Forest Colonization of Savannas: Patterns and Process

by

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Thesis submitted in fulfilment of the requirements for the degree of Master of Science

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I DEDICATE MY WORK TO

MY BELOVED LATE GRANDMOTHER

(MUNZHEDZI KHAVHAGALI-NETSHIMBONI)

I WILL ALWAYS LOVE AND REMEMBER YOU

BECAUSE YOU WILL ALWAYS LIVE IN MY WORLD

Declaration

I, the undersigned, hereby declare that the work contained in this thesis in my own original work. It is being submitted for the degree of Master of Science in the University of Cape Town. It has not been submitted before for any other degree or examination in any other University.

Vhalinavho Patterson Khavhagali

(Signature of candidate)

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Abstract

In this study, I explored factors that influence forest colonization in a South African savanna. I used a 50 year fire experiment in the Kruger National Park to explore patterns of forest colonization in a mesic *Terminalia sericea* savanna. I studied woody seedling and sapling distribution in relation to different burning treatments, including no burning, and microsite position – in the open or under the canopy of tall trees. The study showed that species richness and abundance was greatest under *Sclerocarya birrea*, low under *Terminalia sericea* and lowest in the open habitats. Low fire frequency increased species richness and abundance under *S. biirea,* but not under *T. sericea* or the open habitats. Fire sensitive or fire-intolerant species were highest under tree canopies on unburnt and triennial burn plots, whereas frequently burnt (annual or biennial) plots, had fire tolerant and typical savanna species. Frequent burning reduced woody plant biomass by killing seedlings, saplings and adult trees. Fire exclusion led to a higher seedling and sapling recruitment under *S. birrea* and *T. sericea* than open habitats.

I sampled soil nutrients and water content in the same study sites to explore the effects of trees and fire regime on resource availability. The influence of trees on soil moisture and nutrient availability was found to be species specific. Results showed that soils under *S. birrea* were richer in K, Ca, Mg and C when compared to *T. sericea* and open habitats. Triennial burns favoured high pools of Na and N. Canopy effects were larger than fire effects for most soil properties and canopy effects varied greatly between *S. birrea* and *T. sericea.* High nutrients and water content under *S. birrea* suggest that this microsite is important in promoting colonization of forest seedlings and might be a preferred site for seedling establishment. I studied the effects of grass competition, water and nutrient supply on seedling establishment and growth in two field experiments. It has been suggested that tree seedlings might avoid competition with grasses by growing into the dry season when grasses are dormant. To test this hypothesis, I grew seedlings of the dominant savanna species,

T. sericea and manipulated water, nutrients and grass competition in the dry season. *T. sericea* seedlings showed no significant responses to the treatments and the seedling initial height was the most important predictor of final seedling height. These results suggest that seedlings do not grow during the dry season but use available resources to maintain their daily photosynthetic activities. At least for this species, tree seedlings do not escape competition with grasses by growing when grasses are dormant in the dry season.

The second field experiment compared the growth and survival of two savanna (*Terminalia sericea* and *Acacia gerrardii*) and two forest species (*Ekebergia capensis* and *Kiggelaria africana*) with or without grass competition and with nutrient and water additions. *T. sericea*, *K. africana*, *A. gerrardii* and *E. capensis* along the resource supply gradient. Survival was 90% for *T. sericea,* 75% for *K. Africana*, 65% for *A. gerrardii* and 30% for *E. capensis*. Both forest and savanna seedlings responded differently to treatment effects on their stem height and diameter growth. Grass biomass was strongly influenced by the addition of nutrients and water and also varied through the growing season. The additions of nutrients and water together have extra effects on grass biomass, causing 25 % increase on grass biomass when compared to addition of nutrients and water separately. Mortality was high on the grass plots and grass*water treatment. Nutrients seem to be the limiting factor to savanna and forest seedling establishment and growth. This experiment suggests grass competition influences both establishment and growth of seedlings. Overall, this study suggests that a significant effect of the canopy is increased nutrients promoting seedling establishment and growth. Greater availability of nutrients under the canopy of tall trees promotes high seedling recruitment.

Long term fire exclusion was not enough to cause savannas to be completely invaded by forest. Forest colonization was restricted to below canopy sites. Thus there was an interaction between fire and growing conditions, especially nutrients, in the process of thicket colonization. I predict that forest expansion will be greatest in higher rainfall areas on nutrient rich sites.

Chapter 1. Introduction

Although savannas cover a large part of the world's terrestrial vegetated area, there is still limited understanding about what determines the structure and distribution of savannas. Savannas are broadly defined as tropical seasonal ecosystems with a continuous grass layer, mixed with forbs and sedges with a variable cover of trees and shrubs (Scholes & Archer 1997). Forests and other woody formations differ from savannas in lacking a continuous grass cover (Bond *et al.* 2005). Forests are known to be ecosystems with large trees and overlapping tree layer. Savannas occur in seasonal climates with a distinct dry season and wet season (Scholes & Archer 1997). Savannas have sometimes been seen as a transitional zone between forests or woodland regions and grassland or desert regions but patches of forest or dry thicket occur across the entire climatic range of savannas. Savannas are important socio-economically in tropical regions (Scholes & Archer 1997).

An increase in woody plant density has been reported as a problem in grassland and savanna ecosystems, because increased woody cover can result in decreased herbaceous production and diversity (Archer *et al.* 2001, Dalle *et al.* 2006). Trees, shrubs and thicket species invade open grasslands through a process known as 'bush encroachment', and thicken up in already wooded areas to form woodlands through a process known as "woody plant encroachment" (Trollope 1980). To avoid confusion, I will refer to both processes as woody encroachment, being more specific where necessary. Woody encroachment has occurred in many parts of the world, including Africa (Trapnell 1959, O'Connor 1995, Dalle *et al.* 2006), Australia (Walker & Gillison 1982, Bowman *et al.* 2001) and North America (Archer 1989, Briggs *et al.* 2002).

Conversion of savanna woodlands to forest/thicket stands will be referred to as forest colonization. Forest colonization is a process whereby forest/thicket species colonize savannas to form a closed woody stand. At times, grasslands and savannas are replaced by scrub thicket and eventually closed forest (Bond *et al.* 2005). Forest colonization also takes place in the savanna landscape, but the colonizing woody species differ from savannas in species composition. Invasion of forest species in savannas eventually causes a complete replacement of savannas by forest/thicket formations – a biome shift. Several studies have reported forest invasion, forest expansion, conversion and/or forest colonization of savannas by forest/thicket species worldwide (Trapnell 1959, Archer *et al.* 1988, Bowman *et al.* 2001).

Replacement of savannas by forests is a phenomenon apparently restricted to mesic areas (>650 mm rainfall) (Swaine *et al.* 1992, Bond *et al.* 2003a, Fensham *et al.* 2005, Sankaran *et al.* 2005) and seems to be occurring in many such areas in South Africa (Hoffmann & O'Connor 1999, O'Connor & Crow 1999, Bond *et al.* 2003b) and Australia (Bowman *et al.* 2001) over the last half century. It is much more difficult and costly to reverse the process of forest invasion than to control changes in abundance of savanna trees or shrubs. An ecosystem switch from savanna to forest brings about changes in species composition, loss of grasses, an increase in fire intolerant plant species, reduction in grazing and fire fuel, and a total biome shift. Several studies have proposed climate change, increase in atmospheric CO_2 concentration, changing fire regimes, grazing by livestock & wild herbivores, canopy cover, and soil resources as factors influencing woody plant encroachment (Knoop & Walker 1985, Bond & van Wilgen 1996, Hoffmann 1996, Callaway & Walker 1997, Scholes & Archer 1997, Eckhardt *et al.* 2000, Higgins *et al.* 2000, Hoffmann 2000, Bond *et al.* 2003a, Hoffmann *et al.* 2004, Ludwig *et al.* 2004, Bond *et al.* 2005, Bond & Keeley 2005, Sankaran *et al.* 2005, Govender *et al.* 2006). It is not well known whether the same factors that influence woody encroachment are also responsible for forest colonization.

Forest and thicket patches are common, if small in extent, in most savanna landscapes. Determinants of forest and savanna boundaries have long been debated with some arguing strongly for soil and climate limitations, others for fire, and rarely, an interaction between fire and site conditions in determining forest distribution (Furley (1992) for South America, Bowman *et al.*

(2001) for Australia, Bond *et al.* (2003a) for South Africa). Bond *et al.* (2003a) have argued that most of the higher rainfall eastern grasslands and savannas of South Africa have the climate potential to support forests. They suggest that most grassy biomes with > 750 mm mean annual precipitation (MAP) in this region would switch to forest in the long absence of fire. According to their predictions, most of the Kruger National Park, a savanna-dominated region, is too dry to support forest. Only the south-western region of the Park, in the vicinity of Pretoriuskop, has rainfall close to, or exceeding, 750 mm MAP.

In this study I explored the interactions between fire, water and nutrients in limiting forest colonization of the Pretoriuskop savannas in Kruger National Park (KNP). The park offers excellent opportunities to explore fire effects on forest colonization because of the availability of long-term Experimental Burn Plots (EBP's) in which fire has been manipulated in diverse treatments, including fire exclusion, since 1955 (Van der Schijff 1958, Biggs *et al.* 2003). This study is the first to address and investigate factors limiting forest colonization in South African savannas, specifically looking at the interaction between fire, climate and soil factors that may limit or promote forest colonization. The KNP experimental burn plots were set up in the 1950s and have been maintained to the present day (Biggs *et al.* 2003, Govender *et al.* 2006). Various combinations of season and frequency of burning have been applied (including no burning) in four different 'landscapes' (major plant communities) in KNP with four replicates in blocks ('strings') in each area (Govender *et al.* 2006).

In the Pretoriuskop area of KNP, forest/thicket species first appear in the shade of large savanna trees (*Sclerocarya birrea, Pterocarpus angolensis, Terminalia sericea*) through a process known as facilitation (Kellman 1979, Callaway & Walker 1997). Spread of forest elements beyond the shade of the nurse tree is slow since forest extension beyond nurse tree canopies is rare even where fire has been excluded for 50 years. In this study, I addressed the question: what are the factors that influence forest colonization in savannas, and to what extent do these factors interact to influence this process and where is it likely to take place? I investigate the pattern and process in which forest/thicket tree species invade savanna ecosystems (Chapter 3). I test whether fire exclusion increases forest/thicket species recruitment and woody plant recruitment, with frequent fires known to reduce woody plant density (Bond *et al.* 2005) and whether savanna trees provide nucleation sites for forest seedling establishment (Archer *et al.* 1988).

It has been implied that forest seedling recruitment takes place beneath canopies of savanna trees because they increase resource availability (Belsky *et al.* 1989, Belsky 1994). For example, *Acacia tortilis* and *Adansonia digitata* have been shown to increase herbaceous productivity, lower soil temperatures and increase soil fertility beneath their canopies (Belsky *et al.* 1989). Here I test whether similar patterns and impacts of savanna trees exist in Pretoriuskop savannas using *S. birrea* and *T. sericea* (both savanna trees) and an adjacent open site (no canopy effects), to determine whether large savanna trees do provide better growing conditions that may facilitate tree establishment and growth (Chapter 4).

Grasses influence woody plant recruitment indirectly by promoting a distinct fire regime with very frequent fires. However they also have direct effects on woody plants by competition for resources, especially in the establishment phase when saplings and seedlings are shaded by grasses and roots have to compete with grass roots. I conducted a field experimental study to test how soil resources and competition with grasses influence *T. sericea* seedling growth during the dry season (Chapter 5). This experiment tested the importance of the temporal niche for tree seedling recruitment (Scholes & Archer 1997) and investigated whether tree seedlings continue to grow into the dry season after grasses have dried out. I supplied water, nutrients and removed grasses on other plots and then recorded growth and survival of *T. sericea* seedlings on eight different treatments.

Lastly, I wanted to determine possible differences between savanna and forest tree species in terms of seedling requirements in a savanna ecosystem. I compared the response and growth of savanna and forest seedlings to treatments manipulating water, nutrient and grass competition (Chapter 6). Savanna and forest tree species differ in allocation patterns and requirements for seedling establishment (Hoffmann *et al.* 2003). I supplied water, nutrients and removed grasses on other plots and then recorded growth and survival of *Terminalia sericea*, *Acacia gerrardii* (both savanna species) and *Ekebergia capensis*, *Kiggelaria africana* (both forest species) seedlings in eight different treatments.

Thesis outline:

Each chapter of this thesis was prepared as an individual report.

Chapter 2: I present a detailed description of the study site.

Chapter 3: Focuses on the effects of fire and savanna trees on woody plant recruitment. I investigate how fire frequency and different canopy types influence woody plant recruitment in Pretoriuskop savannas. I test whether there is an interactive effect of fire and savanna trees on woody plant recruitment.

Chapter 4: Investigates the influence of fire frequency on nutrient availability, and how different canopy types influence soil moisture and nutrient availability in Pretoriuskop mesic savannas.

Chapter 5: Investigates how water and nutrient addition and competition with grass influence *T. sericea* seedling growth during the dry season. I test the importance of the temporal niche for tree seedling recruitment as a mechanism for reducing competition with grasses.

Chapter 6: Investigates the influence of water, nutrients and grass on savanna and forest seedling establishment and growth in savanna environments. I test if there are different seedling requirements for savanna vs. forest seedlings and the magnitude of grass competitive effects.

Chapter 7: Synthesis and conclusion. I discuss results and summarize the findings of this study.

Chapter 2. Study Site

Pretoriuskop is located in the southwestern region of the Kruger National Park (KNP), in the north east of South Africa (31° 10' E, 25° 10' S) (Fig. 1). It has the highest annual rainfall and the most nutrient poor soils in the park. Pretoriuskop lies on granite rock, in moderately undulating plains below the lower foothills of the Great Escarpment. Soils form a catenary sequence from moderately leached red sands and loam to yellow then pale grey hydromorphic sands to clays on the bottom of the slopes (Gertenbach 1983, Venter 1990, O' Regan 2005).

Climate

Annual rainfall in the Pretoriuskop region ranges from 700-1000 mm with an average of about 750 mm, which is higher than the rest of the KNP (Figure 2A; O' Regan 2005). Most rain falls in the summer months but the winter dry season usually experiences some rain (Figure 2B). Average spring (Sep-Nov) temperature ranges from a mean minimum of 15°C to mean maximum of 28°C, average summer (Dec-Feb) temperature ranges from a mean minimum of 18°C to mean maximum of 30°C, average autumn (Mar-May) temperature ranges from a mean minimum of 15°C to mean maximum of 29°C and average winter (June-Aug) temperatures ranges from mean minimum of 9°C to mean maximum of 25°C (Gertenbach 1983, O' Regan 2005, Zambatis 2006). Mean monthly maximum and minimum temperatures are shown in Figure 3.

Vegetation

Pretoriuskop is an area of savanna woodlands, tall grass and unpalatable sour veld (Fig 4a & b). Pretoriuskop vegetation is classified as the Lowveld Sour Bushveld by Acocks (1953) and as Pretoriuskop Sour Bushveld in the latest vegetation classification for South Africa (Mucina and

Rutherford 2007). It is broad-leaved deciduous woodland with tall grass (Van der Schijff 1958) and is characterized by the predominance of the trees *Terminalia sericea* and *Sclerocarya birrea* and mixtures of the shrubs *Dichrostachys cinerea* associated with *Euclea spp, Ziziphus mucronata*, *Ximenia caffra*, *Gymnosporia senegalensis* and *Strychnos madagascarensis*. Characteristic species of forest affinities include *Phyllanthus reticulatus*, *Bridelia cathartica*, *Trichilia emetica* and *Diospyros mespiliformis*. Common grasses include *Hyperthelia dissoluta*, *Setaria sphacelata* and *Panicum maximum* growing under large trees. Pretoriuskop is a mesic savanna with a complex vegetation mosaic.

Animals

There is a high chance of seeing herds of sable and eland. Pretoriuskop is also home to impalas, buffalo, rhinos and elephants. The numerous rocky outcrops are inhabited by klipspringer. A visit to dams can produce hippopotamus. Carnivores such as leopard, lions, spotted hyena and wild dogs can be spotted in the area. Several sunbird species, Redheaded *Weaver*, Brown-headed Parrot and Green-capped *Eremomela* can be seen in the surrounding area.

Experimental Burn Plot (EBP)

The Experimental Burn Plot (EBP) experiment was introduced in the mid 1950s as part of an investigation reviewing the policy on fire management. The objective of this program was to determine the effects of burning on major veld types (Van der Schijff 1958). Four replicates of twelve plots, namely Numbi, Shabeni, Kambeni and Fayi, were laid out in the Pretoriuskop region. This project was conducted in the Kambeni plot because it is the only one that had not experienced accidental burns in the no burn treatment. Kambeni EBPs are predominantly occupied by *Terminalia sericea*, *Sclerocarya birrea* and the common understorey shrub, *Dichrostachys cinerea.* The Kambeni string consists of twelve treatments varying in fire season (the season of burn), and fire frequency (intervals between fires) and includes a 'no burn' plot where fire has been excluded for ca. 50 years (Fig. 5). Each treatment plot occupies ~7 hectares.

The treatments are: an annual burn in August; biennial burns in February, April, August, October and December; triennial burns in February, April, August, October and December and the no burn (Table 1). According to Trollope & Potgieter (1983), Kambeni replicates had the highest average fire intensity of 4059 (kJ/s/m). The mean fuel moisture content was significantly higher in April than in August and December ($p < 0.01$), and the fire intensity on the April Triennial treatments (1787 kJ/s/m) was significantly lower than on the August and October Triennial treatments (5155 kJ/s/m and 2854 kJ/s/m respectively) ($p < 0.05$) (Trollope and Potgieter 1983). The mean fire intensity was higher on the August Triennial treatment (5155 kJ/s/m) lower for the August Biennial treatment (3518 kJ/s/m), and still lower on the August Annual treatment (2567 kJ/s/m) (Trollope and Potgieter 1983). An analysis of fire intensity in all four study regions of the experimental burn plots has been recently published (Govender *et al.* 2006).

Table 1: The twelve fire treatments (EBP's) in Kambeni, Pretoriuskop. The table shows the treatment code which is used throughout this document in tables and figures, the month at which the fire takes place, fire frequency, the field conditions in which they burn, and the season of fire.

Code	**Month**	**Frequency**	**Conditions**	**Season**
Control/Gravel Pit	None	No burn	None	None
AUG B1	August	Annual	Dry	Late winter
AUG B2	August	Biennial	Dry	Late winter
AUG B3	August	Triennial	Dry	Late winter
APR B2	April	Biennial	Wet-dry	Autumn
APR B3	April	Triennial	Wet-dry	Autumn
FEB B2	February	Biennial	Wet	Late summer
FEB B3	February	Triennial	Wet	Late summer
OCT B2	October	Biennial	Dry	Spring
OCT B3	October	Triennial	Dry	Spring
DEC B2	December	Biennial	Wet	Mid-summer
DEC B3	December	Triennial	Wet	Mid-summer

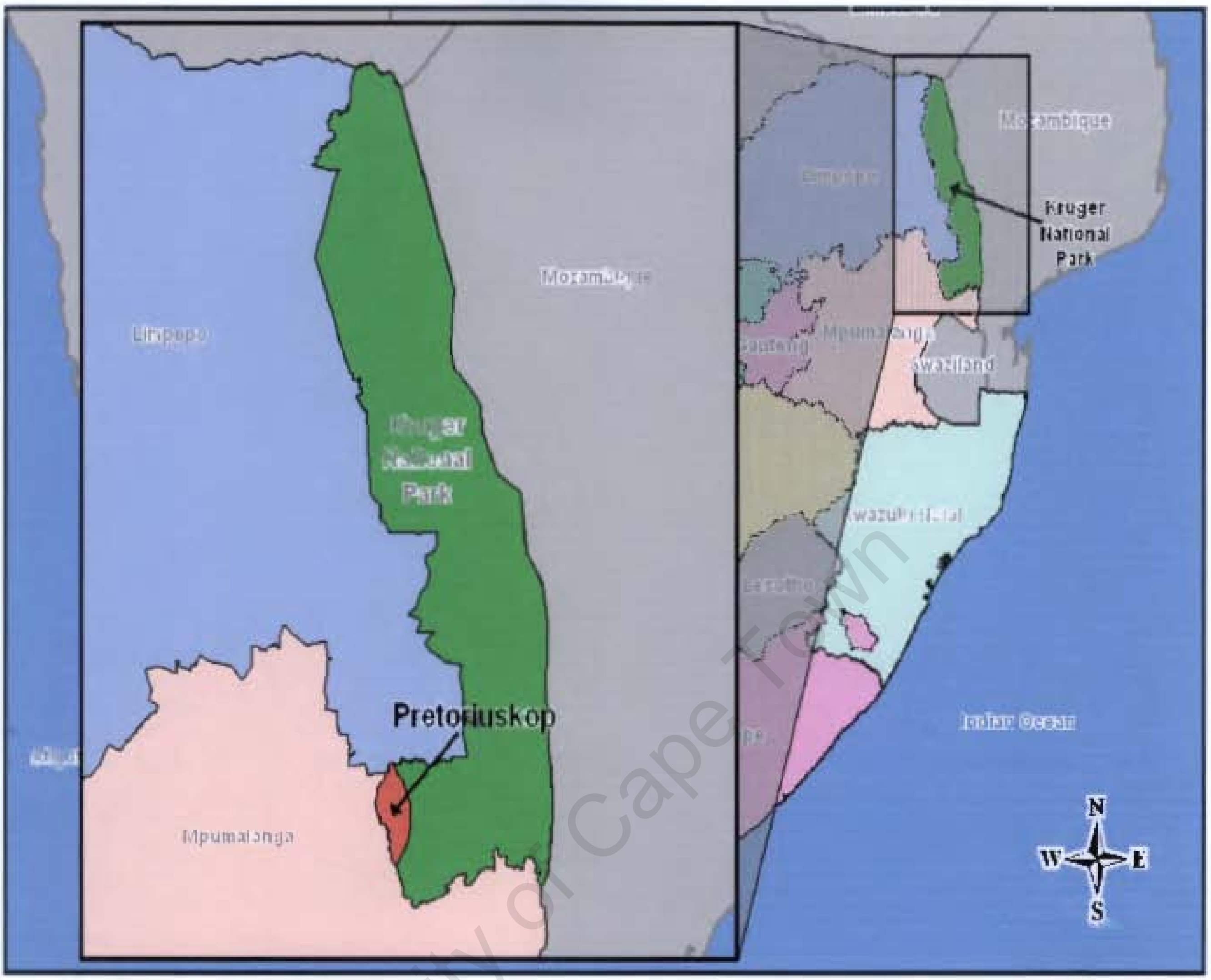

Figure 1. Pretoriuskop is located in the south west of the Kruger National Park (adapted from O' Regan 2005).

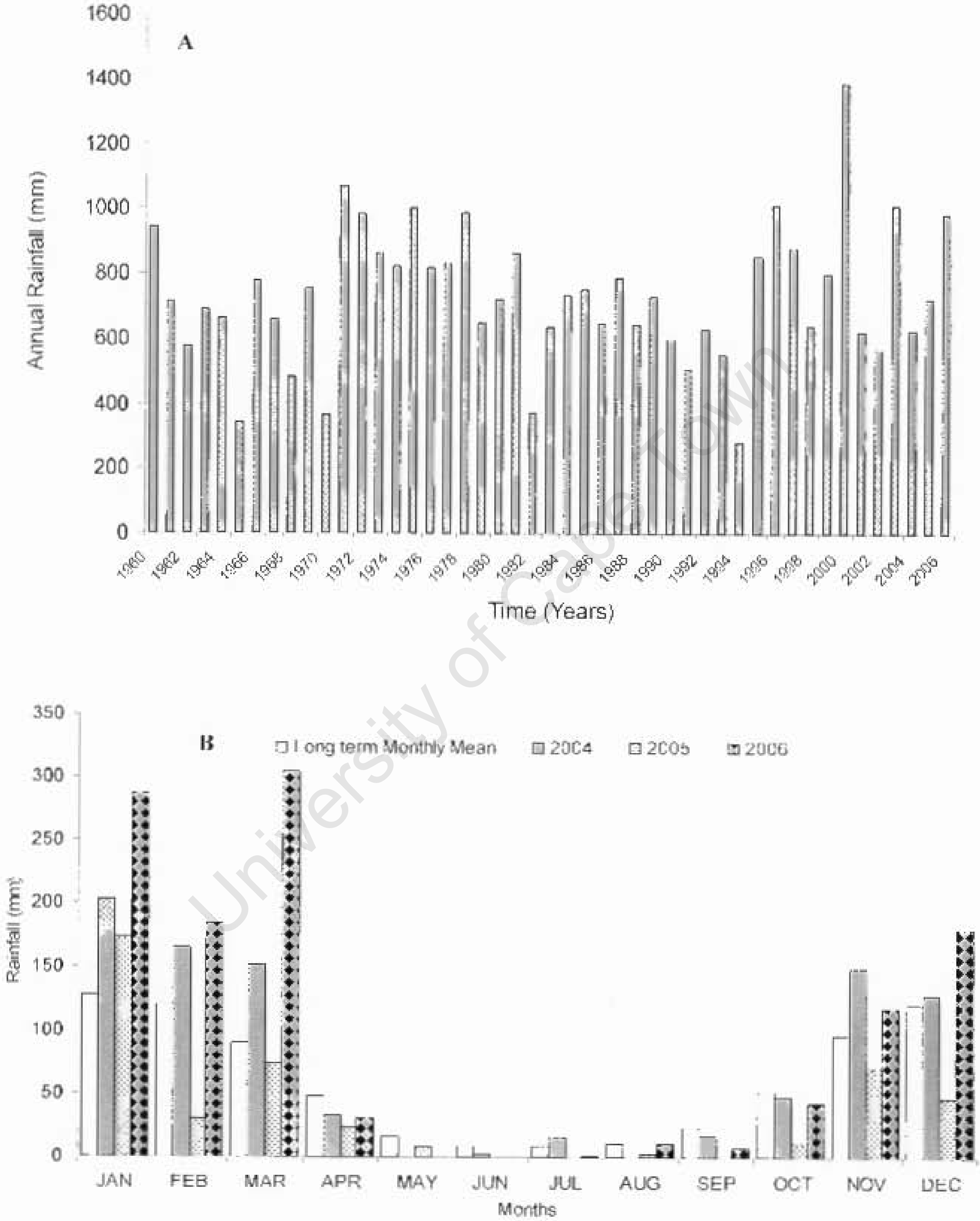

Figure 2. (A) The long term annual rainfall (mm) from 1960 to 2006, and (B) the monthly average rainfall (mm) and rainfall over the study period, 2004, 2005 and 2006, for the Pretoriuskop region.

