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UNIVERSITY OF CAPE TOWN

YUNIVESITHI YASEKAPA • UNIVERSITEIT VAN KAAPSTAD

**Water and available nitrogen as co-determinants of a
mesic savanna in Kruger National Park, South Africa**

Moagiemang Thomas Keretetse

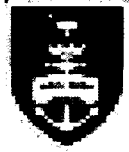
**Thesis presented for the degree of Master of Science
In the Department of Botany
University of Cape Town
February 2009**

DIGITISED

- 2 APR 2013

**To the late Nomvuyiso Joy Matokazi, who passed away while writing up
her M.Sc. thesis. May her soul rest in peace.**

University of Cape Town



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(YUNIBESITHI YASEKAPA • UNIVERSITEIT VAN KAAPSTAD)

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DECLARATION

I know the meaning of plagiarism and declare that all of the work in the document, save for that which is properly acknowledged, is my own.

Moagiemang Thomas Keretsetse
(Signature of candidate)

_____ 16th _____ Day of February _____ 2009

ABSTRACT

Savanna is a summer rainfall, tropical and subtropical vegetation type with a continuous grass cover and discontinuous cover of trees. Rainfall plays an important role in savanna as it triggers many ecosystem processes such as nitrogen mineralization. This rainfall is however extremely variable with cycles of wet and dry years. The impacts of rainfall variability on N mineralization rates and tree-grass dynamics are not well known. This study seeks to provide a quantitative understanding on the influence of rainfall amount on N mineralization rates, and how this interaction (of water and available N) may affect structural diversity in savannas.

Rainfall manipulation treatments were set up to simulate different rainfall amounts. These treatments included a wet treatment which received normal rainfall regime plus irrigation (150 % of rain). The control treatment had no rainfall manipulation and received the normal rainfall regime of the year (100 % rain). The dry treatment received half of the normal rainfall (50 %). Furthermore, the treatments had different plant cover combinations of tree-grass, grass only and tree only. Volumetric soil water content and nitrogen mineralization rates were determined in all treatments from August to June for two growing seasons. N mineralization rates were determined by incubating soil cores *in situ* for +/- 28 days. Grass biomass, tree saplings height and basal area were measured to determine the treatment effects on plant growth. Leaf area and nutrient contents of leaves were quantified to establish physiological response of saplings to different rainfall regimes was also determined.

N mineralization rate was highest in wet treatments (0.55 - 0.29 $\mu\text{g N/ g soil/ day}$) and lowest in dry treatments (0.33 – 0.11 $\mu\text{g N/ g soil/ day}$). Grass biomass increased in wet treatments (1901.3 – 2079.2 Kg/ha) and decreased in dry treatments (722.3 – 880.6 Kg/ha), while the saplings' growth decreased in wet treatments (190 cm) and increased in dry treatments (265 cm). However, saplings experienced greatest growth when grass was removed, than when grass growth was suppressed by dry conditions.

These results show that increase in water and available N in wet treatments led to high grass productivity and intense competition on tree sapling which showed little growth. In dry treatments, grasses were limited by water and low N availability as shown by the

reduction in grass productivity. Reduced grass competition in dry treatments, and lack of competition in grass removal treatments opened an opportunity for saplings to grow faster. This shows that grass competition plays an important role as it can limit saplings from growing beyond sizes where they are vulnerable to fire and browsing. This study shows that it is not only the impact of rainfall that is driving tree-grass coexistence and structural diversity in savannas, but the combined effects of rainfall and available nitrogen.

Keywords: Tree-grass, savanna, rainfall, nitrogen, competition

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CHAPTER 1

INTRODUCTION

Savannas are a tropical vegetation type characterized by the co-dominance of trees and grasses (Scholes and Archer 1997; Sankaran *et al.* 2004). Covering some 12% of the land surface of the world (Huntley and Walker 1982; Scholes and Walker 1993), savanna biomes have a wide geographic and climatic distribution. As a result, the structure of savanna varies from open grassland with few trees, through deciduous woodlands to dry forests with heterogeneous grass cover (Walter 1971; Scholes and Walker 1993; Scholes and Archer 1997; House *et al.* 2003). Wiegand *et al.* (2006) defined savannas as patch-dynamic systems, meaning savannas have many patches which are in different states of transition between herbaceous and woody dominance.

Rainfall is recognized as an important driver of heterogeneity because of its variability in space and time. A key feature in savannas is a climate of hot wet summer, also known as the growing season, usually from October to March, followed by a dry warm winter April to August (Scholes 1997, Tainton 1999). While moisture availability is acknowledged as one of the main drivers in determining savanna structure (Walter 1971; Sankaran *et al.* 2005; February 2007), few studies have investigated the importance of moisture and nitrogen interactions as co-determinants in savanna systems. Here I examine how the interaction of water and available nitrogen influence the growth of grasses and trees in a mesic savanna. The primary objective is to ascertain how water and nitrogen availability interact to determine the structural differences observed in savannas. Emphasis is placed on how competition effects of grass impact the ability of tree saplings growth to recruit into adult sizes and grow beyond the height were they are susceptible to the effects of fire (top-kill) and browse by herbivores.

The coexistence of trees and grasses in savanna has intrigued researchers for a number of years (Silvertown 2004). Coexistence occurs as trees and grasses occupy the same space and utilize the same resources ranging from water, light, and nutrients (Silvertown 2004). As opposed to competitive exclusion, both life forms do not exclude each other, rather

they co-dominate within the same ecosystem. A fundamental issue in savanna ecology has since been to understand the mechanisms that make it possible for trees and grass to coexist (Sarmiento 1984; Scholes & Walker 1993). Several models and hypotheses that seek to explain tree-grass coexistence have been proposed. They can be broadly grouped into two categories, the competition based models (Walter 1971; Walker and Noy-Meir 1982) and the disturbance based models (Higgins *et al.* 2000; Jeltsch *et al.* 2000). In a review article Sankaran *et al.* (2004) described the different models that account for tree-grass coexistence in savanna, this summary makes extensive use of that review.

Walter (1971) was probably the first to suggest that water is the main determinant of tree-grass coexistence in savanna. He proposed that coexistence is possible because trees and grasses source water at different levels in the soil, with trees accessing water at the deeper soil layers while grasses source water closer to the surface. Walker and Noy-Meir (1982) subsequently developed this rooting niche separation model into an analytical model. According to this model, trees and grasses would coexist when there is enough precipitation to satisfy the requirements of grasses with excess water penetrating deeper into the soil to become available for trees. Periods of less rainfall will favour grasses while trees will be more suited by wetter conditions with more water filtering through the soil to deeper layers.

A number of studies dispute with this model and argue that there is little experimental evidence to support it (Hipondoka *et al.* 2003; Schieter and Higgins 2007). Hipondoka *et al.* (2003) suggested that niche separation based on time and not on soil depths accounts for tree-grass coexistence. The rooting niche hypothesis has been criticized for being too simplistic to explain the complex nature of tree-grass coexistence in savannas (Scholes and Walker 1993). It has been suggested that simple mechanisms that explain tree-grass coexistence are defective as the behavior of a mixed tree-grass system is complex and non-linear (House *et al.* 2003; Sankaran *et al.* 2004).

In contrast to the competition model (Walter 1971; Walker and Noy-Meir 1982), disturbance models (Higgins *et al.* 2000; Jeltsch *et al.* 2000) advocate that drought, fire

and herbivory are the primary drivers for tree-grass coexistence in savannas. The demographic bottleneck model (Higgins *et al.* 2000) argues that the impact of drought and fire at different life stages of trees is responsible for tree-grass coexistence. Drought limits the establishment of tree seedlings, while recruitment of seedlings to adult stages is constrained by fire (Higgins *et al.* 2000). However, trees persist in savanna systems due to resprouting of smaller trees and the longevity of adult trees (Higgins *et al.* 2000). This model further suggests that recruitment of seedlings to adult classes of trees occurs episodically, when there is less frequent and less intense fires, and under favourable climatic conditions. Thus, it is variation in climatic conditions over the years that will facilitate tree-grass coexistence. As opposed to the Walter (1971) hypothesis, this model suggest that trees will be favoured by dryer conditions as grass biomass will be lower resulting in reduced fire intensity.

Another mechanism for disturbance, called ecological buffering (Jeltsch *et al.* 2000), focus on the processes that prevents savannas from crossing the “savanna boundary” and becoming either grassland or forest. Jeltsch *et al.* (2000) argue that disturbances such as fire and herbivory prevent the transition of savanna to woodland, whereas heavy grazing pressure and high nutrient patches provide conditions for tree establishment and impedes the system from changing into grassland. This model suggests that tree-grass coexistence in savannas is made possible by mechanisms that prevent transition to either grassland or forest.

Though the disturbance models have shaped the recent understanding of tree-grass interactions (San Jose and Montes 2007), the storage mechanisms that enable tree longevity in savannas as proposed by Higgins *et al.* (2000) may not be universal in all savannas (Schieter and Higgins 2007). Competition based models and disturbance models differ in mechanism and conceptual approach (House *et al.* 2003; Sankaran *et al.* 2004). Competition based mechanisms (Walter 1971) support the view that niche separation with regard to water usage leads to tree-grass coexistence, whereas the disturbance models (Higgins *et al.* 2000) argues that fire, herbivory and rainfall variability promote tree-grass co-existence (Sankaran *et al.* 2004).

Integrating these two models, Sankaran *et al.* (2005) proposed that the wide climatic distribution of savannas influences their resultant structure. This study focused on woody cover as the important component in savanna structural diversity. In mesic savannas, with mean annual rainfall of above ~650 mm, rainfall is sufficient to permit trees to form closed woodland, and disturbances such as fire and herbivory play a major role in constraining trees, allowing coexistence with grasses (Sankaran *et al.* 2005). For semi-arid and arid savannas with a mean annual rainfall lower than ~650mm, woody cover is limited by water allowing grasses to coexist. While fire, herbivory and soil properties interact to further reduce woody cover.

While tree-grass coexistence has been the subject of much scientific debate, of equal interest is why this vegetation type differs so fundamentally in structure (February *et al.* 2007). The availability of resources such as water and nutrients, and the disturbances regimes such as fire and herbivory are recognized as the primary determinants of savanna structure as they regulate woody plant density (Scholes & Walker 1993; Jeltsch *et al.* 1996; Sankaran *et al.* 2005). The impact of fire, rainfall and herbivory on savanna structure have been comprehensively examined (Sankaran *et al.* 2004; Sankaran *et al.* 2005). However, fewer studies have examined the combined effects of water and nutrients on the structure of savannas.

Soil fertility and organic matter turn-over have a significant effect in savanna ecology primarily because these determine plant productivity and palatability, as well as the distribution of plant and animal species in the system (Scholes and Walker 1993; Bustamante *et al.* 2006). Macro-nutrients such as Nitrogen (N) and Phosphorus (P) are key elements which are important for growth and functioning of any organisms (Shaver *et al.* 1980), with N often the most limiting nutrient for plant growth in savanna systems (Scholes and Walker 1993; Scholes *et al.* 2003; Zhe-Ke and Makeschin 2006). Understanding the factors that influence availability of N and its impacts on the vegetation is therefore imperative.

Nitrogen moves through the system via different pathways (Figure 1.1.) and in different forms (Scholes and Walker 1993). Dinitrogen (N_2) from the atmosphere reaches the soil through wet deposition as rain or through dry deposition as dust (Scholes and Walker 1993; Mphapye *et al.* 2006). Ammonium is the main component in dry deposition, whereas wet deposition comprises ammonium and nitrate in equal proportions (Scholes *et al.* 2003). Nitrogen is also introduced into the soil by leguminous plants which are able to fix dinitrogen directly from the atmosphere (Jacobs *et al.* 2006).

In soil, nitrogen is found in different pools with different rates of turnover (Scholes *et al.* 2003), the largest pool being the soil organic nitrogen (SON) (Scholes and Walker 1993). Soil organic nitrogen is chemically and physically resistant to microbial degradation (Zhe-Ke and Makeshin 2006) resulting in only a small part of soil nitrogen being available as a substrate for nitrogen mineralization.

Soil organic nitrogen is mineralized into inorganic forms of nitrogen in a process known as N mineralization, which then becomes available for plant uptake (Binkley and Vitousek 1989). In the first step of mineralization, soil organic nitrogen is converted to ammonium (NH_4^+) in a process known as ammonification (Scholes and Walker 1993). However, microbes responsible for ammonification can also take up inorganic nitrogen to supplement their nitrogen needs through immobilization process (Chaplin *et al.* 2002). Ammonium produced during mineralization, can be converted to nitrite and then to nitrate (Chaplin *et al.* 2002) in a process called nitrification. Denitrification occurs when nitrogen oxides, like nitrate (NO_3^-) and nitrite (NO_2^-), are reduced to the gases nitric oxide (NO), nitrous oxide (N_2O), and dinitrogen (N_2) (Scholes and Walker 1993).

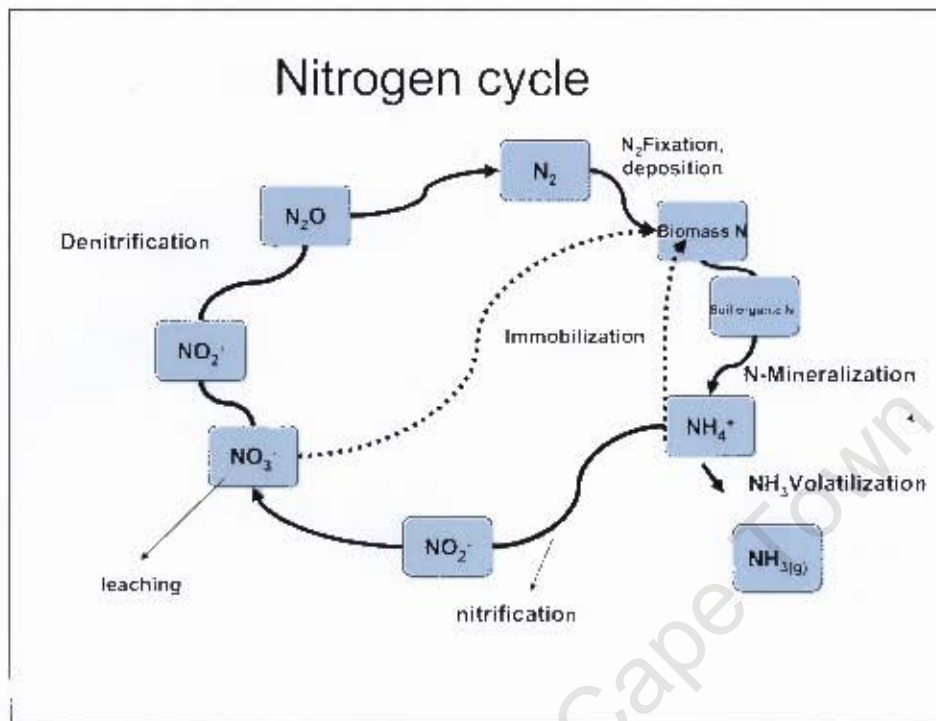


Figure 1.1 Schematic presentation of Nitrogen cycle (Binkley and Vitousek 1989; Scholes and Walker 1993).

Nitrogen mineralization is used as an indicator of nitrogen available to plants in terrestrial ecosystems (Robertson *et al* 1999). It is measured as net nitrogen mineralization which is the difference between gross mineralization and gross immobilization (Bruun *et al.*, 2006; Chen *et al.*, 2006).

This process of mineralization may be illustrated with the following equation;



↓

Soil microbial biomass (Immobilization)

Mineralization of nitrogen depends on favourable climatic or environmental factors, the activity of microbes, substrate chemistry and soil texture (Binkley and Vitousek 1989, Chapin *et al.* 2002; Bechtold and Naiman 2006). Organic matter turn-over in savannas

is regulated by interactions of water and available nutrients (Bustamante *et al.* 2006). Water plays an important role in savanna systems as it initiates savanna processes like the mineralization of nitrogen (Scholes and Walker 1993; Schwinning and Sala 2004). This is because mineralization of nitrogen to inorganic forms is driven by microbes which are sensitive to water stress (Scholes *et al.* 2003). Several studies have found higher rates of mineralization during the wet warmer months of the season, whereas lower rates of N mineralization as well as immobilization occurred during winter season (Scholes *et al.* 2003, Feig 2004, Fischer 2006).

