8 ± 5.7[b]
	Wet	4 (7)	275.8 ± 18.7
Steenbok	Dry	14 (16)	136.1 ± 5.8[b]
	Wet	3 (5)	215.3 ± 71.7

Table 4.4: Intake and faecal output (mean ± SE) of common duiker, categorised by age, sex, diet and season. Diet codes and age categories as per text.

Category	Diet[a]	Total DM intake (g)		Total DM ouput (g)		Apparent digestibility (%)		Defecation rate (/24 h)		Mass per deposit (g)	
	Season	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet
Male, young	LFD	519.1±24.6	515.0±28.6	162.6±13.0	166.0±15.0	68.7	67.8	7.0±1.1	5.8±1.4	23.4±1.1	36.1±18.3
N=2	HFD	190.1±16.5	346.5±14.6	180.4±16.8	209.3±15.7	5.1	39.6	7.4±0.9	7.0±2.3	24.5±0.1	33.7±11.1
2.1±0.3 yr	Pooled	354.6±95.7	430.8±50.4	171.5±26.1	187.7±68.8	51.6	56.4	7.2±1.0	6.3±1.8	23.9±0.5	35.1±14.8
Male, Old	LFD	532.7±9.3	526.0±12.0	143.2±4.3	134.6±8.8	73.1	74.4	4.9±1.2	4.7±1.6	36.0±15.5	38.8±12.8
N=3	HFD	186.9±17.2	344.7±38.1	152.1±17.5	113.1±40.7	18.6	67.2	4.6±0.7	2.7±0.7	34.8±8.5	44.4±8.7
11.4±1.4 yr	Pooled	359.8±77.8	435.3±44.3	147.6±17.8	123.8±53.9	59.0	71.6	4.8±0.9	3.6±1.1	35.1±11.5	41.0±10.7
Male, All	LFD	527.3±9.9	521.6±11.5	150.9±5.5	147.1±7.1	71.4	71.8	5.8±0.9	5.1±1.0	31.0±9.0	37.7±9.1
N=5	HFD	188.2±10.8	345.4±21.4	163.4±11.0	151.6±22.9	13.2	56.1	5.7±0.8	4.4±1.3	30.7±5.3	40.1±6.5
7.7±2.4 yr	Pooled	357.7±56.9	433.5±31.5	157.2±14.0	149.4±40.0	56.1	65.5	5.7±0.8	4.7±1.0	30.7±6.9	38.6±7.7
Female, Young	LFD	527.1±21.8	538.3±15.6	154.1±8.9	167.2±4.3	70.8	58.9	2.5±0.5	3.1±0.5	66.3±11.5	57.4±11.5
N=3	HFD	197.9±9.9	414.3±10.0	149.7±10.1	180.8±10.7	24.4	56.4	3.0±0.6	3.5±0.5	56.4±14.1	51.2±12.4
2.9±0.9 yr	Pooled	362.5±74.4	476.3±28.9	151.9±16.7	174.0±63.0	58.1	63.5	2.8±0.5	3.3±0.5	60.9±12.9	54.0±11.9
Female, Old	LFD	445.9±83.5	492.6	153.2±6.7	161.5	65.7	67.2	3.2±0.2	2.5	47.6±5.7	55.8
N=2(1)[b]	HFD	200.8±14.4	411.2	158.2±14.6	178.4	21.2	56.6	3.9±0.7	3.2	39.9±9.3	71.6
15.2±0.2 yr	Pooled	323.4±78.8	451.9±40.7	155.7±30.8	170.0±154.5	51.9	62.4	3.5±0.4	2.9	43.7±7.7	61.9
Female, All	LFD	494.6±35.2	526.8±15.9	153.7±9.4	165.8±8.4	58.9	58.5	2.8±0.3	3.0±0.4	58.8±8.0	61.0±8.8
N=5(4)[b]	HFD	199.1±7.1	413.5±7.1	153.1±7.2	180.2±7.6	23.1	56.4	3.4±0.4	3.4±0.4	50.0±9.2	61.0±8.8
7.8±3.0 yr	Pooled	346.8±52.1	470.2±22.9	153.4±15.0	173.0±54.7	55.8	63.2	3.1±0.4	3.2±0.4	54.0±8.6	56.0±8.7
Pooled sexes	LFD	510.9±18.1	523.9±8.9	152.3±5.2	155.4±5.7	70.2	70.3	4.3±0.7	4.0±0.7	44.9±7.3	48.0±7.3
N=10(9)[b]	HFD	193.6±6.4	375.7±16.7	158.3±6.5	164.3±17.9	18.3	56.3	4.5±0.6	4.2±0.7	40.2±5.9	45.5±5.4
7.8±1.8 yr	Pooled	352.3±37.6	449.8±20.2	155.3±10.0	159.9±32.3	55.9	64.5	4.3±0.6	4.0±0.6	42.3±6.5	46.3±6.2

[a] Ingested fibre fractions both seasons: (a) ADF % = 0.48 (HFD) and 0.10 (LFD) ; (b) NDF % = 0.54 and 0.59 (HFD in dry and wet seasons, respectively) and 0.12 and 0.17 (LFD in dry and wet seasons, respectively). SE << 0.001 in all cases.

[b] One female was unavailable for trials in the wet season, reducing sample size to 1 (old females) and 4 (all females).