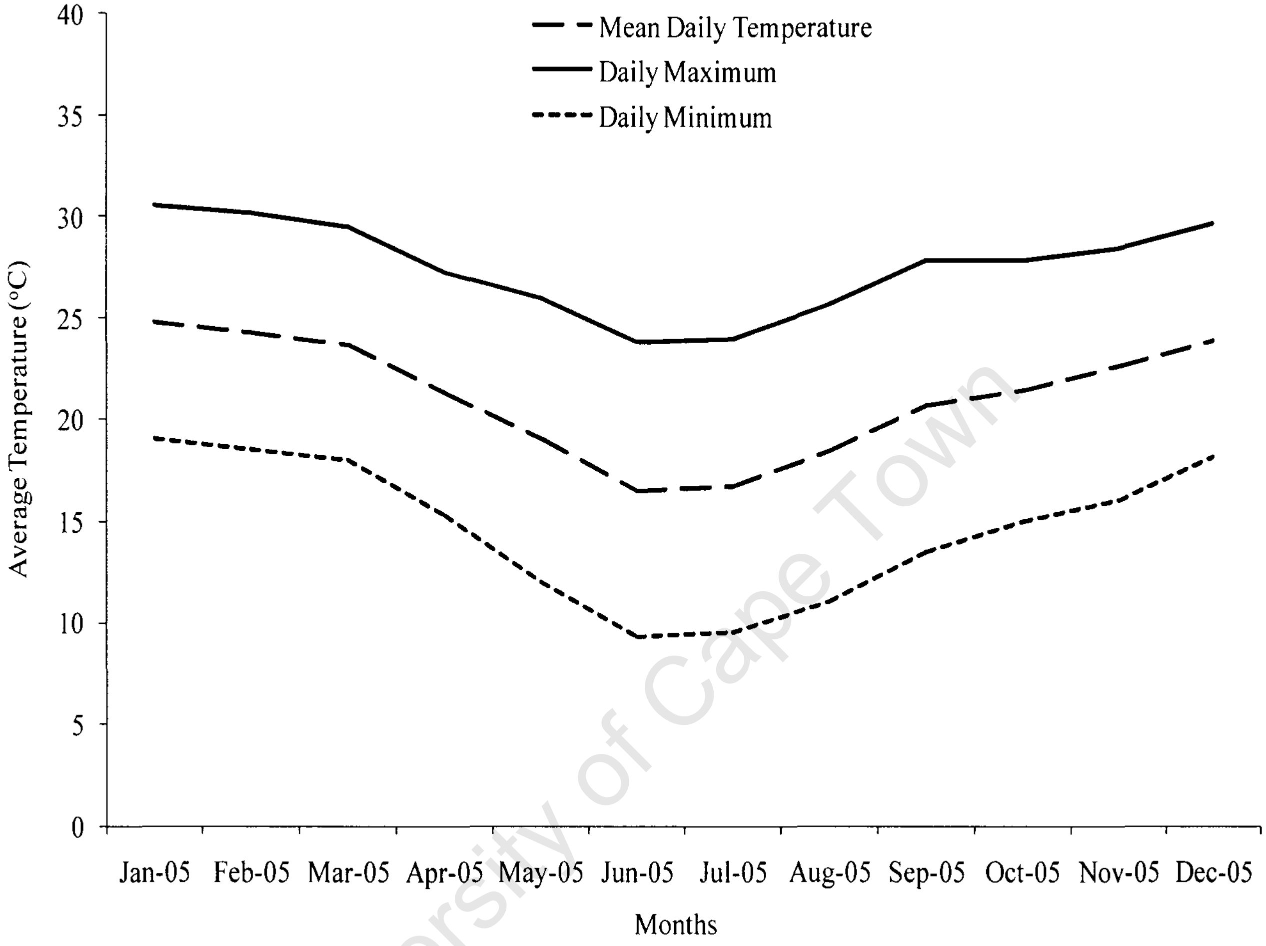

Figure 3. The long term average minimum and maximum temperatures (^{o}C) for the Pretoriuskop region.

Figure 4a. View of savanna landscape of Pretoriuskop Sour Bushveld with scattered trees, south-western region of Kruger National Park.

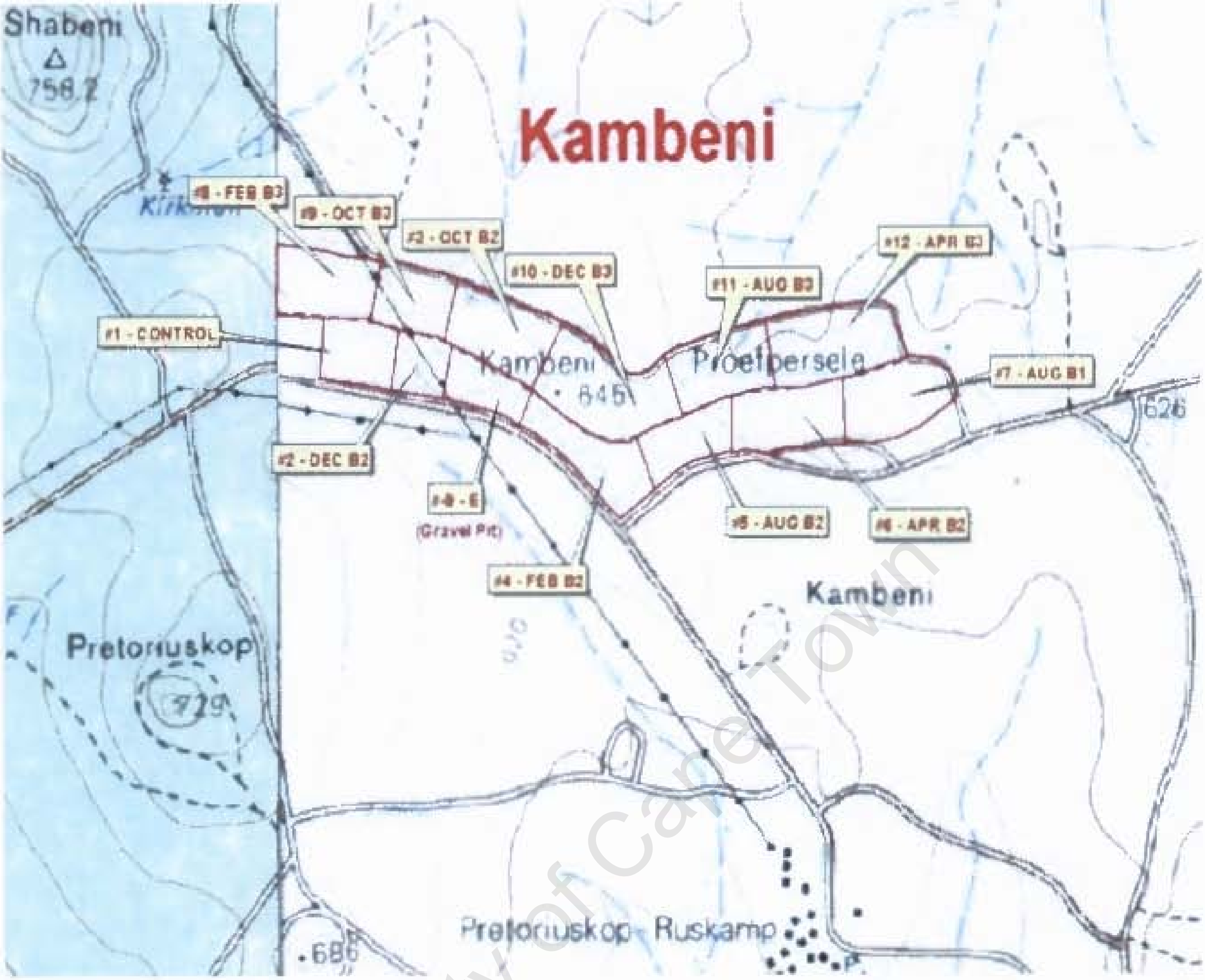

Figure 5. Layout of the Experimental Burn Plot, Kambeni string, in Pretoriuskop region, showing the treatments that were applied to each burn plot. The site marked "Gravel Pit" (#9 - E) was used for the no burn treatment.

Chapter 3. Effects of fire regime and savanna trees on woody plant recruitment.

Abstract

Increasing density of woody plants, "bush encroachment" has many cascading ecosystem consequences, but little is known about factors that influence the pattern and process in which forest/woody species colonize savannas. In a broad-leaved deciduous woodland ecosystem in Pretoriuskop, southwestern region of the KNP, we collected data on woody plants on the Experimental Burn Plots under the canopies of *Sclerocarya birrea* and *Terminalia sericea* and the open habitats to investigate the ecological effects of fire frequency and savanna trees on woody plant recruitment.

Species richness was greatest under *S. birrea*, low under *T. sericea* and lowest on the open habitats. Species abundance was highest under *S. birrea*, low on the open habitats and lowest under *T. sericea*. Decreasing fire frequency was associated with decreased species abundance under *T. sericea* and on the open habitats, but increased species abundance under *S. birrea*. Decreased fire frequency increased species richness under both *S. birrea* and *T. sericea* and on the open habitats. Fire sensitive or fire-intolerant species were highest under tree canopies on unburnt and triennial burn plots than in open habitats, whereas frequently burnt plots, annual and biennial plots had fire tolerant and typical savanna species.

Frequent burning reduced woody plant biomass seedlings, saplings and adult trees. Species composition under *S. birrea* differed significantly from that under *T. sericea*. Conclusively, canopy cover provides better growing conditions to new establishing species. Fire exclusion alone did not lead to forest invasion because few new saplings were found on the open sites and under *T. sericea*, but there was a shift to dense trees and a shift in species composition with no burn under *S. birrea*. Forest colonization is likely to take place under *S. birrea* canopies on low fire frequency burn plots.

Introduction

Bush encroachment is the successful establishment of trees and shrubs into open grasslands and savannas, creating a dense thicket (Trollope 1980). Woody plant encroachment is the increase in abundance or density of woody plants in savanna grasslands resulting in savanna woodlands (Archer *et al.* 2001). Both processes describe the increase in tree/shrub density in a particular area. To avoid confusion, I will refer to both processes as woody encroachment. Woody encroachment has occurred in many parts of the world, including Africa (Trapnell 1959, O'Connor 1995, Dalle *et al.* 2006), Australia (Walker & Gillison 1982, Bowman *et al.* 2001) and North America (Archer 1989, Briggs *et al.* 2002).

Woody encroachment has long been a concern to land managers because it degrades grasslands and savanna ecosystems by turning them into woodlands, reducing grass productivity and affecting biodiversity (Dalle *et al.* 2006). In the most extreme cases of woody encroachment, savannas are replaced by scrub thicket and eventually closed forest. Replacement of savannas by forests is a phenomenon apparently restricted to mesic areas (>650 mm rainfall) (Archer *et al.* 1988, Bond *et al.* 2003a, Fensham *et al.* 2005) and seems to be occurring in many such areas in South Africa (Hoffmann & O'Connor 1999, O'Connor & Crow 1999, Bond *et al.* 2003b) and Australia (Bowman *et al.* 2001, Fensham *et al.* 2005) over the last half century.

Establishment of forest species is known as forest colonization. Forest colonization means a change in tree species composition, reduction or loss of the grass layer and therefore a reduction in fire frequency and intensity and loss of mammal grazers. This is effectively a biome shift- from savanna to closed woodland formations with little or no grass. Several factors, including fire, herbivory, soil moisture and nutrients are thought to influence woody encroachment in savannas (Scholes & Archer 1997). However, it is not known whether factors governing an increase in savanna trees and shrubs are the same factors influencing forest colonization. The main aim of this study was to investigate factors limiting and promoting the pattern and process of forest colonization into savanna ecosystems.

In Kruger National Park (KNP), the experimental burn plots (EBPs) provide an excellent opportunity to explore forest colonization under different fire regimes and to investigate interactive effects of fire, climate and other factors in maintaining savanna structure or promoting forest colonization. The EBP's were set up in the 1950s and have been maintained to the present day (Biggs *et al.* 2003). Various combinations of season and frequency of burning have been applied (including no burn) in four different 'landscapes' (major plant communities) in the park with four replicates set in blocks ('strings') in each area (Govender *et al.* 2006). The layout of the experiments is described in Biggs *et al.* (2003).

Preliminary explorations suggested that only the Pretoriuskop sites, the most mesic of the four landscapes, show successional trends to forest. Woody forest/thicket species first appear in the shade of large savanna trees *Sclerocarya birrea*, *Pterocarpus angolensis* and *Terminalia sericea.* Spread of forest elements beyond the shade of the nurse tree is slow since forest extension beyond nurse tree canopies into open grassy areas remained incomplete even where fire has been excluded for 50 years.

What limits forest colonization at particular sites? Several researchers reported that recruitment of forest species into savannas is limited by soil nutrients (Kellman 1979), frequent fires (Hoffmann & Franco 2003, Hoffmann *et al.* 2004, Bond *et al.* 2005), and drought or seasonal water logging (Knoop & Walker 1985, Bowman & Panton 1993, Fensham *et al.* 2005). Establishment of forest species in savannas may also be limited by high light intensity and high temperatures characteristic of the savanna environment (Hoffmann 2000). As a result, the establishment and growth of forest species may be low in open savannas as shown by Hoffmann *et al.* (2004), and may be facilitated by the presence of adult savannas trees (Kellman 1979, Li & Wilson 1998). Increase in woody encroachment and forest invasion is attributed to fire exclusion (Swaine *et al.* 1992, Moreira 2000, Bond *et al.* 2005), fire-herbivory interactions (Eckhardt *et al.* 2000, Briggs *et al.* 2002, van Langevelde *et al.* 2003), facilitation by large savanna trees (Kellman 1979, Belsky *et al.*1989, Hoffmann 1996, Callaway & Walker 1997, Ludwig *et al.* 2004), atmospheric CO_2 and climate change (Bond & Midgley 2000, Bond *et al.* 2003b, Sankaran *et al.* 2005).

Savanna trees ameliorate soil moisture deficits (Ludwig *et al.* 2003) and reduce nutrient stress for establishing seedlings (Hoffmann 1996) by increasing soil fertility under their canopies (Belsky *et al.* 1989, Ludwig *et al.* 2004) resulting in the formation of "fertile islands". Phillips (1930), Bond *et al.* (2003a) and Bond *et al.* (2005) suggested that fire is the main factor maintaining mesic savannas because the climate can potentially support closed forests. Thus fire suppression can trigger rapid forest invasion (Swaine *et al.* 1992) or increase tree cover by favoring woody seedling establishment (Bond 2000, Moreira 2000, Hoffmann 2000) or allowing existing saplings to escape the flame zone and grow into adult trees (Higgins *et al.* 2000, Bond *et al.* 2005, Dalle *et al.* 2006, Sankaran *et al.* 2005).

High rainfall indirectly restricts forest invasion because it enables grass fuel to accumulate to support frequent fires (Higgins *et al.* 2000) that burn down tree seedlings and stimulate coppice growth (Bond 2000, Hoffmann 2000). In Brazil, forest species are more sensitive to fire than savanna species (Hoffmann 1996, Hoffmann & Moreira 2002), so savanna fires restrict forest species from colonizing the savanna environment (Hoffmann 2000, Hoffmann *et al.* 2004).

To understand the dynamics of forest invasion in savannas, I studied the pattern of forest colonization in a savanna ecosystem subjected to different burning treatments including fire exclusion for 50 years. I compared the effects of fire frequency and savanna trees on woody plant recruitment to test the following hypothesis:

1) Woody plant recruitment responds differently to fire frequency, with greater recruitment *where fires are infrequent and less recruitment with frequent fires.* Reduced fire frequency may allow establishment of fire sensitive species resulting in changes in tree species composition. Fire suppression should promote woody plant recruitment and forest species establishment initiating a biome shift. Fire frequency may affect fire intensity and fuel which in turn influences plant response to fire.

2) Woody plant recruitment would be high beneath canopies of large savanna trees and low on the open habitats. The presence of a tree canopy would promote forest colonization by increasing resource availability under their canopies, promoting seedling establishment and sapling growth. Canopy shading may provide safe sites and better growing conditions to tree seedling recruitment. The presence of a large tree might also increase seed dispersal, especially of bird-dispersed fruits, to the under-canopy environment while grazing and browsing may also be reduced.

3) There is an interaction between fire regime and the canopy effect of large trees such that saplings would colonize most readily where fires are less frequent and where resources are concentrated beneath the canopies of the large trees. Interactive effects between fire regime and canopy may influence woody recruitment greatly. Besides direct effects of burning on seedlings and saplings, reduced fires may increase canopy effects because of reduced fire damage to large trees enhancing "island effects" whereby tree canopies alter the availability of both nutrients and water thereby promoting tree seedling establishment.

Material and Methods

Study area

This study was conducted in Pretoriuskop, in the southwestern region of the Kruger National Park (KNP), in the north east of South Africa (31° 10' E, 25° 10' S). Pretoriuskop lies on granite rock.

Soils form a catenary sequence with red sandy soils on the crest, yellow soils at mid-slope positions, switching to pale grey hydromorphic sands and then clay soils on the bottom of the slopes (Gertenbach 1983, Venter 1990, O' Regan 2005). The average annual rainfall at the sites is ≈ 750 mm, which is the highest in the KNP. Pretoriuskop hosts one of the large long term Experimental Burn Plots (EBP). The experiment was introduced in the mid 1950s as part of an investigation to determine the effects of burning on major veld types (Van der Schijff 1958). Four replicates ('strings') of twelve plots, namely Numbi, Shabeni, Kambeni and Fayi, were laid out in the Pretoriuskop region.

This project was conducted in the Kambeni string because other plots had experienced unscheduled wildfires. Kambeni EBPs are predominantly occupied by *Terminalia sericea*, *Sclerocarya birrea* and the shrub, *Dichrostachys cinerea*. The Kambeni string consists of twelve treatments with respect to fire season (season of burn), fire frequency (the number of burns over a certain period) and the no burn plot where fire has been excluded for ca. 55 years. Each treatment occupies al least 7 hectares.

Experimental layout

Four fire treatments were selected, Aug B1, Aug B2, Aug B3 and No Burn (see Table 1) and within each treatment, three sampling sites (referred to as "microsites" hereafter), under the canopies of savanna trees *S. birrea* and *T. sericea* and an adjacent open habitat (without canopy effect) were selected. Four replicates of each microsites, *S. birrea*, *T. sericea* and open habitat were selected, with canopy area ranging from 5-14 m^2, giving a total of 12 microsites per burn plot. The entire canopy area under trees was used as a sampling plot and a similar area was sampled in adjacent open sites. All individual woody plant species were identified, measured, counted and recorded. The height and basal diameter of the recorded plants were measured by means of calipers and/or tapes. Multi stemmed species were counted as one individual plant. Woody plant species were classified as saplings (height >1.1 m) or as 'seedlings' (height < 1.1m). Specimens that could not be identified in the field were collected for identification in the herbarium. Due to accidental wildfires, there are no replicate plots for each of the four burn treatments used in this experiment. A summary of fire treatments sampled in Kambeni is provided in Table 1.

Effects of fire frequency and savanna trees on woody plant recruitment

I used number of species and number of individuals, standardized to per m^{-2} by dividing total species and individuals by the area of the sampling plot, as a response variable to both fire frequency and microsites. To determine the effects of fire frequency, I compared the number of individuals and species per unit area in four of the fire treatments. To determine the effects of canopy cover, seedling and sapling density was compared under and away from the canopy environments. Scatter plot graphs were used to show the relationship between species density and individual density under different microsites on different fire treatments. Bar charts were used to compare sapling and seedling species density and individual density under different microsites on different fire treatments.

A two dimensional ordination was performed using Primer 5, to determine possible changes in species composition in response to fire frequency and microsites. I used MDS (Multi-dimensional scaling) as the ordination technique based on Bray-Curtis similarity coefficients (Clarke & Gorley 2005). I used descriptive statistics by groups and Analysis of Covariance (ANCOVA) to analyze and compare species and plant density under different microsites on all fire treatments. I compared species composition under different microsites across different fire treatments to determine species response to fire and microsites. Treatments were not replicated in this study, only microsites were replicated within each treatment. Data analysis and statistical tests were performed using MS Excel, Statistica 7 and Jump 5.0.1, and all factors were considered to be significant at $p \leq 0.05$.

Results

Effects of fire frequency and savanna trees on woody plant recruitment

Effects of fire frequency on woody plants was determined by (1) evaluating species density and individual stem density in the different fire treatments , (2) establishing the influence of number of plants on species density under different fire treatment and (3) investigating the response of seedling and sapling density to fire frequency. Species density and individual density varied between fire frequencies (Fig. 1). Fire frequency had a significant effect on species density ($F_{3, 63}$=0.49, p=0.02) but no effect on individual density ($F_{3, 63}$=10.23, p=0.60). When tested over different fire treatments using Tukey test, species density was highest on the no burn plot, and significantly different from Aug B1 (p=0.02) and Aug B2 (p=0.02) but not from Aug B3 (p=0.45) at (MS =0.01, DF =62).

The number of individual stems showed no significant response to fire frequency. Species density increased in the No burn plot and Aug B3 treatments and number of stems increased in the Aug B1 treatment. Since species number is often correlated with number of stems (Gotelli & Colwell 2001), I determined the relationship between the number of stems and number of species per unit area for each fire treatment. The regression showed a strong relationship in Aug B3 (r^2 =0.89, p< 0.001), the no burn plot (r^2 =0.87, p< 0.001), and Aug B1 (r^2 =0.82, p<0.001) plot, and a weaker relationship in the Aug B2 (r^2 =0.76, p< 0.001) (Fig. 1). Sapling density on the no burn plot was significantly different from Aug B2 (p<0.01). No burn and Aug B3 plot had increased seedling species density, with the no burn plot significantly different from Aug B1 (p=0.02) and Aug B2 (p=0.04), but not significantly different from Aug B3 (p=0.5). Sapling species density on the no burn plot was significantly different to Aug B1 and Aug B2 (p<.001) and to Aug B3 (p<.01) (Table 2).

The strength of the relationship between number of individuals and number of species of saplings and seedlings differed with response to fire frequency. Regression results were on the Aug B1, sapling (r^2=0.02), seedling (r^2=0.88); Aug B2, sapling (r^2=0.37), seedling (r^2=0.30); Aug B3, sapling (r^2=0.29), seedling (r^2=0.88); and no burn, sapling (r^2=0.64), seedling (r^2=0.78). There were higher densities of individuals and species of both saplings and seedlings in the No burn and Aug B3 plot. Both the Aug B1 and Aug B2 treatment had low sapling density and high seedling density (Fig. 2). Large savanna trees had significantly greater sapling and seedling densities beneath their canopies. *S. birrea* and *T. sericea* were highly significantly different from open habitats in both seedling ($p< 0.0001$) and sapling ($p<0.001$) densities. There were highly significant differences ($p< 0.001$) between *S. birrea* and open habitat (Fig. 3).

Interactive effects of fire frequency and large savanna trees on woody plants

Individual stems on the open habitats decreased with the decrease in fire frequency (Fig. 4A). The species density of saplings under *S. birrea* and *T. sericea* on the Aug B3 and the No Burn plots was double that of *S. birrea* and *T. sericea* on Aug B1 and Aug B2 treatments while the open habitats had consistently lower species richness on all fire treatments. The effect of fire regime on sapling densities is most readily seen on the annual burn vs. the no burn. Even though fire has been excluded from the No Burn for approximately 55 years, there were very few individuals in the open habitats (Fig. 4C).

There was no significant difference between individual seedling densities on similar sampling sites on different fire treatments suggesting that fire treatments did not play a major role in 'general' woody establishment (Fig. 4B). But this measure does not take into account differences in the species favoured by frequent fires or infrequent fires. Microsite had strong effects on seedling location with significantly more seedlings under *S. birrea* and *T. sericea* than in the open habitats in all fire treatments (Fig. 4D). The seedling species increased linearly from high frequency to low frequency fires below the canopy of *S. birrea* and on the open habitats, except for *T. sericea* microsites on the Aug B2 treatment where the seedling species diversity decreased.

Effects of fire and microsite on species composition

Ordinations of all woody plants separated out along Axis 1 according to fire frequency and Axis 2 separates out different canopy types. On the positive side of Axis 1, the ordination grouped No burn *S. birrea* sites with No burn *T. sericea*, No burn Open habitat, Aug B3 *S. birrea*, and Aug B2 *S. birrea*. No burn plots are similar to each other and *S. birrea* sites on Aug B3 and Aug B2, but different from Aug B1. Axis 2 shows a strong dissimilarity between open habitat and *S. birrea* canopy sites, but some *T. sericea* sites that are similar to open habitat (Fig. 5).