Several studies on different stages of N cycling have been carried out in Kruger National Park (KNP). Mphepya *et al.* (2006) calculated wet N deposition in KNP, Skukuza, to be $2.8 \text{ kg N ha}^{-1} \text{ yr}^{-1}$. This value was higher by an order of magnitude when compared with a similar study that was carried out in the savanna of Banizoumbou in Niger. Scholes *et al.* (2003) suggested that deposition in Kruger is a major factor because KNP is located down hill from major coal driven power stations. These findings further necessitate that the role of N availability and its impacts in determining savanna structure be investigated.

Studies on the impact of soil texture on N mineralization revealed that fine textured soils had higher N mineralization, higher total N, and high total carbon than coarse textured soil (Feig 2004). Fine textured soils like clay soils are important in regulating N retention and mineralization because of their particle size (Bechtold and Naiman 2006). Other studies in KNP which focused on the impacts of fire on N, found that frequently burned areas had higher mineralization rates (Aranibar *et al.* 2003), but that fire frequency had no effect on total N (Aranibar *et al.* 2003; Feig 2004).

San Jose and Montes (2007) investigated differences between two structurally different savannas, herbaceous savanna (i.e., open savanna dominated by grass) and the woodland savanna (closed savanna dominated by trees). They found that these structurally different savannas had varied in precipitation and soil bulk density (low bulk density is related to increased storage of nutrients and water, while high bulk density signifies reduced storage of nutrients and water by the soil). They found that in herbaceous savanna, woody

cover was limited by reduced precipitation at the beginning of the rainy season and increased soil bulk density. While in the woodland savanna, woody cover and net primary productivity increased with an increase in precipitation at the beginning of the rainy season and low bulk density. This study shows the importance of water and available nutrients as major determinants of savanna structure.

The above-mentioned studies looked at various aspects which affect N mineralization, like fire, wet deposition, soil texture and topography, precipitation and bulk density (Aranibar *et al.* 2003; Feig 2004; Bechtold and Naiman 2006; San Jose and Montes 2007). Even though the dependence of N mineralization on soil water content has been shown (Scholes and Walker 1993; Feig 2004; Fischer 2006; Singh and Kashyap 2006), fewer studies examine the combined effects of water and nitrogen availability on plants.

The nitrogen cycle in the soil is characterized by the pulsing of mineralization rates immediately after the first major rainfall events during the growing season (Scholes *et al.* 2003). This period which has the highest rate of mineralization throughout all seasons, is also coupled with active plant growth (Singh and Kashyap 2006). The increased rate of plant growth during this time suggests that the activity of microorganisms in the soils may provide plants with the much needed N to supplement their growth in this period (Singh and Kashyap 2006; February *et al.* 2007). James *et al.* (2006) proposed that differences in phenology and timing of optimum growth in co-existing species might facilitate different times of N uptake and ultimately permit coexistence. Scholes (1997) suggested that the early-season flush of nutrients to which trees have first access might be the important limitation rather than water. These are some of the studies which investigate and link nutrients, especially N availability, to tree-grass coexistence in savannas. It is possible that it is not only water but also the interaction of water and nitrogen that cooperate to produce the structural diversity witnessed in savannas.

Objectives

Bottom-up controllers, such as water and nutrients, play an important role in determining the structural diversity seen in savannas (Scholes *et al.* 2003). This study investigates the role of the interaction between water and available nitrogen as co-determinants of savanna structure. A focus is placed on the impact of varying water treatments on N availability. Furthermore, the effects of the interaction between water and available N on tree-grass dynamics are also studied. Different treatments with varying water levels and different tree-grass combinations are set-up to test the combine effects of water and nitrogen availability in a mesic savanna. The role of grass competition in dry and wet conditions, on the growth rates of saplings is also investigated.

In a preliminary study (Chapter 2), I first show the relationship between N mineralization rate and rainfall for my study site at Pretoriuskop in the KNP. The relationship between water and N availability was investigated on a monthly and seasonal basis, under rainfall manipulation treatments of dry and wet conditions. The role of grass cover as a potential regulator of available water was also investigated. In Chapter 3, I show the effects of the interaction of water and N availability on plant growth under different treatments. Here I focus especially on how grass competition effects on tree sapling are regulated by the various rainfall manipulation treatments. Information on how trees and grasses respond to varying levels of water and nitrogen availability will contribute towards understanding how the interaction of water and nitrogen availability shape tree and grass interactions. Differences in mineralization rates of nitrogen caused by varying water treatments will have significant effects on plant growth and resultant structure (Scholes *et al.* 2003). I hypothesize that competition will affect the ability of saplings to recruit to adult stages, but its effects will be regulated by variability in rainfall.

Kruger National Park

The Kruger National Park (KNP) (Figure 2.1) is located in the Lowveld of north-eastern South Africa (22° 20'S-25°30'S and 31°50E-32°00'E). It covers a land surface of 2 million hectares, with a length of 350 km from north to south and a width of about 60 km (Venter *et al.* 2003). The southern part of the park is in Mpumalanga province of South

Africa, whereas the upper part of the park extends into Limpopo province. Furthermore, the KNP is a part of a larger trans-frontier conservation area which includes private game reserves on the western side, and protected areas from Mozambique and Zimbabwe on the east and north-eastern side.

Kruger National Park is separated into 56 land types and 11 land systems based on soil, climate and vegetation (Venter 1990). The study was carried out on the southern part of KNP at Pretoriuskop. The Pretoriuskop land type is situated in the Skukuza land system according to the classification of land systems of Kruger National Park (Venter 1990). The Pretoriuskop land type, which has a size of 47 267 ha, occupies 12.1% of the Skukuza land system (Venter 1990). The field site was placed in an animal enclosure at the Shabeni string of the Pretoriuskop Experimental Burning Plots (EBP).

The Pretoriuskop land type is a sour bushveld savanna, which is mainly uplands dominated by *Terminalia sericea* while the dense grassy layer is dominated by *Hyperthelia dissoluta* (Rutherford *et al.* 2006). *Terminalia sericea* is a deciduous tree, shedding its leaves annually during the winter season (van Wyk *et al.* 2000), while *Hyperthelia dissoluta*, also known as yellow thatching grass, is a perennial grass with culms often reaching the height of 3 m (van Oudsthoorn 2004).

The Kruger National Park is a sub-tropical region with periods of hot wet summers and cool dry winters (Rutherford *et al.* 2006). The wet season which occurs between October and March, is generally very hot with temperatures around 35⁰ C (Venter *et al.* 2003). The dry winter season spans from April to August with moderate temperatures. The rainfall increases from north to south, Pafuri in the north receives about 400mm/yr and Pretoriuskop in the south receives around 750mm/yr (Venter *et al.* 2003).

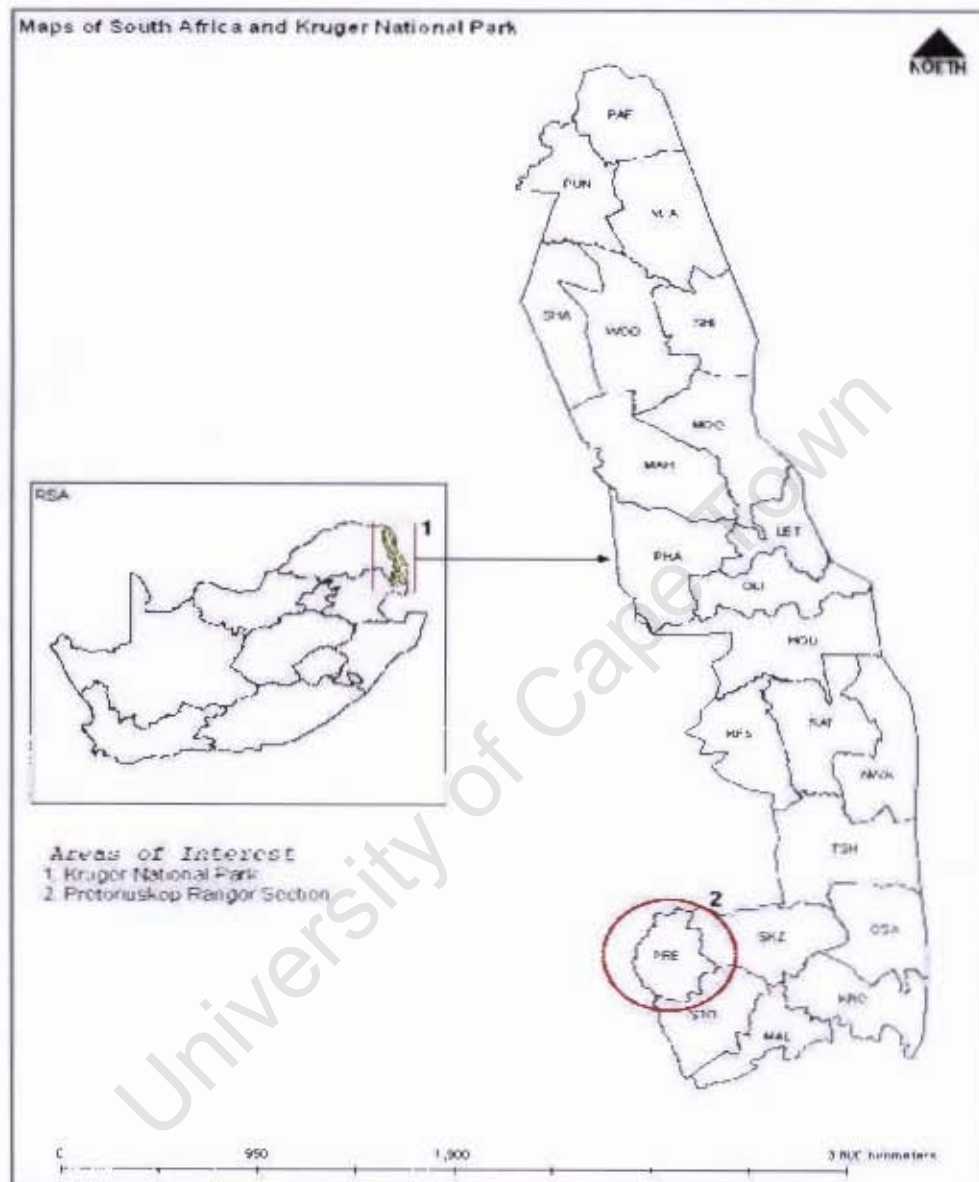


Figure 1.2 Map of South Africa (SA) and the Kruger National Park (KNP). The KNP is located in the north-eastern corner of SA (1), bordering Mozambique on the east. Pretoriukop is found on the southern part of KNP (2).

The KNP is separated geologically with the soil layer on the western side being mainly nutrient-poor sandy soil underlain by granite, whereas the eastern side is dominated by nutrient-rich clay soil on the basalts (Venter *et al.* 2003). Pretoriuskop is characterized by nutrient poor, coarse sandy soil on granites (Venter 1990).

Several studies have classified the physical and chemical properties of the soil at Pretoriuskop and at the Shabeni EBP (Table 1.1) (Mills 2003; Feig 2004; Coetsee 2007). Feig (2004) characterized the soil type at Shabeni as sandy loam with a pH of 6.1 - 6.3, with a soil texture comprised of 78.5% sand, 14% clay and 7.5 % silt. Mills (2003) measured the bulk density at Pretoriuskop to be 1.64 – 1.66 g/cm³.

Table 1.1 Total soil nutrients C, N (%), and P for Pretoriuskop land type

<i>Soil nutrients</i>	Mills (2003)	Feig (2004)	Coetsee (2007)
Total soil C	0.7 – 0.9	0.77 - 1.05	1.10 – 1.53
Total soil N	0.06 – 0.08	0.04 – 0.06	0.08 – 0.11
Soil P		201±18 mg/P/kg	2.83 – 5.05 µg/g
C:N		15.1 – 19.3	14

The differences in annual rainfall, temperatures and geology across KNP results in heterogeneous plant communities and structure. Venter *et al.* (2003) reports that woody plant cover in KNP savannas is variable with areas having total tree cover as little as 5 percent, while other areas have near-closed canopy cover of around 60 percent. Pretoriuskop is classified as a bushveld with tree cover less than 35 percent (Venter *et al.* 2003).

CHAPTER 2: The effects of rainfall variability and plant cover on nitrogen mineralization rates in a mesic savanna of Kruger National Park, South Africa

INTRODUCTION

Savannas are defined as tropical and subtropical vegetation types with a continuous grass cover and discontinuous cover of trees (Frost *et al.* 1986). Rainfall in savannas like KNP is variable both annually and seasonally. On an annual basis, there are cycles of above and below average rainfall years, and on a seasonal basis rainfall occurs primarily in summer (5-7 months) and little or no rainfall in winter (5-7 months) (Gertenbach 1980; Scholes *et al.* 2003; Rutherford *et al.* 2006). During the wet summer season savannas have abundance of water for growth and development, however, savannas are water limited during the dry winter season (Scholes and Archer 1997). This rainfall seasonality will have an enormous impact on the nitrogen (N) cycle in the soil as water availability is strongly correlated with N availability (Scholes and Walker 1993; Feig 2004; Fisher 2006). This seasonality in rainfall results in a series of drying and rewetting of soils which is stressful to microorganisms responsible for nutrient cycling (Cui and Caldwell 1997; Austin *et al.* 2004). The impacts of these wet and dry rainfall cycles on N mineralization and plant interactions are however not well known.

Recent studies suggest that the variability in plant available moisture plays an important role in determining savanna structure (Sankaran *et al.* 2005; February *et al.* 2007; Hempson *et al.* 2007). Soil water availability is recognized as the key factor constraining maximum woody cover in savannas where mean annual precipitation (MAP) is less than 650mm (Sankaran *et al.* 2005). Where MAP exceeds 650mm fire and herbivory are said to constrain tree distribution (Sankaran *et al.* 2005). However, water does not play a solitary role in savannas as it triggers many ecosystem processes such as N mineralization (Schwinning and Sala 2004). Water availability regulates nutrient availability in semi-arid ecosystems as it creates suitable conditions for drought-sensitive microorganisms that carry out nitrogen mineralization (Cui and Chadwell 1997; Chaplin ; Fischer 2006).

Nitrogen mineralization is the process in which organic N is converted to inorganic N, with ammonium and nitrate as the two forms of inorganic N (Scholes and Walker 1993). Microorganisms break down organic matter in soil to take-up carbon and releases inorganic N (Scholes and Walker 1993). As plants are only able to take up inorganic N, this process is essential in determining the availability of N to plants. Nitrogen mineralization can also be the limiting factor for plant growth because plants use N for their productivity (Binkley and Vitousek 1989).

Quantitative information on the effects of rainfall variability on nutrient cycling is relatively scarce (Austin *et al.* 2004). Here I propose that it is not only the impact of water that is driving the structural change in savannas, but the combined effects of both water and nitrogen. Information on the relationship between rainfall and N mineralization rates will reveal the importance of N availability as one of the determinants of savanna structure.

While the primary objective of this chapter is to determine the relationship between available water and N mineralization, I also examine the effect of vegetation cover on the interaction between rainfall and available N. Previous studies (Scholes and Walker 1993; Feig 2004) looked at the relationship between water and N availability, my studies investigates this relationship over different seasons.

METHODS

Experimental layout

The study consisted of eight treatments (Figure 2.1), three tree-grass combination treatments on a water gradient of wet, dry and control, and three grass-only treatments on the same water gradient. One tree-only (No-grass) treatment and one bare-ground treatment in which all grass cover was removed. Bare ground treatments were then covered with 40% shade cloth to simulate grass cover and prevent soil crusting. The sizes of the plots were 4 x 4 meters, and all treatments were replicated six times giving a total of 48 plots.

Experimental design*
(8 treatments x 6 reps = 48 plots per site)

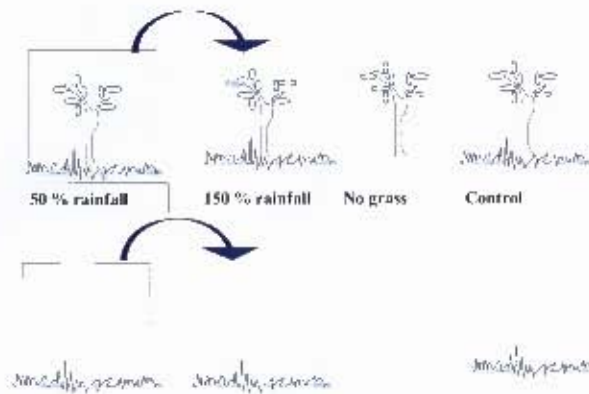


Figure 2.1 Experimental layout showing treatments of different combinations of tree and grass on a water gradient.