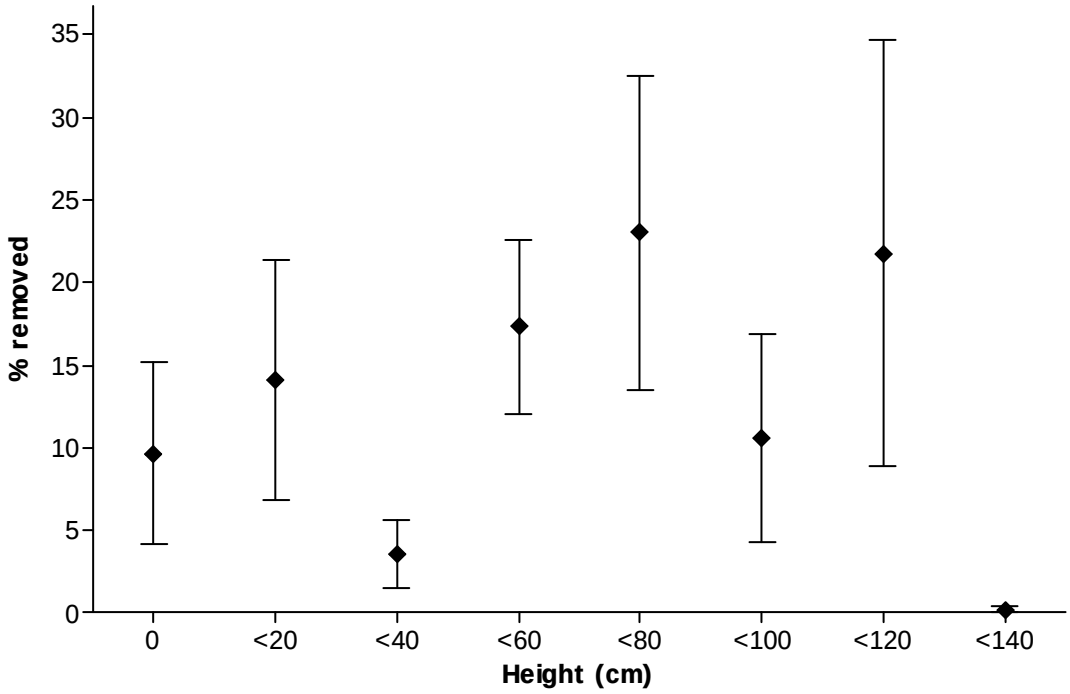


Figure 4.1: Proportion of total tissue removal (due to common duiker browsing) at 20 cm height intervals. Data are means ± SE pooled across individuals (N = 5).

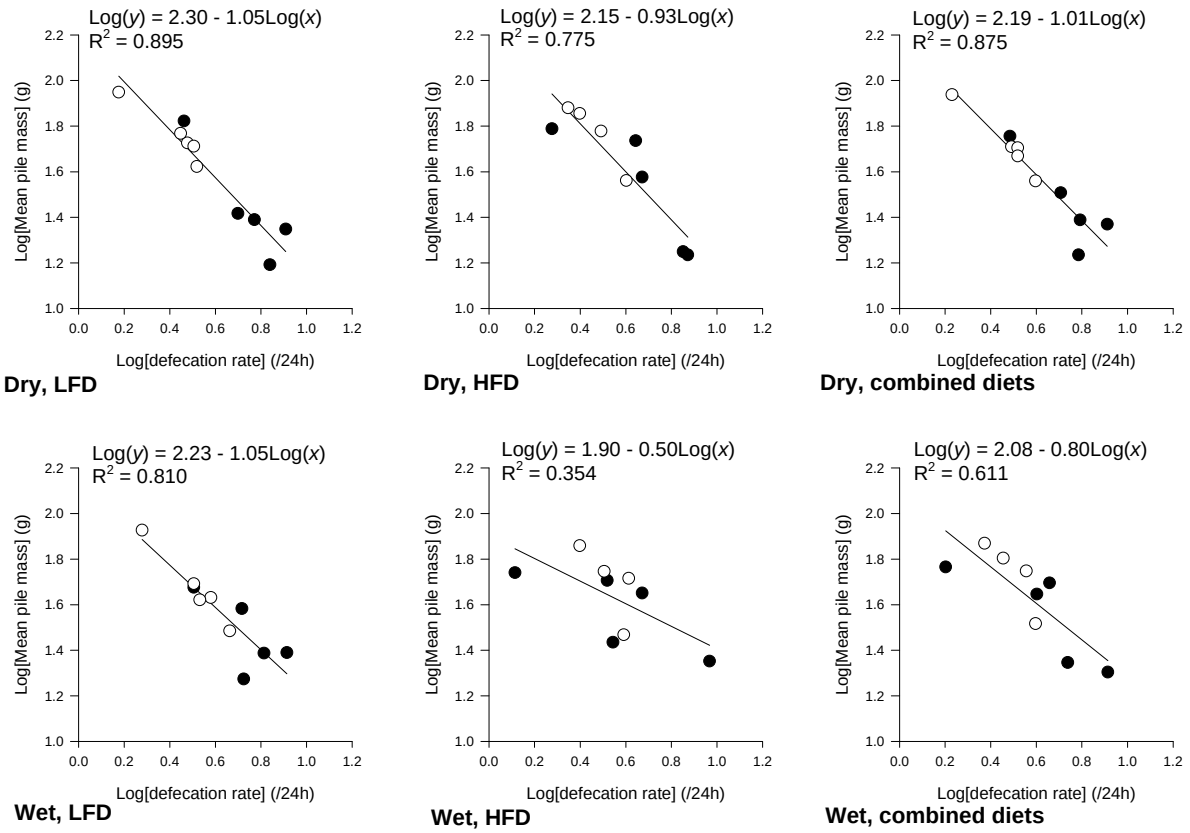


Figure 4.2: Relationship between mean faecal pile mass (g) and daily defecation rate for male (closed circle) and female (open circle) common duiker on each diet (LFD/ HFD/ combined) in each season (Wet/ Dry). See text for diet and season descriptions.