Species responded differently to fire treatments and microsite effect. This test shows that there is high forest/thicket species composition on the no burn plot when compared to triennial, biennial and annual burns. Species such as *Bridelia cathartica*, *Gardenia volkensii* and *Xeromphis obovata* are forest species only occurring on the no burn plot. Other species such as *Canthium ventosum*, *Securinega virosa* and *Zanthoxylum capense* occur on the triennial and no burn plots. Species such as *Diospyros mespiliformis*, *Euclea natalensis*, *Rhus pyroides*, *Ochna natalitia* and *Phyllanthus reticulatus* are forest/thicket species occurring on biennial and triennial burn plots but with highest density on the no burn plot. The no burn plot had the highest species density of forest/thicket species when compared to other fire treatments (Fig. 6a, b, and c).

Forest/thicket species composition was highest under *S. birrea*, low under *T. sericea* and lowest on open habitats. Decreased fire frequency increased species density of savanna species such as *Dalbergia melanoxylon*, *Grewia flavescens*, *Gymnosporia senegalensis* and *Rhus leptodictya* under the canopies of *S. birrea*. Common savanna species such as *Dichrostachys cinerea*, *Senna petersiana*, *Terminalia sericea* and *Ziziphus mucronata* had high species density on annual burn, low on biennial burn and lowest on the triennial and no burn plots. Species such as *S. birrea* and *Strychnos madagascariensis* did not show any pattern of response to either fire frequency or microsite (Fig. 6a, b, c).

Table 1: The four fire treatments sampled in Kambeni, Pretoriuskop. The table shows the treatment code by which the treatment is referred to throughout this document in tables and figures, the month at which the fire takes place, the fire frequency, the field conditions in which they burn, and the season of fire.

Code	Month	Frequency	Conditions	Season
AUG B1	August	Annual	Dry	Late winter
AUG B2	August	Biennial	Dry	Late winter
AUG B3	August	Triennial	Dry	Late winter
NO BURN	None	No burn	None	None

Table 2. ANOVA comparing individual density of seedlings and saplings in three microsites (open habitat, *S. birrea*, *T. sericea*), and the size of the sampling plot unit area (SUA).

ANOVA	**Seedlings**				**Saplings**			
Source	*DF*	*SS*	*F*	*P*	*DF*	*SS*	*F*	*P*
Microsite	2	0.59	18.89	***<.0001***	2	0.13	7.46	***0.001***
Sample Unit Area	1	0.25	15.89	***<0.001***	1	0.01	1.88	*0.174*
Microsite*SU Area	2	0.13	4.31	***0.0177***	2	0.05	3.04	*0.059*
Error	*60*	*0.94*			*59*	*0.51*		

Table 3. Comparison of means of densities (m^{-2}) of species and individuals of saplings and seedlings under different microsites in response to different fire treatments.

Treatment	Microsite	Indiv/area-Saplings	Indiv/area-Seedlings	Spp/area-Saplings	Spp/area-Seedlings
Aug B1	Open habitat	0.14	0.1	0.02	0.02
Aug B1	*S. birrea*	0.1	0.32	0.02	0.05
Aug B1	*T. sericea*	0.13	0.41	0.03	0.06
Aug B2	Open habitat	0.12	0.17	0.02	0.03
Aug B2	*S. birrea*	0.1	0.3	0.03	0.08
Aug B2	*T. sericea*	0.07	0.33	0.03	0.04
Aug B3	Open habitat	0.11	0.16	0 .02	0.04
Aug B3	*S. birrea*	0.21	0.29	0.06	0.08
Aug B3	*T. sericea*	0.15	0.35	0.05	0.09
No Burn	Open habitat	0.08	0.1	0.04	0.04
No Burn	*S. birrea*	0.26	0.38	0.1	0.1
No Burn	*T. sericea*	0.2	0.28	0.1	0.1

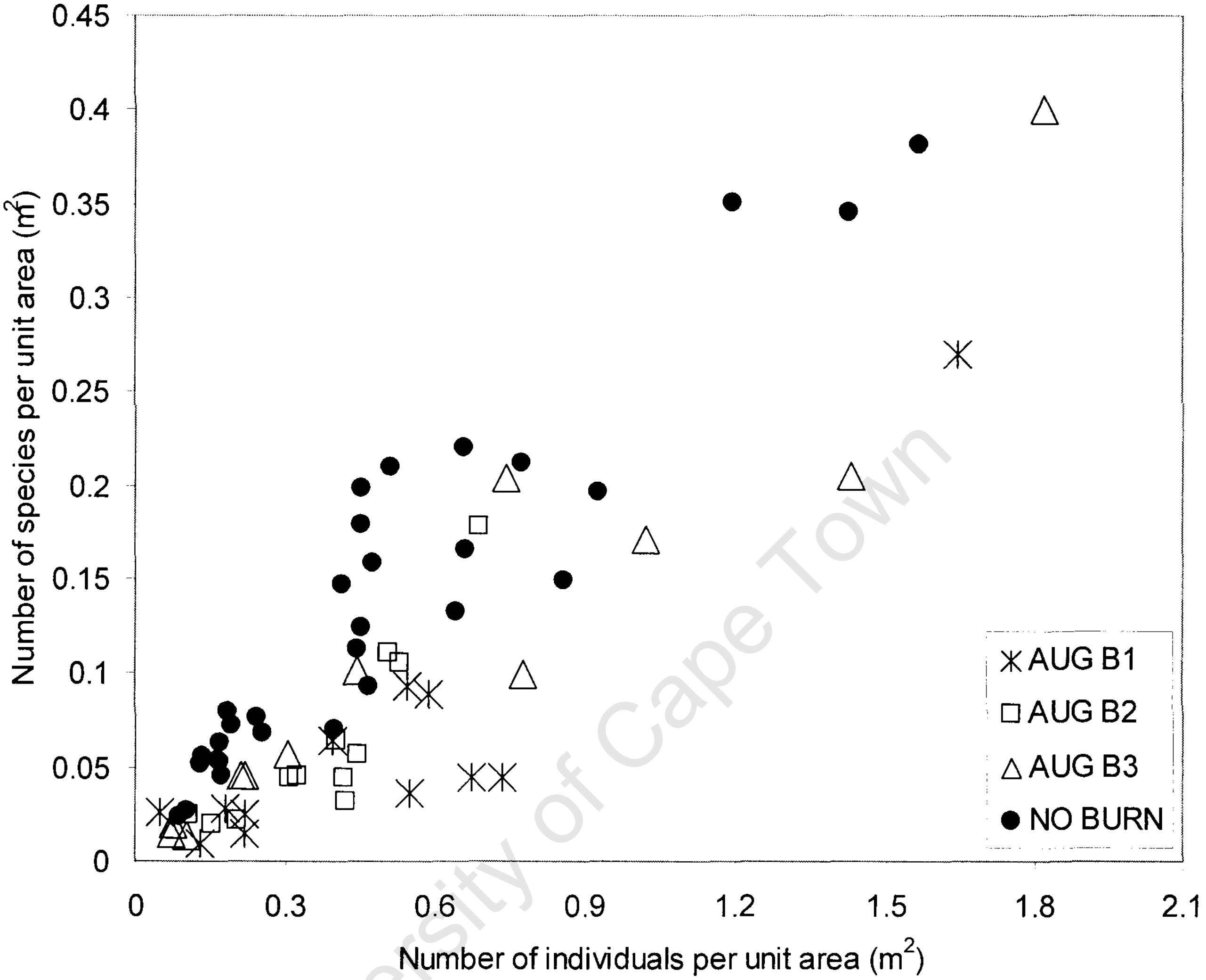

Figure 1. A scatter plot showing the relationship between the number of species per unit area (m^2) and the number of individual stems per unit area (m^2) for different fire regimes. Aug B1= annual burns in August, Aug B2 = biennial burn in August, Aug B3 = triennial burn in August, No Burn = no fires for ca. 50 years.

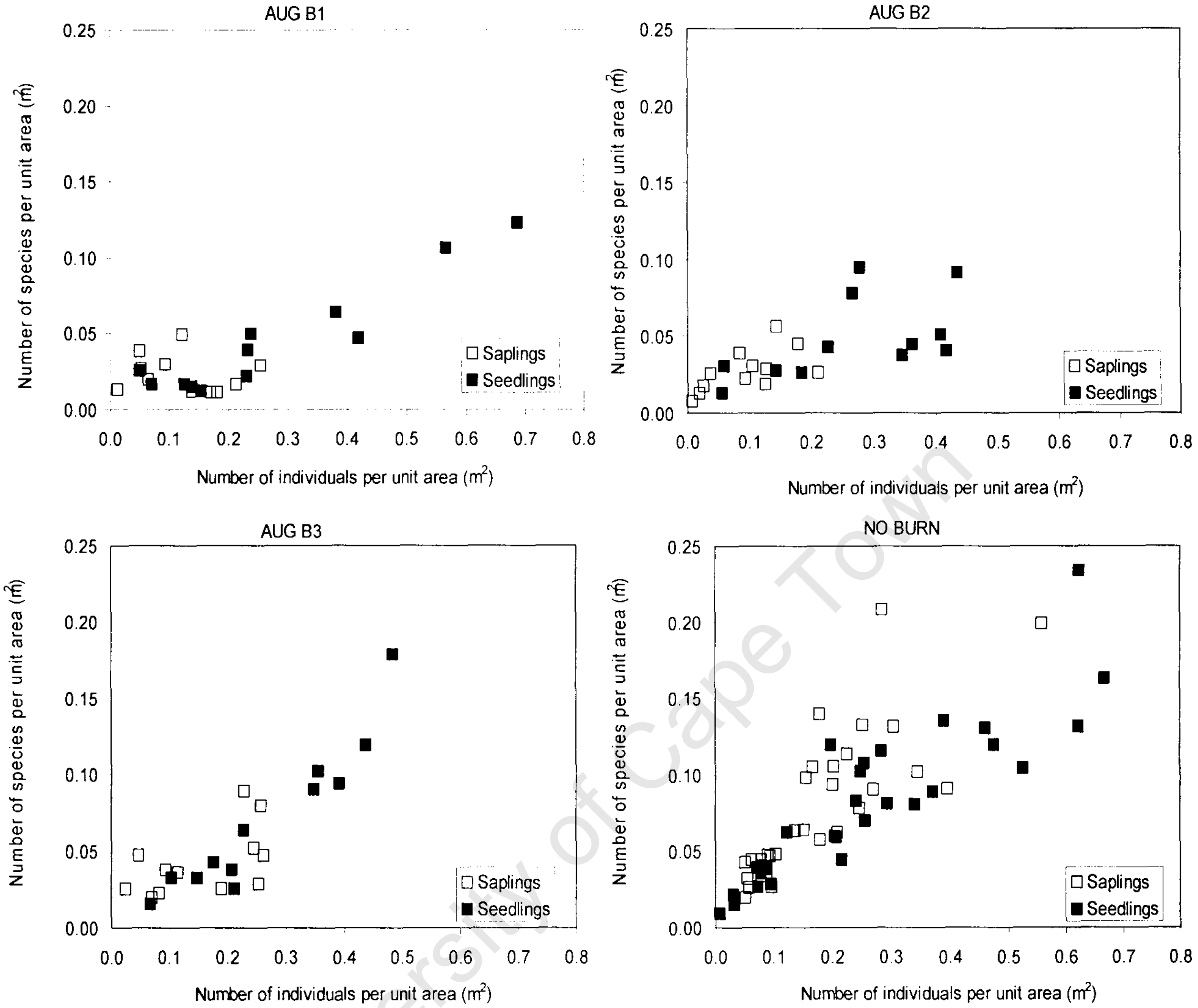

Figure 2. Individual and species density response of seedlings and saplings to different fire regimes. Aug B1= annual burns in August, Aug B2 = biennial burn in August, Aug B3 = triennial burn in August, No Burn = no fires for ca. 50 years.

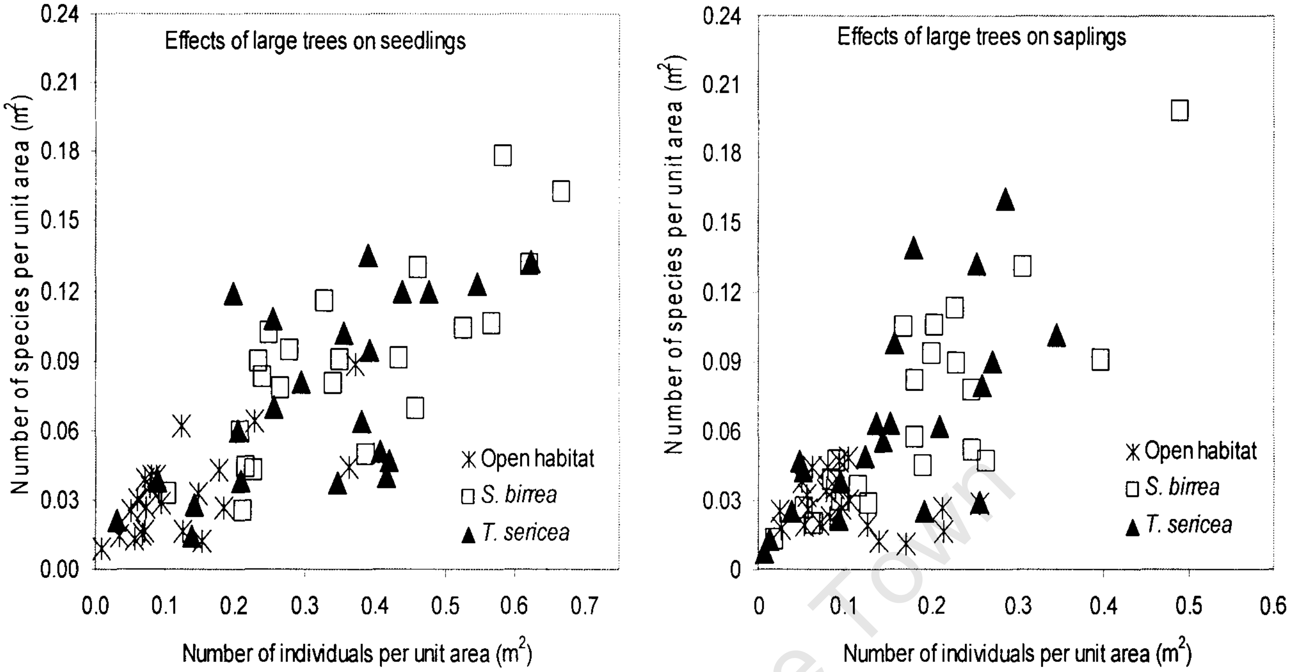

Figure 3. Individual and species density response of seedlings and saplings to different sampling plots, i.e. Open habitat, *S. birrea* and *T. sericea*.

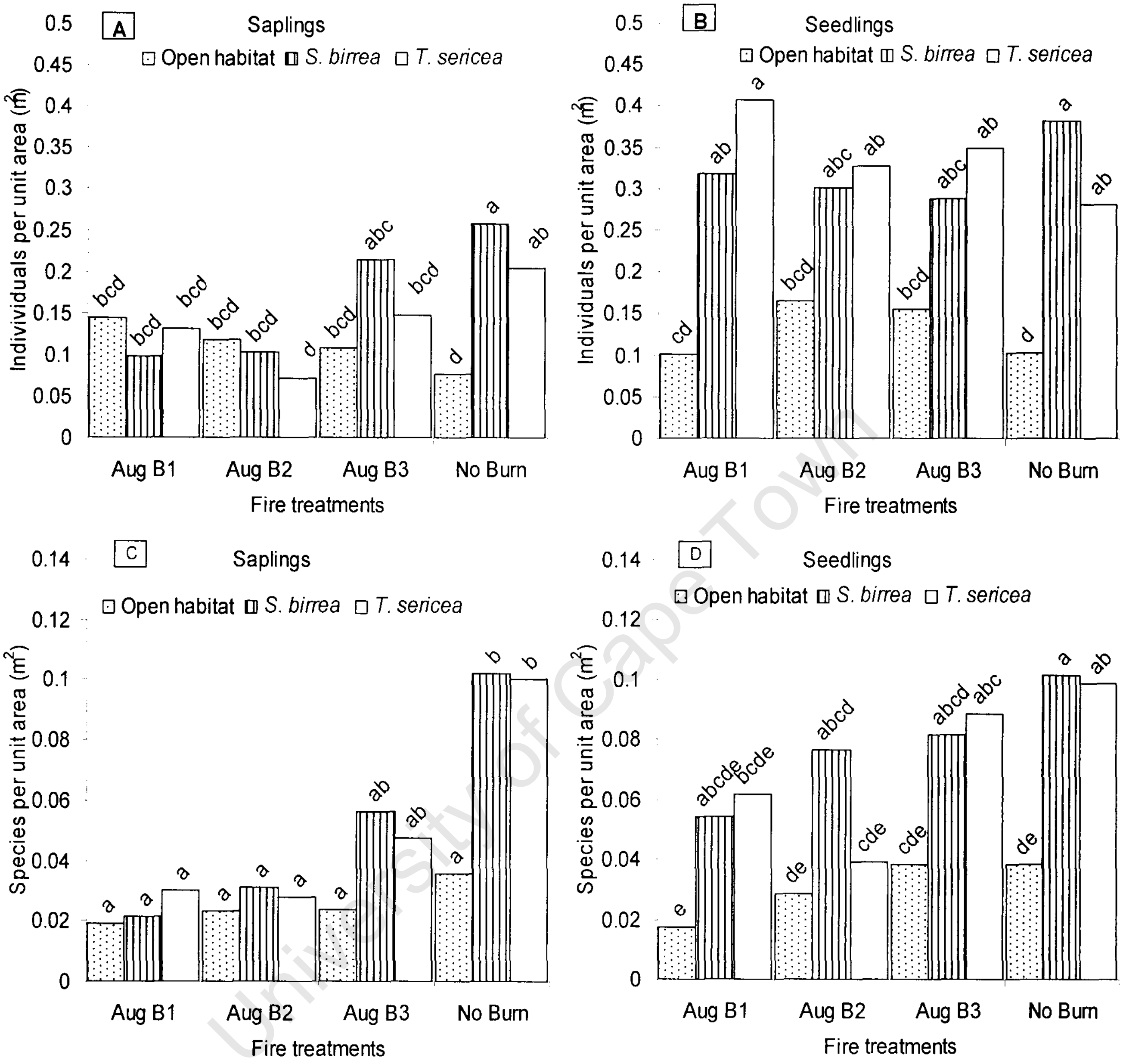

Figure 4. Response of individual stems of saplings (A) and seedlings (B); species density of sapling (C) and seedlings (D) to canopy cover and fire frequency. Levels not connected by same letter are significantly different.

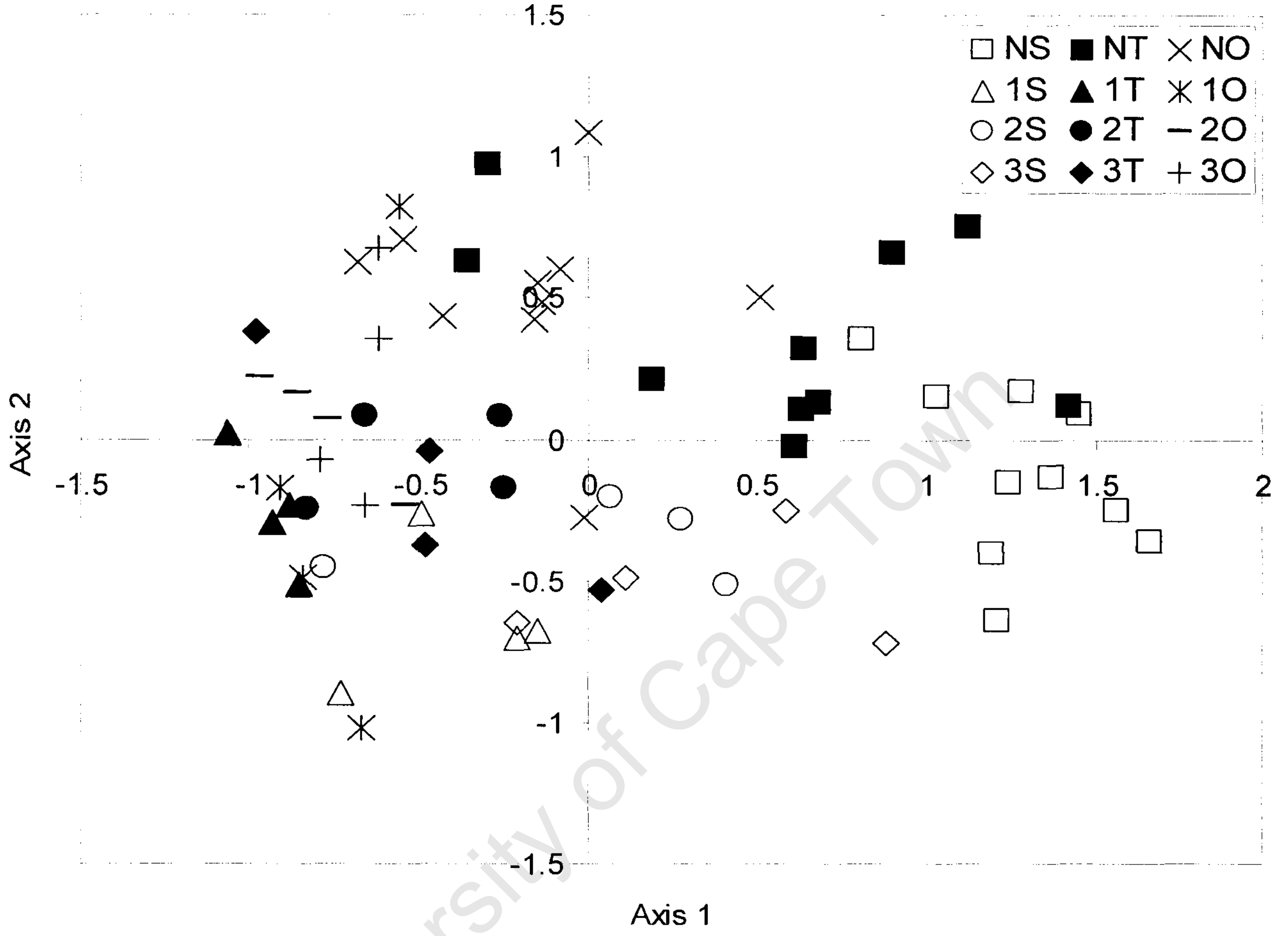

Figure 5. Two dimensional ordination (MDS) of woody plants under three microsites (open habitat, *S. birrea*, *T. sericea*) and four fire treatments, based on the importance scores for woody plants, showing an interactive role of microsite and fire treatment: NS- No Burn *S. birrea*, NT-No Burn *T. sericea*, NO-No Burn Open habitat; 1S- Aug B1 *S. birrea*, 1T- Aug B1 *T. sericea*, 1O-Aug B1 Open habitat; 2S- Aug B2 *S. birrea*, 2T- Aug B2 *T. sericea*, 2O-Aug B2 Open habitat; 3S- Aug B3 *S. birrea*; 3T- Aug B3 *T. sericea*, 3O-Aug B3 Open habitat.

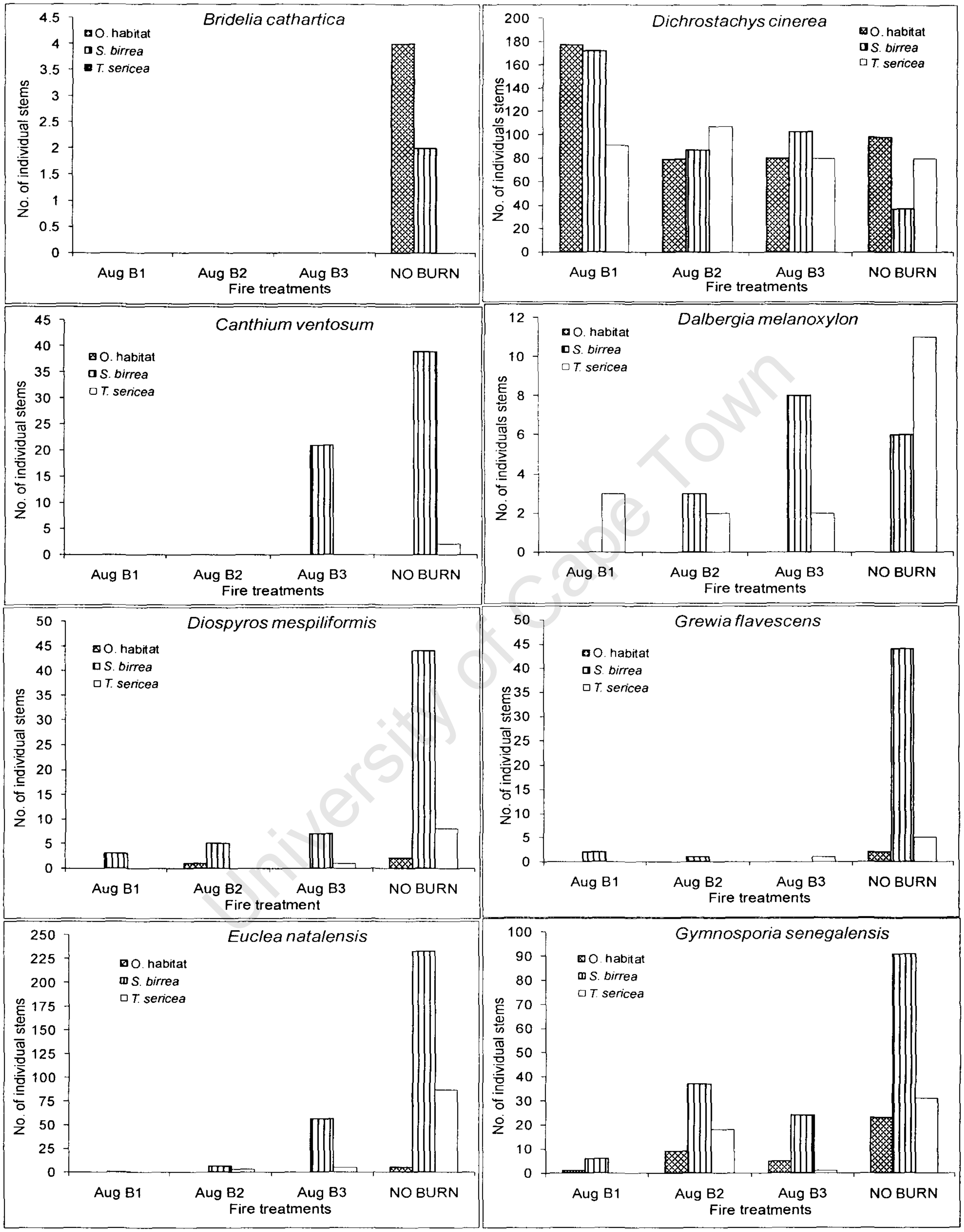

Figure 6a. Individual species densities in relation to fire treatment and microsite. Species on the left are characteristic of closed thicket/forest communities, species on the right are typical savanna trees and shrubs.