Fixed location shelters were used to manipulate the amount of rainfall on the dry treatments. This shelter consisted of four 4m long poles, covered with a roof made out of eight bands (0.2m x 1m) of transparent corrugated polycarbonate roof sheeting configured to intercept 50% of the rainfall. Water trapped on the roof flowed through a gutter into a 100 L water container. This water was then funneled from the dry treatment through a 20 mm diameter pipe to an adjacent wet treatment. In the wet treatment, the pipe transporting water from the dry treatment diverted into eight 8 mm diameter tubes that were spread parallel to each other 0.5 m apart across the entire plot. These tubes had regular spaced holes that were 100 mm apart to ensure that the whole wet treatment plot was evenly irrigated. In this way the dry treatment received 50% of the rainfall, and the wet treatment received an additional 50% from the dry treatment giving it a total of 150% rainfall. The control treatments had no rainfall manipulation and thus received 100% of the rainfall.

Nitrogen mineralization

Nitrogen (N) mineralization rate is used as an indicator of nitrogen available to plants in terrestrial ecosystems (Robertson *et al.* 1999). Net N mineralization was measured using the *in situ* core field incubation method as described by Robertson *et al.* (1999). Field incubations provide an estimation of N mineralization for the soil moisture at the time of sampling (Eno 1960; Vitousek and Matson 1985). Mineralization rates were determined monthly during the period from September to March for two successive years, 2005 to 2007. In each treatment, a stainless steel pipe with a length of 15 cm and diameter of 4cm was driven into the soil to a depth of 10 cm. Soil cores were covered with punctured plastic caps to prevent leaching losses by rain but still permit aeration (Nadelhoffer *et al.* 1984; Gelfand and Yakir 2007). These soil cores prevented uptake of inorganic N by roots (Adams and Attiwill 1986).

Two samples were taken for determining N mineralization, namely the initial sample and the final sample. In both samples, nitrate and ammonium values were taken. The initial soil sample was taken within 30 cm from the final sample and placed in a 10 x 8 cm plastic Ziploc bag at the site. This sample was transported to the laboratory in a cooler box and stored in a fridge at 4°C overnight before extraction with potassium chloride (KCl). For the incubated sample, soil cores were left *in situ* for a period of 28 ± 5 days. After an incubation period of 28 days, the soil cores were removed for extraction and analysis. At the same time, a new set of immediate and incubation cores were installed at new randomly selected locations within the plot.

In the laboratory large roots and stones were manually removed from the sample after which the soil was passed through a 2 mm sieve to remove any smaller organic particles. A ten gram subsample was treated with 45 ml of KCl and the solution was shaken together for one hour and then centrifuged at 5000 rpm for 5 minutes. The supernatant (10 ml) was then sent to the Institute of Soil, Climate and Water of the Agricultural Research Council (ARC), Pretoria, for analyses of ammonium and nitrate.

The rate of net nitrogen mineralization was calculated as the difference between the final (28 days incubation) and initial levels of ammonium and nitrate.

The following equation was used to calculate daily net N mineralization rates:

$$N_{\text{mineralized}} = [(\text{Nitrate}_f + \text{Ammonium}_f) - (\text{Nitrate}_0 + \text{Ammonium}_0)] / T_{\text{days}}$$

Where; Nitrate_f is the final value of Nitrate, Ammonium_f is the final value of Ammonium, Nitrate₀ is the initial value of Nitrate, Ammonium₀ is the initial value Ammonium, and T_{days} is time measured in days. N mineralization is expressed in the following units: µg N/soil/ day. Gravimetric soil water content was used with the concentration of ion in the extract, mass of soil and volume of extract to calculate mass N concentration in the soil (Robertson *et al.* 1999).

Gravimetric soil water content was determined by using a 20g sub-sample of the soil from the soil core sample. This sub-sample was then weighed in the laboratory, oven-dried at 60 °C for 48 hours and reweighed (Robertson *et al.* 1999). Gravimetric soil water content was then calculated from the following equation; $\Theta_g = [(Mw) - (Md)] / (Md)$ Where; Mw is the Mass of soil in grams before drying, Md is the Mass of soil after drying, and Θ_g is the gravimetric water content as ml H₂O/g dry soil

The following equation was used to correct for soil moisture on the concentration results of ammonium and nitrate;

1. Volumetric extract (V) = gravimetric water content (Θ_g) + 40

2. µg element/g soil = (C x V)/ W

where C is the concentration of either ammonium or nitrate, V is volumetric extract and W is the dry mass of the soil.

Volumetric soil water content

Volumetric soil water content in the top 10 cm of the soil was used as a measure of how much soil water was available for N mineralization. At each plot, an access tube for a Diviner 2000 (Diviner 2000 series2, Sentek environmental technologies, Adelaide, Australia) moisture probe was inserted in the soil to a depth of 100cm. Diviner 2000 is a capacitance probe with a length of 110 cm and a diameter of 5 cm. Diviner 2000 uses

time domain reflectometry (TDR) sensors to measure soil water content at 10 cm intervals from the surface to a depth of 100 cm throughout the soil profile. The TDR sensors measure soil volumetric water content by converting a dielectric constant of a soil into an equivalent estimate of soil volumetric water content (Noborio 2001, Mwale *et al.* 2005). Readings were taken on a monthly basis from July to March for each of the two growing seasons of sampling. The results are presented as % of volume water in volume of soil.

Volume soil moisture % = volume of water (cm³) / volume of soil (cm³).

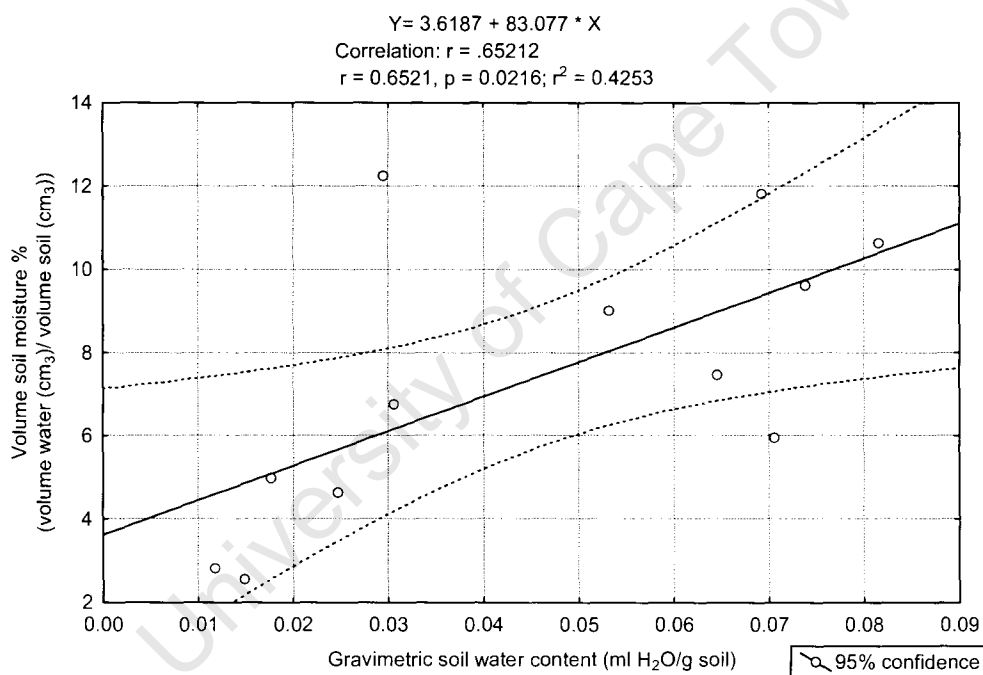


Figure 2.2 Scatter plot of Volumetric soil water content versus gravimetric soil water content. Each point represents an average of six replicates. Straight line show the positive trend in the relationship, while dotted line shows the 95 % confidence area.

The diviner probe volumetric soil water content data was calibrated against the results of gravimetric water content. There was a positive relationship between volumetric soil water content obtained from the diviner probe and gravimetric soil water content, ($r = 0.65$; $p < 0.02$) (Figure 2.2). Both volumetric water content and gravimetric water content

were sampled at 10 cm soil depth. Although both volumetric and gravimetric water content were taken from the same plot, these values are from different parts of the plot, so they need not necessarily agree or be the same. Consequently, the volumetric soil water content obtained from the diviner probe was used as a measure of available water in the soil.

Rainfall data

The two years of sampling had different rainfall patterns. The first year (2005-2006) had below average rainfall from August to October, but had above average rainfall towards the end of the growing season from January to March (Table 2.1). The highest monthly rainfall occurred in March (204.2 mm), and lowest rainfall occurred in August and September with 2.3 mm and 0 mm (Table 2.1).

The second year (2006-2007) of sampling had rainfall as early as August and exceeded the average rainfall levels during the period between September to November (Table 2.1). The second year had a less variable monthly rainfall as compared to the first year with the highest rainfall being 133.8 mm in November and the lowest being 12.2 mm in September and 23.8 mm in February. Contrary to the first year, the second year had a below average rainfall towards the end of the season from January to March.

Table 2.1 Total monthly rainfall in (mm) during the two years of sampling at Pretoriuskop, included is the long term rainfall average. Long term climate data are from archives in the Kruger National Park compiled by Nick Zambatis.

Months	2005/2006rainfall	2006/2007 rainfall	Long term rainfall average
Aug	2.3	26	12
Sep	0	12.2	28
Oct	10.5	55.6	55
Nov	70.3	133.8	100
Dec	46.5	133.2	119
Jan	185.2	55.2	129
Feb	185	23.8	111
Mar	204.2	59.8	92
Apr	29.2	71.8	52
Total	733.2	571.4	698

Temperature data

In the first year of sampling, only 5 out of 9 months had temperatures that were higher than the long term monthly average (Table 2.2). The second year was warmer with 7 out of 9 months with temperatures that were above the long term average (Table 2.2). In both the first and second year the average monthly minimum temperature was recorded in August with temperature of 20⁰C and 17⁰C. The average monthly maximum temperature were recorded in February for both years with temperature of ± 25⁰C.

Table 2.2 Average monthly and long term temperature ($^{\circ}\text{C}$) at Pretoriuskop for 2005/2006 and 2006/2007 periods of sampling. Long term climate data is from archives in the Kruger National Park compiled by Nick Zambatis.

Months	2005/2006 temperatures	2006/2007 temperatures	Long term temperature averages
Aug	20	17.3	18.4
Sep	22.6	20.2	20.7
Oct	23.5	22.9	21.4
Nov	23.7	22.8	22.6
Dec	22.5	25.2	23.9
Jan	24.4	24.5	24.8
Feb	24.5	25.8	24.3
Mar	21.6	24.6	23.7
Apr	20.3	21.4	21.3

Statistical analysis

Statistical analysis were carried out using STATISTICA 8 (Statsoft Inc. Tulsa, OK, USA) computer software package. The effects of the grouping/categorical variables such as different rainfall treatments, seasons, and cover on the dependent variables such as volume soil moisture percentage and nitrogen mineralization rates were tested. Factorial and one-way ANOVA were used to test the statistical significance of the differences between means of dependent variables. When data differed significantly ($p < 0.05$), either Tukey HSD for equal N or Tukey unequal N HSD test was used to show which treatments differed significantly. Levene's Test was performed for determining homogeneity of variance on the dependant variables, and residuals of dependant variables were tested for normality.

RESULTS

The effect of varying soil moisture levels on Nitrogen mineralization rates

The wet treatment had the highest volumetric soil water content followed by the control and dry treatments for both years of sampling (Figure 2.3). This trend remained the same throughout different months of both years of sampling (Figure 2.4). In the first year (2005-2006), all treatments differed significantly ($p < 0.0001$) (Figure 2.4). In the second year (2006-2007), the wet treatment differed significantly from the dry treatment ($p < 0.05$), but there were no significant differences between wet and control, and control and dry treatments (Figure 2.4).

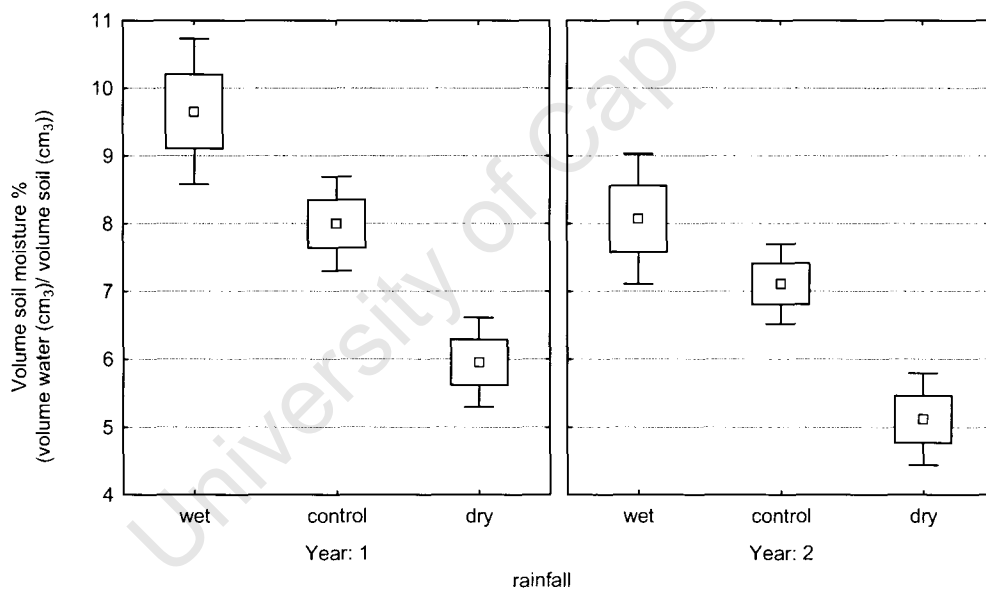


Figure 2.3 Means of volumetric soil water % over dry, wet and control treatments for the two years of sampling. The bars represents +/- 1.96 standard error of means, the bigger box represents the +/- standard error of means.

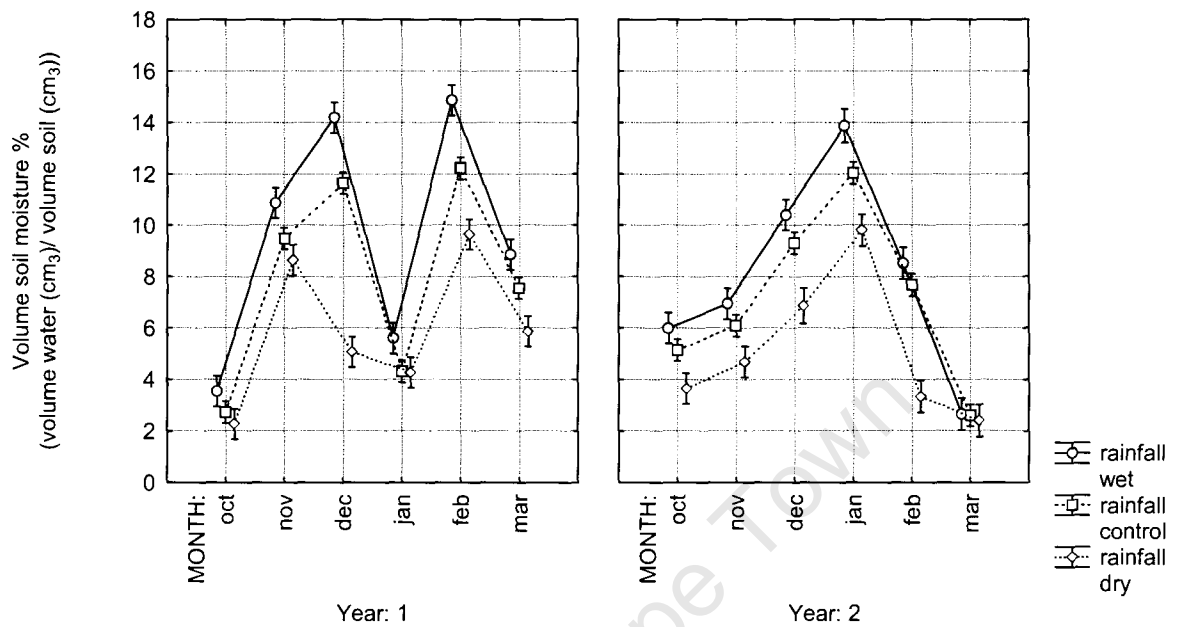


Figure 2.4 Monthly volumetric soil water % over dry, wet and control treatments for the two years of sampling. Vertical bars denote standard error.