5. SYNTHESIS

5.1. PREAMBLE

The primary aim of this study was to investigate the role that medium-sized indigenous herbivores, *viz.* small antelope (Bovidae: Cephalophinae and Antilopinae: Neotragini), play in a savanna ecosystem. It was hypothesized that morphological, physiological and behavioural characteristics of small antelope would have important implications for savanna structure. This would be due to their direct impacts, such as selective feeding and trampling, and indirect impacts such as nutrient cycling. Experiments were established that investigated several aspects of antelope impacts on vegetation and nutrient cycling, with comparison of the effects of small antelope with those of larger sympatric browsers. A secondary aim, which was introduced part-way through the study as a result of an unplanned fire, was to investigate the short-term interactive effects of fire and mammalian herbivores at a community scale.

5.2. SMALL ANTELOPE, FIRE AND VEGETATION DYNAMICS

5.2.1. Disturbance effects on vegetation

All terrestrial animals exert frictional and mechanical pressure on vegetation and the ground as they move through the environment, although body size determines the magnitude of damage incurred (Cumming and Cumming, 2003). These pressures and fire provide gaps for the establishment of new plant growth, and hoof action mixes surface litter into the top layer of soil (Augustine and McNaughton, 1998). In the Matobo study site, relatively low mammalian biomass (Chapter 2) precluded extensive trampling that may have resulted in erosion (Boelhouwers and Scheepers, 2004). The combined effects of herbivory, fire and mechanical damage incurred through animal movement, generated patterns that were consistent at the community scale but differed at the level of the plant species (Chapter 3). Thus, community-scale effects supported previous findings (Augustine and McNaughton, 2004; Belsky, 1984; Levick and Rogers, 2008; Sheuyange *et al.*, 2005; Strang, 1973), and variation in fine-scale effects underscored the importance of defining the scale of measurement (Belsky, 1987; Skarpe et al., 2007) and the constraints imposed by prior conditions (Skarpe, 1992).

Despite the preponderance of browsers, animal presence limited grass development and promoted species richness of both grasses and forbs (Chapter 3), which demonstrates the

impact of mechanical effects on vegetation structure. Similarly, fire, in the absence of animals, promoted herbaceous species richness. However, the combination of fire and animal pressures limited species richness. Woody vegetation showed a different trend: species richness increased in the absence of mammalian (especially smaller species) browsers, declined in the presence of browsers, and increased across the board following fire (Chapter 3). These effects demonstrate that moderate disturbance affects the trajectory of plant succession in the short term (Davidson, 1993; Fuhlendorf and Engle, 2004; Ritchie *et al.*, 1998; Seagle and Liang, 2002), and support previous studies that indicate that woody and herbaceous plants compete with each other (Meyer et al., 2007; Vandenberghe et al., 2008; Veblen, 2008). Such competition is frequently mediated by water availability and herbivory pressure (Veblen, 2008), although only the latter effect was investigated in this study.

Spencer (1995), using spinal and cranial features, predicted that the common duiker (*Sylvicapra grimmia*) and klipspringer (*Oreotragus oreotragus*) feed primarily at ground level, and du Toit (1990; 1993) demonstrated that the steenbok (*Raphicerus campestris*) also feeds at this level. *Ex situ* experiments on the common duiker, the largest small antelope species present in the MNP study area, showed a bimodal feeding height preference, with the majority of plant tissue selected from below 20 cm and between 40 and 80 cm above ground level (Chapter 4). Woody plant recruitment and development were apparently limited more by small antelope than by large antelope (Chapter 3, Augustine and McNaughton, 2004; Belsky, 1984), which suggests that regulation of woody plants occurs through limitation of smaller stems (e.g. seedlings and resprouts) rather than through reduction in growth rates of established stems.

Seedlings of a number of palatable woody plant species became established or increased in density in the absence of antelope (Chapter 3). By contrast, with the exception of the over-compensating shrub *Lippia javanica*, it was primarily unpalatable species that increased in the presence of herbivores. This further supports the contention that browsing antelope regulate the establishment of woody vegetation (Belsky, 1984), and at first glance would suggest that the community would become dominated by unpalatable plants over time (de Mazancourt and Loreau, 2000b). However, although dominance was by unutilised (e.g. *Burkea africana*) or rarely browsed (e.g. *Terminalia brachystemma*) species, highly preferred species persisted in the community (Chapter 3). At least one species persisted through "associational refuges" among rarely browsed species (Miller *et al.*, 2006) and others were

able to compensate for herbivory damage (Agrawal, 2000; Focardi and Tinelli, 2005). Temporary refugia may occur in a vertical plane when plants enter the height classes that are avoided by small antelope (e.g. 20 to 40 cm for common duiker), and as a result of the territorial behaviour of small antelope and the spatiotemporal shifts in core areas of their home ranges (de Chantal and Granstrom, 2007; Lunt *et al.*, 2007). Therefore, although small antelope apparently regulate woody development at the local scale (e.g. individual plant and plants in core use areas), vegetation heterogeneity would be promoted at the community scale, reducing the probability of local extinction of highly palatable plant species (O'Connor et al., 2007). Importantly, in experimental plots accessible to all animals, woody: herbaceous cover ratios and within-season species richness and diversity of the herbaceous layer changed little, indicating a system in equilibrium.

It is also important to note that species that were apparently unpalatable to mammalian herbivores were utilised by insects (e.g. Lepidopteran larvae on *Burkea africana*, pers. obs.), and such unmeasured impacts inevitably affect community dynamics. That *Burkea africana* was dominant lends some support to the hypothesis that the scale of measurement is important (Belsky, 1987). Small herbivores that cycle nutrients locally (e.g. lepidopteran larva frass deposited beneath the canopy) may be more advantageous to the individual plant than larger herbivores that deposit faeces and urine away from the host plant (Belsky, 1987; de Mazancourt and Loreau, 2000b), but the combination of local- and community scale effects maintain heterogeneity.