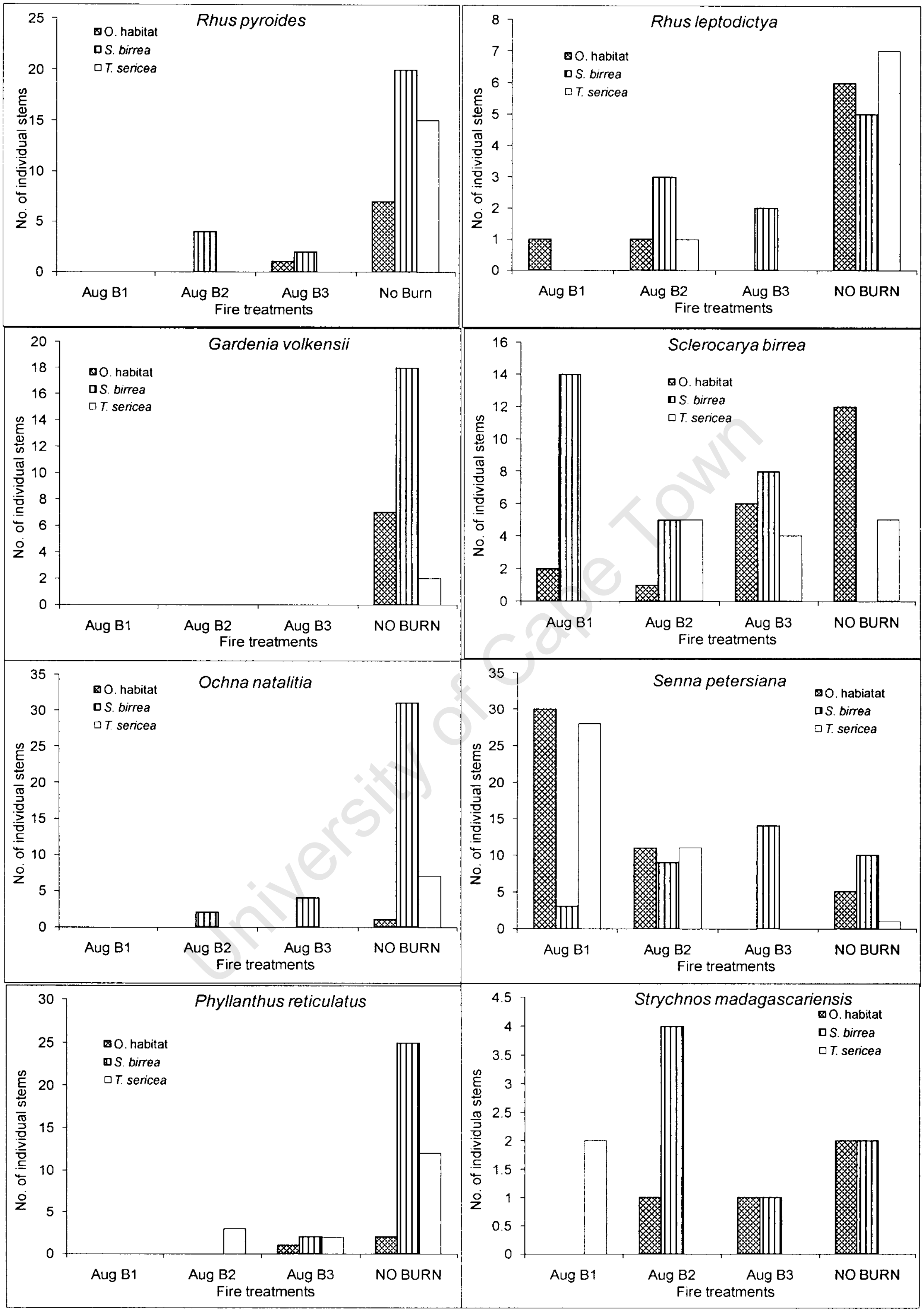

Figure 6b. Individual species densities in relation to fire treatment and microsite. Species on the left are characteristic of closed thicket/forest communities, species on the right are typical savanna trees and shrubs.

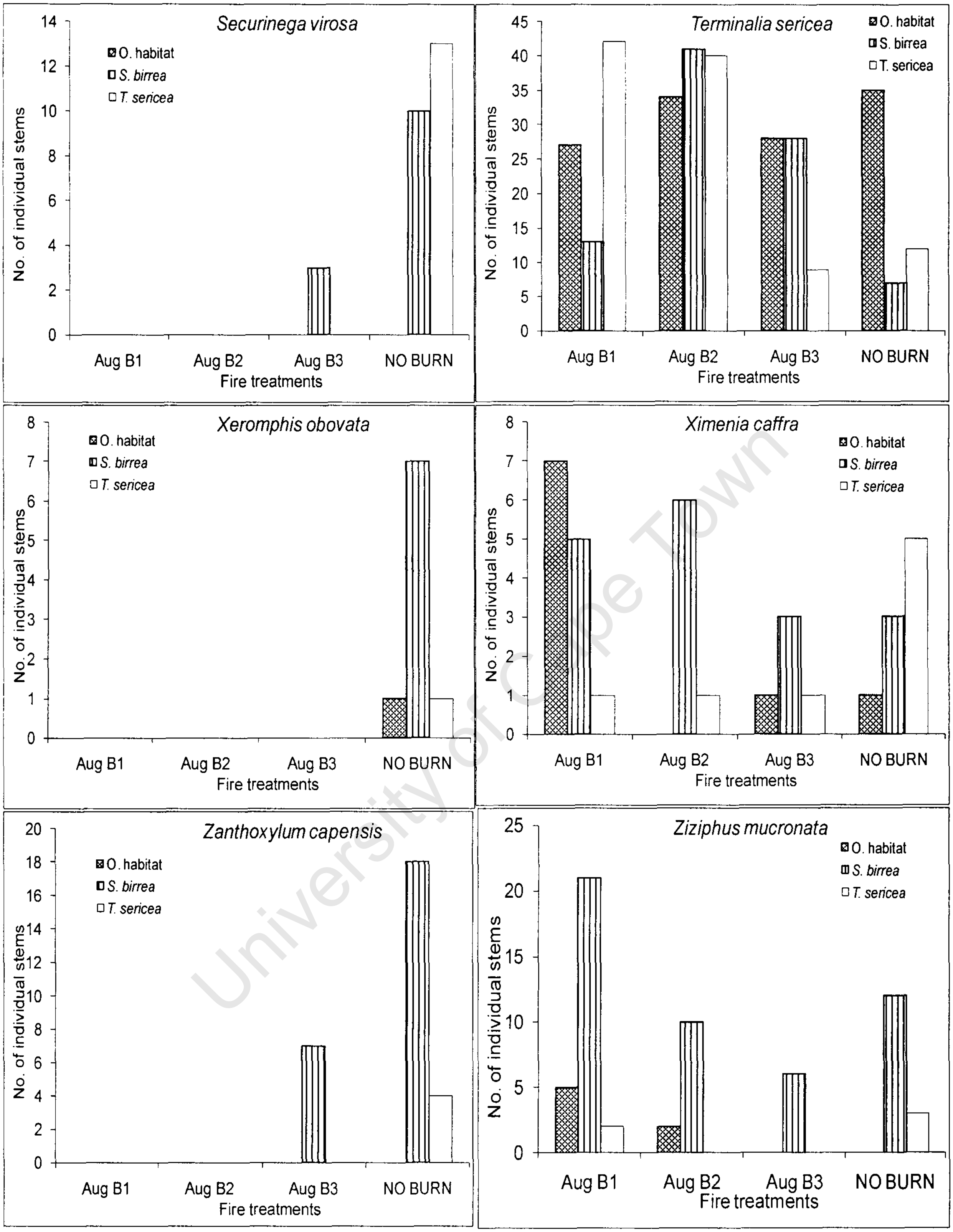

Figure 6c. Individual species densities in relation to fire treatment and microsite. Species on the left are characteristic of closed thicket/forest communities, species on the right are typical savanna trees and shrubs.

Discussion

O' Regan 2005, Enslin *et al.* 2000, and Shackleton & Scholes 2000 investigated effects of fire regime on woody plants in the savannas of KNP. Shackleton & Scholes (2000) found that woody plant density decreased with increasing fire frequency in a semi-arid savanna at Kruger (*Acacia nigrescens – Sclerocarya birrea* community) and Williams *et al.* (2003) also showed that tree density increases in the absence of fire in a *Eucalyptus* savanna and was highest in the no burn plots. I found similar patterns in the more mesic savanna at our study area, with greater woody density in the triennial and no burn plot, whereas frequently burned plots (Aug B1 & Aug B2) had few woody plants and few species (Fig. 1).

The frequently burnt plots had fewer species per stem counted as predicted in the hypothesis. High individual density of woody plants was recorded on the annual burn but low species density, so frequent fires reduced establishment of new species. There were also shifts in tree species composition with more seedlings and saplings on the no burn and Aug B3, as compared to Aug B1 and Aug B2. Tree species found on the triennial and no burn plot included fire sensitive and broadleaved species, whereas species found on the frequently burned plots included the most fire tolerant species. Govender *et al.* (2006) reported that triennial burn winter fires have a high fuel load generating high fire intensities that can torch the vegetation. However, my study shows that in the Pretoriuskop area, triennial winter burns lead to a change in species composition, increase in fire intolerant species, and a declining grass layer that does not support damaging fires under tree canopies.

Tester (1989) reported that frequent burning led to a decrease in forest species and an increase in true prairie species in the tall grass prairie biome. Therefore, forest species are fire sensitive and intolerant of frequent savanna fires whereas savanna trees can survive very frequent fire. In my study area, species like *Kraussia floribunda*, *Mystroxylon aethiopicum*, *Bridelia cathartica* and *Catunarega spinosa* only occurred on the no burn plot. Their typical habitat is montane forest, riverine forest or thicket (Schmidt *et al.* 2002). In general, the most common savanna species in the area *Dichrostachys cinerea*, *Gymnosporia senegalensis*, *Ximenia caffra* and *T. sericea* can survive multiple burns and they are capable of resprouting after disturbance, as sprouting seems to be a savanna species trait of survival after disturbances such as fire, clipping and/or herbivory (Hoffmann 2000, Bond & Midgley 2001).

Triennial burn and no burn plots favoured the introduction of broadleaved savanna trees, savanna-forest species, and fire intolerant and shade tolerant species as predicted by Moreira (2000) and Petersen & Reich (2001). These results support Swaine *et al.* (1992) who found that fire suppression led to forest development in African Guinea savannas and Dalle *et al.* (2006) who found that fire suppression caused woody encroachment in Borana lowlands. The most surprising pattern in my study was the few individuals and species found in the open microsites in the no burn plot. The fire hypothesis predicts that, with suppression of fire, closed woody vegetation will develop. In my study, sapling stems did not increase in the open sites (defined by the absence of a tree canopy) after 50 years of fire exclusion (Fig. 4A). However, concerning sapling species density, there was a slight increase in the number of species as fire frequency decreased (Fig. 4C).

Seedling recruitment showed no consistent trends among fire treatments (Fig. 4B) also contradicting the predictions of the hypothesis. I hypothesised that seedling recruitment will increase with the decrease in fire frequency. Instead, the results suggest that recruitment and establishment of new species depends on the "canopy effect", and this result supports Hoffmann (1996) who found that seedling establishment was highest under the canopies than in open grassland. The nature of the canopy seems to be more important than fire in terms of recruitment. Despite many seedlings found on these fire treatments (Fig. 4B), very few survive fire, drought and herbivory, and recruitment to mature trees is slow or rare in frequently burnt areas.

In contrast, on the no burn and the Aug B3 plot, the process of woody plant colonization is faster particularly under the canopies of *S. birrea* and *T. sericea*. There were more woody stems on the no burn plot and Aug B3 as compared to Aug B1 and Aug B2. These findings support Trapnell (1959), Archer *et al.* (1988), Swaine *et al.* (1992), Scholes & Archer (1997), Moreira (2000) and Bond *et al.* (2005) who suggested that fire suppression result in an increase in woody species. Frequent fire plays a major role in maintaining the structure of savannas because it limits woody plant recruitment and it also eliminates or kills seedlings, saplings and possibly mature trees (Phillips 1930, Tester 1989, Bond & van Wilgen 1996, Higgins *et al.* 2000, Bond *et al.* 2003a, and Bond *et al.* 2005). Reduced fire frequency also favours seedling recruitment and sapling growth to adult trees as reported by Bond (2000), Hoffmann (2000) and Hoffmann *et al.* (2004). Low woody density under the canopies of *S. birrea* and *T. sericea* on frequently burnt plots may be a direct effect of fire on young plants or an indirect effect of fire reducing canopy cover of large trees.

In summary, fire reduced woody plant recruitment and inhibited forest invasion by killing seedlings and saplings and thereby reduced the chance of saplings escaping the fire trap to grow into mature trees. In this savanna, effects of fire on forest colonisation are contingent on the presence and density of large trees. Canopy sites promoted nucleation sites which appear to favour colonisation of woody plants in general and forest species in particular. A large tree canopy influences many ecological factors such as soil nutrients, shade, fire intensity, dispersal of propagules and soil moisture.

Though the density of individual plants was not significantly different between *S. birrea* and *T. sericea*, species response to fire frequency and microsites shows that species composition under *S. birrea* canopies differs significantly from that under *T. sericea* canopies. So, Marula, *S. birrea* acts as a nurse plant for forest invasion and a haven to forest/thicket species more than *T. sericea*. The no burn fire treatment had high species diversity and a switch in species composition with increasing forest/thicket species. Forest colonization is likely to take place under the canopies of *S. birrea* and on the no burn plots and/or low frequency fire plots.

Chapter 4. Ecological effects of fire and savanna trees on resource availability in savannas

Abstract

Throughout the grasslands and savannas of the world, fire and savanna trees affect and influence soil moisture and nutrient availability in the ecosystem, but the pattern in which these factors affect resource and vegetation distribution is not well understood. In a broadleaved mesic savanna in Pretoriuskop, Kruger National Park, soil samples were collected under the canopies of *Sclerocarya birrea* and *Terminalia sericea* and on open habitats on four fire treatments, i.e. annual burn (Aug B1), biennial burn (Aug B2), triennial burn (Aug B3) and fire exclusion (No Burn), to investigate the influence of fire and savanna trees on soil moisture and nutrient availability.

Soil moisture availability was significantly greater on the deeper soils when compared to topsoil layers and differed with sampling sites. Soils under *S. birrea* were moderately acidic. Soils under *T. sericea* and in open habitats were strongly acidic. Soils under *S. birrea* were significantly richer in K, Ca, Mg and C when compared with *T. sericea* and open habitats. There was no significant effect of fire treatment and fire treatment*sampling sites on exchangeable ions, and no significant effect of fire treatment and fire treatment*sampling sites on soil organic matter (SOM).

The effect of savanna trees on their microenvironment varied with species with high levels of K, Ca, Mg, C, SOM and exchangeable ions under *S. birrea* canopies but not under *T. sericea*. These results have shown that effect of trees on soil moisture and nutrients availability depends on the species, and that low fire frequencies favour high pools of Na and N.

Introduction

Throughout the grasslands and savannas of the world, productivity of an ecosystem depends on the amount of nutrients stored in various compartments such as vegetation, litter, soil and animal biomass and on the rates of nutrients transfer among those compartments (Holt & Coventry 1990, Cook 1994, Cotsee 2007). Savannas vary greatly in soil fertility with some on nutrient rich, and others on nutrient-poor soils (Cook 1994 for Australian savannas, Weltzin & Coughenour 1990 for African savannas). Several factors such as fire, herbivores, and the canopy effect of savanna trees may influence soil fertility. Fire is an active agent of nutrient cycling (Holt & Coventry 1990), and is regarded as a global "herbivore" because it consumes plant biomass (Bond & Keeley 2005) and thereby increases decomposition rate. According to Kauffman *et al.* (1994), fire is an ecological factor that dramatically influences ecosystem structure, composition and nutrient cycling, and it affects long-term site productivity by nutrient losses during fire and redistribution after fire in Brazilian cerrado.

Savanna trees are believed to strongly influence environments under their canopies by altering the spatial distribution and cycling of nutrients, microbial activities, soil moisture, light availability and by concentrating organic matter beneath their canopies resulting in the formation of "fertile islands" (Kellman 1979, Belsky *et al.* 1989, Weltzin & Coughenour 1990, Belsky 1994, Scholes & Archer 1997, Anderson *et al.* 2001, Reich *et al.* 2001, Hudak *et al.* 2003, Ludwig *et al.* 2004 and Caylor *et al.* 2005). Both factors, fire and savanna trees, seem to have an interactive effect and influence on soil fertility. However, while many studies have shown how fire and trees influence soil resources in the ecosystem, the role of fire and trees on soil resources varies from one area to the other and is not well understood.

In Australian savannas, Cook (1994) reported that burning facilitates the local redistribution of nutrients, with fire causing a flush of nutrients (P, K, Ca, & Mg) and a high loss of nitrogen through volatilization. When fire is excluded from savannas, nutrients are primarily cycled through herbivory and decomposition by microbes. In North America (Texas), Ansley *et al.* (2006) reported that fire and its season of occurrence can significantly alter ecosystem processes and storage of C and N in savanna ecosystems. In African savannas, Aranibar *et al.* (2003) and Mills & Fey (2004) found that repeated burning resulted in a decline in soil organic matter (SOM) because of removal of vegetation which increases mineralization of organic matter and microbial activities. Pereira (1982) for South American savannas and Cook (1994) for Australian savannas reported that loss of nitrogen to the atmosphere from frequent fires is substantial. However, Aranibar *et al.* (2003) reported that the effects of fire on nitrogen are unpredictable in the Kruger National Park and Ansley *et al.* (2006) for North American savannas reported that two or three fires within 5 years may either increase or have no effect on soil organic carbon and total nitrogen in mixed-grass/mesquite savanna. Mills & Fey (2004) for African savannas suggested that frequent burning can increase the tendency of soil to crust leading to reduced infiltration of rainfall.

Hoffmann *et al.* (2004) in Brazilian cerrado, manipulated water, light and nutrients to determine the relative importance of these resources vs. fire, in limiting the distribution of forest and savanna woody species. They showed that below-ground allocation was the single most important difference between forest and savanna seedlings and concluded that fire tolerance, rather than resource requirements was the key difference between forest and savanna species. If this was also the case in South African savannas, we would expect fire-intolerant forest species to readily colonise savannas from which fire has been excluded for long periods. Alternatively, if forest species require higher nutrients, water, or shade we would expect forest species to preferentially colonise under-canopy areas – if resources are indeed more available beneath trees.

In this chapter I set out to explore the relative magnitude of the canopy effect and different fire regimes, and their interaction, on soil properties in a mesic savanna at Kruger National Park, South Africa. A long term burning experiment was initiated in the 1950s and is still being maintained. The experiment varied fire frequency, season and also included a fire exclusion treatment. The experiment thus provides an excellent opportunity for determining the relative importance of fire and canopy effects on soil resources and their interactions.

To understand how fire and tree canopies influence resources, I collected soil samples under two savannas trees, *S. birrea* and *T. sericea* and adjacent open sites from plots in the Kambeni string of the Pretoriuskop Experimental Burn sites. I expected that nutrient status would differ amongst fire treatments and tree canopy types, but that soil moisture would not be affected by fire treatment (unless crusts develop under frequent burning as suggested by Mills & Fey 2004). I predicted that the presence of a tree canopy would increase nutrient, moisture and organic matter content under their canopies, and there would be lower moisture, nutrients and organic matter content on unshaded open sites. Under tree canopies, shade cast would reduce light intensity, water stress and temperature and increase nutrient concentration (Weltzin & Coughenour 1990). It has been shown that some savanna trees modify soil moisture by hydraulic lift (Ludwig *et al.* 2003).

Materials and Methods

Effects of fire frequency and savanna trees on soil moisture and soil nutrients.

I determined the effects of fire on nutrient availability by collecting soil samples in four fire treatments (Table 1) of the Kambeni string under the canopies of large *S. birrea* and *T. sericea* trees and in adjacent open habitats. The entire canopy area was used as the sampling site under each tree and an adjacent circular plot of similar area (without effects of large trees) was sampled in open habitats. Four sampling sites under each of the tree species and four open habitats were located on each treatment giving a total of twelve samples in each burn treatment (sampling sites and canopy types are called "microsites" hereafter). Soil samples for nutrient analysis were collected in April 2005 at 10-15 cm depth, one sample at each replicate microsite. Soil samples were placed inside zip-loc plastic bags and brought to the Ecophysiology lab, in the Botany Department (University of Cape Town) for organic matter analysis, BemLab (Stellenbosch) for nutrients and Scientific Services Lab in Skukuza (Kruger National Park) for moisture analysis. Soil moisture was measured using the gravimetric method (Rowell 1994).

Soil samples for moisture analysis were collected under the host trees, *S. birrea* and *T. sericea* and on the open habitats at different soil depth, 5, 15, 25 and 45 cm respectively, to determine the moisture content below and away from the canopy sites on different fire treatments. Soil samples for moisture estimation were collected in April 2005 towards the end of the rainy season and in July 2006 during the dry season. A soil auger was used to dig the soil samples from different soil depths, and all the soil samples were placed in sealable plastic bags and placed in a cooler box to keep samples at a moderate temperature. In the lab, the samples were thoroughly mixed to ensure uniform distribution of moisture. Approximately 30 g of wet soil was weighed and the samples were placed in the oven to dry at 110°C for 24 hours. After 24 hours, the dry soil mass was weighed and recorded. The moisture content was calculated as:

Soil moisture content = (soil wet mass – soil dry mass)/ soil dry mass; and was expressed as g H_2O g^{-1} oven dry soil (Rowell 1994).

For soil organic matter (SOM), oven dried soil samples were weighed into crucibles, placed in a furnace at 450°C for 16 hours and reweighed. SOM was calculated as:

Soil organic matter content = (soil dry mass – furnaced soil mass)/ soil dry mass and was expressed as a percentage (Rowell 1994).

Soil pH was determined using a KCl solution. Approximately 10 g of soil was weighed into a centrifuge tube, 15 ml of KCl added and mixed for 30 minutes on a whirl mix. After 30 minutes, the pH readings were taken and recorded (Rowell 1994). For soil exchangeable cations (Mg, Na, K, Ca), Nitrogen, Phosphorous and Carbon content, soil samples were processed in

BemLab using standard methods (Rowell 1994). Available exchangeable cations (AEC) were expressed as cmol kg^{-1}, and total exchangeable cations (TEC) were expressed as a percentage.

Analytical Methods

Statistical analyses were performed using the software package of JMP 5.0.1 and STATISTICA 7. Dependent variables were tested for normality. A two-factor model was used to test the effects and influence of fire treatments and microsite (under or away from tree canopy) on soil moisture and nutrients. Fire treatments were unreplicated, only microsites were replicated in each treatment. Significant differences ($P < 0.05$) among treatments and microsites were determined using the Post-hoc, Tukey HSD test.

Table 1: The four fire treatments sampled in Kambeni, Pretoriuskop. The table shows the treatment code used in subsequent tables and figures, the month at which the fire takes place, the fire frequency, the field conditions in which they burn, and the season of fire.

Code	Month	Frequency	Conditions	Season
NO BURN	None	No burn	None	None
AUG B1	August	Annual	Dry	Late winter
AUG B2	August	Biennial	Dry	Late winter
AUG B3	August	Triennial	Dry	Late winter

Results

Soil Moisture

Average soil moisture was highest in April 2005 (2.76 g H_2O g^{-1}) when compared to July 2006 (0.02 g H_2O g^{-1}). Soil moisture differed significantly amongst fire treatments, microsites and soil depth in both the wet and the dry season. In April 2005, moisture content was highest on triennial burn (3.38 g H_2O g^{-1}) and no burn (3.10 g H_2O g^{-1}) treatments, and lower on biennial burn (2.29 g H_2O g^{-1}) and annual burn (2.26 g H_2O g^{-1}) treatments. Moisture content in April 2005 was highest under *S. birrea* (3.08 g H_2O g^{-1}), low on open habitats (2.66 g H_2O g^{-1}) and lower under *T. sericea* (2.56 g H_2O g^{-1}). Deeper soil layers (45 cm) had the highest moisture content (3.76 g H_2O g^{-1}), high on top soil layers 5 cm (2.78 g H_2O g^{-1}), and lower on middle layers 25 cm (2.38 g H_2O g^{-1}) and 15 cm (2.15 g H_2O g^{-1}) respectively.