Nitrogen mineralization rates for both years of sampling followed the same trend as the volumetric soil water content with high mineralization rates in the wet treatment, followed by the control and then the dry treatments (Figure 2.5). In the first year, the wet treatment differed significantly from the dry treatment ($p < 0.001$) and from the control ($p < 0.003$). However, dry and control treatments did not differ significantly. The second year (Figure 2.5) showed no significant differences among treatments.

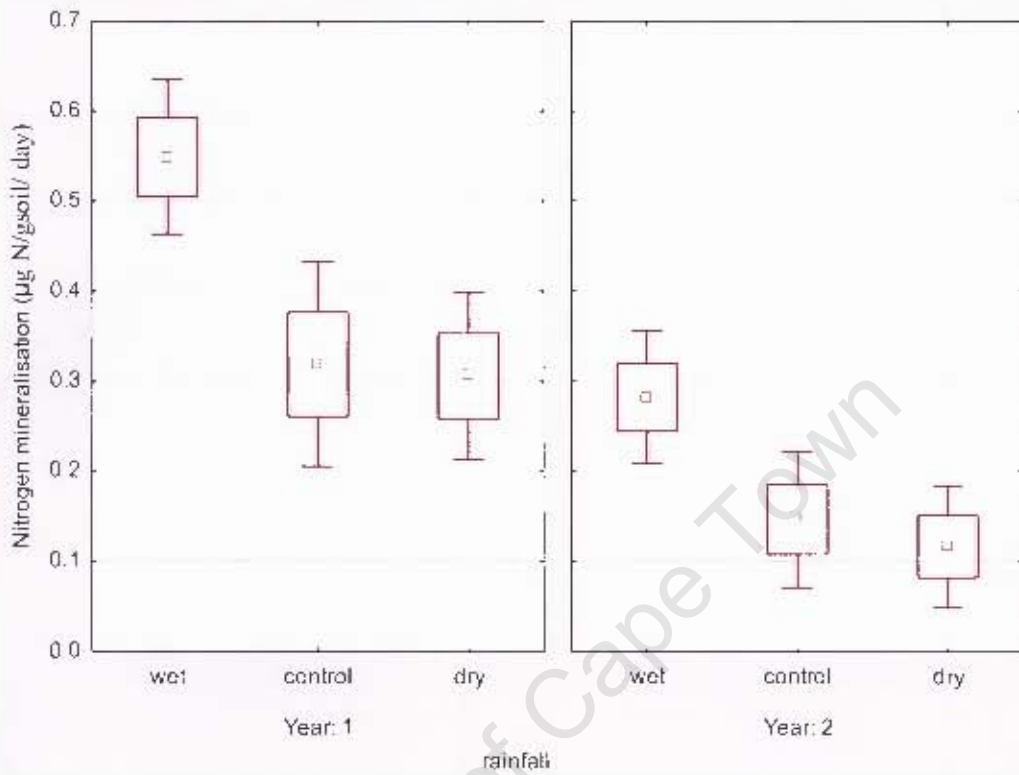


Figure 2.5 Mean nitrogen mineralization rates over wet, control and dry treatments for two years of sampling. The bars represents ± 1.96 standard error of means, the bigger box represents the \pm standard error of means, and the smaller box represents the means.

Wet treatments had the highest N mineralization rates throughout the different months of the first year of sampling, followed by both dry and control treatments (Figure 2.6). In the second year, wet treatments had the highest mineralization rates followed by control and dry in all the months, except for January (Figure 2.6).

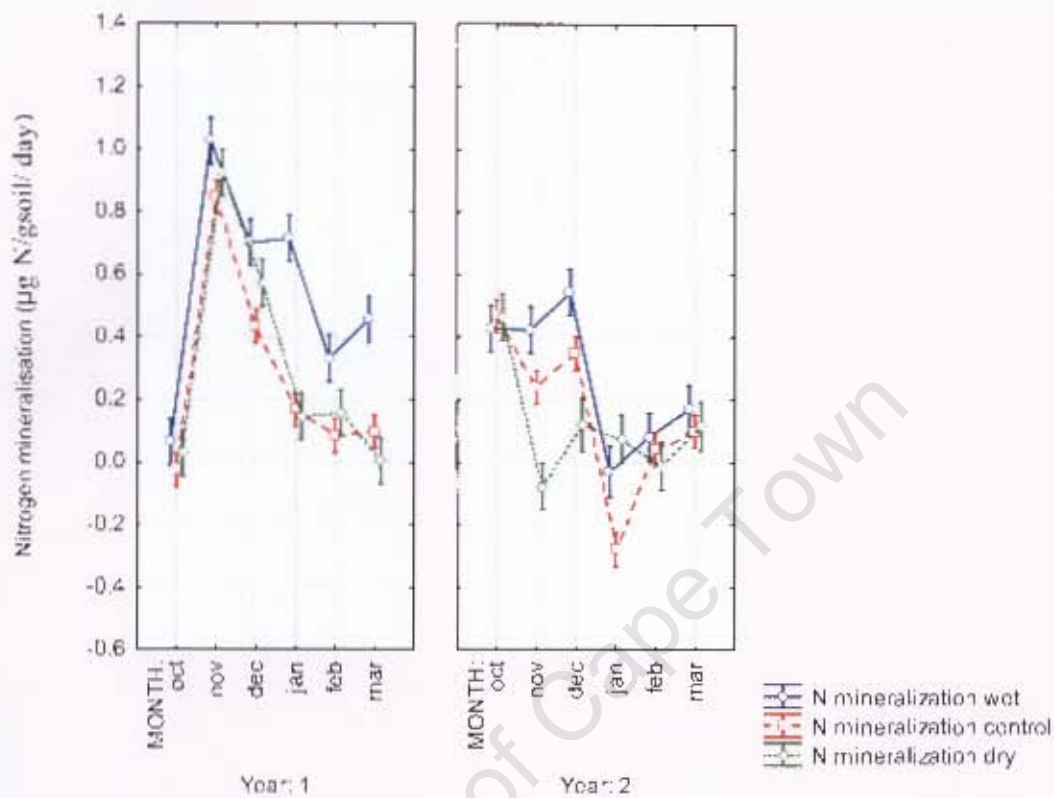


Figure 2.6 Monthly nitrogen mineralization rates over dry, wet and control treatments for the two years of sampling. Vertical bars denote standard error.

The effect of cover treatment on N mineralization rates

To test for the effect of grass cover on soil volumetric water content and N mineralization, tree-only and bare ground treatments were combined into one treatment called “without grass”, and tree-grass and grass treatments were also combined into one treatment called “with grass”.

Volumetric water content was highest in the with-grass treatments and lowest in without grass treatment for both years of sampling, but there were no significant differences with $p < 0.09$ in the first year, and $p < 0.08$ in the second year (Figure 2.7).

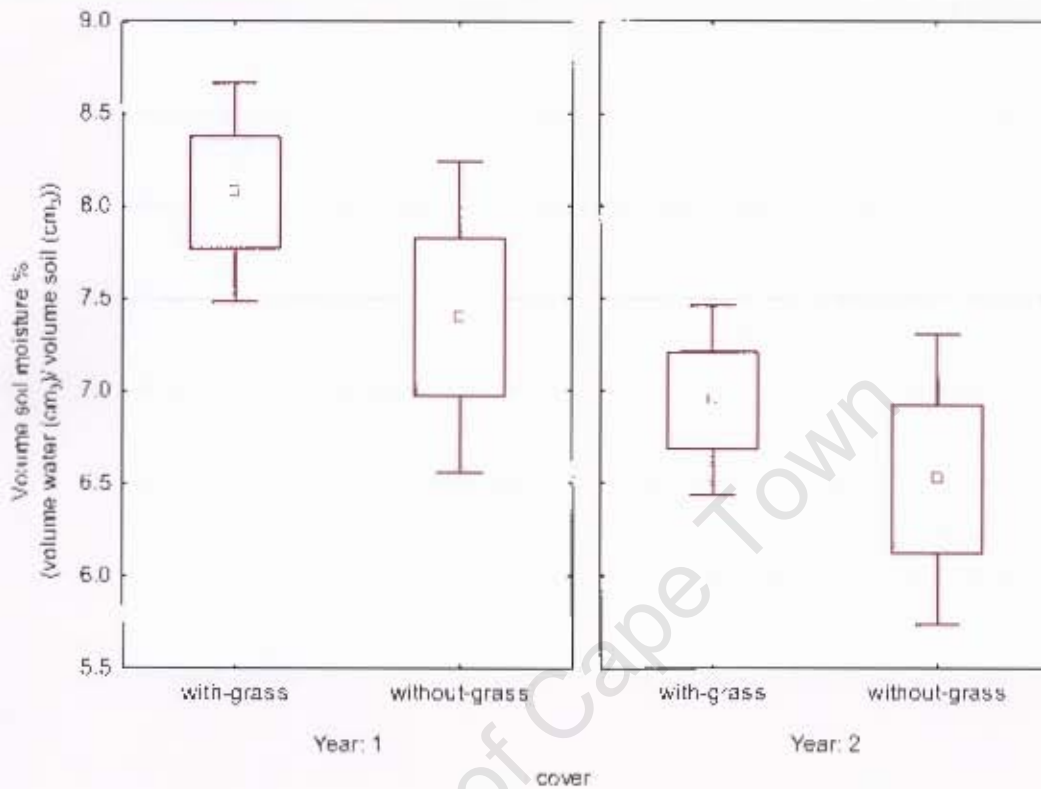


Figure 2.7 Percentage volumetric soil water content in with-grass and without-grass treatments for two years of sampling. The bars represents ± 1.96 standard error of means, the bigger box represents the \pm standard error of means, and the smaller box represents the means.

The with-grass treatment had higher N mineralization rates than the without-grass treatment in both years of sampling. The with-grass and without-grass treatments differed significantly in the first year ($p < 0.03$), but there were no significant results between the two treatments in the second year (Figure 2.8)

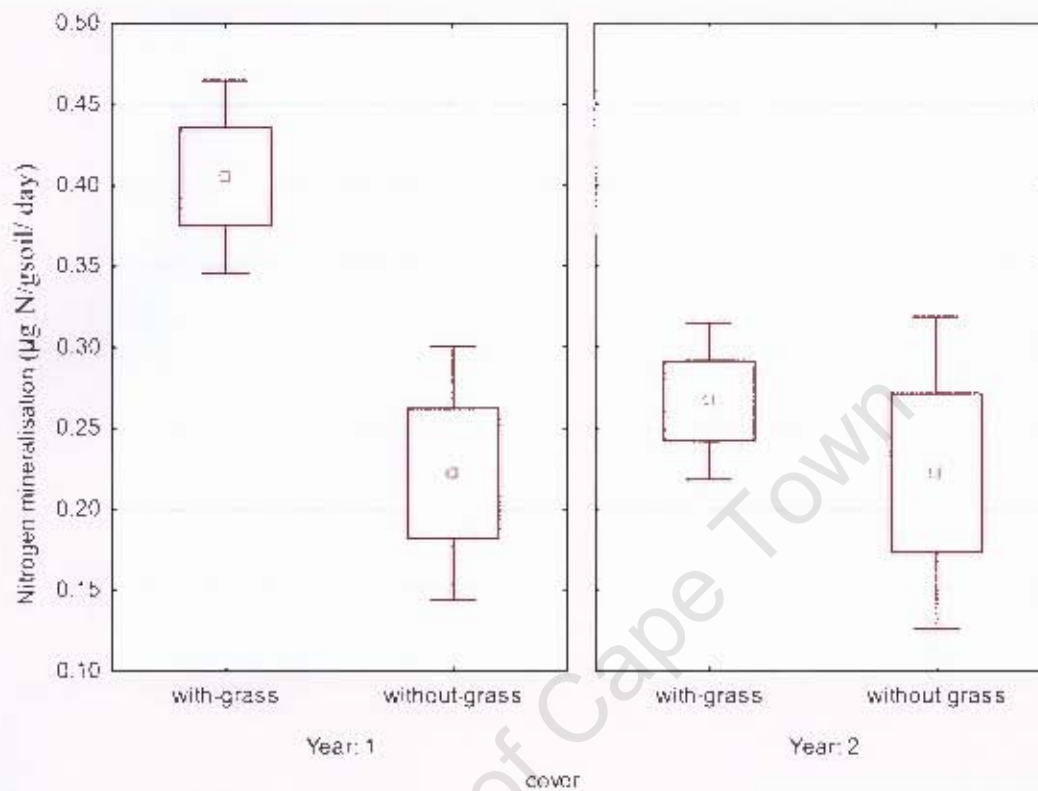


Figure 2.8 Nitrogen mineralization rates for two years of sampling in treatments with and without grass. The vertical bars represents ± 1.96 standard error of means, the bigger box represents the \pm standard error of means, and the smaller box represents the means.

The effect of season on N mineralization rates

To determine the effects of season on N mineralization rates, data were grouped into three seasons. The period before the onset of the rains from August to October is late dry season. Peak rainy season from November to January is early wet season, and the late wet season, which is the end of the rainy season, is between February and March.

The trend for volumetric soil water content (VWC) differed between the two years due to differences in rainfall patterns, i.e., late rainfall in the first year and early rainfall in the second year. Volumetric soil water content was lowest in the late dry season, increased in the early wet season, and was highest in the late wet season for the first year of sampling

(Figure 2.9). There were significant differences in VWC among the treatments ($p < 0.002$). In the second year, early wet season differed significantly with both late dry and late wet seasons ($p < 0.001$), but there was no significant differences between late dry and late wet seasons (Figure 2.9).

In the first year of sampling, N mineralization rates were lowest in late dry season, increased in early wet and decreased again in late wet season (Figure 2.10). Nitrogen mineralization rates in early wet season differed significantly with both late dry and late wet seasons ($p < 0.001$). However, there were no significant differences between late dry and late wet seasons. In the second year, a different pattern prevailed as N mineralization peaked in the late dry season and continued to decrease through out the growing season (Figure 2.10). Late dry season differed significantly from both early wet and late wet seasons ($p < 0.001$). Early wet and late wet seasons were not however significantly different.

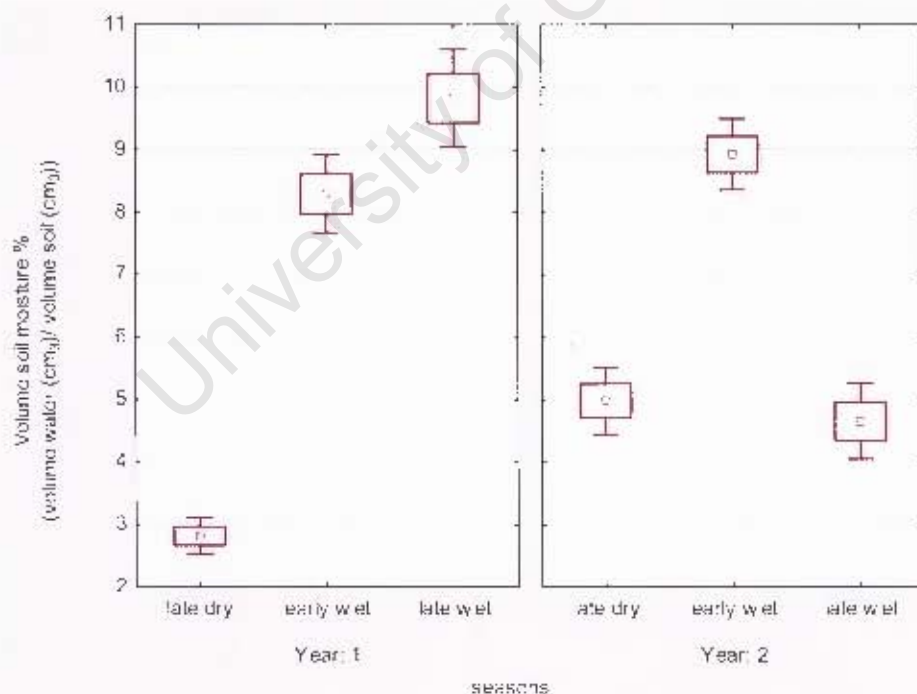


Figure 2.9 Percentage volumetric soil water content over late dry, early wet and late wet seasons for the two years of sampling. The vertical bars represents ± 1.96 standard error of means, the bigger box represents the \pm standard error of means, and the smaller box represents the means.