5.2.2. Small antelope as seed dispersers

Small antelope ingest a wide range of savanna fruits of a variety of sizes (du Toit, 1993; Kingdon, 1982b; Prins *et al.*, 2006; Wilson, 1966,2005), although only three fruit species were identified in the dung of small antelope in a Mozambican study (Prins et al., 2006).

Matching disperser and seed is important. Soft-seeded species, such as *Euclea divinorum* in this study, may be destroyed during mastication (Feer, 1995), so small antelope are potential dispersers of hard seeds, seeds protected by a woody stone, or very small seeds that escape mechanical damage and that can tolerate gut chemicals (Feer, 1995; Janzen, 1984). Other species (e.g. *Grewia monticola*), despite being hard-seeded and possessing a pulp layer, may be bird-dispersed (Tews *et al.*, 2004). Incidental dispersal by antelope through accidental ingestion during browsing is possible, but unlikely to be the primary mechanism of dispersal

(Janzen, 1984; Tews et al., 2006). However, disperser mismatch is unlikely to be a contributing cause for the lack of germination in duikerberry (*Pseudolachnostylis maprouneifolia*): ripe fruits are highly sought after by common duiker and other antelope (Coates-Palgrave, 1996), aggregations of depulped stones are frequently found at antelope resting sites (pers. obs.), and common duiker latrine sites are often associated with this tree (pers. obs.) which may indicate resource defence.

As shown by Traveset (1998), Traveset *et al.* (2008) and duikerberry experiments (Chapter 4), intact passage through the gut does not necessarily result in improved germination success or post-germination growth. While marula (*Sclerocarya birrea*) germination was enhanced following antelope ingestion, stone size had an apparent effect. I suggest that this may be an adaptive response by *S. birrea* to take advantage of a large suite of mammalian dispersers with a range of mechanical and chemical characteristics (Chapter 4).

The results from this set of experiments illustrate several important points. Firstly, successful endozoochorous dispersal is reliant on the matching of the fruit and animal disperser (Traveset, 1998). Secondly, post-deposition factors affect germination success of endozoochorous species (Calviño-Cancela, 2004). Thirdly, multiple cues may be necessary for seed germination. For example, in the case of marulas, germination only occurred when ambient temperatures increased. Finally, although only four species were investigated here, small antelope are probably important dispersers of a number of species of savanna seeds, although germination success may not be enhanced following endozoochory (Traveset, 1998). For species such as the marula that have nutritional and economic value to humans (Aganga and Mosase, 2001; Emanuel *et al.*, 2005; Glew *et al.*, 2004), understanding the factors influencing germination and development is vital.

5.2.3. Small antelope as nutrient cyclers

Small antelope's selection of high-quality forage, relatively rapid throughput rates of digesta, and clumped distribution of dung (Chapter 4) ensure localised soil enrichment. This study was limited in duration, but it would be expected that long-term effects of small antelope feeding ecology and defecation behaviour would be profound. Zoochorous seed dispersal may influence plant species composition in the medium term (Heinken et al., 2006b), and community succession processes may be interrupted or accelerated by local enrichment, depending on the pre-enrichment conditions (Davidson, 1993).

5.2.4. Extrapolations in time and space

This study was restricted to a short time period and focused on a single plant community in a browser-dominated system. Extrapolations to a larger scale are therefore limited. However, given the similarity in results to previous studies of woodland ecosystems (Augustine and McNaughton, 2004; Belsky, 1984), it is clear that mammalian browsers – especially smaller antelope – are important regulators of woody vegetation, and potentially on the species composition of herbaceous vegetation. It has also been demonstrated that small antelope play an important role in ecosystem function (Chapter 3 & 4). Perturbations to the browser guild would therefore be expected to have substantial effects on medium- and long-term vegetation dynamics of woodland ecosystems.

In woodland, increased density of small browsers would promote the development of large savanna trees, through the removal of seedlings and growth limitation of saplings (Belsky, 1984; Strang, 1973). In the long-term, it would be expected that open-canopy woodland would develop, dominated by relatively unpalatable species but with palatable species persisting in spatiotemporal refugia. Resilient palatable species with zoochorous seeds (e.g. *Flacourtia indica*) would remain relatively common in the community. Frictional effects, selective browsing of forbs and the actions of grazers (at low- to moderate stocking rates) would maintain the diversity of the herbaceous layer. However, heavy browsing pressure on forbs may favour the dominance of unpalatable species (Davidson, 1993).

The loss of the browser guild would promote woody development, resulting in closed-canopy woodland. Obligate zoochorous species would ultimately be lost unless alternative dispersers were present. In the absence of all large herbivorous fauna, the reduction in frictional effects and tissue removal would result in a depauperate herbaceous layer, dominated by unpalatable species. Fire intensity would increase due to the high fuel load, ultimately leading to altered soil chemistry (Mills and Fey, 2004) and negatively affecting plant development. Fire may limit woody growth in the short term, but colonisation of newly created gaps would promote woody plant recruitment. Inter-stem competition in the mid size ranges would result in few mature plants developing, with a preponderance of small, shrubby plants.

5.3. CONCLUSIONS

The results from this study highlight the importance of small mammalian browsers in ecosystem function. This guild is frequently overlooked in ecological studies, but it is

apparent that small browsers not only regulate woody vegetation, but affect the composition and development of the herbaceous layer as well, through direct (feeding) and indirect (frictional pressure) effects. Thus, management should aim to manage smaller browsers in addition to the traditionally accepted “megaherbivores” that cause obvious changes to vegetation structure (Levick and Rogers, 2008).