In July 2006, during the dry season, soil moisture was slightly higher on biennial and triennial burn plots (both with 0.03 g H_2O g^{-1}) than on the annual burn and the no burn plots (both with 0.02 g H_2O g^{-1}). Microsite effects showed that moisture content was slightly higher under *S. birrea* (0.03 g H_2O g^{-1}) than under *T. sericea* and open habitats (both with 0.02 g H_2O g^{-1}). Deeper soils (45 cm) and lower middle layers (25 cm) had the highest moisture content (both with 0.03 g H_2O g^{-1}), high on upper middle layers (15 cm) with 0.02 g H_2O g^{-1} and lower on top soil layers (5 cm) with 0.01 g H_2O g^{-1}.

In April 2005, interactive effects of fire treatments, microsites and soil depth had an influence on moisture content (Table 2). Topsoil layers were significantly moister under the canopies than away when compared to middle layer (15 cm) during the wet season (Table 2). In July 2006, fire treatment, soil depth, microsite, microsite*depth and fire treatment*microsite significantly influenced soil moisture. Moisture content was highest on triennial burn, higher under *S. birrea* and on open habitat and highest in the deeper soil layers. A positive interactive role was found amongst factors on the soil moisture content (Table 3).

Soil pH

Fire treatment, microsite and fire treatment*microsite influenced soil pH greatly. Soil pH was positively correlated with organic matter ($F= 7.86$, $r^2 = 0.14$, $P< 0.01$) and available exchangeable cations ($F= 45.44$, $r^2 = 0.49$, $P< 0.001$) (see Fig. 1). Soils on the annual burn under *S. birrea* were moderately acidic and significantly different from very acidic soils on open habitats (Fig. 2A). Soils under *S. birrea* canopies were less acidic and significantly different when compared to soils on open habitats on annual burn, triennial burn and no burn plots (Fig. 2A). There were significant differences in pH under *S. birrea* and *T. sericea* on annual burn, biennial and no burn plot, except for the triennial burn plots where soils under *S. birrea* were slightly acidic and strongly acidic under *T. sericea*. No significant differences were found on soils collected under *T. sericea* and on open habitats (Fig. 2A).

Soil nutrients

Potassium (K) (Fig. 2B), Ca (Fig. 2C), Mg (Fig. 2D) and C (Fig. 3A) content did not show any significant differences among fire treatments and fire treatment*microsite, but there were significant differences amongst microsites (K, $F= 5.81$, $P< 0.01$; Ca, $F= 12.09$, $P< 0.001$; Mg, $F= 5.68$, $P< 0.01$ and C, $F= 5.47$, $P< 0.01$) (see Table 4). Soils under *S. birrea* were richer in K, Ca, Mg and C when compared to *T. sericea* and open habitat microsites. Fire treatment had a significant effect on nitrogen (N %) ($F= 6.94$, $P< 0.001$) but there was no microsite effect ($F= 0.82$, $P= 0.44$) or interaction between fire treatment*microsite ($F= 0.42$, $P= 0.85$) (Table 4). The triennial burn plot had the highest N% content (MS=0.06), when compared to no burn (MS=0.05), biennial burn (MS=0.04) and annual burn (MS=0.03).

Fire treatment and microsite had no effect on P content (F-value= 1.44 and $P= 0.19$). Na content was influenced by fire treatment ($F= 5.2$, $P< 0.01$) and treatment*microsite interaction ($F= 3.73$, $P<0.01$) (Table 4). Only the triennial burn was significantly different from annual and biennial burn plots. No significant differences were found amongst microsites, except for open habitat on triennial burn which was significantly different to all microsites on annual and no burn plots (Fig. 2B). Calcium content was highest on soils under *S. birrea*, low under *T. sericea* and lowest on open habitats on all fire treatments, but there were no significant differences between microsites within fire treatments. Soils under *S. birrea* were significantly different to all microsites on the annual and no burn plot (Fig. 2C). Soils under *S. birrea* on the annual, triennial and no burn treatments were highly enriched with Mg content and fairly rich under *T. sericea* and open habitats (Fig. 2D). No significant differences were found between microsites within fire treatments, except for open habitat to *S. birrea* on the annual burn and *S. birrea* to *T. sericea* and open habitat on the no burn plot (Fig. 2D).

Carbon content was highest under *S. birrea*, low under *T. sericea* and lowest on open habitat. Significant differences were found on microsites within the annual burn plot only (Fig. 3A). Fire treatment*microsite interaction shows that only open habitat on the triennial burn differed significantly from open habitats on the no burn, biennial and annual plots, and *T. sericea* on the biennial and no burn plot when comparing Na content (Fig. 3B). There was no significant effect of fire treatment (F= 0.38, P= 0.76) and fire treatment*microsites (F= 1.35, P= 0.26) on available exchangeable cations. Soils under *S. birrea* had the highest available exchangeable cations (F= 11.88, P< 0.001) (Table 4) as compared to *T. sericea* and open habitats (Fig. 3C).

Total exchangeable cations under *S. birrea* were significantly greater than under *T. sericea* and open habitats. There was no fire treatment effect and fire treatment*sampling site effect on total Na. Total Na content was highest on open habitat (MS= 1.76), low under *T. sericea* (MS= 1.42) and lowest under *S. birrea* (MS= 1.01). Total K and Mg content did not show any response on different fire treatments and microsite (F=1.40, P=0.21, r^2= 0.30) (see Table 4). Microsites had a significant effect on total Ca (F= 21.65, P<0.001), with soils under *S. birrea* having the highest total Ca (MS= 58.88), lower under *T. sericea* (MS= 41.31) and lowest on open habitat (MS= 58.88). Microsites had significant effects on SOM (F= 6.77, P< 0.01) but there were no significant effect of fire treatment (F= 1.57, P= 0.21) or fire treatment*microsite (F= 0.57, P= 0.74) on SOM (Fig. 3D). Neither soil exchangeable cations nor organic matter content showed consistent variation with fire frequency. For both variables, there was an increase from annual burns to the triennial burn, but surprisingly a decrease in the no burn treatment (Table 4).

Table 2. Comparison of soil moisture (g H_2O g^{-1} oven dry soil) content under the canopies of *S. birrea* and *T. sericea* and on the open habitats, on different fire treatments, AUG B1, AUG B2, AUG B3 and NO BURN at different soil depth.

Soil Moisture Table		Soil depth							
		Wet season (April 2005)				Dry season (July 2006)			
Fire Treatment	Microsite	5 cm	15 cm	25 cm	45 cm	5 cm	15 cm	25 cm	45 cm
AUG B1	Open habitat	1.34	1.69	2.03	3.04	0.01	0.02	0.02	0.03
AUG B1	*S. birrea*	3.51	1.98	2.23	4.28	0.02	0.02	0.02	0.03
AUG B1	*T. sericea*	1.89	1.28	1.76	2.38	0.01	0.01	0.02	0.02
AUG B2	Open habitat	1.91	1.88	2.14	2.24	0.02	0.02	0.03	0.04
AUG B2	*S. birrea*	2.77	2.15	2.17	3.45	0.02	0.02	0.03	0.04
AUG B2	*T. sericea*	2.15	1.80	1.87	2.98	0.01	0.02	0.03	0.03
AUG B3	Open habitat	3.82	2.27	2.54	5.52	0.02	0.03	0.04	0.04
AUG B3	*S. birrea*	3.19	2.69	2.87	4.06	0.03	0.03	0.03	0.03
AUG B3	*T. sericea*	2.47	2.72	3.02	5.39	0.02	0.02	0.03	0.03
NO BURN	Open habitat	2.55	2.43	2.86	4.23	0.01	0.02	0.02	0.03
NO BURN	*S. birrea*	4.92	2.68	2.78	3.61	0.03	0.03	0.03	0.05
NO BURN	*T. sericea*	2.76	2.22	2.35	3.89	0.02	0.02	0.02	0.03

Table 3. A Three factor model showing F-value and significance levels (***P < 0.001, **P < 0.01 and *P < 0.05) on the effects of fire treatment, microsites and depth on soil moisture in April 2005 and July 2006. For factors: fire treatments (FT), microsites (SS: under tree and away from trees) and depth (Topsoil: 5 cm, Middle layer 1: 15 cm, Middle layer 2: 25 cm, Deeper soils: 45 cm) on soil moisture.

Properties	**April 2005**	**July 2006**
Whole model	(F= 4. 77, r^2= 0.88***)	F= 12.13, r^2=0.95***)
Fire Treatment (FT)	13.32**	27.59**
Microsite (SS)	4.40*	8.63**
Depth (DE)	21.14***	53.92***
FT X SS	1.54	8.10***
FT X DE	1.05	2.04
SS X DE	1.23	3.84*

Table 4. A Two factor model showing F-values, r-squared and significance levels (***$P < 0.001$, **$P < 0.01$ and *$P < 0.05$) on the effects of fire treatment and canopy sites on soil properties. For factors: fire treatments (FT) and microsites (SS: under tree and away from trees) on soil pH, available exchangeable cations (AEC) (Na, P, K, Ca, Mg) and total exchangeable cations (TEC) (Na %, K %, Ca %, Mg %) and organic matter (SOM). Soils for nutrients analysis were collected at 15 cm depth.

Properties	**F-value**	**R^2**	**Fire treatment (FT)**	**Microsites (SS)**	**FT X SS**
pH	5.74	0.64***	7.15***	12.05***	2.94*
Na	3.70	0.53**	5.20**	1.38	3.73**
K	2.24	0.41	1.42	5.81**	1.47
Ca	2.86	0.47**	0.40	12.09***	1.01
Mg	2.65	0.45*	2.36	5.68**	1.78
AEC	3.00	0.48**	0.38	11.88***	1.35
P	1.44	0.31	2.81	0.08	1.20
N %	2.27	0.41*	6.94***	0.82	0.42
C %	1.72	0.35	0.87	5.47**	0.89
Na %	3.59	0.52**	2.26	10.74***	1.87
K %	1.40	0.30	2.61	0.002	1.26
Ca %	5.22	0.61***	2.27	21.65***	1.22
Mg %	1.86	0.36	2.03	4.17	1.01
TEC	4.78	0.59***	1.76	17.87***	1.93
SOM	1.97	0.38	1.57	6.77**	0.57

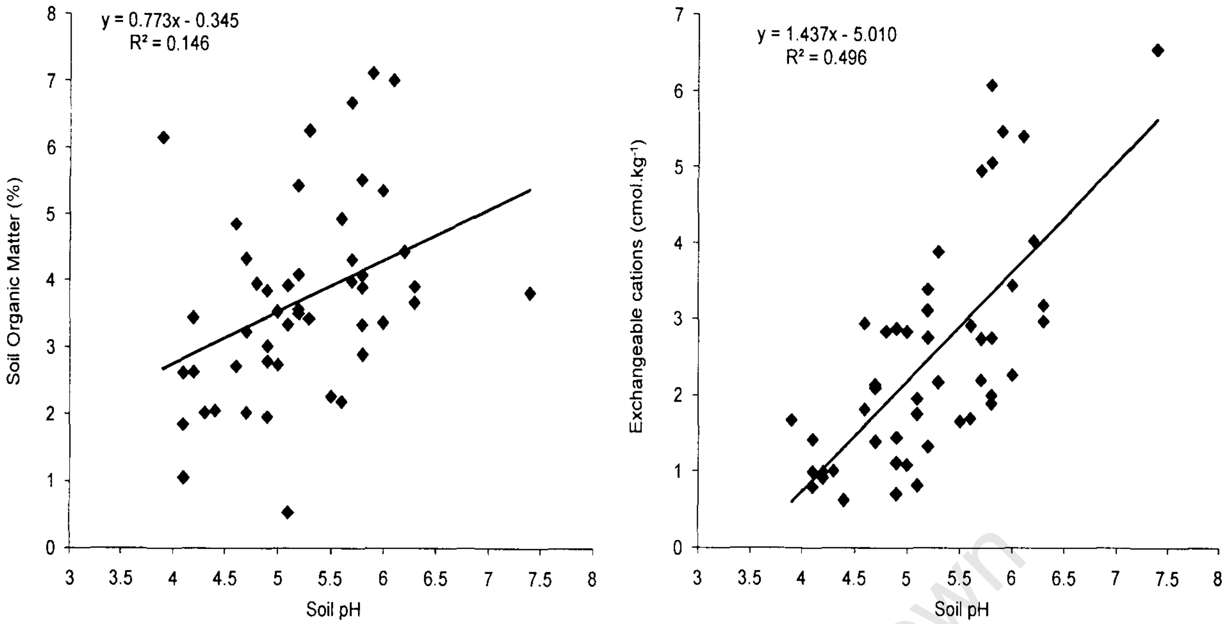

Figure 1. Relationship between soil pH and soil organic matter (r^2= 0.15) and exchangeable cations (r^2= 0.50). Soils for nutrient analysis were collected at 15 cm depth.

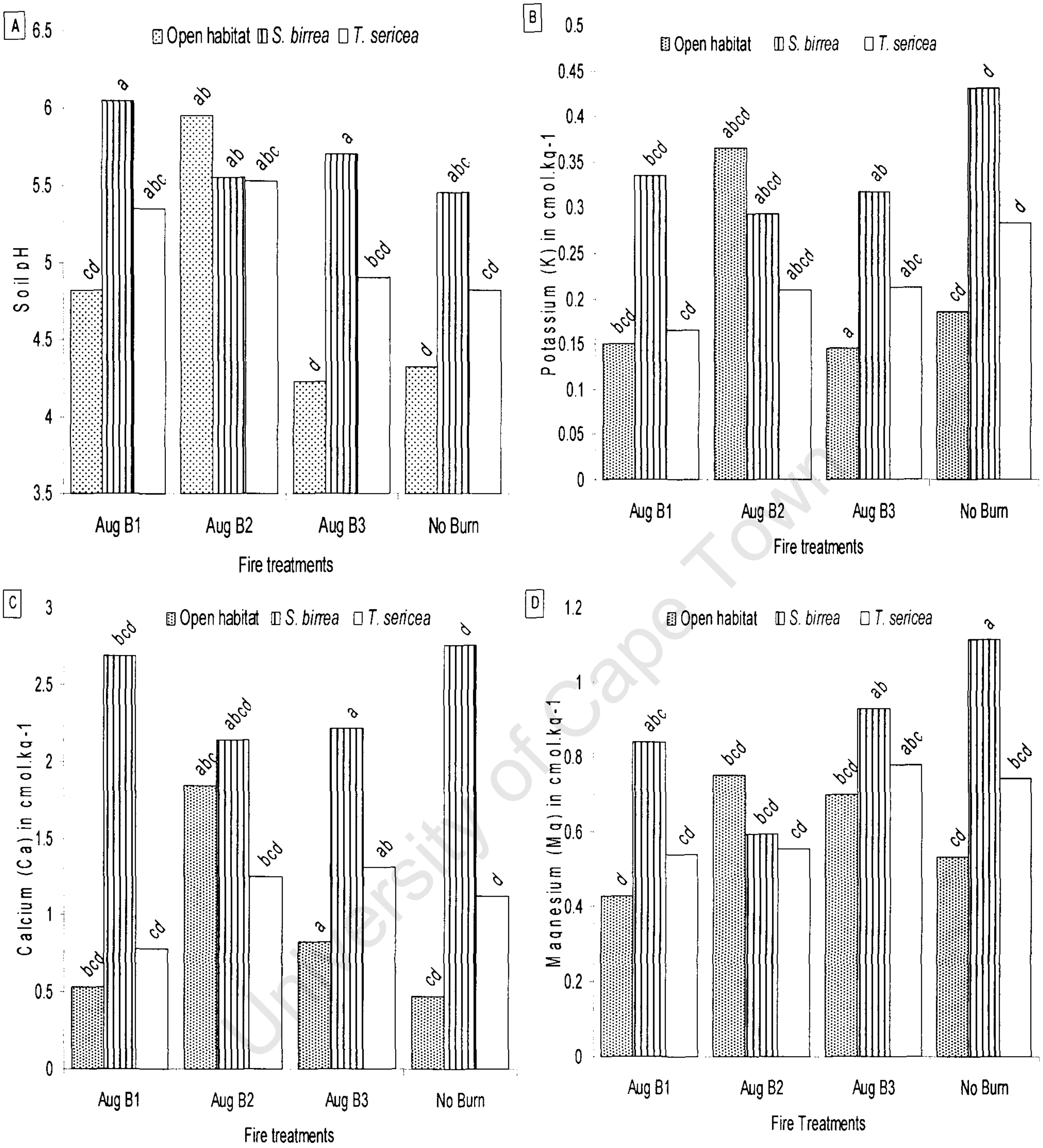

Figure 2. Response of soil pH (A), Potassium (B), Calcium (C) and Magnesium (D) to canopy cover and fire frequency. Microsite levels not connected by the same letter are significantly different. Soils for nutrient analysis were collected at 15 cm depth.

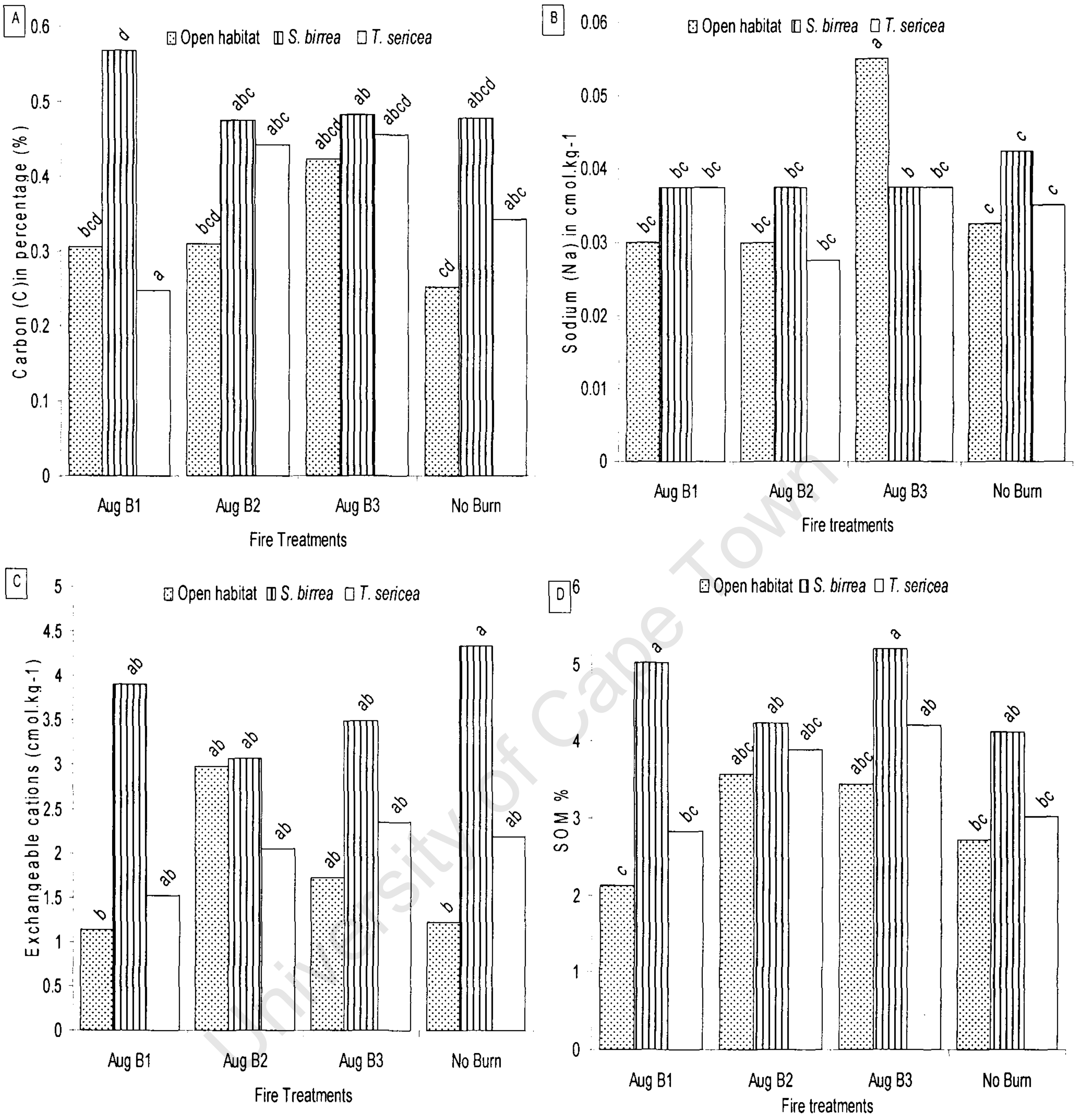

Figure 3. Response of Carbon (A), Sodium (B), Exchangeable cations (C), SOM (D) to canopy cover and fire frequency. Microsite levels not connected by the same letter are significantly different. Soils for nutrient analysis were collected at 15 cm depth.

Discussion

Effects of fire frequency and savanna trees on soil moisture and nutrients.

The effect of savanna trees on soils have been investigated in a wide variety of savanna ecosystems and reported in several studies (Kellman 1979; Belsky *et al.* 1989, Belsky 1994, Ludwig *et al.* 2004). In this study, soil moisture showed significant differences when comparing fire treatment, soil depth and microsite. Top soil layers under *S. birrea* had highest soil moisture when compared to *T. sericea* and open habitats, whereas there was no statistical difference for other soil layers. These results suggest that, either through hydraulic lift (as suggested by Ludwig *et al.* 2003) and/or canopy cover reduces evapotranspiration (Belsky 1994); a canopy of *S. birrea* improves surface soil moisture content. It was not possible to track soil moisture variation across different growth seasons for each microsite in this study and the pattern found here may differ for other seasons. The triennial and no burn plots had the highest soil moisture whereas biennial and annual burn plots had the lowest. There was higher soil moisture across all soil depth in April than in July because April is in the wet season and July is in the middle of the dry season.

I had expected that soil moisture would be higher under tree canopies than in the open at all depths. However there was no consistent pattern of moisture content. Soils under *S. birrea* were not significantly different from open habitats but both were significantly different from *T. sericea* in April. These results contradict the hypothesis that under - tree sites would have higher moisture content than open sites. However, Anderson *et al.* (2001) noted that it has proved difficult to predict the effects of savanna trees on soil moisture. It was clearly shown that deeper soils had higher soil moisture in both seasons. Soil moisture remains an unpredictable factor in savanna ecosystems. My results suggest that both fire treatment, (particularly fire frequency) and microsite are important in determining soil pH, with soils on the frequently burnt plots being moderately acidic. Soils under *S. birrea* were the most neutral with soils under *T. sericea* and the open habitat being strongly acidic resulting in low soil nutrient availability. As expected, soil pH was positively correlated with available and total exchangeable cations so that soils beneath *S. birrea* canopies would have higher nutrient availability than open habitats and *T. sericea* sites. Patterns of soil organic matter and exchangeable cations showed that this was indeed the case with *S. birrea* soils having the highest nutrient content when compared to *T. sericea* and open habitats, whereas there was no significant difference between *T. sericea* and open habitats. Soils under the canopies of savanna trees are often more fertile than soils from the surrounding environment, and though this island of fertility under savanna trees is a well known phenomenon, the mechanism through which the soil is enriched by the trees is still poorly understood (Scholes & Archer 1997). In a study in a more arid savanna replicate of the Kruger Burn Experiments, Shackleton & Scholes (2000) also reported significant differences for soil variables except for SOM and Mg in response to fire treatment but did not analyse canopy effects.

Although the presence of adult savanna trees has been reported to increase soil fertility under the canopies (Kellman 1979, Belsky *et al.* 1989, Weltzin & Coughenour 1990, Belsky 1994, Scholes & Archer 1997, Reich *et al.* 2001, Hudak *et al.* 2003, Ludwig *et al.* 2004 and Caylor *et al.* 2005), my results suggest that the phenomenon is species specific. Marula, *S. birrea*, had enriched soils beneath the canopy but not *T. sericea* relative to open sites. These species differences are useful for testing the influence of shade and other canopy effects, such as perch sites for dispersers, on where forest species colonize a savanna. If forest colonization depends on greater nutrient availability, then forest saplings should be most common under *S. birrea* with fewer under *T. sericea* or open habitats.

In Chapter 3, I reported that species such as *Canthium venosum*, *Diospyros mespiliformis*, *Euclea natalensis*, *Gardenia volkensii*, *Ochna natalatia*, *Xeromphis obovata* and *Zanthoxylum capensis* were largely restricted to the no burn treatment with double to many fold more individuals under *S. birrea* than *T. sericea* or open sites. This is consistent with greater nutrient demand in these forest precursor species. I suggest that enrichment of soils under the canopies is caused by (1) litter fall that releases nutrients to the soil during and after decomposition (2) animals that visit the canopy areas frequently for foraging and for shade, in the process trampling and breaking twigs, and adding urine and faeces to the ground, (3) the leaves and fruits of *S. birrea* are big and palatable, whereas small and unpalatable for *T. sericea,* suggesting that there might be higher nutrient content in leaves and fruit of *S. birrea* than *T. sericea*, (4) large area with a sub-canopy with a low temperature and soil pH may increase microbial biomass and activities that may improve decomposition under the canopies, hence enhancing soil fertility.