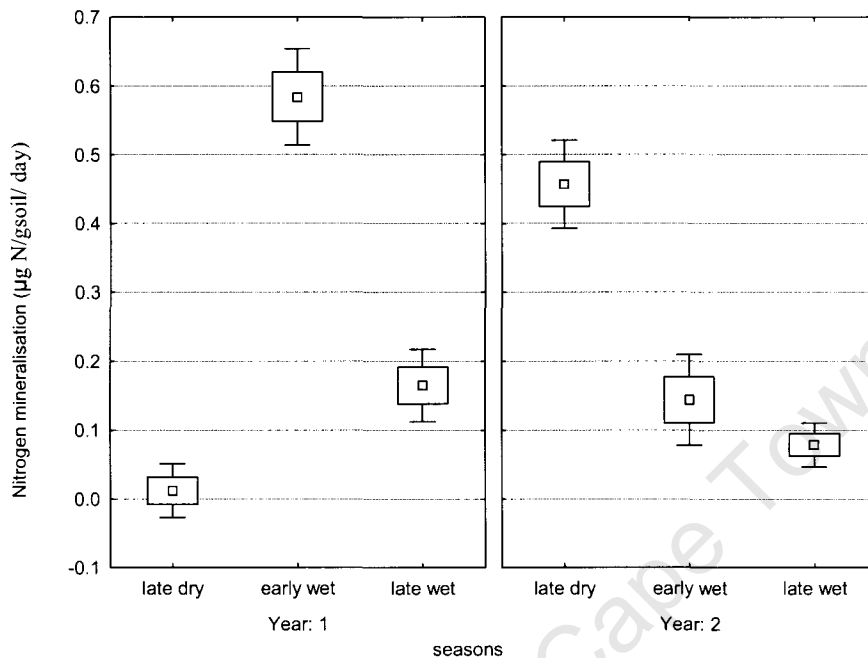


Figure 2.10 Means of Nitrogen mineralization rates over late dry, early wet and late wet seasons for two years of sampling. The vertical bars represents ± 1.96 standard error of means, the bigger box represents the \pm standard error of means, and the smaller box represents the means.

To identify the time of N mineralization pulse in both years of sampling, rainfall and N mineralization were plotted against time (Figure 2.11). In the first year of sampling, the N mineralization rate pulse was recorded in November when rainfall amount increased from below 20 mm per month in October to above 50 mm in November (Figure 2.11).

Nitrogen mineralization rates then dropped steadily from November to April even when rainfall increased.

Rainfall started earlier in the second year with August recording 26 mm and October 56 mm. The increase in rainfall in the late dry season caused the highest N mineralization rate during this period. Nitrogen mineralization rate in the second year was much lower than in the first year but the initial mineralization pulse again occurred when rainfall exceeded 50 mm per month.

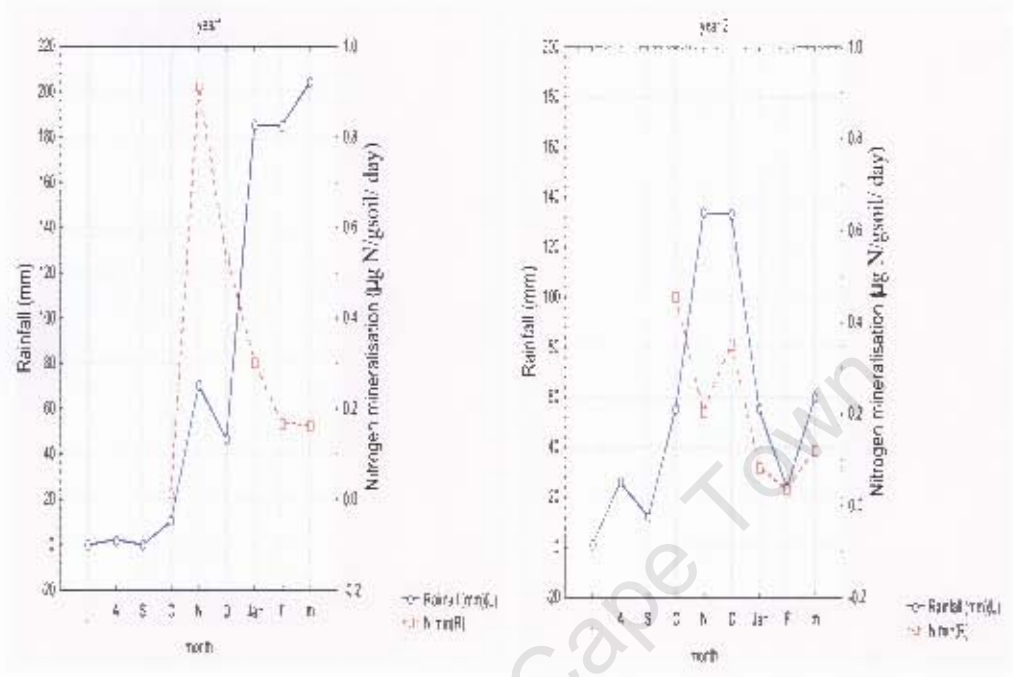


Figure 2.11 Graph of rainfall and Nitrogen mineralization rates for the two years of sampling. Rainfall data ranges from July to March, while N mineralization data ranges from October to March.

DISCUSSION

The results for this study show that the relationship between rainfall and N mineralization is different in different seasons. The lack of moisture in late dry season affected N mineralization rates as it was at its lowest during this period. Other studies have also shown that low temperatures and lack of moisture which characterize the late dry season constrain microbial activity, resulting in slow N turnover (Fierer and Schimel 2002; Austin *et al.* 2004) (Figure 2.12).

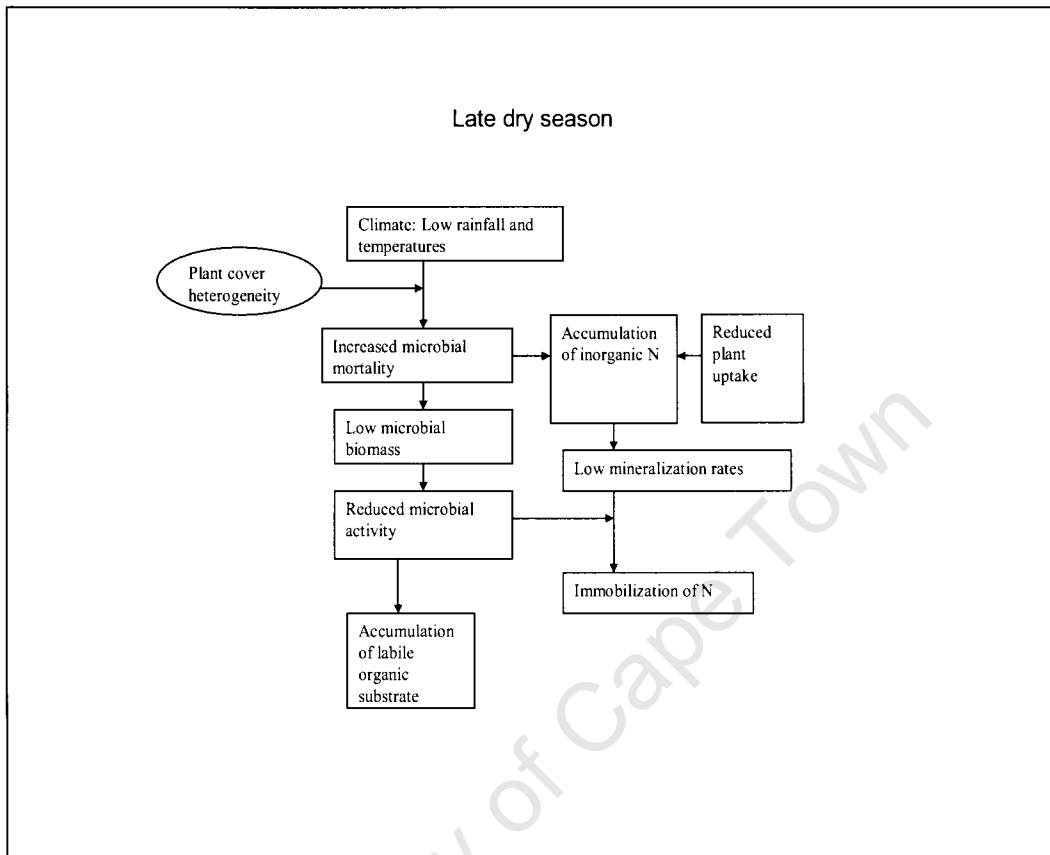


Figure 2.12 Schematic diagram of the relationship between rainfall and N mineralization in the late dry season. Microbial mortality and reduced microbial activity results in accumulation of labile organic substrate.

The early wet season is characterized by the advent of the rains and increased temperatures which triggers microbial activity and results in high rates of N mineralization. The early wet season experienced the highest rate of N mineralization, as it was the period when the first major rainfall induced mineralization pulse. An increase in rainfall above 50 mm at the beginning of the wet season triggers a massive increase in microbial activity and N mineralization rates. This sudden surge in N mineralisation rates after the first major rains has been observed in a number of other studies in the Kruger National Park. Woghiren (2002), observed slower rates of N mineralisation in winter and autumn (-0.05 and $-0.16 \mu\text{g N/g soil/day}$) and had the highest rates of N mineralization ($0.2 \mu\text{g N/gsoil/day}$) in spring after the first rains. Fisher (2006) had the highest N

mineralization in October ($0.78 \mu\text{g N/gsoil/day}$) and lowest N mineralization in July ($-0.65 \mu\text{g N/gsoil/day}$). The present study is however the first to show that the increase in N mineralization rate is directly related to mean monthly rainfall above 50 mm. This increase in N mineralization rates immediately after the first rains is the result of a release of inorganic N with microbial activity (Cui and Chadwell 1997; Beater 2002; Fierer and Schimel 2002; Austin *et al.* 2004).

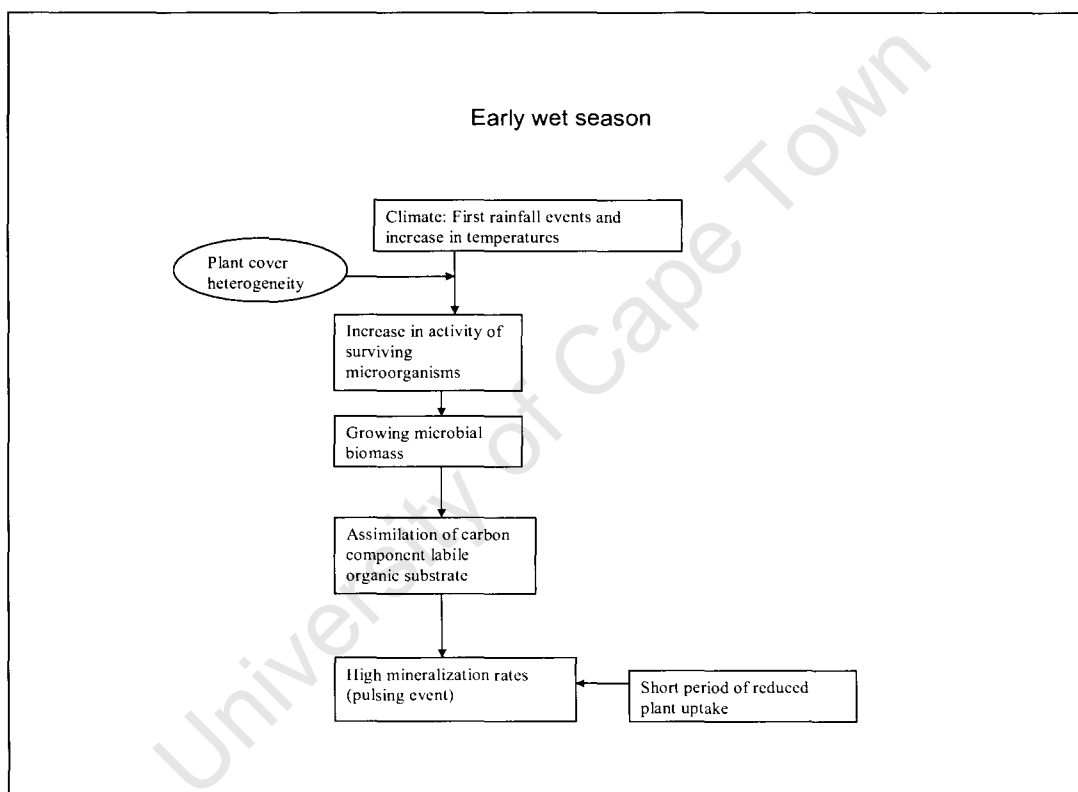


Figure 2.13 Schematic diagram of the relationship between rainfall and N mineralization in the early wet season. Increase in microbial activity and reduced plant uptake leads to high rates of N mineralization.

Labile organic materials which accumulate in winter lead to faster rates of N mineralization immediately after the first rains, termed mineralization pulses (Scholes *et al.* 2003; James *et al.* 2006). Mineralization pulses are short periods of high nitrogen availability that normally occurs immediately after the first rains (Scholes *et al.* 2003;

Schwinning and Sala 2004). This pulse is limited to a few days because of increased plant and microbial uptake resulting in immobilization (James and Richards 2004). Schwinning and Sala (2004) suggest that the increase in nitrogen availability in the soil during this time can supply all the N demands of plants for the rest of the growing season. The first major rainfall of the early wet season triggers microbial activity and a period of high rates of N mineralization (Figure 2.13).

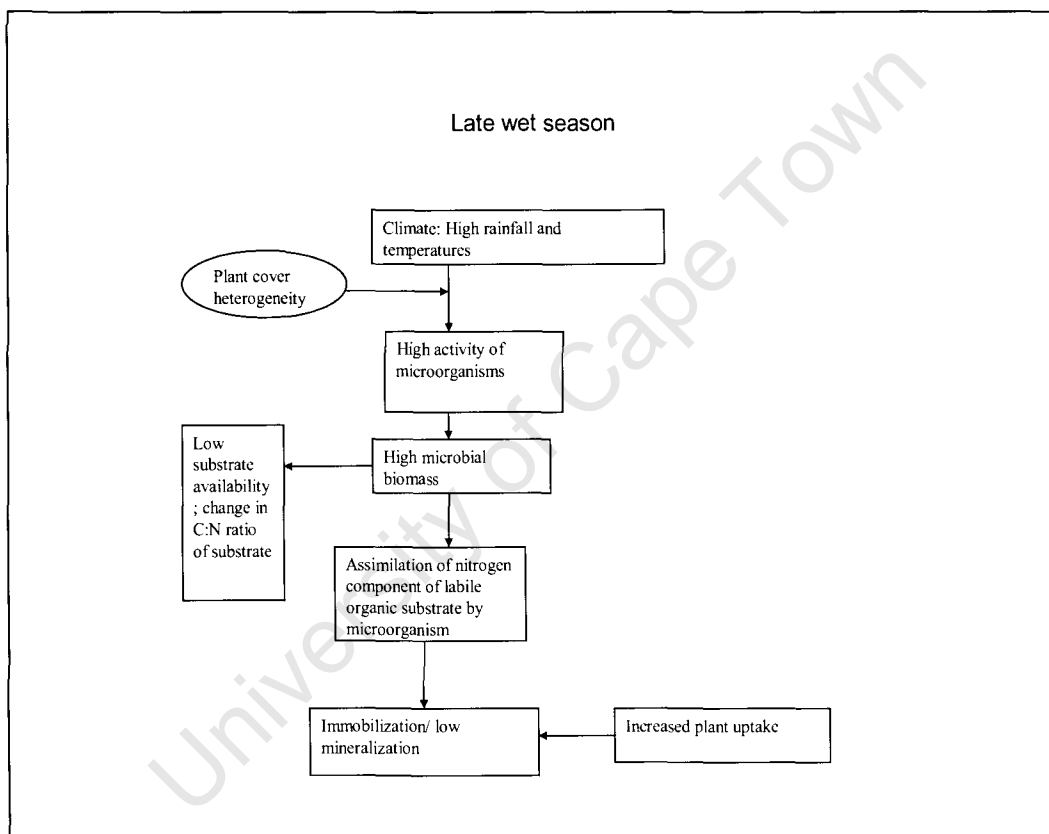


Figure 2.14 Schematic diagram of the relationship between rainfall and N mineralization in the late wet season.