6. APPENDICES

APPENDIX 1: HERBIVORES LARGER THAN 2 KG ENCOUNTERED IN THE MATOBO HILLS STUDY SITE

Family: Subfamily: Tribe	Common name	Scientific name (Authority)	Status and habitat
Cercopithecidae	Chacma baboon	*Papio ursinus* (Kerr, 1792)	Common resident; all habitats
Cercopithecidae: Cercopithecinae	Vervet monkey	*Cercopithecus pygerythrus* (F. Cuvier, 1821)	Relatively common resident; all habitats especially near water
Leporidae	Scrub hare	*Lepus saxatilis* (F. Cuvier, 1823)	Common resident; woodland/ grassland
Leporidae	Jameson's red rock hare	*Pronolagus randensis* (Jameson, 1907)	Locally common resident; rocky outcrops
Hystricidae	Porcupine	*Hystrix africaeaustralis* (Peters, 1852)	Relatively common resident; all habitats except dwalas
Procavidae	Rock hyrax	*Procavia capensis* (Pallas, 1766)	Locally common resident; rocky outcrops
Procavidae	Yellow-spotted hyrax	*Heterohyrax brucei* (Gray, 1868)	Locally common resident; rocky outcrops
Rhinocerotidae	White rhinoceros	*Ceratotherium simum* (Burchell, 1817)	Uncommon late dry season visitor (< 4 animals); open woodland/ grassland
Suidae	Warthog	*Phacochoerus africana* (Pallas, 1766)	Uncommon resident; woodland
Suidae	Bushpig	*Potamochoerus larvatus* (Linnaeus, 1758)	Common resident; all habitats except bornhardts

Family: Subfamily: Tribe	Common name	Scientific name (Authority)	Status and habitat
Bovidae: Bovinae: Tragelaphini	Greater kudu	*Tragelaphus strepsiceros* (Pallas, 1766)	Common resident; woodland/ gentle slopes
Bovidae: Bovinae: Tragelaphini	Bushbuck	*Tragelaphus scriptus* (Pallas, 1766)	Common resident; woodland
Bovidae: Cephalophinae	Common duiker	*Sylvicapra grimmia* (Linnaeus, 1758)	Common resident; woodland/ grassland
Bovidae: Antilopinae: Neotragini	Klipspringer	*Oreotragus oreotragus* (Zimmerman, 1783)	Common resident; kopjes/ woodland/ grassland
Bovidae: Antilopinae: Neotragini	Steenbok	*Raphicerus campestris* (Thunberg, 1811)	Locally common resident; open woodland/ grassland
Bovidae: Reduncinae	Reedbuck	*Redunca arundinum* (Boddaert, 1785)	Common resident; grassland/ vlei
Bovidae: Alcelaphinae	Blue wildebeest	*Connochaetes taurinus* (Burchell, 1823)	Dry season visitor (small herds of <20); open woodland
Bovidae: Alcelaphinae	Tsessebe	*Damaliscus lunatus* (Burchell, 1823)	Rare dry season visitor; open woodland/ grassland
Bovidae: Hippotraginae	Sable antelope	*Hippotragus niger* (Harris, 1838)	Rare dry season visitor; tall grassland/ vlei

APPENDIX 2: TIMING OF *IN SITU* AND SEASON-DEPENDENT *EX SITU* EXPERIMENTAL ASSESSMENTS.

Activities	2004		2005			2006			2007			2008			
Season[1]	CD	HD	HW	CD	HD	HW	CD	HD	HW	CD	HD	HW	CD	HD	HW
CHAPTER 2															
Vegetation assessments	Jun	Oct	Mar	Jun											
Antelope density estimates	Apr	Oct		Apr	Oct		May	Oct		May	Oct		Apr	Oct	
CHAPTER 3															
Exclosure construction							Jul								
Shoot extension							Jul		Feb						
Herbaceous layer (forb, grass, seedling)								Sep	Feb	May		Mar	Jul		
Herbaceous biomass								Oct	Mar	Jul		Feb	Jul		
Seedbank assessments											Sep				Nov
Woody biomass assessments								Oct			Oct	Jan			Dec
CHAPTER 4															
Dung decomposition					Fortnightly; Sep 05 – Apr 07										
Seed viability trials									Mar		Aug	Apr			
SIGNIFICANT EVENTS															
Political violence (delay fieldwork)										May					
Fire											Jul				
Theft of fence (one replicate lost)												Apr			

[1]Season codes are CD = cool, dry (Apr to Jul); HD = hot, dry (Aug to mid-Nov); HW = hot, wet (mid-Nov to Mar)

APPENDIX 3: WOODY PLANTS AND GRASSES RECORDED IN THE MATOBO HILLS STUDY SITE

Table 6.1: Conservative list of grasses (excluding sedges) identified in the Matobo study site.

This list is not complete, as some vegetative species were not identified, and members of some genera were not unambiguously identified. The list is thus of more commonly encountered and readily identified species.

Andropogon gayanus Kunth
Aristida congesta barbicollis Trin. & Rupr.
Aristida congesta congesta Roem. & Schult.
Brachiaria brizantha (Hochst.) Stapf
Brachiaria deflexa (Schum.) C.E. Hubbard ex Robyns
Cymbopogon sp. Spreng.
Cynodon dactylon (L.) Pers.
Digitaria spp. Heist.
Eragrostis nindensis Ficalho & Hiern
Eragrostis rigidior Pilg.
Eragrostis viscosa (Retz.) Trin.
Heteropogon contortus (L.) Beauv.
Hyparrhenia filipendula (Hochst.) Stapf
Hyperthelia dissoluta (Nees ex Steud.) Clayton
Loudetia simplex (Nees) C.E. Hubbard
Melinis nerviglumis (Franch.) Zizka
Melinis repens (Willd.) Zizka
Panicum maximum Jacq.
Phragmites sp. Trin.
Pogonarthria squarrosa (Licht.) Pilg.
Schizachyrium jeffreysi (Hack.) Stapf
Setaria ustilata de Wit
Sporobolus fimbriatus Nees
Sporobolus nitens Stent
Themeda triandra Forsk.
Tricholaena monachne (Trin.) Stapf
Trichoneura grandiglumis (Nees) Stapf & C.E. Hubbard
Urochloa oligotricha (Fig. & De Not.) Henrard

Table 6.2: Woody plant species list and occurrence in each plant community (data from 2004/05).
Relative frequency (Rel. frequency) calculated as [number of individuals assessed/(number of sites*5)] since a maximum of five individuals were assessed at any site. Browse intensity is [number of individuals browsed/number of individuals assessed]. Dominant or indicator species are typed in boldface. Species identified using Coates-Palgrave (1996) and van Wyk & van Wyk (1997).