In comparison with the canopy effect, especially of *S. birrea*, fire had only a minor effect on most soil nutrients. However the different fire treatments did show an effect on nitrogen, with the triennial burn and no burn having significantly higher N content than the annual burn. Could this mean that high fire frequency reduces nitrogen pools? According to Kauffman *et al.* (1994), Cook (1994) and Ansley *et al.* (2006), fire is reported to increase nitrogen loss through volatilization resulting in less nitrogen becoming available for plant use. Mills & Fey (2004) reported that there was a reduction in tree cover as a result of frequent burning at Kruger so that fire indirectly affects soils by reducing tree cover and hence canopy effects. However, Aranibar *et al.* (2003) and Coetsee (2007) found no consistent effects of fire on nitrogen cycling or N availability to plants in the Pretoriuskop fire treatments.

In conclusion, the effect of trees on soil moisture and nutrient availability is species specific and low fire frequencies favour high pools of Na and N. Canopy effects are larger than fire effects for most soil properties but canopy effects vary greatly between *S. birrea* vs. *T. sericea.* High nutrient and water content under *S. birrea* suggest that this microsite is important in promoting colonization of forest seedlings and might be a preferred site for seedling establishment. The results in this chapter support findings in Chapter 3 that there was high seedling recruitment under the canopies of *S. birrea* and suggest that nutrients make a difference for forest colonization.

Chapter 5. Effects of water, nutrients and grass on *T. sericea* seedling growth over the dry season.

Abstract

Competition for resources between established grass species and tree seedlings is high. However seedlings may avoid competition by continuing to grow in the dry season when grasses are dormant. We studied the establishment and growth of *Terminalia sericea* seedlings in the dry season in a mesic savanna in Pretoriuskop under different levels of resource availability. To examine the effects of water and nutrients on *T. sericea* growth, competition for resources between *T. sericea* and grass species and effects of grass on *T. sericea* seedling growth we conducted an experiment under field conditions with manipulation of water and addition of nitrogen and phosphorous.

We tested the hypothesis that (i) *T. sericea* growth will be highly influenced by the addition of water and nutrients in the absence of grasses, (ii) grass will compete for resources with *T. sericea* seedlings, and (iii) high belowground biomass of grasses will reduce seedling growth rate by limiting available resources.

Grass biomass increased with the addition of water and nutrients. *T. sericea* seedlings did not show significant responses to the addition of water and nutrients in the presence and absence of grass. Results suggest that the initial height (May) was the most important predictor of final (September) seedling height, followed by the addition of nutrients. The initial stem diameter was the most important predictor of final (September) stem diameter followed by grass layer. Since there were negligible treatment effects on seedling growth, we conclude that seedlings do not grow during the dry season but use the little resources available to maintain their daily photosynthetic activities.

Introduction

A savanna is a landscape with a continuous grass layer mixed with herbs, and a discontinuous tree layer of varying density, in climates with a distinct dry and wet season (Scholes & Archer 1997). Savannas are targets of regular fires. Most savannas experience fire at least twice a decade and annual fires are common in many savanna types. These fires either kill or suppress tree seedlings, thus preventing the establishment of a continuous tree canopy which would prevent further grass growth (Hoffmann 1996).

Despite their recognized importance to human welfare and economy, the origin, nature and dynamics of savannas are poorly understood (Scholes & Archer 1997, Sankaran *et al.* 2004). Mechanisms permitting trees and grasses to coexist without one displacing the other, and factors determining the ratios of woody, herbaceous and grass cover across different savanna types remain unclear (Scholes & Archer 1997). Savanna structure is a result of interacting factors including fire, competition, climate and grazing that operate independently and simultaneously at various spatial and temporal scales (Scholes & Archer 1997).

The co-existence of the two life forms, grasses and trees has raised the question, how do tree and grass co-exist in this system without one dominating the other? Do grasses and trees compete for water, nutrients or light or do they partition resources reducing competition? Two contrasting theories on what drives co-dominance of tree and grasses in savanna ecosystem have been proposed. The Walter hypothesis proposes a niche separation model, where trees and grasses coexist by accessing resource from different soil depths, trees using deeper soils and grasses using shallower layers, thereby reducing resource competition. In this model, coexistence results because of spatial/temporal niche differences in resource use between trees and grasses (Walter 1971, Walker & Noy-Meir 1982). In contrast Higgins *et al.* (2000) suggest that problems for savanna trees are demographic not competitive. Their demographic bottleneck model suggests that trees and grasses persist in savannas because of climatic variability and/or disturbance such as fire and herbivory which limit successful recruitment of tree seedlings, and prevent trees from dominance of savannas. In contrast to the demographic bottleneck model, the root niche separation model does not consider juvenile stages of trees. However, since both tree seedlings and grasses use the same soil horizon, who is the better competitor and for which resources?

Tree seedlings growing in savanna regions are exposed to complex and dynamic interactions among climate, topography, soils, geomorphology, herbivory and fire (Walker 1987, Scholes & Archer 1997). Seedling recruitment, survival and growth is a critical life stage for woody plants during which they compete with grasses for resources such as light, space, water and nutrients (Scholes & Archer 1997). Competition in plant communities implies that the supply of light, water or nutrients to plants is reduced by the presence of neighbouring plants (Tilman 1987). The trade-off hypothesis assumes that biomass allocation to root systems cannot be simultaneously allocated to tissues used to acquire light (Tilman 1988). Having the mechanisms to acquire resources and survive the juvenile stage would be an important attribute of a savanna tree.

Thus, grasses may regulate woody plant recruitment directly through competition for water and nutrients or indirectly by increasing fuel load to influence fire severity (Scholes & Archer 1997). Schmidt & Stubbendieck (1993) have shown that, although survival of an evergreen tree (*Juniperus virgianiana*) was highest in grazed pastures (57%), survival of seedlings in pastures that had not been grazed for >50 years was still 40 %. In South African savannas, O'Connor (1995) showed that reduction in grass competition did little to affect seedling establishment. Therefore even though competition with grasses may potentially reduce establishment, growth and survival of woody seedlings, the magnitude of the effect may be too small to result in complete exclusion of tree seedlings.

In contrast, Florentine & Fox (2003) showed that neighboring grasses increased mortality rate of *Eucalyptus victrix* seedling and reduced resources necessary for seedling growth. Competition from grasses for moisture is a major cause of the failure of *Eucalyptus* *camaldulensis* Dehnh. seedling establishment (Dexter *et al.* 1986) and stunted growth of valley oak seedlings (Danielsen & Halvorson 1991). In some savannas, seedling establishment appears to be episodic and dependent on rainfall. Kraaij & Ward (2006) noted that an above-average rainfall year may be adequate for seedlings to establish.

Though the Walter hypothesis emphasises spatial separation of grass and tree roots in promoting niche differentiation, Scholes and Archer (1997) suggested that temporal differences in the phenology of growth may also lead to niche differentiation. They noted that savanna trees often leaf out before the rains and maintain leaves longer into the dry season than grasses. Thus, though grasses may out-compete trees for resources during their growing season, trees would have sole access to resources when grasses are dormant during the dry season. This temporal niche differentiation hypothesis has received little attention. It might account for establishment and growth of tree seedlings when woody plants are at their most vulnerable stage in competing with grasses. For example, tree seedlings that continue growing into the dry season, after grasses have dried out, might have greater establishment success and higher initial growth rates because of their longer growing season.

To test the potential importance of the temporal niche for tree seedling recruitment, I established a competition experiment in which I tested the effects of adding resources, with or without grasses, during the dry season. In this chapter, I report an investigation of competition between *T. sericea* seedlings and grasses at different supply of water and nutrients using a field experiment conducted over the dry season. Treatments included a complete factorial combination of water, nutrients and grass addition with two levels for each factor (water added/not added, nutrients added/not added, and grasses present/removed). The field experiment was designed to test the following hypothesis for *T. sericea*: (1) seedling growth would be enhanced by addition of water and nutrients during the dry season, (2) the removal of grasses would reduce competition for water and nutrients, and tree seedlings would grow much better in the absence of grasses. This experiment also tests whether tree seedlings benefit from a temporal niche, i.e. whether tree seedlings continue to grow over the dry season when grasses are dormant.

Materials and Methods

Seedling transplants

The study was conducted at Pretoriuskop Rest Camp, in the southwestern region of the KNP. During the first growing season, December 2004-December 2005, four species were selected for the study: *Terminalia sericea, Sclerocarya birrea, Ziziphus mucronata* and *Diospyros mespiliformis*. *T. sericea* and *S. birrea* are the most common savanna tree species found around in the study area. *Z. mucronata* and *D. mespiliformis* are mostly restricted in their distribution; they mainly occur along river banks and in forest/thicket stands (Schmidt *et al.* 2002). Sixty-four seedlings of each species were used in the experiment. Seedlings were transplanted from the field to the experimental site in the rest camp on December 2004. Four different seedlings were planted in 1 m^2 quadrat. The monitoring of seedlings response to treatment effects started from the first week of transplantation until May 2005. During the first growing season, seedling mortality was very high and no data could be used to answer the experimental questions. During the second growing season, January-October 2006, *Terminalia sericea* was chosen as the study species, because it was the only species that survived the first experiment and because it is the dominant savanna tree species, particularly in Pretoriuskop. Transplants were conducted in April 2006.

Treatments

A fully factorial experimental design was used with two levels of each treatment; water, nutrients and grass giving a total of eight treatments (Table 1). Each treatment combination had eight replicates to provide a total of 64 experimental quadrats. The 1 m^2 quadrats were constructed and treatments were applied to the entire area. The site was fenced to exclude grazing and browsing vertebrates. To reduce the effect of competition between grasses and seedlings, the grass layer was removed/cleared using spades. Thirty-two quadrats were cleared of grass. Water and nutrients were manipulated to determine the effects of water and nutrients on seedling growth during the dry season. The amount of water to be added was determined using the long term monthly mean rainfall data (1960-2006) (Table 2). Monthly mean rainfall differed across seasons from wet (Dec-Feb) to dry (Jun-Aug) seasons.

The control treatment (No water addition) plots received natural rain, while water addition treatments received natural rain supplemented with an amount equivalent to mean monthly rainfall for that period (Table 3).Water addition treatments were made at two day intervals. Fertilizers were added at the beginning of the experiment, 30 g/meter square ($g.m^{-2}$) of each of ammonium nitrate (NH_4NO_3) and super phosphate (Ca $(H_2PO_4)_2$. NH_4NO_3 is a high-nitrogen fertilizer and Ca $(H_2PO_4)_2$ is a high phosphate fertilizer. Seedling growth measurements were taken by measuring the stem diameter and height and grass biomass was determined using a Disk Pasture Meter reader on a monthly basis. DPM readings were converted to total biomass in $g.m^{-2}$ using the equation:

Total Biomass = 12.33+26.12*DPM value, and was expressed as grams per square meter ($g.m^{-2}$).

Seedling growth (height) and survival was measured monthly, and growth rate was calculated by measuring initial height and final over the period of the experiment I used ANCOVA to analyze seedling growth under all treatments using initial seedling dimensions as the covariate. Tukey HSD tests were used for comparisons of means. All statistical tests were performed using Jump 5.0.1. Tests were considered to be statistically significant when $p \leq 0.05$.

Results

Treatment codes are listed in Table 1. Seedling survival was highest on G, N, NW and W treatments with all 8 seedlings surviving, whereas –GWN had 6 survivors and GW, GN and GWN had 7 survivors each. Despite irrigation, nutrient addition, and grass removal, there was little growth of *T. sericea* seedlings over the experimental period, effectively the dry season from April to October and November (Table 3). Grass biomass decreased mid-dry season and picked up late September after the first rains (Fig. 1). Seedling growth showed no response to treatment effect for seedling height measured in October, the end of the dry season (Fig. 2a), and seedling stem diameter similarly showed no response to treatment as shown in Fig. 2b. In October, seedling height was highly dependent on initial (May) height ($p<0.0001$) and grass layer ($p<0.0001$) (Table 4), and the stem diameter was determined by initial (May) stem diameter ($p<0.0001$) and grass ($p<0.0001$) (Table 5).

No interactive effects of treatments on October height and stem diameter were found when testing all treatments. In November, after the start of the rains, seedling height (Fig. 2a) and stem diameter (Fig. 2b) showed no response to treatment. Initial height strongly influenced seedling height ($p<0.0001$, Table 4) and stem diameter was highly influenced by initial stem diameter ($p<0.0001$, Table 5). An interactive role between grass and water contributed to p-level of 0.01 on seedling stem diameter (Table 4). Seedlings on the plots without grass did well in October and November with water addition increasing the seedling growth, whereas nutrient addition did not show any influential role (Fig. 3).

Table 1. Summary of the factorial experimental design of all treatments and treatment codes, water added/not added, nutrients added/not added and grass present/removed in the field experiment.

Treatments	G+ N+ W+	G+ N- W+	G+ N+ W-	G+ N- W-	G- N+ W+	G- N- W+	G- N+ W-	G- N- W-
Treatment Code	GWN	GW	GN	G	NW	W	N	-GWN

Table 2. Summary of the irrigation treatment adding water equivalent to the long term monthly mean rainfall to the normal monthly rainfall that fell during the period of the study (May-November 2006).

	May	Jun	Jul	Aug	Sep	Oct	Nov
Long term monthly mean rainfall (mm)	18	9.5	9.5	11.4	24.8	53	96.6
No Water (Normal rainfall (mm)	18	9.5	9.5	11.4	24.8	53	96.6
Irrigation Treatment (Normal rainfall + Long term Monthly mean) (mm)	36	19	19	22.8	49.6	106	193.2

Table 3. Summary of means ± Std errors of treatments for May, October and November seedling stem diameter (cm) and height (cm).

	May stem diameter	May stem height	October stem diameter	October stem height	November stem diameter	November stem height
Level	Mean± Std errors	Mean± Std errors	Mean± Std errors	Mean± Std errors	Mean± Std errors	Mean± Std errors
-GWN	0.42±0.09	18.33±2.69	0.48±0.06	19.17±2.9	0.60±0.08	25.17±4.23
G	0.30±0.08	12.29±2.49	0.30±0.05	12.43±2.52	0.29±0.08	16.14±3.91
GN	0.38±0.09	15.83±2.69	0.28±0.05	16.50±2.69	0.33±0.08	18.17±4.23
GW	0.30±0.09	20.00±2.69	0.33±0.05	20.33±2.52	0.47±0.08	26.17±4.23
GWN	0.37±0.08	17.86±2.49	0.33±0.05	17.86±2.69	0.49±0.08	24.00±3.91
N	0.41±0.08	17.50±2.33	0.51±0.05	19.88±2.52	0.49±0.07	24.25±3.66
NW	0.56±0.08	20.88±2.33	0.63±0.05	23.13±2.52	0.60±0.07	27.50±3.66
W	0.60±0.08	19.38±2.33	0.60±0.05	23.25±2.52	0.54±0.07	27.13±3.66

Table 4. ANOVA of the effects of initial (May) height, grass, water and nutrients on seedling height of *T. sericea* in October and November 2006.

		October Height			November Height		
Source	DF	SS	F	P	SS	F	P
May Height(cm)	1	1958.79	259.55	***<.0001***	2925.46	61.81	***<.0001***
Grass	1	59.67	7.90	***0.00***	47.59	1.00	0.32
Water	1	6.55	0.86	0.35	14.65	0.30	0.58
Nutrients	1	0.02	0.00	0.95	8.47	0.17	0.67
Grass*Water	1	8.89	1.17	0.28	16.05	0.33	0.56
Grass*Nutrients	1	0.07	0.01	0.92	0.19	0.00	0.94
Water*Nutrients	1	14.59	1.93	0.17	0.99	0.02	0.88
Grass*Water*Nutrients	1	3.58	0.47	0.49	13.60	0.28	0.59

Table 5. ANOVA of the effects of initial (May) stem diameter, grass, water and nutrients on seedling stem diameter of *T. sericea* in October and November 2006.

		October Stem Diameter			November Stem Diameter		
Source	DF	SS	F	P	SS	F	P
May Stem diam(cm)	1	0.45	37.56	***<.0001***	0.75	28.03	***<.0001***
Grass	1	0.34	28.71	***<.0001***	0.05	2.14	0.14
Water	1	0.02	1.77	0.18	0.03	1.15	0.28
Nutrients	1	0.00	0.02	0.87	0.00	0.07	0.78
grass*water	1	0.00	0.00	0.95	0.19	7.18	***0.01***
grass*nutrients	1	0.02	1.90	0.17	0.00	0.00	0.99
Water*nutrients	1	0.00	0.05	0.81	0.02	0.95	0.33
grass*water*nutrients	1	0.00	0.00	0.95	0.04	1.48	0.22

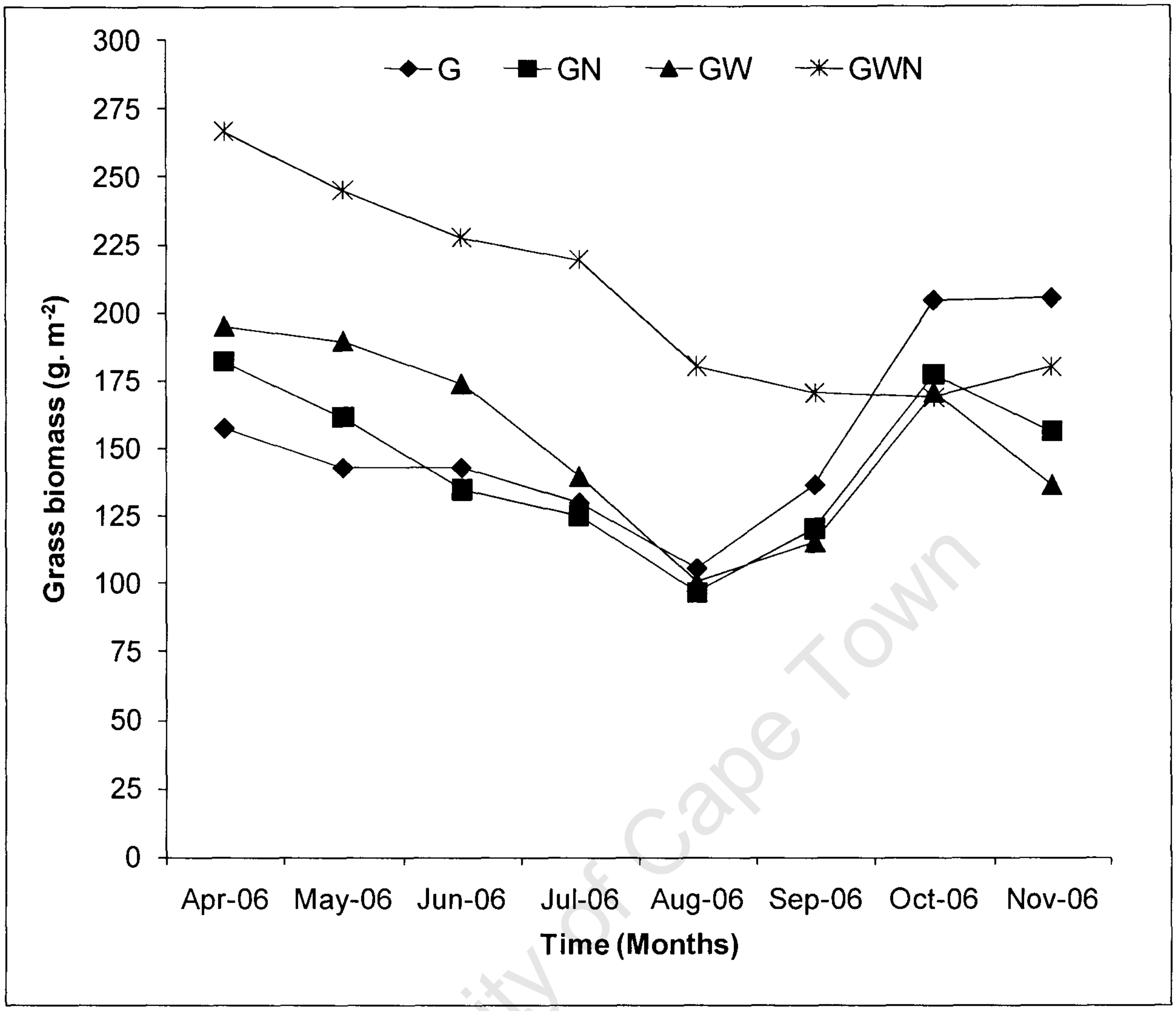

Figure 1. Total grass biomass measured during the period of the experiment on different plot treatments, from April 2006 to November 2006.

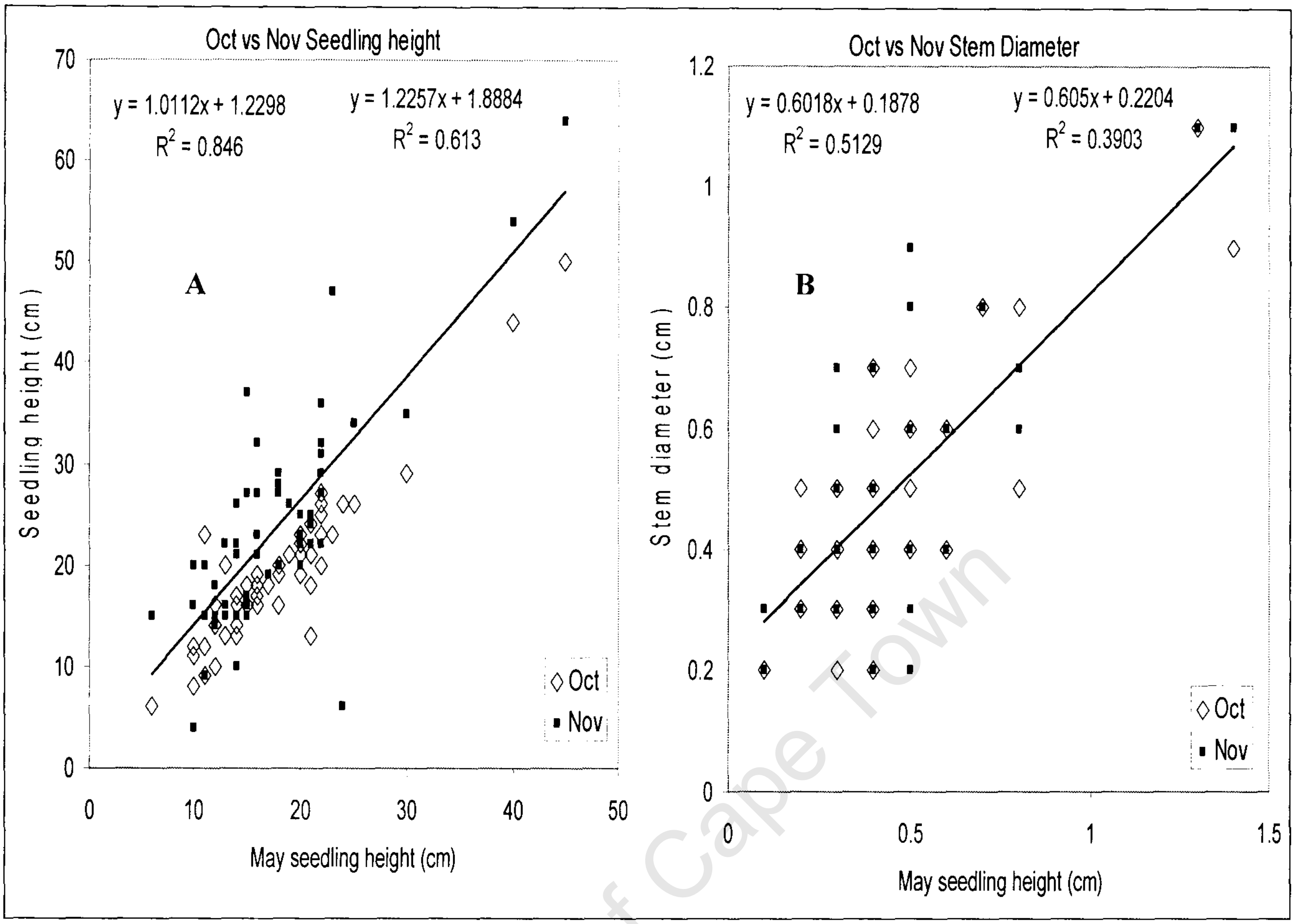

Figure 2. Growth indicated by (A) Seedling height and B) Stem diameter (B), in October and November 2006 relative to initial size measured in May 2006.