As the growing season progresses the magnitude of the N mineralization pulse decreases resulting in a general pattern of high resource pulse immediately after the first rains and lower resource pulses towards the end of the season (James *et al.* 2006). This study showed that N mineralization dropped gradually throughout the season even when rainfall continued to be very high. This reduction in available N is caused by the

depletion of the labile organic substrate, rapid growth of microbial biomass and assimilation of N by microorganisms to meet their growth demands, and increase in plant uptake of inorganic N (James *et al.* 2004; Mikha *et al.* 2005). During this period, N availability is limited by low substrate availability, immobilization by microorganisms and increased plant uptake (Figure 2.14).

This relationship is however not uniform across the landscape as mineralization rates are highest under grasses and lowest in bare patches. These changes in available N across the landscape might form an important constraint on the ability of trees to establish in savanna that goes beyond merely competing with grasses for resources. In the first year of sampling N mineralization pulse occurred in November when monthly rainfall was 70mm. Whereas in the second year it occurred in October when rainfall was 50mm. Consequently, the study proposes that the key trigger for a pulse in N mineralization is rainfall above 50 mm in a month. This amount of rainfall only occurs from October to March resulting in a very strong seasonality of growth. The intense competition for this initial pulse in N between trees, grasses and microbes indicates the enormous constraints for trees establishing in savanna. Nitrogen mineralization rates are sensitive to changes in rainfall patterns and seasonality, hence N mineralization rates and pattern will differ from year to year based on rainfall amount.

CONCLUSION

My study shows that N mineralization rates are low in the dry season, and increase in the early wet season with the advent of major rainfalls. Nitrogen mineralization rates shows that they are limited by available water and/ or temperature in the dry season and stimulated by first major rainfall events in the early wet season. However temperature was not measured in this study even though it might be important for N mineralization rates. The late season period showed low N mineralization even though water was not limiting. Other studies show that substrate availability and increased plant uptake in the late wet season might be responsible for the low N mineralization rate in the late wet season (Cui and Chadwell 1997).

A number of recent studies have shown that the amount of plant available water plays an important role in determining the structure of savanna, while overlooking the impact that rainfall have on nitrogen mineralization (Sankaran *et al.* 2005; February *et al.* 2007; Hempson *et al.* 2007). This study is in agreement with previous studies (Scholes and Walker 1993; Scholes *et al.* 2003; Feig 2004) which showed that N mineralization rates are influenced by rainfall, however my study show that this relationship is not the same throughout the different seasons.

Wet and dry rainfall treatments had different levels of N availability, as N mineralization rates increased with increase in available water. Therefore I propose that it is not only the impact of water that is driving the structural change in savannas, but the combined effects of both water and nutrients, especially available N. Savanna structural diversity cannot be explained only by rainfall while ignoring the water-nutrient interaction.

This relationship is however not uniform across the landscape as mineralization rates are highest under grass and lowest in bare patches. Vegetation cover regulates the effects that rainfall may have on N mineralization rates. Plant cover heterogeneity in savanna will results in different levels of available N which may also influence tree-grass relations. I therefore accept the hypothesis that variability in rainfall, coupled with plant cover heterogeneity results in different levels of N availability across the savannas systems. This variability in N across the savanna ecosystem can shed more information in understanding tree-grass coexistence and plant structural heterogeneity in savannas.

CHAPTER 3

The role of grass competition on tree sapling growth under wet and dry rainfall cycle in a mesic savanna

INTRODUCTION

The coexistence of trees and grasses and the resultant structural diversity in savannas has intrigued researchers for decades (Walter 1971; Scholes 1997; Sankaran *et al.* 2004; Silvertown 2004). Savannas vary in structure from open grassland with few trees, through deciduous woodlands with a herbaceous layer to dry forest (Scholes and Walker 1993, Scholes 1997, House *et al.* 2003). Savannas are heterogeneous and dynamic, and they have patches which are in different states of transition between herbaceous and woody dominance (Wiegand *et al.* 2006). This interaction between trees and grasses lead to an important question in savanna ecology; understanding how trees and grass coexist without one becoming dominant (Sarmiento 1984).

Different hypothesis and models that explain tree-grass coexistence have been proposed in the past. They can be grouped into two main categories, those with competition-based mechanisms and those with disturbance-based mechanisms. Competition –based mechanisms such as the ‘rooting niche’ hypothesis focuses on the competition of trees and grass for resources such as water. The rooting niche hypothesis proposes that coexistence is possible as grass use water in the upper layers of the soil, while trees use water deeper down in the soil profile (Walter 1971). This hypothesis also suggest that grass will grow best under drier conditions as compared to trees because of limited infiltration of water to the deeper levels of the soil. On the other hand, trees will benefit from above-average rainfall years as more water will infiltrate deep into the soil profile.

Disturbance-based mechanisms such as the demographic bottleneck model (Higgins *et al.* 2000) are generally supported by recent literature as compared to the competition-based mechanisms (Scholes 1997, Hipodonka *et al.* 2003; House *et al.* 2003; Sankaran *et al.* 2004). The demographic bottleneck model as proposed by Higgins *et al.* (2000) suggests that variability in rainfall and fire intensity, coupled with the longevity of adult

trees, facilitates tree-grass coexistence. The model shows that seedling establishment is limited by drought, while sapling recruitment is limited by fire.

Both of these hypotheses highlight the importance of rainfall as a driver of savanna dynamics. However, the effects of rainfall on savanna dynamics cannot be separated from available nutrients as studies have shown that rainfall is correlated with available nitrogen (Scholes and Walker 1993; Feig 2004). Schwinning and Sala (2004) have shown that rainfall triggers ecosystem processes like nitrogen (N) mineralization in the soil. Furthermore, the response of organisms to resources such as rainfall in terrestrial systems is hierarchical and interconnected (Schwinning and Sala 2004). Microorganisms respond to available water by mineralizing organic substance into inorganic forms, which plants then assimilate for growth purposes (Schwinning and Sala 2004).

The role of available nutrients in determining savanna structure is overshadowed and made complex by the interconnectedness of factors such as fire, herbivory and rainfall (Higgins *et al.* 2000; Jeltsch *et al.* 2000; Aranibar *et al.* 2003). However, other studies have shown that N plays an important role in terrestrial systems and can affect species richness and diversity (Stevens *et al.* 2004; Gundale *et al.* 2006). More-over, N is an important nutrient as it limits productivity of plants, particularly in nutrient-poor systems like savannas (Lata *et al.* 2004; Singh and Kashyap 2006). In nutrient-limited arctic tundra, N availability shapes the species composition of the plant community, and species dominance is related to the availability of either NO_3^- or NH_4^+ (McKane *et al.* 2003). Even though Knoop and Walker (1985) have long suggested that nutrients could play an important role in determining savanna structure, few studies have investigated this possibility.

The previous chapter (Chapter 2) shows that microorganisms respond to the first rainfall in the growing season by mineralizing nitrogen and making it available for plant uptake. Chapter 2 also shows that dry and wet rainfall manipulation treatments had significant consequences for N availability in the soil as N mineralization rates increased in the wet treatments and decreased in the dry treatments. As nitrogen is an important nutrient for

plant growth (Grant and Scholes 2006), different levels of N mineralization rates facilitated by varying moisture availability and vegetation cover, can have significant effects on tree-grass dynamics and savanna structure.

Nitrogen mineralization is a process whereby soil microbes make N available to plants (Binkley and Vitousek, 1989). This process occurs mainly in the surface of the soil, and is strongly correlated to water availability as it increases with an increase in soil moisture (Chapter 2). Hipodonka *et al.* (2003) showed that in arid savannas of Southern Africa trees and grasses utilize the same soil volume for water and nutrients. Consequently, it is important to understand the effects of competition for resources between trees and grasses, and how that influences structural diversity in savannas. Recruitment of saplings to adult sizes of trees is important with regard to structural diversity in savannas (Scholes and Archer, 1997). Saplings are often hindered by both fire and herbivory from reaching adult size classes (Midgley and Bond, 2001), resulting in a more open savanna dominated by small trees and shrubs. However, I believe that without competition for resources trees would rapidly grow to escape the flame-browse height (Midgley and Bond, 2001).

In chapter 2 I show that N mineralization is strongly, positively correlated with available water. I also show that N mineralization rate is highest under grasses and lowest in bare patches. These changes in available N across the landscape form an important constraint on the ability of trees to establish under the pressures of fire and herbivory. As N mineralization is highest under grasses, competition for N with grasses places an enormous constraint on tree growth. Here I test the effects that competition for resources may have on biomass production by removing grasses around trees and removing trees among grasses. The primary objective is to ascertain the extent to which savanna structure is determined by competition for resources between trees and grasses.

I do this through determination of plant productivity and physiological responses of trees and grasses under manipulative experiments as described in Chapter 2. In this experiment, trees and grasses are subject to a regular annual amounts of rainfall (control treatments), 50% reduction in rainfall (dry treatments) and 50% increase in rainfall (wet

treatments) was set up to determine the effect of varying levels of moisture on tree-grass dynamics.

METHODS

Study site

The study was conducted in the south-western part of the Kruger National Park at Pretoriuskop. The dominant soil at Pretoriuskop is the nutrient poor sandy soils underlain by granite (Gertenbach 1983). The dominant tree species are *Terminalia sericea* and dominant grasses are *Hyperthelia dissoluta* (Gertenbach 1983).

Experimental layout

Tree-grass and grass combination treatments on a rainfall gradient as described in chapter 2 where rainfall was manipulated in a wet, dry and control treatment were used. Consequently, seven treatments were used to determine plant productivity under different tree-grass combination treatments and under the rainfall manipulation treatments. These seven treatments included three tree-grass combination treatments on a water gradient of 50% rainfall addition, 50 % rainfall reduction and control where rainfall was not manipulated. Three grass-only treatments on the same water gradient, and one tree-no grass treatment with no rainfall manipulation. All treatments were replicated six times. Refer to figure 2.1 for the experimental design. Data were collected for two consecutive growing seasons, 2005 – 2006, referred to as Year 1, and 2006 – 2007 referred to as Year 2.

Grass standing crop

Grass standing crop was measured in both grass and tree-grass combination treatments using a disc pasture meter (DPM). Grass standing crop was used to determine the response of grass to different water treatments and associated available N, as well as the effect of competition from tree saplings. A Disc pasture meter is widely used as a simple and rapid method for measuring compressed grass height (Trollope and Potgieter 1986; Trollope 1990; Zambatis *et al.* 2006). The DPM was lowered on top of the grass and the settling height was recorded in cm. Six permanent points were placed across the plot to

mark the sward of grass that was measured. These points (together with other replicates), were then averaged to get a single reading for the treatment. The grass height as determined by the DPM was converted to grass biomass with the following equation;

$$[31.7176 (0.3218^{1/x}) x^{0.2834}]^2 = \text{kg} / \text{ha}$$

Where x is the mean DPM height in cm of a site (Zambatis *et al.*2006).

The measurements were carried out on a monthly basis during the growing season from September 2005 to April 2006 and from September 2006 to April 2007.

Tree height

Terminalia sericea saplings were used as the study species because of their dominance in the Pretoriuskop area. A measuring rod with a total height of 3 m was used to determine the height of these saplings. Tree height was used as an indicator for growth under the different manipulative experiments. Tree height was measured in four treatments, three tree and grass combination treatments which were on a rainfall gradient of wet, control and dry, and the fourth treatment with a tree but no grass. The height measurements from all six replicates of each treatment were pooled together to get the average tree height for each treatment. In total, 24 trees were measured. At the beginning of the study heights of the saplings were from The measurements were carried out on a monthly basis for two growing seasons from September 2005 to April 2006 and from September 2006 to April 2007.

Stem growth

Tree saplings (ranging in diameter from 2 – 5 cm) were fitted with a manual dendrometer bands (Agricultural Electronics Corporation, Tucson, AZ, USA) and monitored monthly for radial increments. Dendrometer bands are 3 mm wide bands of metal placed around the stem of a tree and held under tension by a spring loaded vernier gauge. Changes in radial diameter, which include both the expansion and/or contraction of the stem, were read manually from the vernier gauge at a resolution of 0.1 mm at the end of the month from September 2006 to April 2007 (February *et al.* 2007). Dendrometer bands were fitted on the trees in four treatments in total, three tree-grass combination treatments on a water gradient of 50% rainfall addition (wet), 50 % rainfall reduction (dry) and control,

and one treatment with tree but no grass. In total, 24 dendrometer bands were placed on trees (four treatments replicated six times).

Physiological response of *Terminalia sericea* saplings

To test for the physiological response of *Terminalia sericea* saplings to differing amounts of plant available water and competition from grass, plant moisture stress, specific leaf area and foliar nutrients (nitrogen, phosphorus and carbon) were determined. Four treatments were used to test sapling response under these different conditions, three treatments with both trees and grasses under wet, control and dry conditions, and one treatment with tree but no grass.

Plant moisture stress

Water lost through transpiration is continuously replaced by available soil water through the roots (February *et al.* 2007). The amount of water available to plants is reflected in the amount of tension on the water column (Scholander *et al.* 1965; Miller *et al.* 1984; February *et al.* 2007; Hempson *et al.* 2007). Xylem Pressure Potentials which are a measure of the tension on the water column were determined using a Scholander Pressure Chamber (PMS instrument Co., Corvallis, OR, USA). Six saplings from each of the three tree-grass combination treatments on a gradient of dry, wet and control were measured for moisture stress in summer. The experiment was carried out at mid-day on sunny cloudless days during January 2007 (February *et al.* 2007).

Specific leaf area index

Specific leaf area is the ratio of leaf area to leaf dry mass (Reich *et al.* 1999; Nasahara *et al.* 2008). Twelve fully expanded leaves were randomly selected per tree. The leaves that were chosen were without serious pathogen or herbivore damage (Garnier *et al.* 2001). The leaves were placed on a white background and photographed to ensure separation from the background. Average leaf area was then determined for the 12 leaves using image processing software by SigmaScan. The leaves were then oven-dried at 60⁰C for two days and weighed to determine the dry mass. Specific Leaf Area (SLA) was

determined as the area of leaves per dry mass (cm^2/g). Specific leaf area was determined in late summer season during the month of January 2006.

Foliar Nutrients

Foliar nutrients of plants were used to determine the effects of competition and water availability on foliar chemistry. Foliar samples were collected from *Terminalia sericea* saplings and *Hyperthelia dissoluta* grass in all the treatments. On each tree, 15 leaves were collected randomly from all sides of the tree and placed in a paper bag. Samples were oven-dried at 60°C for 2 days and ground to a fine powder using a Wiley mill. A 10g sample was then sent to the Agricultural Research Council in Pretoria for analysis of the total percentage of nitrogen, carbon and phosphorus using the Dumas combustion method (Leco, St. Joseph, MI, USA). The Dumas method as implemented in the Leco CNS 2000, quantitatively determines foliar nutrient content using an induction furnace and a thermal conductivity detector (Etheridge *et al.* 1998, Horneck and Miller 1998).

Statistics

Statistical analysis were carried out using STATISTICA 8 (Statsoft Inc. Tulsa, OK, USA) computer software package. A factorial ANOVA was used to determine the treatment effects on grass and tree growth over different months and years. One way ANOVA was used to determine significant differences among treatments on specific leaf area, xylem pressure potentials and foliar nutrients. A scatter plot was used to determine the correlation between volume soil moisture % and grass biomass. When data differed significantly ($p < 0.05$), either Tukey HSD for equal N or Tukey unequal N HSD test was used to show which treatments differed significantly. A Levene's Test was performed for determining homogeneity of variance on the dependant variables, and residuals of dependant variables were tested for normality.

RESULTS

Productivity: Grass biomass

Grass biomass in all the treatments declined during the dry season from August 2005 to October 2005 when mean monthly precipitation was less than 10.5 mm (Figure 3.1 and 3.3). There was a steady growth between November and April as rainfall remained high and above the monthly average.

In the 2006 – 2007 growing season, grass biomass ranged between 1200 – 1400 kg/ha, and peaked in the period between December and February where it reached 1800 kg/ha (Figure 3.2 and 3.3). All treatments peaked between November and February as rainfall peaked to 133 mm. Rainfall for January (55mm) and February (24 mm) were below average resulting in a decline in grass biomass in all treatments with a slight increase in April as rainfall increased to 72 mm.

The growth trend in both growing seasons differed towards the last months of the season, from February to March. Grass biomass in 2005 – 2006 growing season remained high, while it declined in 2006 – 2007 growing season as rainfall fell below the average.