Species		***Burkea***	***Combretum***	**Dwala**	**Kopje**	**Miombo**	**Mixed**	***Pterocarpus***	***Terminalia***	**Vlei**
Acacia ataxacantha DC.	Rel. frequency				0.13			0.11	0.01	
	Browse intensity				0.10			0.00	0.00	
*Afzelia quanzensis*Welw.	Rel. frequency				0.01		0.01			
	Browse intensity				0.00		0.00			
Albizia amara (Roxb.) Boiv.	Rel. frequency				0.01	0.01				
	Browse intensity				0.00	0.00				
Albizia tanganyicensis E.G. Baker	Rel. frequency			0.05	0.05					
	Browse intensity			0.00	0.00					
Annona senegalensis Pers.	Rel. frequency									0.01
	Browse intensity									0.00
Apodytes dimidiata E. Meyer ex Arn.	Rel. frequency				0.07					
	Browse intensity				0.20					
Azanza garckeana (F. Hoffm.) Exell & Hillcoat	Rel. frequency	0.08	0.03		0.01	0.05	0.01	0.01		
	Browse intensity	0.17	0.00		0.00	0.00	0.00	0.00		
Boscia angustifolia A. Rich.	Rel. frequency	0.01			0.03	0.03	0.07			
	Browse intensity	0.00			1.00	0.50	0.40			
Brachystegia boehmii Taub.	Rel. frequency					0.99				
	Browse intensity					0.00				
Bridelia mollis Hutch.	Rel. frequency	0.36	0.33	0.13	0.45	0.35	0.25	0.32	0.11	0.01
	Browse intensity	0.00	0.12	0.40	0.03	0.08	0.00	0.00	0.13	0.00
Burkea africana Hook.	Rel. frequency	**0.95**	0.36		0.15	0.21	**0.57**	0.39	**0.71**	0.04
	Browse intensity	0.00	0.00		0.00	0.00	0.05	0.00	0.00	0.00
*Carissa edulis*Vahl	Rel. frequency					0.01			0.03	
	Browse intensity					0.00			0.00	
Cassia abbreviata Oliver	Rel. frequency	0.04	0.05		0.03	0.03	0.01	0.04	0.05	0.01
	Browse intensity	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00
Catha edulis (Vahl) Forsk. Ex Endl.	Rel. frequency				0.07					
	Browse intensity				0.20					

Species		*Burkea*	*Combretum*	Dwala	Kopje	Miombo	Mixed	*Pterocarpus*	*Terminalia*	Vlei
Catunaregam spinosa (Thunb.) Tirveng.	Rel. frequency						0.03			
	Browse intensity						0.00			
Clerodendrum glabrum E. Meyer	Rel. frequency				0.01					
	Browse intensity				0.00					
Combretum apiculatum Sonder	Rel. frequency		**0.76**		0.05	0.07	0.40	0.03	0.15	
	Browse intensity		0.00		0.00	0.00	0.07	0.00	0.00	
Combretum collinum Fresen.	Rel. frequency	0.01					0.01			
	Browse intensity	0.00					0.00			
Combretum hereroense Schinz	Rel. frequency		0.15		0.04	0.04	0.03		0.04	
	Browse intensity		0.00		0.00	0.00	0.00		0.00	
Combretum molle R. Br. ex G. Don	Rel. frequency	0.07	0.01	0.08	**0.55**	0.03	0.15	0.29	0.05	
	Browse intensity	0.00	0.00	0.50	0.00	0.00	0.09	0.00	0.00	
Combretum zeyheri Sonder	Rel. frequency	0.01	0.05		0.07			0.03		
	Browse intensity	0.00	0.00		0.00			0.00		
Commiphora africana (A. Rich.) Engl.	Rel. frequency				0.16		0.07			
	Browse intensity				0.00		0.00			
Commiphora mollis (Oliver) Engl.	Rel. frequency		0.08	0.03	0.05		0.03	0.04		
	Browse intensity		0.00	0.50	0.00		0.00	0.33		
Commiphora sp.	Rel. frequency	0.01		0.08	0.09					
	Browse intensity	0.00		0.00	0.00					
Cussonia arborea Hochst. ex A. Rich.	Rel. frequency		0.03							
	Browse intensity		0.00							
Dichrostachys cinerea (L.) Wight & Arn.	Rel. frequency	0.40	0.48	0.01	0.12	0.21	**0.67**	0.15	**0.76**	0.17
	Browse intensity	0.20	0.28	1.00	0.00	0.25	0.34	0.18	0.32	0.38
Diplorhynchus condylocarpon (Muell. Arg.) Pichon	Rel. frequency		0.19		0.04	0.21	0.08		0.03	
	Browse intensity		0.00		0.00	0.00	0.00		0.00	
Dodonaea angustifolia L.f.	Rel. frequency									0.07
	Browse intensity									0.40
Dombeya rotundifolia (Hochst.) Planchon	Rel. frequency	0.20	0.32		0.08		0.49	**0.81**	0.23	0.05
	Browse intensity	0.00	0.21		0.00		0.11	0.00	0.00	0.00
Elaeodendron matebelicum Loes.	Rel. frequency	0.03	0.15		0.09		0.12	0.11	0.08	
	Browse intensity	0.00	0.00		0.00		0.00	0.00	0.00	