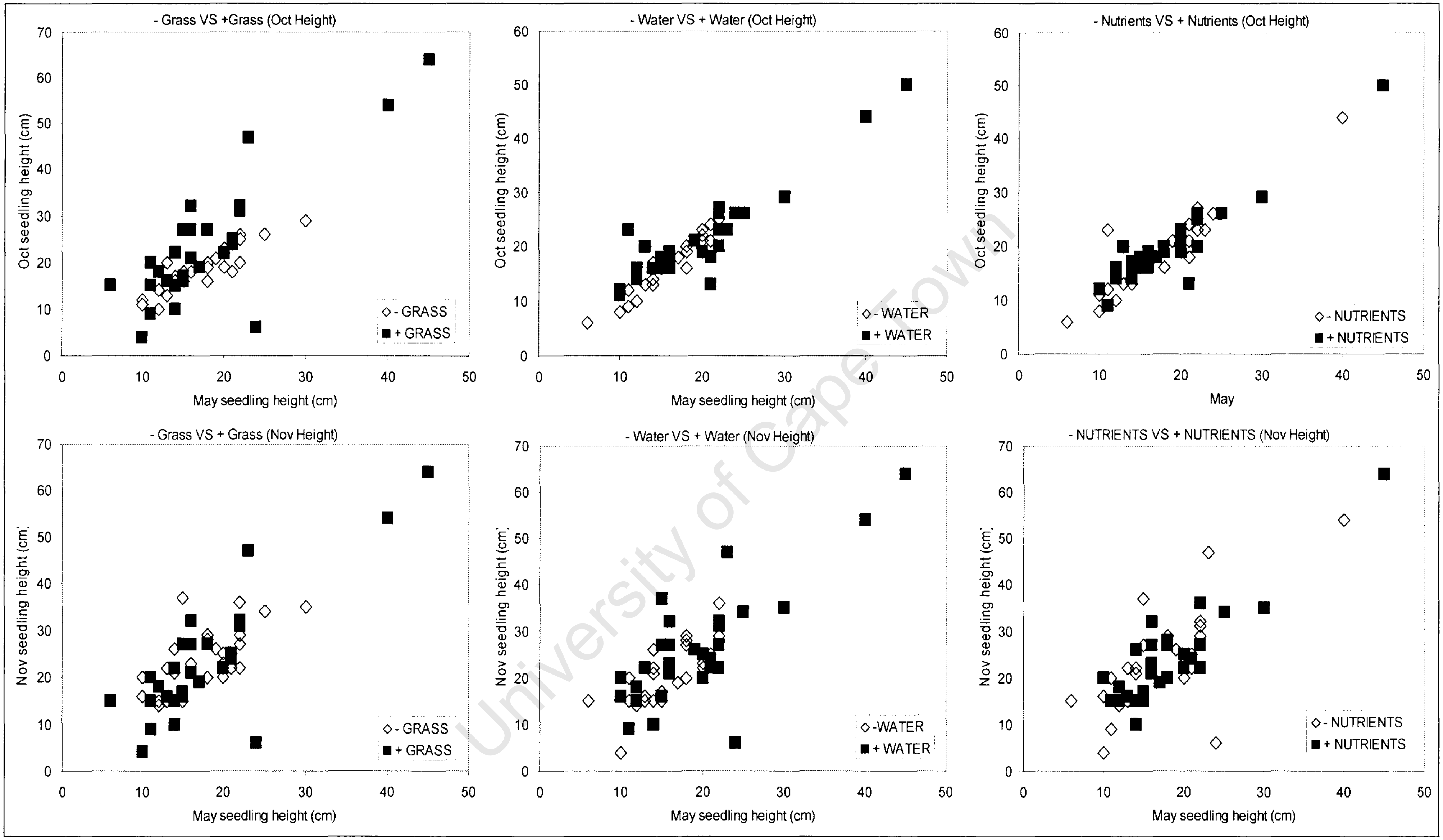

Figure 3. The effect of grass, water, nutrients on seedling growth in October and November 2006 relative to the initial size measured in May 2006.

Discussion

This experimental design tested the effects of water and nutrient addition on growth and survival of tree seedlings in competition with grass. The experiment was conducted over the dry season when grasses are generally dormant but tree seedlings may continue to grow. The "temporal niche", where woody plants retain foliage in the dry season after grasses become dormant, has been suggested as an additional mechanism reducing tree/grass competition (Scholes & Archer 1997). It could be important in the early seedling establishment phases when trees are most vulnerable to direct competition from grasses since their roots completely overlap. This experiment found very little evidence that *T. sericea* saplings utilize the dry season for growth while grasses are dormant. Reported seedling mortality on – GWN, GW, GN, GWN treatments could be a result of transplantation and adaptation to a new environment under different conditions. Treatment effects had insignificant effects on seedling growth. Growth, both of height and stem diameters, was negligible in the period from April to October and November. Thus it would seem that seedlings of this species do not use the temporal niche of the dry season to grow and establish while grasses are dormant. Seedlings began to show significant growth only in November, after the rains had started and after grasses had grown new leaves.

The initial height and stem diameter of seedlings taken during transplantation appears to be a major factor determining seedling growth. Although there was a factorial treatment of water, nutrient addition and grass removal, initial seedling and stem diameter were by far the most statistically significant determinants of both October and November seedling dimensions. I expected seedlings to grow well when watered and fertilized, but no treatment effect was observed. Even if watered, no seedlings growth was recorded during the dry season. However, seedlings lost only 25% of their leaves and grasses were 75% dormant on irrigation plots, grasses dried out on the grass plots without water and nutrient addition. Thus, for this species, there is no evidence that tree seedlings escape competition with grasses by continuing to grow into the dry season when grasses are largely dormant.

Chapter 6. Response of savanna and forest seedlings to resource supply and competition with grasses.

Abstract

I hypothesized that both savanna and forest seedling growth and survival would be limited by competition with grasses for moisture and nutrients, but that savanna seedlings would perform better than forest seedlings in competition with grasses. I conducted a field experiment (1) to compare savanna vs. forest seedling growth rate and survival across treatments manipulating water, nutrients and competition with grass. Seedling survival was highest for *Terminalia sericea* (savanna, 90 %), high for *Kiggelaria africana* (forest, 75 %), and low for *Acacia gerrardii* (savanna, 65 %) and lowest for *Ekebergia capensis* (forest, 30 %).

Grass presence caused low growth and high mortality of *E. capensis* and *A. gerrardii* seedlings, stunted growth and low growth rate for *K. africana* and *T. sericea* seedlings. Addition of nutrients increased the survival and growth rate of all seedlings with or without grasses present. Addition of nutrients and water not only improved the competitive ability of seedlings, but also promoted grass productivity. Grass removal and nutrient addition increased seedling survival of savanna seedlings. There were no differences in survival rate of *K. africana* seedlings with or without grass.

Seedling establishment, growth and survival in a savanna environment were limited by competition with grass, primarily for nutrients. The process of forest invasion may therefore be limited by low nutrients and low water availability and competition with grasses, but promoted by high resource availability in the *Terminalia* savannas of Kruger Park. In higher rainfall regions, forest invasion would be taking place with minimum nutrient requirement for seedling establishment.

Introduction

Tropical savannas and forest ecosystems are characterized by distinct tree communities with most species occurring almost exclusively in only one of the two environments (Hoffmann *et al.* 2004). The distribution of these two vegetation types is often associated with soil properties, fire, hydrology, climate and herbivory (Furley 1992). Forest ecosystems have an overlapping canopy cover and they often occur on sites of greater nutrient and water availability (Furley 1992), whereas savanna ecosystems consist of a continuous grass cover and scattered trees, coupled with strong alternation of wet and dry seasons in tropical regions (Scholes & Archer 1997). The boundary of savanna and forest is characterized by a transition not only in the tree density, but also in species composition (Hoffmann *et al.* 2005).

Over the last decades, the increase in tree density in savannas has become a major concern for farmers and for conservation scientists. Tree biomass increase produces dense woodlands and/or closed forest/thickets. A major problem for woody seedlings in grasslands and savanna is how to escape injury from frequent fires, grazing and intense competition for resources with grasses. Though savanna and forest species differ in fire tolerance, allocation patterns and requirements for seedling establishment (Hoffmann *et al.* 2004), establishment and survival of tree seedlings in savannas is often low because they are exposed to complex and dynamic interactions among climate, fire, soils and herbivory (Walker 1987, Scholes & Archer 1997). Seedling recruitment is periodical, occurring when there is enough moisture availability and minimal competition with grasses for water and nutrients (Scholes & Archer 1997).

Water has been long recognized as a key resource affecting plant distribution and performance in savannas (Scholes & Archer 1997), while nutrient availability has been reported to determine the distribution of savanna and forest ecosystems, yet little is known about differences in nutrient and water requirements of both savanna and forest species (Hoffmann *et al.* 2005). Both savanna and forest seedlings compete with grasses for resources. According to Tilman (1988), competition in plant communities implies that the supply of light, water and/or nutrients to plants is reduced by the presence of neighbouring plants. Tree seedlings compete with grasses for water and nutrients, and the outcome depends on effectiveness of both functional groups.

Grasses have been reported to limit seedling survival (Noble 1984) causing major seedling failure (Dexter *et al.* 1986, Florentine & Fox 2003). Florentine & Fox (2003) reported that neighboring grasses increased mortality rate of *Eucalyptus victrix* seedlings and reduced resources necessary for seedling growth. Competition from grasses for moisture is a major cause in the failure of *Eucalyptus camaldulensis* Dehnh. seedling establishment (Dexter *et al.* 1986) and stunted growth of valley oak seedlings (Danielsen & Halvorson 1991). Though grasses have been reported to reduce seedling emergence, growth and survival, the competitive reduction is not large enough to cause complete exclusion (Scholes & Archer 1997). Studies examining competition between grass and tree seedlings demonstrate that recruitment success is influenced by the ability to survive and grow in direct competition with grasses (Davis *et al.* 1999) and depends on effective competition with grasses (Noble 1984, Florentine & Fox 2003).

Previous chapters have shown that forest species appear under the canopies of large savanna trees through the process of facilitation forming forest patches and/or thickets. The process whereby forest species invade savannas is not well understood. In some savannas, fire exclusion leads to rapid forest invasion (Swaine *et al.* 1992; Bond *et al.* 2005) whereas in others the process is slow with only a few scattered forest trees even after one or two decades of fire exclusion (Bowman & Fensham 1991). Both the occurrence, and the rate, of forest colonization in the absence of fire may be limited by low soil moisture and low nutrient levels, high temperature and high light intensity. It is far from clear what limits forest species in savanna environments, and how forest species differ from savanna trees in terms of seedling establishment requirements.

In this study, I compared savanna and forest seedling responses to different resource supply levels and to competition with grasses. I compared the growth and survival of savanna and forest seedlings to contrasting water and nutrient levels with and without grass competition. I hypothesized that savanna and forest seedlings would differ in their ability to establish and survive in competitive environments. Under conditions of high resource supply with grass competition, increased grass productivity might result in suppression of tree seedlings; however seedlings might survive regardless of increased grass productivity. In the absence of grass, competition would be minimal and both savanna and forest seedling would grow and survive better. Light is a limiting resource in forests but not in savannas, whereas nutrients and water may be limiting resources in savannas.

Materials and Methods

Seedling transplants

The study was conducted at Pretoriuskop Rest Camp, in the southwestern region of the KNP. During the December 2006 growing season, four species were transplanted to the field for the study: *Terminalia sericea, Ekebergia capensis, Kiggelaria africana* and *Acacia gerrardii. T. sericea* and *A. gerrardii* are typical savanna trees found in the study area. *E. capensis* and *K. africana* are forest trees (Schmidt *et al.* 2002).

Treatments

A fully factorial experimental design was used with two levels of each treatment, water (water addition and no water addition), nutrients (nutrient addition and no nutrient addition) and grass (grass present and grass removed) (Table 1). Each treatment combination had eight replicates to provide a total of 64 experimental quadrats. The 1 m^2 quadrats were constructed and treatments were applied to the entire area. The site was fenced to exclude grazing and browsing vertebrates. To reduce the effect of competition between grasses and seedlings, the grass layer was removed using spades. Seedling growth rate and survival was determined at monthly intervals.

Water and nutrients were manipulated to determine their effect on seedling growth during the wet season. Monthly mean rainfall differed across seasons from wet (Dec-Feb) to dry (Jun-Aug) seasons. The control treatment (No water addition) plots received natural rain, while water addition treatments received natural rain supplemented with an amount equivalent to mean monthly rainfall for that period (Table 2). Water addition treatments were irrigated at two day intervals. Fertilizers were added once at the beginning of the experiment, 40 grams per square meter ($g.m^{-2}$) of each of ammonium nitrate (NH_4NO_3) and super phosphate ($Ca\ (H_2PO_4)_2$). NH_4NO_3 is a high nitrogen fertilizer and $Ca\ (H_2PO_4)_2$ is a high phosphate fertilizer. Seedling growth measurements were taken by measuring the stem diameter and height. Grass biomass was determined using a Disk Pasture Meter read on a monthly basis and converted to above-ground dry biomass using the equation:

Total Biomass = 12.33 + 26.12*DPM Value, expressed as grams per square meter ($g.m^{-2}$).

I used ANCOVA to analyze seedling growth under all treatments, using initial seedling size as covariate. Tukey HSD and Post hoc tests were used for comparisons of means between seedlings and treatments. All statistical tests were performed using STATISTICA 7 and Jump 5.0.1 and all factors were considered to be significant at $p \leq 0.05$.

Results

Each seedling species was examined under different treatments for the period of four months (December 2006 to April 2007). Seedling mortality and growth was recorded during this period. Grass presence reduced stem diameter growth of *T. sericea* dramatically, caused high mortality to *E.*

capensis seedlings and stunted growth of both *K. africana* and *A. gerrardii* seedlings. Seedling survival was highest for *T. sericea* (90 %), high for *K. africana* (75 %), lower for *A. gerrardii* (65 %) and lowest for *E. capensis* (30 %) (Fig. 1). The presence of grass in the control treatment led to a complete exclusion of *E. capensis* seedlings, and caused high mortality of *A. gerrardii*. Seedling survival for *K. africana* and *T. sericea* was much less sensitive to the presence of grasses. The addition of nutrients increased the survival rate of *K. africana*, *A. gerrardii* and *T. sericea*.

Nutrient addition together with grass reduced survival rate compared to without grasses for savanna seedlings, *A. gerrardii* and *T. sericea*. Nutrient addition nullified the grass effects on *E. capensis* seedling survival which showed no difference between grass present or grass removed. The addition of water increased the survival rate of *T. sericea* seedlings in the absence of grass. Water addition in the grass removal treatment caused high mortality rate of *E. capensis* and *A. gerrardii* seedlings. Addition of water and nutrients together increased the survival rate of all seedlings, with forest species *K. africana* and *E. capensis* and a savanna species *T. sericea* showing better survival rates on grass removed treatments. Water and nutrient addition increased the survival rate of *A. gerrardii* seedlings with the grass treatment having the highest seedling survival compared to no grass treatment (Fig. 2).

Forest and savanna seedling growth was influenced by nutrients, grass, initial stem height, water* grass treatment and nutrient*grass treatment. The seedling height of *K. africana* seedlings was highly influenced by nutrient addition ($P<0.001$), water*grass ($P<0.01$), nutrients*grass ($P=0.04$) (Table 3). No treatment response was observed when examining the stem diameter (Table 4). *T. sericea* seedling height responded strongly to nutrient addition ($P<0.001$) and initial stem height ($P<0.0001$) (Table 3); and the stem diameter was highly influenced by initial stem diameter ($P<0.0001$) and grass treatment ($P=0.001$) (Table 4). *A. gerrardii* seedling height was significantly influenced by initial stem height ($P<0.01$) and grass treatment ($P=0.05$) (Table 3), whereas the stem diameter was influenced by initial stem diameter ($P=0.03$) and nutrients*grass treatment ($P<0.01$) (Table 4). There were too few surviving seedlings of *E. capensis* to perform statistical analysis of treatment effects on size and growth.

Grass biomass was strongly influenced by the addition of nutrients and water and also varied through the growing season. The addition of nutrients and water increased grass biomass significantly, with the water and nutrient addition treatment having 341.8 g.m^{-2}, water treatment with 243.6 g.m^{-2}, nutrient treatment with 238.6 g.m^{-2} and the control with grass only having the lowest grass biomass of 181.6 g.m^{-2}. Mean grass biomass was highest in December 2006 (303 g.m^{-2}), declining in January 2007 (265 g.m^{-2}), February 2007 (229.6 g.m^{-2}), March 2007 (195 g.m^{-2}) and lowest in April 2007 with 179.6 g.m^{-2} (Fig. 3).

Seedling height growth was strongly suppressed by grasses in the control treatment for *T. sericea*, a savanna species and *K. africana*, a forest species. *A. gerrardii*, a nitrogen fixing legume, showed much less reduction in growth with vs. without grass. The addition of nutrients strongly promoted growth in all three species, *K. africana*, *T. sericea* and *A. gerrardii*, effectively removing the competitive effect of grass which had no significant effect relative to grass removals for this treatment. The watering treatment suppressed growth of *K. africana*, *T. sericea* and *A. gerrardii*, relative to nutrient addition treatments. Reduced growth was not due to increased grass competition because growth was similarly reduced by irrigating in grass removal treatments. Addition of both water and nutrients promoted growth for *K. africana*, *T. sericea* and *A. gerrardii* seedlings, but there was no significant difference from the nutrient addition treatment. Thus nutrient availability seems to be the main constraint on seedling growth and not water. Increased nutrient supply effectively removed the effects of grass competition (Fig. 4).

The stem diameter growth of all seedlings was highly influenced by nutrient addition in the absence of grass (Fig. 5). Addition of nutrients showed grass competitive effects on all seedlings.

Addition of water increased the stem diameter growth of *T. sericea* greatly; the same cannot be said for *K. africana* and *A. gerrardii*. Water and nutrient addition together, increased the stem diameter growth of savanna seedlings, *A. gerrardii* and *T. sericea* than forest seedlings *K. africana* and *E. capensis*. Grass removal treatments improved survival and stem diameter growth of *T. sericea* greatly, with grass presence causing slow growth in all treatments (Fig. 5).

Table 1. Summary of the factorial experimental design of all treatments and treatment codes, water added/not added, nutrients added/not added and grass present/removed in the field experiment

Treatments	G+ N+ W+	G+ N- W+	G+ N+ W-	G+ N- W-	G- N+ W+	G- N- W+	G- N+ W-	G- N- W-
Treatment Code	GWN	GW	GN	G	NW	W	N	-GWN

Table 2. Summary of the irrigation treatment using long term monthly mean rainfall and normal monthly rainfall applied during the period of the study (December 2006 to April 2007).

	Dec 06	Jan 07	Feb 07	Mar 07	Apr 07
Long term monthly mean rainfall (mm)	128	125	128	87	44
No Water (Normal rainfall (mm))	119	130	111	92	52
Irrigation Treatment (Normal rainfall + Long term Monthly mean) (mm)	247	255	239	179	96

Table 3. ANOVA of the effects of initial height (Jan SH) and stem diameter (Jan SD), grass, water and nutrients on seedling height of *K. africana, A. gerrardii, T. sericea* and *Ekebergia capensis* in April 2007.

		K. africana			*T. sericea*			*A. gerrardii*		
Factors	DF	SS	F	P	SS	F	P	SS	F	P
Water	1	1.61	0.09	0.76	95.62	2.33	0.13	16.85	0.56	0.46
Nutrients	1	250.83	14.77	<.***001***	646.65	15.77	<.***001***	7.08	0.24	0.63
Grass	1	26.02	1.53	0.22	109.59	2.67	0.11	120.00	4.01	***0.05***
Jan SH	1	38.60	2.27	0.14	1296.93	31.64	<.***0001***	238.26	7.96	<.***01***
Jan SD	1	45.38	2.67	0.11	27.41	0.67	0.42	1.56	0.05	0.82
W*N	1	54.91	3.23	0.08	9.59	0.23	0.63	89.36	2.98	0.09
W*G	1	176.69	10.41	***<0.01***	64.67	1.58	0.22	52.11	1.74	0.19
N*G	1	80.92	4.77	***0.04***	0.01	0.00	0.99	38.97	1.30	0.26
W*N*G	1	15.72	0.93	0.34	147.61	3.60	0.06	0.44	0.02	0.90

Table 4. ANOVA of the effects of initial height (Jan SH) and stem diameter (Jan SD), grass, water and nutrients on seedling stem diameter of *K. africana, A. gerrardii, T. sericea* and *Ekebergia capensis* in April 2007.

		K. africana			*T. sericea*			*A. gerrardii*		
Factors	DF	SS	F	P	SS	F	P	SS	F	P
Water	1	0.02	0.90	0.35	0.01	0.41	0.52	0.04	2.40	0.13
Nutrients	1	0.05	2.03	0.16	0.01	0.45	0.51	0.02	1.07	0.31
Grass	1	0.05	1.89	0.18	0.34	12.31	***0.001***	0.05	2.85	0.10
Jan SH	1	0.06	2.26	0.14	0.00	0.04	0.84	0.00	0.00	0.95
Jan SD	1	0.02	0.71	0.40	1.77	63.61	***<.0001***	0.08	4.85	***0.03***
W*N	1	0.03	0.95	0.34	0.01	0.24	0.63	0.00	0.35	0.56
W*G	1	0.00	0.02	0.90	0.00	0.00	0.99	0.00	0.05	0.83
N*G	1	0.07	2.58	0.12	0.00	0.03	0.87	0.16	8.98	***<.01***
W*N*G	1	0.00	0.25	0.62	0.06	2.16	0.15	0.02	1.17	0.289

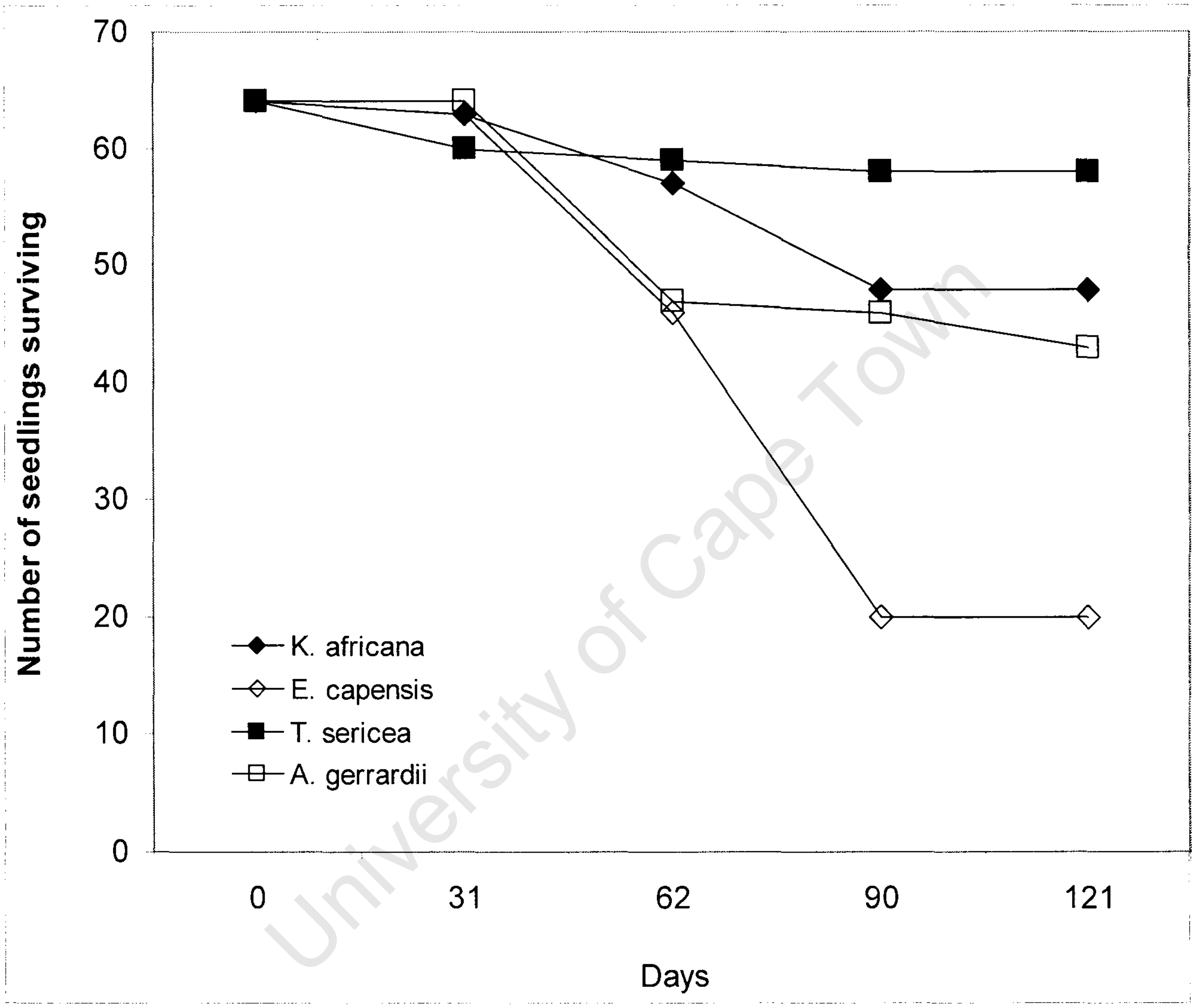

Figure 1. Survival of *K. africana, E. capensis, T. sericea* and *A. gerrardii* seedlings in the field experiment from December 2006 to April 2007. *K. africana* and *E. capensis* are forest species while *T. sericea* and *A. gerrardii* are savanna trees.