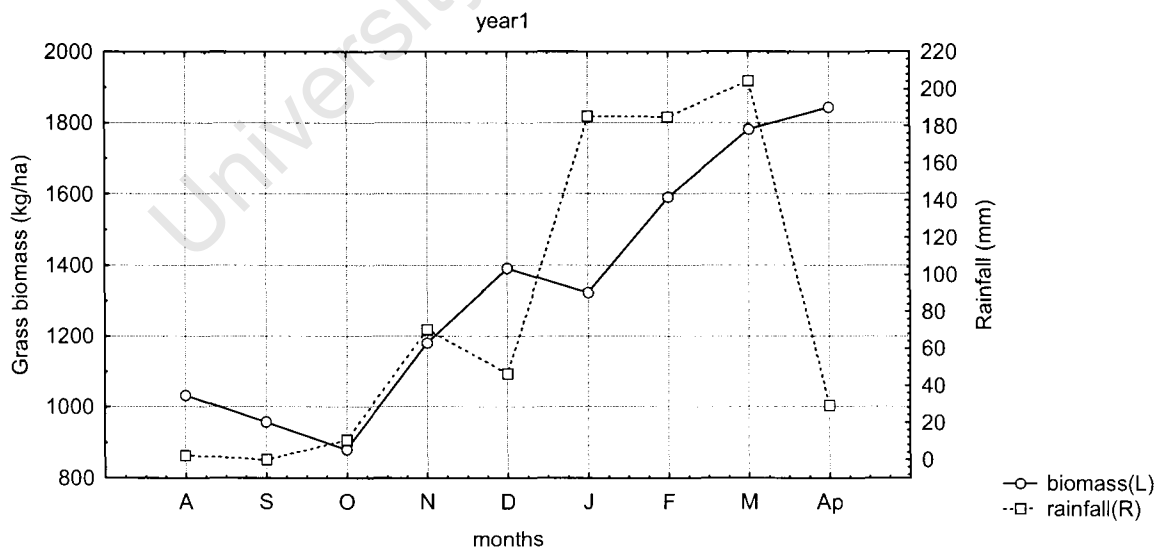


Figure 3.1 Graph of grass biomass and rainfall for the first year of sampling from August 2005 – April 2006.

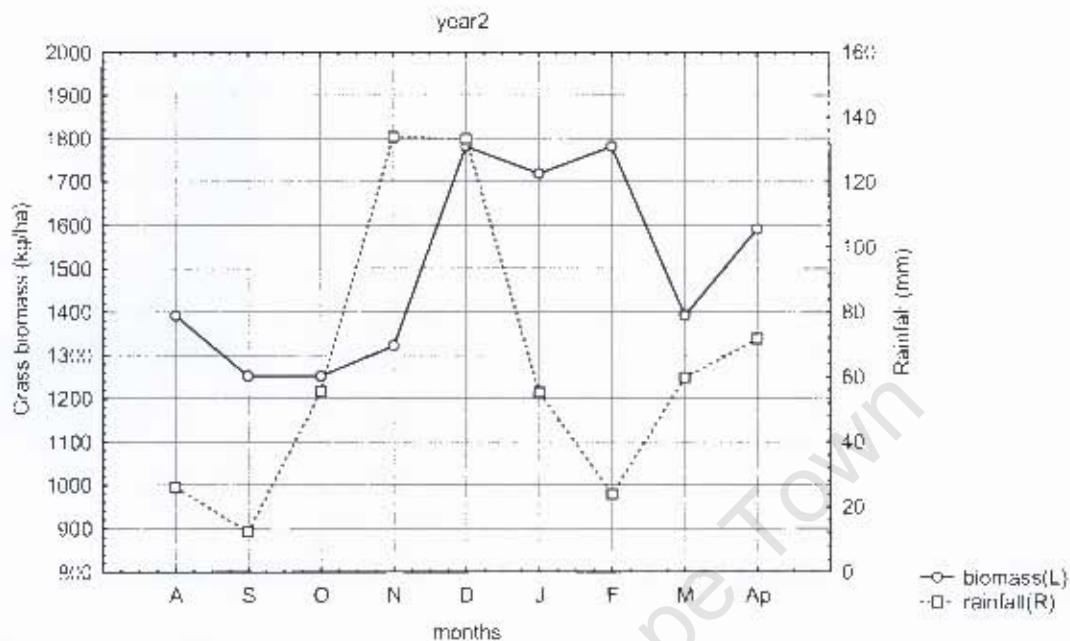


Figure 3.2 Graph of grass biomass and rainfall for the second year of sampling from August 2006 – April 2007.

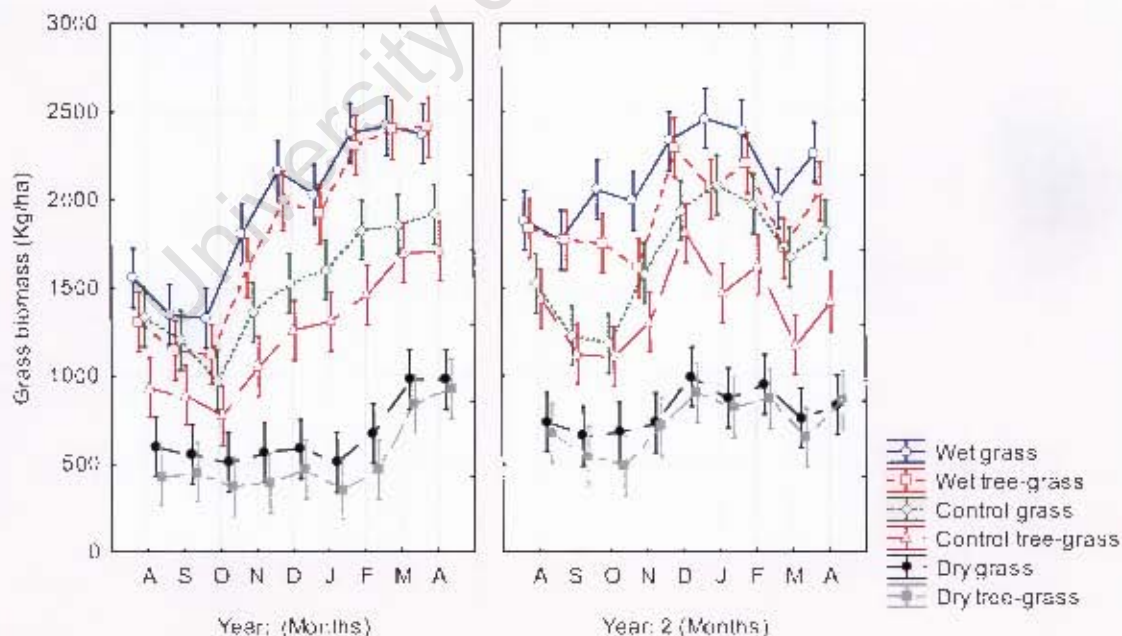


Figure 3.3 Graph of grass biomass showing individual treatments as determined using disc pasture meter at three rainfall treatments of wet, dry and control for the 2005 – 2006, and 2006 – 2007 growing season. Vertical bars denote +/- standard errors.

The wet treatments had a higher grass biomass (1843 – 2079.2 kg/ha; Table 3.1) in both years of sampling, while dry treatments had the lowest grass biomass (561.1 – 722.1 kg/ha; Table 3.1). There was a significant difference among all treatments ($p < 0.001$). However, grass only treatments had a highest biomass than tree-grass combination treatments (Table 3.1).

Table 3.1 Mean standing crop and grass biomass for two consecutive growing seasons, 2005-2006, and 2006 – 2007. Standing crop was converted to grass biomass according to a calibration by Zambatis *et al.* (2006).

Treatment	Mean standing crop (cm)		Grass biomass (Kg/ha)	
	2005-2006	2006-2007	2005-2006	2006-2007
Wet grass	6.1	6.6	1901.3	2079.2
Wet Tree & grass	5.8	6.3	1843	1962.8
Control grass	4.6	4.9	1459	1591.5
Control tree & grass	4.2	4.6	1322.4	1459.3
Dry grass	2.6	3.1	722.3	880.6
Dry tree & grass	2.2	2.7	561.1	722.1

Grass biomass was high (1380 – 1540 kg/ha) in plots without trees and low (1180 – 1540 kg/ha) in plots with trees for two growing seasons (Figure 3.4). However, there were no significant differences between the plots in both growing seasons.

Tree height

Tree height in the wet treatments was lowest (year 1: 186 cm and year 2: 238 cm) among all treatments for both years of sampling, but increased in both dry and control treatments (Figure 3.4). When grass was removed, tree height in the tree no-grass treatment was significantly (Year1: $p < 0.005$; Year2: $p < 0.03$) higher than in wet, dry and control treatments (Figure 3.5).

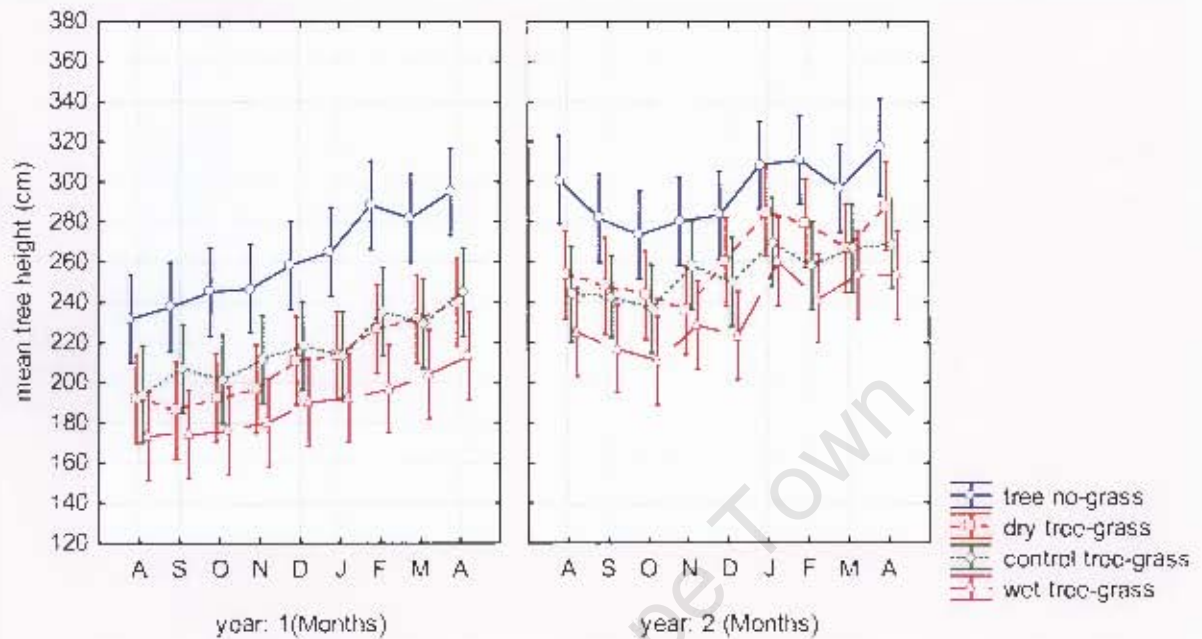


Figure 3.4 Average tree heights at four treatments, three different rainfall treatments of wet, control and dry, and one tree no grass treatment. Vertical bars denote \pm standard errors.

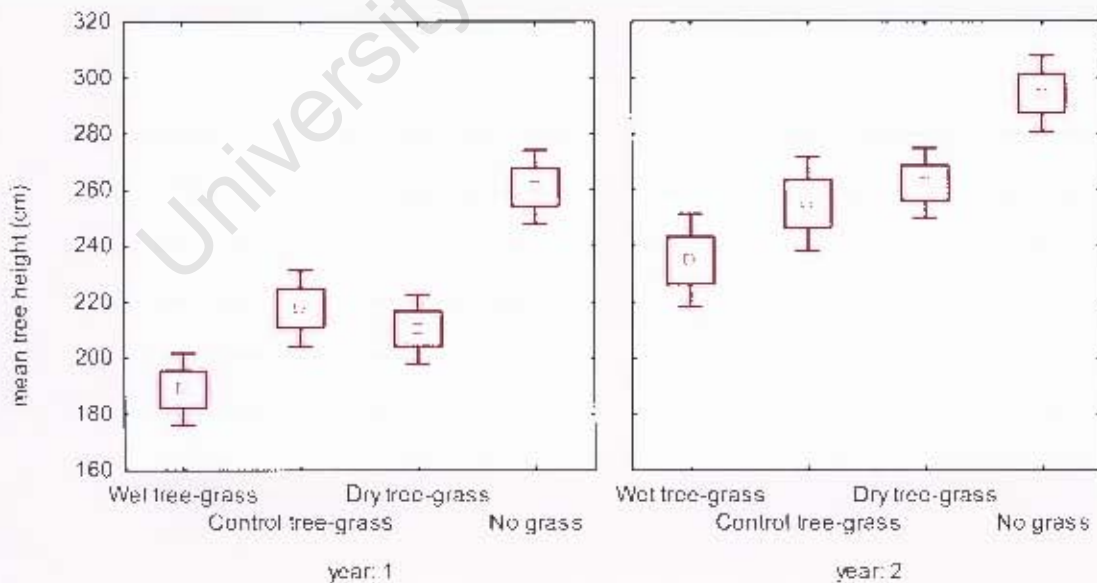


Figure 3.5 Average heights of trees in different treatments over two years of sampling. The bars represents ± 1.96 standard error of means, the bigger box represents the \pm standard error of means, and the smaller box represents the means.

Stem growth

The results for dendrometer band measures show negative growth when rainfall is below 5 mm between the months of August and September for both growing season (2005-2007). Thereafter there was a constant positive growth from October to January as rainfall increased. The growth pattern stabilized for the months of February, March and April. The tree no-grass treatments showed the highest increase in stem diameter (6.5cm), followed by the control (4.5 cm) and dry treatments (4.2 cm) (Figure 3.6, 3.7).

The wet treatments had the lowest stem growth throughout the growing season (4 cm). The difference in water availability between wet, dry and control treatments did not have significant effects on tree growth. However, when grass was removed on the tree-no grass treatments, there was increased growth and a significant difference between tree-no grass treatments and dry ($p < 0.03$). This difference was much stronger with $p < 0.02$ between the tree-no grass treatments and wet treatment which had the lowest growth among all treatments.

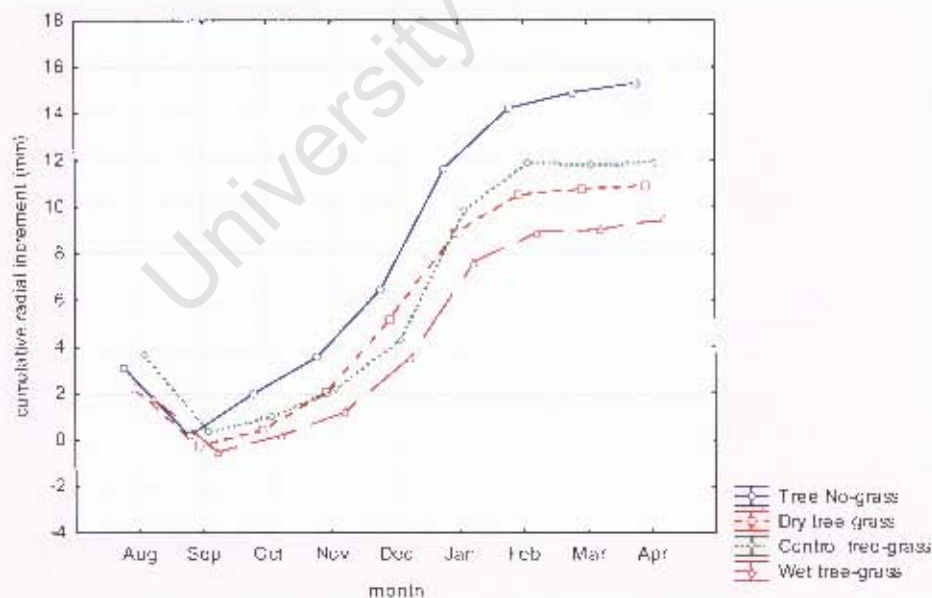


Figure 3.6 Mean cumulative radial increments in stem growth of *Terminalia sericea* saplings in different rainfall manipulation treatments and tree no-grass treatments over the growing season.