Species		*Burkea*	*Combretum*	Dwala	Kopje	Miombo	Mixed	*Pterocarpus*	*Terminalia*	Vlei
Elephantorrhiza goetzii (Harms) Harms	Rel. frequency			0.44						
	Browse intensity			0.03						
Entandrophragma caudatum (Sprague) Sprague	Rel. frequency			0.19						
	Browse intensity			0.07						
Euclea divinorum Hiern	Rel. frequency	0.16	0.35	0.01	0.63	0.19	0.43	0.20	0.15	
	Browse intensity	0.00	0.00	0.00	0.04	0.00	0.03	0.00	0.00	
Euclea natalensis A. DC.	Rel. frequency	0.21	0.12		0.49	0.17	0.17	0.23	0.19	
	Browse intensity	0.00	0.00		0.03	0.00	0.00	0.00	0.00	
Euphorbia ingens E. Meyer ex Boiss.	Rel. frequency					0.01				
	Browse intensity					0.00				
Faurea saligna Harvey	Rel. frequency	0.24	0.48			0.01	0.16	0.08	0.17	0.13
	Browse intensity	0.00	0.06			0.00	0.00	0.00	0.00	0.00
Ficus abutilifolia Miq.	Rel. frequency		0.01	0.11	0.07					
	Browse intensity		0.00	0.25	0.00					
Ficus ingens (Miq.) Miq.	Rel. frequency								0.04	
	Browse intensity								0.00	
Ficus thonningii Blume	Rel. frequency			0.01	0.03	0.01	0.03	0.05		
	Browse intensity			1.00	0.00	0.00	0.00	0.00		
Flacourtia indica (N.L. Burm.) Merr.	Rel. frequency	0.11	0.17		0.01	0.13	0.28	0.12	0.08	0.09
	Browse intensity	0.13	0.15		0.00	0.00	0.29	0.33	0.50	0.14
Flueggea virosa (Roxb. ex Willd.) Pax & K. Hoffm.	Rel. frequency	0.01	0.25	0.13	**0.55**	0.05	0.47	0.20	0.19	0.08
	Browse intensity	1.00	0.21	0.20	0.29	0.75	0.57	0.73	0.07	0.17
Garcinia buchananii Baker	Rel. frequency				0.01		0.01			
	Browse intensity				0.00		0.00			
Gardenia resiniflua Hiern	Rel. frequency	0.43	0.29		0.03	0.41	0.28	0.11	0.20	0.01
	Browse intensity	0.19	0.14		1.00	0.35	0.10	0.25	0.00	0.00
Gardenia volkensii K. Schum.	Rel. frequency		0.01			0.07			0.03	
	Browse intensity		0.00			0.00			0.00	
Grewia bicolor Juss.	Rel. frequency						0.03			
	Browse intensity						0.00			
Grewia flavescens Juss.	Rel. frequency	0.11	0.01	0.03	0.15	0.21	0.33	0.05	0.20	0.05
	Browse intensity	0.25	1.00	0.50	0.18	0.31	0.28	0.00	0.20	0.75
Grewia monticola Sonder	Rel. frequency	0.56	0.65	0.01	0.31	**0.51**	**0.76**	0.51	0.28	0.01

Species		*Burkea*	*Combretum*	Dwala	Kopje	Miombo	Mixed	*Pterocarpus*	*Terminalia*	Vlei
	Browse intensity	0.05	0.04	0.00	0.00	0.05	0.00	0.03	0.05	0.00
Gymnosporia senegalensis (Lam.) Loes.	Rel. frequency	0.61	0.49		0.07	0.07	0.35	0.44	0.51	0.33
	Browse intensity	0.02	0.00		0.00	0.20	0.04	0.06	0.03	0.08
Heteropyxis natalensis Harvey	Rel. frequency	0.07	0.03		0.01	0.03		0.19		0.03
	Browse intensity	0.00	0.00		0.00	0.00		0.00		0.00
Julbernardia globiflora (Benth.) Troupin	Rel. frequency					**0.67**				
	Browse intensity					0.00				
Kirkia acuminata Oliver	Rel. frequency	0.01	0.04	0.04	0.13			0.01		
	Browse intensity	0.00	0.00	0.00	0.00			0.00		
Lannea discolor (Sonder) Engl.	Rel. frequency	0.09	0.27	0.01	0.16	0.04	0.07	0.13	0.08	0.07
	Browse intensity	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lippia javanica (Burm.f.) Spreng.	Rel. frequency	0.75	0.45		0.07	0.17	0.59	0.49	0.68	0.17
	Browse intensity	0.21	0.21		0.00	0.31	0.43	0.19	0.24	0.38
Lonchocarpus capassa Rolfe	Rel. frequency					0.01				
	Browse intensity					0.00				
Mimusops zeyheri Sonder	Rel. frequency				0.17					
	Browse intensity				0.00					
Mundulea sericea (Willd.) Chev.	Rel. frequency				0.01					
	Browse intensity				0.00					
Olea europea L.	Rel. frequency		0.09		0.04		0.05	0.09	0.01	
	Browse intensity		0.29		0.00		0.00	0.00	0.00	
Olea sp.	Rel. frequency					0.07				
	Browse intensity					0.40				
Ozoroa insignis	Rel. frequency	0.09	0.19	0.01	0.09	0.13	0.15	0.17	0.08	
	Browse intensity	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17	
Pappea capensis Ecklon & Zeyher	Rel. frequency	0.12	0.31	0.01	0.21	0.05	0.35	0.09	0.13	0.01
	Browse intensity	0.00	0.13	0.00	0.13	0.25	0.42	0.00	0.00	0.00
Parinari capensis Aubl.	Rel. frequency	0.07							0.20	
	Browse intensity	0.20							0.33	
Parinari curatellifolia Planchon ex Benth.	Rel. frequency	0.20	0.07		0.09				0.01	
	Browse intensity	0.07	0.00		0.00				0.00	
Peltophorum africanum Sonder	Rel. frequency	0.07	0.17		0.07	0.03	0.39	0.12	0.15	0.08
	Browse intensity	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00