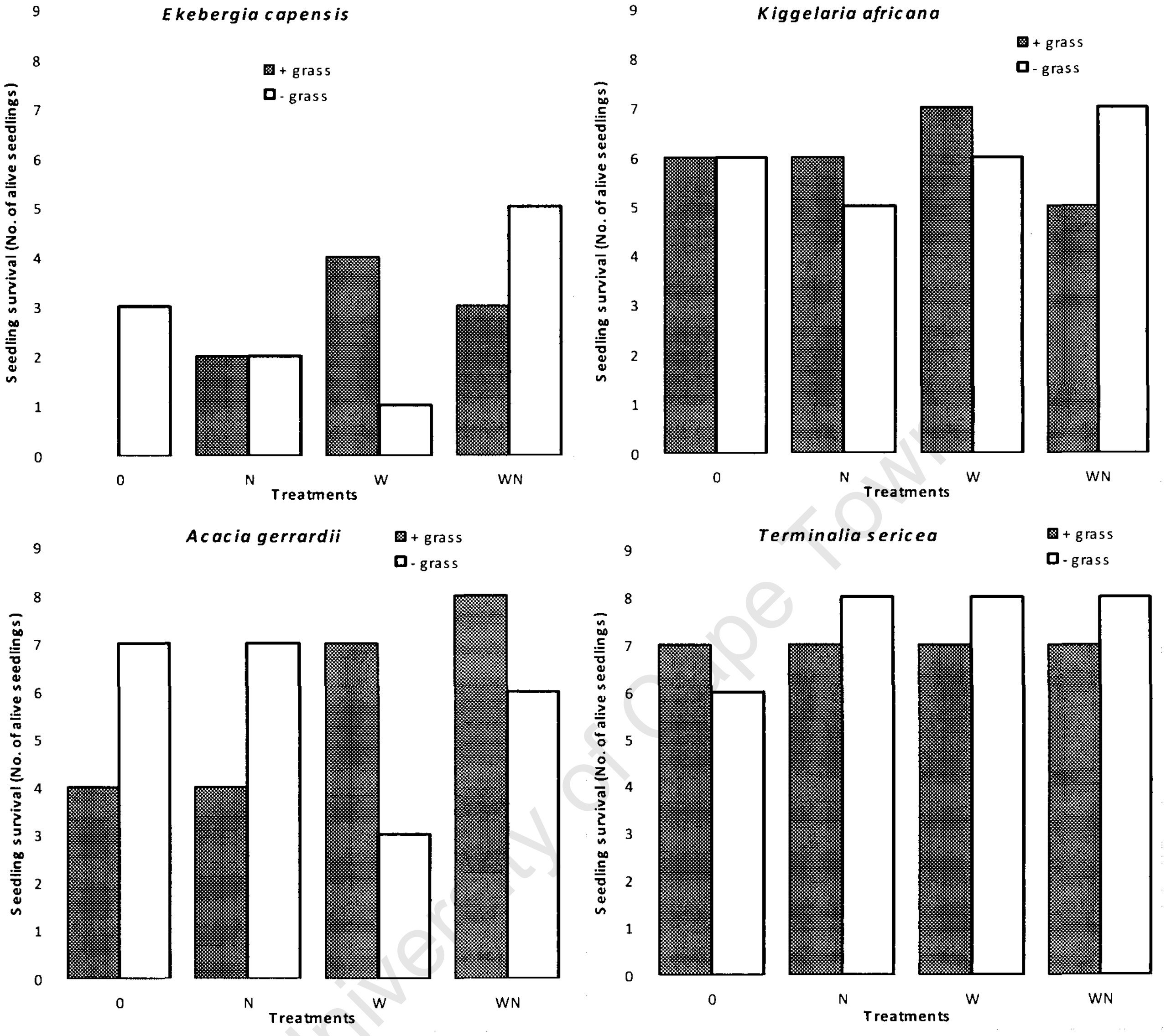

Figure 2. Comparison of seedling survival between forest (*E. capensis, K. africana*) and savanna (*A. gerrardii, T. sericea*) species on different treatments. Solid squares – grass present, open squares – grass removed. Treatments are 0 no water or nutrient addition, N nutrients added, W – irrigated, NW – nutrients and water added.

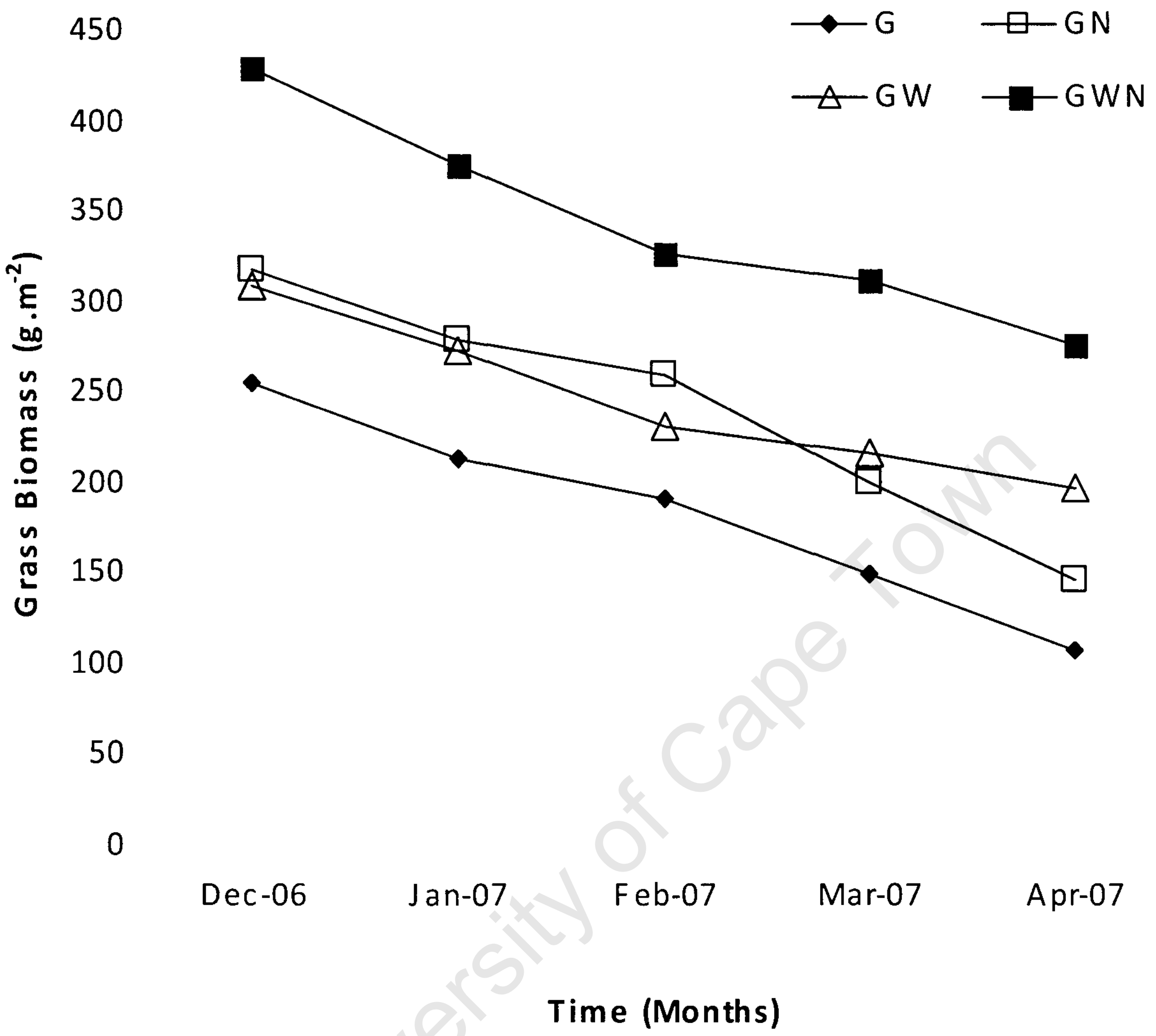

Figure 3. Comparison of grass biomass over time in months, December 2006, January 2007, February 2007, March 2007 and April 2007. Grass biomass was compared on different treatments, that is G- Grass, GN- Grass with nutrients added, GW- Grass with water added and GWN- Grass with water and nutrients added.

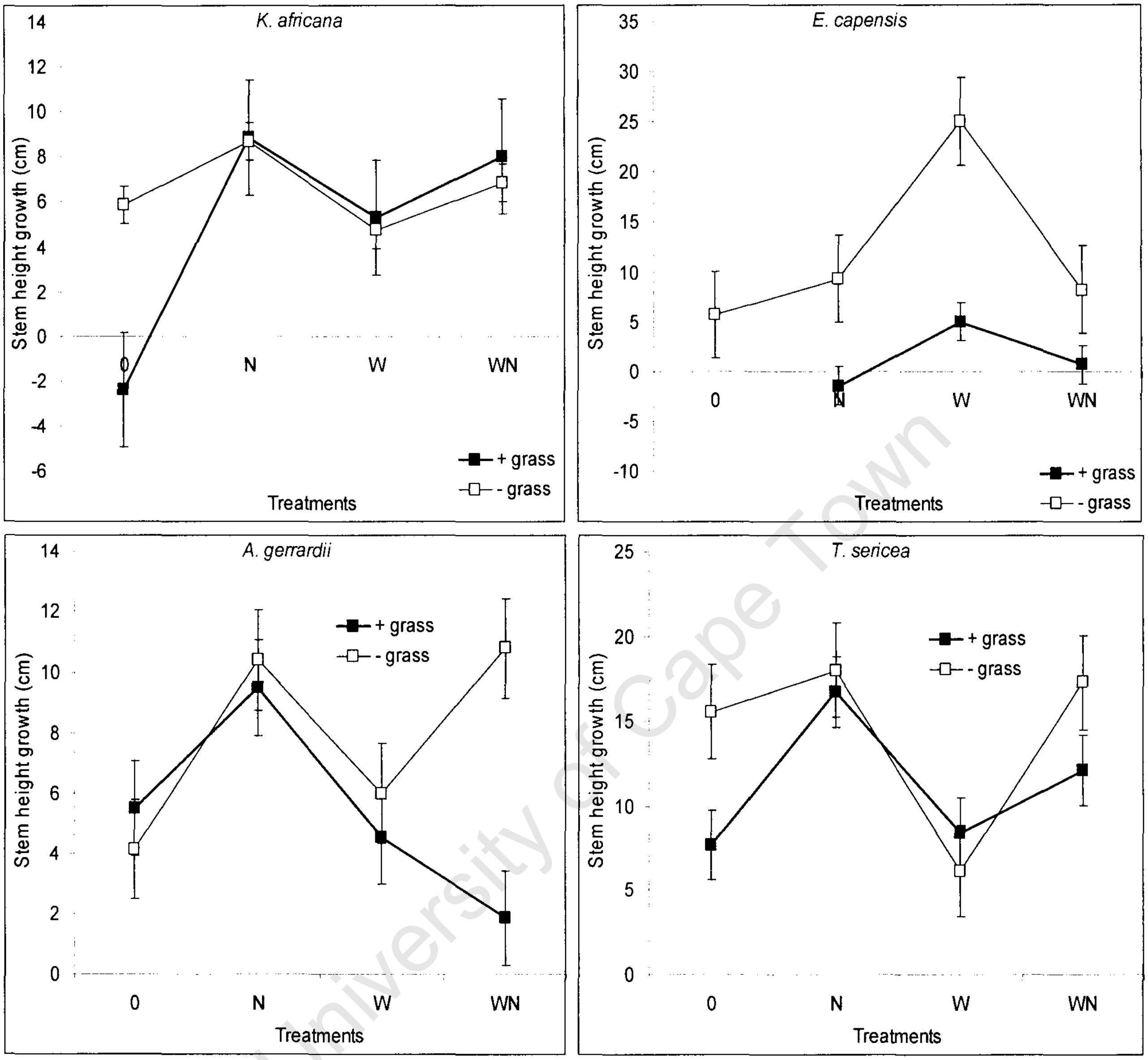

Figure 4. Seedling height growth in relation to treatments for forest (*K. africana* and *E. capensis*) and savanna seedlings (*A. gerrardii* and *T. sericea*). Solid squares shows grass present, open squares shows grass removed. Treatment 0– no water or nutrient addition, N- nutrients added, W- irrigated, WN- water and nutrients added.

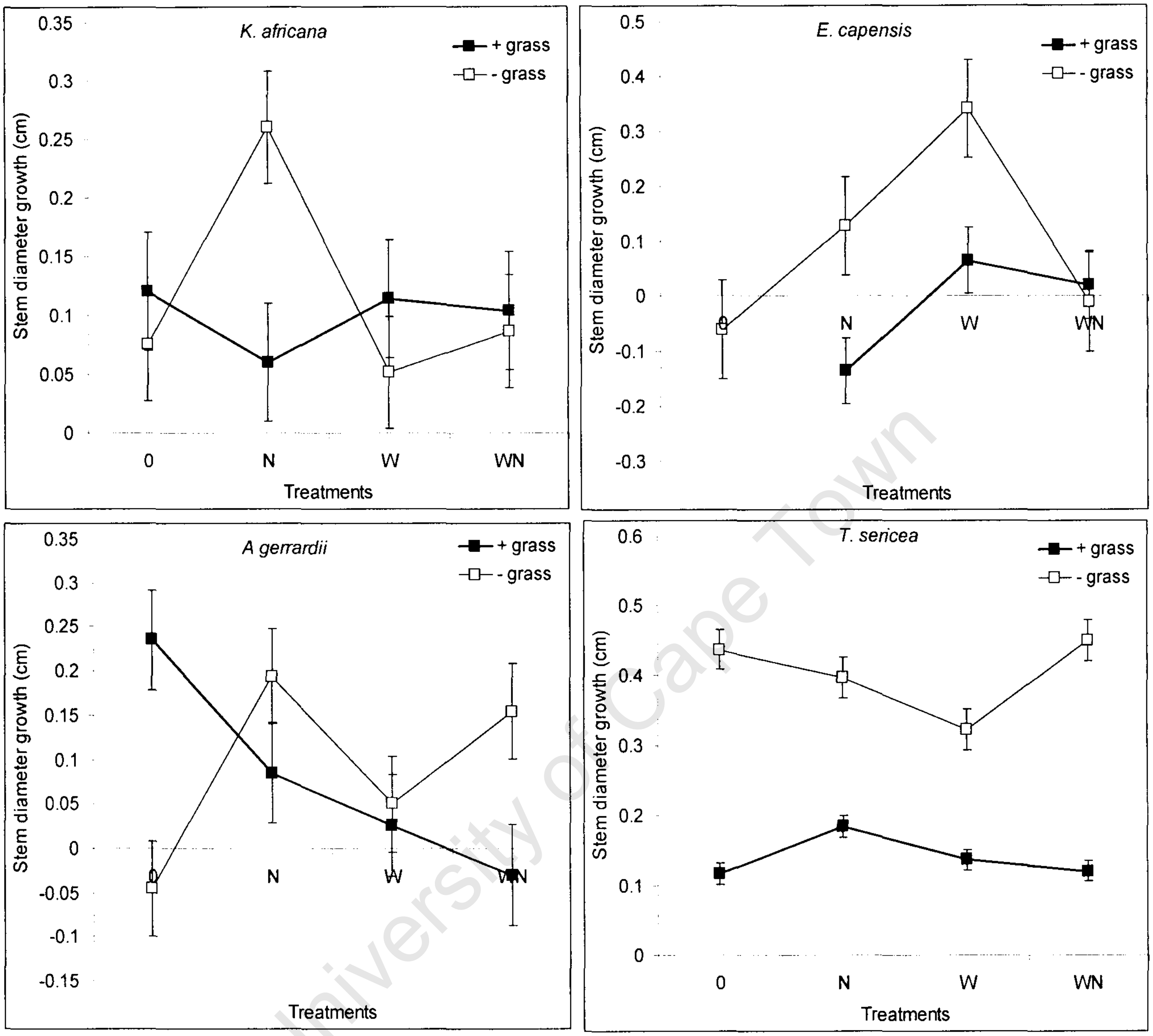

Figure 5. Seedling stem diameter growth in relation to treatments for forest (*K. africana* and *E. capensis*) and savanna seedlings (*A. gerrardii* and *T. sericea*). Solid squares shows grass present, open squares shows grass removed. Treatment 0– no water or nutrient addition, N- nutrients added, W- irrigated, WN- water and nutrients added.

Discussion

Seedling survival showed different responses to the grass treatment but differences were not associated with savanna vs. forest origin. Grass presence increased mortality of *E. capensis* and *A. gerrardii*, a forest and savanna species respectively. Savanna seedlings, *A. gerrardii* and *T. sericea* responded in similar manners to nutrient addition. Seedling survival did not show similar trends with water addition and water and nutrient addition. The results show that nutrients influenced savanna seedling survival. Though there was also an element of competition from grass, the no grass treatment reduced seedling survival in both species. Grass removal and nutrient addition together increased seedling survival of the two savanna species. For the two forest species, grass completely excluded *E. capensis* seedlings, but had no effect on survival rate of *K. africana* seedlings with or without grass treatments.

For three of the four tree species, competition with grasses did not prevent seedling establishment with half or more of the seedlings surviving their first growing season. However competition with grasses significantly reduced growth rates of surviving seedlings. These results contrast with Noble (1984) and Danielsen & Halvorson (1991) who suggested that grass limits survival and causes major seedling failure. In some studies, grasses facilitate seedling establishment or have negligible effects. O'Connor (1995) found that grasses facilitated establishment of *Acacia karroo,* and Brown & Archer (1999) found that grass competition had little effect on *Prosopis glandulosa* seedling emergence. The results in my study show that grass competition did matter for survival of two of the species. Though seedling survival may have been influenced by transplant shock, seedling mortality was relatively minor until 90 days after establishment (Figure 1). Seedlings that did manage to survive showed strong treatment effects of grass on growth.

My results show that grasses responded to treatments with water and nutrient addition each having equivalent effects and the combination having additive effects on grass biomass (Figure 3). Thus both water and nutrients limited grass biomass in this experiment. As we provide resources for seedling growth, a large part of that resource is absorbed by grass for their growth and development. The presence of grass suppressed growth of the broad-leaved savanna species, *T. sericea,* seedlings relative to grass removals. Grass affected seedling growth primarily by competing for nutrients. There were minor differences between seedling height growth with nitrogen addition and nitrogen and water added together. The nitrogen fixing legume, *Acacia gerrardii*, showed much less reduction in growth in the presence of grass relative to the two non-fixing species, consistent with the importance of nutrients, and especially nitrogen, as being the resource most limiting to seedling growth. Cramer *et al.* (2007) have shown that seedlings of African *Acacia* species fix nitrogen in the presence of grass but not where grasses were removed. They suggested that N fixation gives a competive advantage to seedlings competing with grass but provided no information on relative competitive ability of non-fixing non-acacia species. Both broad-leaved non N fixing species (*T. sericea* and *K. africana*) in my study were strongly suppressed by grass competition in the absence of nutrient and water addition in comparison to the *Acacia*. So nutrients seem to be the problem.

I hypothesized that savanna seedlings would survive and compete better than forest species with grass for resources. The results do not support this since the savanna species, *T. sericea* did well in the absence of grass, as did the forest species, *K. africana*. *A. gerrardii* growth showed a significant effect of grasses with high mortality and slow growth rates in the grass plot, although there was also low mortality on irrigated plots. This might be because the soils are sandy and cannot hold water resulting in high infiltration rates. Grass can hold water on surface layers but most of the available water is absorbed into grass roots. *E. capensis* had the highest mortality rate in the grass and water addition treatments, but this may have been caused by transplant shock to the seedlings, therefore further tests need to be conducted. These results suggest that grass competition limits seedling establishment and survival of *T. sericea*, *K. africana* and *A. gerrardii* seedlings, probably by reducing nutrient availability as reported by Florentine & Fox (2003).

Competition for resources seems to be intense because both water and nutrients are limiting resources in savanna ecosystems and in plots where both water and nutrients were added, without grasses, *A. gerrardii*, *E. capensis* and *T. sericea* showed an improved growth rate. Results obtained in this study support the hypothesis that seedling establishment, growth and survival in savannas is limited by competition with grass, primarily for nutrients. Grasses exert an effective competition for underground resources such as water and nutrients by increasing underground biomass allocation (Tilman 1987). For all species, *T. sericea* and *A. gerrardii*, *K. africana* and *E. capensis*, grass removal, nutrient and water addition promoted growth but grass presence suppressed growth. In the presence of grass, growth was very poor without nutrients. But nutrient addition seemed to compensate for no extra water. Nutrient addition in this experiment produced better seedling growth with or without grass competition. Irrigation without nutrient addition, reduced growth suggesting that nutrients were limiting in this experiment.

This study provides a better explanation of why there are few woody plants in grasslands and open savanna. In the previous chapters, it was reported that there is high woody density under canopies of savanna trees which may also be linked to high nutrients and water availability below the canopies. The results of this experiment suggest that the process of forest invasion into grassy open habitats is primarily limited by low nutrient availability in competition with grasses, but promoted by higher nutrient availability under the canopies of tall trees in the *Terminalia* savannas of Kruger Park. Grass competition influences both establishment and growth of seedlings. Under the canopies, we get less grass but there are nutrient hotspots under the big trees (e.g. Belsky 1994, Ludwig *et al.* 2004) than away from trees. This study suggests that a significant effect of the canopy is increased nutrient supply promoting seedling establishment and growth. Greater availability of water under the canopy seems less of an issue. In contrast, Hoffmann *et al.* (2004) found that Brazilian forest species suffered greater moisture stress than savanna seedlings and had different rooting systems (shallower rooted) than savanna trees. That may be true in this ecosystem but I found no obvious difference in irrigation response of savanna and forest seedlings. My experiment compared only a small number of forest and savanna seedlings. There is no previous work comparing forest and savanna species in South Africa, so this is a first for the region but the results are suggestive rather than definitive.

Chapter 7. Synthesis and Conclusions

Though several factors such as fire, herbivory, climate are well known for their impacts on savanna structure, it was not clear as to whether the same factors influence forest invasion in Pretoriuskop savannas. The main aim of this study was to investigate factors limiting and promoting forest invasion in this savanna ecosystem. I used the experimental burn plots to explore forest colonization under different fire regimes and to explore the interaction between fire, climate and other factors in maintaining savanna structure and/or promoting forest colonization.

Results in chapter 3 showed that frequent fires reduced woody biomass whereas triennial burn and no burn plots increased woody biomass. It was also shown that there was high seedling recruitment on the triennial burn and no burn plot. However, there was a strong microsite effect with high woody biomass and high seedling recruitment found under the canopies of savanna trees, *S. birrea* and *T. sericea* in particular and not the open habitats. *S. birrea* also had high species diversity and supported different species composition suggesting facilitation of a biome shift to thicket. It was not clear why there are still few saplings in the open habitats on the no burn plot even though fire was excluded for 50 years. The effect of 50 years of fire exclusion in promoting high densities of woody plants and a change towards forest species composition was largely limited to under canopies of *S. birrea*. Fire reduced forest species in the frequently burnt plots and they could only be seen on the no burn plot under *S. birrea* canopies. *S. birrea* played a facilitative role by acting as a nurse plant to recruiting forest species. This facilitation results in the formation of forest clumps in the savanna ecosystem.

To understand the differences under microsites and fire treatments in terms of soil resources, I collected soil samples under different microsites on different fire treatments to measure nutrients and moisture content. Savanna trees influence soil fertility under their canopies (Belsky et al. 1989) and fire is an active agent of nutrient cycling (Holt & Coventry 1990). Soils under *S. birrea* were highly enriched with K, Ca, Mg, C, SOM & exchangeable cations. Results in this chapter suggested that high seedling recruitment and high woody biomass under the canopies of *S. birrea* was significantly influenced by high moisture and nutrients. *T. sericea* had less effect on soil nutrients and also had less of an effect on forest species colonisation.

These results led to the following questions: What limits forest colonization at a particular site? Is it water, nutrients or both? Are open sites not colonized because of intense seedling competition with grasses? And how do savanna species differ from forest species in terms of seedling growth and response to resource supply and competition with grasses? In chapter 5 and 6, I set up a field experiment to investigate the differences between savanna and forest seedling resource requirements, and to measure seedling growth in competition with grass. In the first experiment, conducted during the dry season, I examined the temporal niche hypothesis: whether *T. sericea* seedlings could maintain growth during the dry season when grasses are dormant. *T. sericea* seedlings did not show any response to treatment effect. This suggests that, at least for this species, seedlings do not avoid competition with grasses by continuing to grow in the dry season.

In December 2006, during the growing season, I set up a similar experiment to determine the resource requirements for savanna and forest seedlings. Savanna and forest seedlings did well in the absence of grass. This result implies that grass has a negative impact on seedling establishment and growth. The results from this experiment lead to an alternative explanation for why there are low densities of woody recruits in grasslands and open savannas. Seedling establishment and growth of savanna and forest seedlings were reduced by grass through competition for resources. Nutrient addition increased forest and savanna seedling growth and survival, whereas grass presence completely excluded seedlings of the forest species, *E. capensis*, and reduced seedling growth for other species. Nutrients in this experiment seem to be the limiting resource in this savanna because nutrient addition caused high seedling survival and high growth rates with or without grasses. However, grass completely prevent *E. capensis* establishment, whereas with other species it only caused slow growth rates. These results further suggest that the rate of forest colonization and woody plant recruitment may be influenced by interactions between seedling growth rates and fire/herbivory.

After all this, I conclude this thesis by emphasizing that there is woody plants are increasing in grasslands and savanna, and forest invasion/colonization is taking place in high rainfall areas in South Africa. Open grasslands are being transformed to open savannas which thicken up to savanna woodlands and/or switch from woodlands to forest/thicket through a process called forest invasion. Where forests/thickets are invading, there is not only an increase in woody plants, but also a change in species composition and a reduction in grasses so that frequent fires and herbivory can no longer be supported, resulting in further formation of forest clumps. Where it is occurring, thicket/forest expansion is a serious conservation and rangeland problem with the biome switch resulting in reduced conservation values of savanna parks and livestock potential. But it does seem as though frequent fires would be enough to limit the process in the *Terminalia* savannas of KNP.

Fire reduces woody biomass whereas large savanna trees influence seedling recruitment under their canopies by creating better conditions for establishment. Therefore, it would be valuable to keep track of savanna/thicket switches under large savanna trees in KNP in future. Forest expansion into grassy ecosystems could become a major problem associated with global change. We really know little about which parts of the savanna world may switch to forest/thicket and what will happen to forest/thicket ecosystems. It is likely that forest invasion would be taking place in higher rainfall areas with minimum nutrient requirement for seedling establishment and/or under tree canopies through facilitation. It is not well known whether the same factors that influence woody encroachment are also responsible for forest colonization.

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