Species		*Burkea*	*Combretum*	Dwala	Kopje	Miombo	Mixed	*Pterocarpus*	*Terminalia*	Vlei
Piliostigma thonningii (Schumach.) Milne-Redh.	Rel. frequency	0.09	0.04				0.15	0.05	0.12	0.04
	Browse intensity	0.14	0.00				0.09	0.00	0.00	0.67
Pouzolzia mixta Wedd.	Rel. frequency		0.03	0.05			0.04			
	Browse intensity		0.50	0.25			0.00			
Protea gaguedi J.F. Gmelin	Rel. frequency	0.07	0.08							0.07
	Browse intensity	0.40	0.00							0.00
Pseudolachnostylis maprouneifolia Pax	Rel. frequency	**0.67**	0.40	0.03	0.41	0.35	0.28	0.36	**0.52**	0.12
	Browse intensity	0.02	0.00	0.50	0.00	0.00	0.05	0.04	0.05	0.11
Ptaeroxylon obliquum (Thunb.) Radlk.	Rel. frequency	0.01	0.12	0.21	0.28		0.05	0.12	0.05	
	Browse intensity	0.00	0.00	0.00	0.00		0.25	0.00	0.00	
Pterocarpus angolensis DC.	Rel. frequency	0.15	0.04		0.01	0.03	0.08		0.01	
	Browse intensity	0.00	0.00		0.00	0.00	0.00		0.00	
Pterocarpus rotundifolius (Sonder) Druce	Rel. frequency	0.43	**0.64**	0.04	**0.55**	0.15	0.49	**0.87**	**0.60**	0.24
	Browse intensity	0.00	0.02	0.00	0.02	0.09	0.00	0.00	0.00	0.00
Rhoicissus tridentata (L.f.) Wild & R.B. Drumm.	Rel. frequency	0.03			0.08			0.01		
	Browse intensity	0.00			0.83			1.00		
Rhus lancea L.f.	Rel. frequency					0.01	0.11		0.03	
	Browse intensity					0.00	0.00		0.00	
Rhus leptodictya Diels	Rel. frequency	0.29	0.31	0.01	0.35	0.49	0.31	0.11	0.17	
	Browse intensity	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
Rhus pyroides Burch.	Rel. frequency					0.04	0.05		0.05	
	Browse intensity					0.67	0.00		0.25	
Rhus tenuinervis Engl.	Rel. frequency	0.01	0.13		0.09	0.01	0.04	0.04		
	Browse intensity	0.00	0.00		0.00	0.00	0.00	0.00		
Schinziophyton rautanenii (Schinz.) Radcl.-Sm.	Rel. frequency								0.01	
	Browse intensity								0.00	
Schrebera alata (Hochst.) Welw.	Rel. frequency		0.01		0.01		0.01		0.01	
	Browse intensity		0.00		0.00		0.00		0.00	
Sclerocarya birrea (A. Rich.) Hochst.	Rel. frequency	0.04	0.04		0.08	0.01	0.17	0.01	0.11	0.04
	Browse intensity	0.00	0.00		0.00	0.00	0.08	0.00	0.00	0.33
Strychnos cocculoides Baker	Rel. frequency						0.01			
	Browse intensity						0.00			
Strychnos madagascariensis	Rel. frequency	0.01	0.09		0.05		0.04		0.03	

Species		***Burkea***	***Combretum***	**Dwala**	**Kopje**	**Miombo**	**Mixed**	***Pterocarpus***	***Terminalia***	**Vlei**
Poiret	Browse intensity	1.00	0.29		0.25		0.00		1.00	
Strychnos potatorum L.f.	Rel. frequency			0.03	0.27					
	Browse intensity			0.50	0.15					
Strychnos spinosa Lam.	Rel. frequency	0.03	0.07			0.01	0.07		0.04	
	Browse intensity	0.00	0.00			1.00	0.20		0.33	
Tarchonanthus camphoratus L.	Rel. frequency		0.11	0.11	0.39	0.03	0.01	0.01		
	Browse intensity		0.00	0.00	0.00	0.00	0.00	0.00		
Terminalia brachystemma Welw.	Rel. frequency	0.41	0.09	0.01	0.07	0.03		0.12	0.17	0.27
	Browse intensity	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.05
Terminalia sericea Burch. ex DC.	Rel. frequency	**0.69**	**0.65**		0.07	0.23	**0.79**	0.35	**1.00**	0.31
	Browse intensity	0.02	0.00		0.00	0.00	0.00	0.00	0.00	0.00
Vangueria infausta Burch.	Rel. frequency			0.01	0.15	0.07	0.03			
	Browse intensity			1.00	0.18	0.40	0.00			
Vangueria randii S. Moore	Rel. frequency	0.09	0.01	0.08	0.24	**0.68**	0.12	0.16	0.05	
	Browse intensity	0.43	1.00	0.83	0.61	0.76	0.89	0.67	0.25	
Vepris reflexa Verdoorn	Rel. frequency	0.01				0.04				
	Browse intensity	0.00				0.00				
Vitex payos (Lour.) Merr.	Rel. frequency			0.15						
	Browse intensity			0.27						
Ximenia caffra Sonder	Rel. frequency	0.07	0.25	0.05	0.05	0.04	0.17	0.11	0.11	
	Browse intensity	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.13	
Ziziphus mucronata Willd.	Rel. frequency	0.33	0.35	0.01	0.41	0.01	0.27	0.48	0.19	0.07
	Browse intensity	0.04	0.08	0.00	0.13	0.00	0.05	0.06	0.00	0.00

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