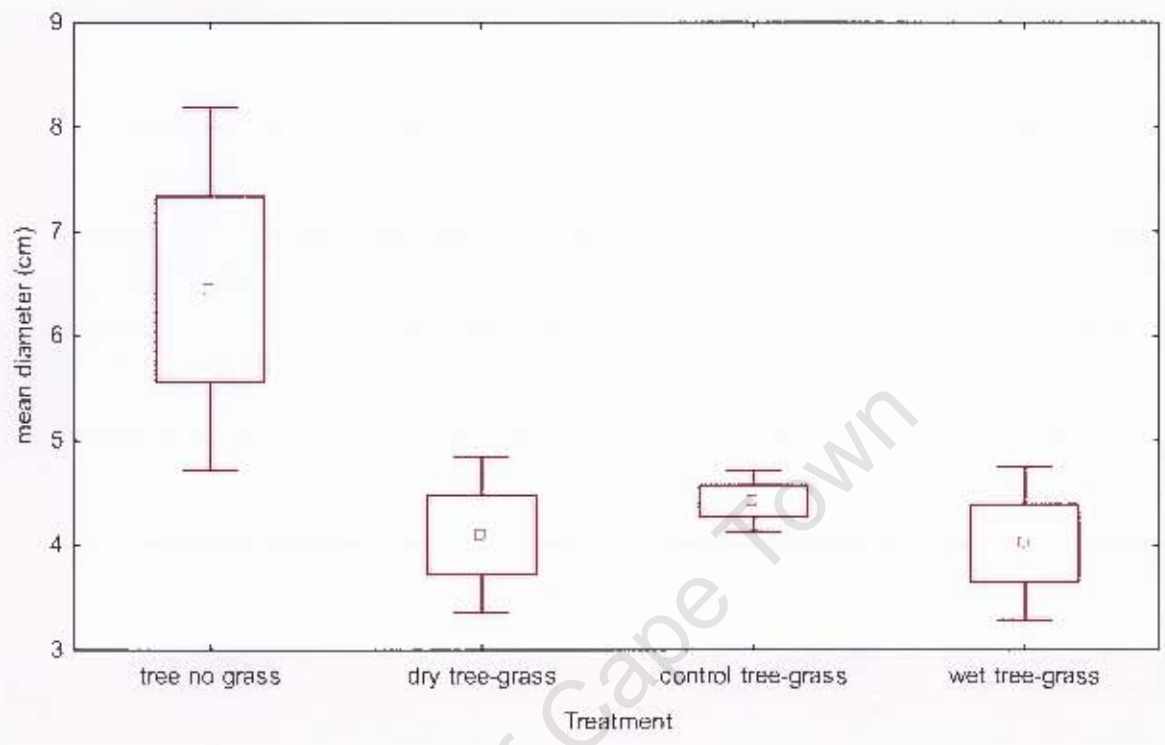


Figure 3.7 Mean stem diameter of *Terminalia sericea* saplings in different rainfall manipulation treatments and tree no-grass treatments at the end of the study.

Physiological response of *Terminalia sericea* saplings

Plant Moisture stress

To test for plant water stress levels in the different treatments, xylem pressure potentials (XPPs) were determined. Trees in the No-grass treatments were under less water stress, than the other treatments (Figure 3.8), there were however no significant differences between treatments.

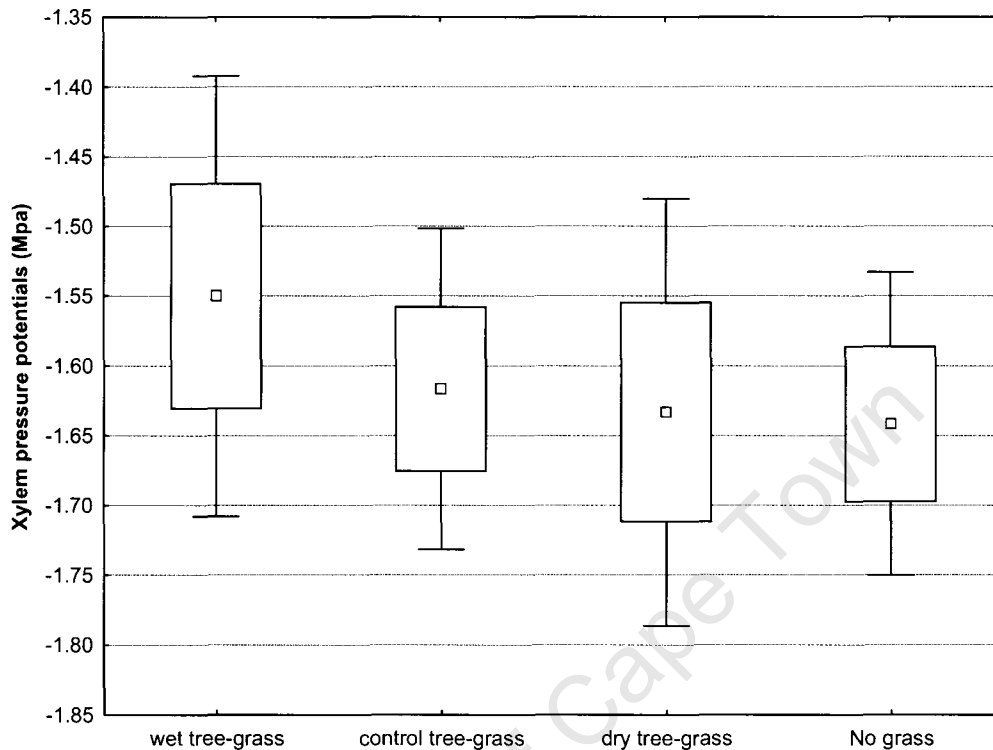


Figure 3.8 Mean mid day xylem pressure potentials for trees in tree-grass combination treatments under wet, dry and control treatments. The bars represents +/- 1.96 standard error of means, the bigger box represents the +/- standard error of means, and the smaller box represents the means.

Specific leaf area index

Specific leaf area index (SLA) was determined for all tree treatments. The dry treatments had the largest SLA followed by the control treatments (Figure 3.9). Wet and No-grass treatments had the lowest SLA, but there were no significant differences among all treatments.

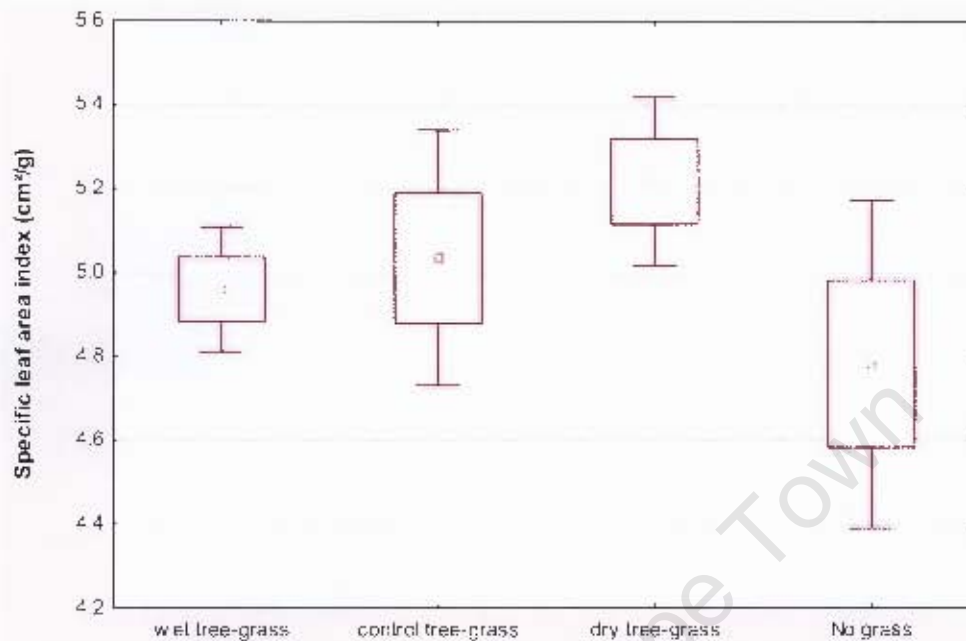


Figure 3.9 Specific leaf area index of trees in tree-grass combination treatments under wet, control and dry conditions. The bars represents ± 1.96 standard error of means, the bigger box represents the \pm standard error of means, and the smaller box represents the means.

Foliar nutrients

There were no trends for leaf total C % and total P % between the different treatments (Table 3.2). The C:N ratio was highest in the wet treatments, followed by control, dry and no grass treatments. Total N % was high in the dry treatments, but low in wet and no grass treatments. These results are, however, not significantly different.

Table 3.2 Means of total N %, total P %, total C %, and C:N ratio of tree foliage in wet, control and dry, no grass treatments. Values of standard error are in brackets.

	Total C %	C:N ratio	Total P %	Total N %
No grass	45.77 (0.17)	2.77(0.10)	0.12(0.004)	1.42 (0.06)
Dry tree-grass	45.53 (0.15)	2.82(0.15)	0.11(0.002)	1.56 (0.05)
Control tree-grass	46.03 (0.15)	2.87(0.11)	0.13 (0.02)	1.52 (0.03)
Wet tree-grass	45.95 (0.20)	2.99(0.13)	0.12 (0.01)	1.43 (0.05)

Table 3.3 Results of an ANOVA performed for total N, P, C, and C:N ratios of tree foliage in wet, control and dry treatments. Reported statistics include the sum of squares (SS), degree of freedom (DF), the F statistic and p value.

	SS	DF	F	p
Total C %	0.87	3	1.75	0.19
C:N ratio	0.16	3	0.57	0.64
Total P %	0.001	3	0.66	0.59
Total N %	0.080	3	2.14	0.13

Total C in grass foliage did not show significant differences among treatments, while C:N ratios were high the wet treatments (84.4), followed by the control treatments (74.5), and were lowest in the dry treatments (61.1) (Table 3.4, 3.5). Total P was highest in the dry treatments (0.08), and lowest in the wet treatments (0.05) (Table 3.4). The dry treatment differed significantly ($p < 0.01$) from the wet treatments, but did not differ significantly from the control (Table 3.5).

Table 3.4 Means and standard error (in brackets) of total N %, total P %, total C %, and C:N ratio of grass foliage in wet, control and dry treatments.

	Total C %	C:N ratio	Total P %	Total N %
Dry tree-grass	42.1 (0.24)	61.1(4.19)	0.08(0.01)	0.71 (0.05)
Control tree-grass	41.4 (0.33)	74.5 (8.19)	0.07(0.01)	0.59 (0.06)
Wet tree-grass	42.3 (0.06)	84.4(2.98)	0.05(0.003)	0.50 (0.02)

Table 3.5 Results of an ANOVA performed for total N %, total P %, total C %, and C:N ratio of grass foliage in wet, control and dry treatments. Reported statistics include the sum of squares (SS), degree of freedom (DF), the F statistic and p value.

	SS	DF	F	p
Total C %	2.306	2	2.96	0.09
C:N ratio	1368	2	3.36	0.07
Total P %	0.003	2	7.19	0.01
Total N %	0.105	2	3.63	0.06

DISCUSSION

In this chapter I test the hypothesis that competition for resources such as N and water may affect the growth rates of trees in savanna systems to such an extent that trees may not establish or recruit into adult size classes. As growth rates of trees are affected by competition with grasses, trees are maintained at heights below 2 m where they will be susceptible to the negative effects of fires which are inherent to the savanna biome (Higgins *et al.* 2000).

Chapter 2 showed that the wetter treatments also have the highest rate of N mineralization, suggesting that it is the increase in available water coupled with an increase in N mineralization rate that elevates grass biomass production. Significant differences in grass biomass among all rainfall manipulation treatments showed that grass biomass production is very sensitive to changes in available moisture and N.

The increased growth of trees in the No-grass treatments show that tree growth is limited by grass competition. However, the effects of grass competition differ with treatment. Competition for N and water was highest in wet treatments as trees showed the slowest growth while grasses had the highest biomass. Based on the results from chapter 2 I speculate that low soil moisture levels in these treatments led to low N mineralization rates and low grass productivity, creating an opportunity for increased tree growth as competition decreased. Tree growth benefited more from grass absence than from reduced grass competition as my results showed that tree growth was highest when grass was removed from the treatments. This finding corresponds with findings from bush encroachment studies which shows that trees grow best after removal of grass by heavy grazing (Skarpe 1990; van Langevelde *et al.* 2003). Competition for resources such as N and water affect the growth rates of trees in savanna systems to such an extent that trees may not establish and reach their full potential. As growth rates of trees are affected by competition with grasses, trees are maintained at heights below 2 m because of the regular fires inherent to the savanna biome (Higgins *et al.* 2000, Midgley and Bond 2001).

Competition for resources between grasses and woody plants has been demonstrated in a number of studies in different ecosystems. A study on plant responses to competition which was carried out across a prairie-forest boundary also showed that competition had much larger impacts on the performances of juvenile plants (Peltzer 2001). Peltzer (2001) showed that both grass and shrub seedling growth was suppressed by competition effects from neighbors. Simmons *et al.* (2007) studied the effects of grasses on woody growth in a temperate savanna, and found that tree basal area increased significantly following removal of grasses. A study in the Australian mesic savanna showed that growth of adult trees decreased in high rainfall and where herbivores were removed, possibly because of increased competition from herbaceous plants (Prior *et al.* 2006).

Knoop and Walker (1985) found that competition between herbaceous and woody plants differed in broad-leaved savannas and fine-leaved savannas because of different soil properties. They found that the effect of grass on mature woody plant growth was negligible in broad leaved savannas, but woody growth was reduced by competition in fine leaved savanna. The results for my study, which was under taken in a broad leaved savanna, differed from that of Knoop and Walker (1985) in that it showed significant negative effects of grass on woody plant growth. The main difference is that in my study I worked with saplings and not mature trees. It is possible that competition for resources such as water and nutrients between grasses and mature trees is eliminated by the expansive and well developed root system of mature trees.

The findings of my study differed with the predictions of Walter (1971) who suggested that low rainfall periods will favor grass as water does not penetrate to the deeper layers of the soil and woody plants can not establish. My study shows that a dry period leads to low available N which limits grass productivity and competition, creating an opportunity for an increase in growth rates of tree saplings. While wetter periods lead to increased N availability and more grass productivity which suppress tree growth. Furthermore, the increased growth of saplings in treatments without grass shows that competition rather than rooting niche between grass and trees is more important (Hipondoka *et al.* 2003).

My study shows that grasses are stronger competitors for water and available N, and tend to support the demographic bottleneck model which proposes that variability in rainfall provide irregular opportunities for tree saplings to reach fire-resistant size class (Higgins *et al.* 2000). The demographic bottleneck model proposes that seedling establishment and recruitment of saplings to adult tree sizes are important stages in determining structural diversity in savannas (Higgins *et al.* 2000, Midgley and Bond, 2001). Slow sapling growth and high grass biomass in wet treatments show that wet years benefit grass more than trees. Whereas trees grows quicker only when grass is completely removed. An Increase in grass biomass also leads to frequent and intense fires which causes topkill in trees and further limits sapling recruitment to adult classes (Higgins *et al.* 2007). However, it is not only the effects of fire that limit sapling recruitment, but also grass competition which retard tree growth significantly. I propose that there will therefore be no recruitment of saplings to adult classes during wet periods (Figure 3.10). When it is dry, reduced grass productivity mitigates the competition effects of grasses resulting in increased growth of saplings. Saplings also benefit from the longer fire return interval during this period of low grass biomass (Higgins *et al.* 2007). Recruitment opportunities occur as grass biomass is low, resulting in reduced competition and cooler fires (Figure 3.11).

CONCLUSION

Grasses are stronger competitors for resources such as water and available N, and this limits the growth of saplings. Grasses limit sapling recruitment directly through competition for resources, and indirectly through providing fuel for fire. However, the impact and intensity of grass competition on trees is regulated by availability of resources such as available water and N.

The study concludes that the recruitment of tree sapling to adult classes will occur in below average rainfall years and/or when grass has been removed through heavy grazing. Consequently, it is variability in rainfall which facilitates tree-grass dynamics in savanna systems (Higgins *et al.* 2000, Sankaran *et al.* 2005). This study concludes that different

levels of N mineralization rates, facilitated by varying moisture levels and differences in vegetation cover, have significant effects on plant growth with implications on tree-grass coexistence and savanna structure (Scholes *et al.* 2003).

My study has also shown that the effects of rainfall in savanna can not be considered in isolation without recognizing its impact on N mineralization rates. Understanding tree-grass coexistence in savanna requires ecologists to appreciate that rainfall, nutrients, fire, herbivory, and soil properties interact at different scales in time and space.

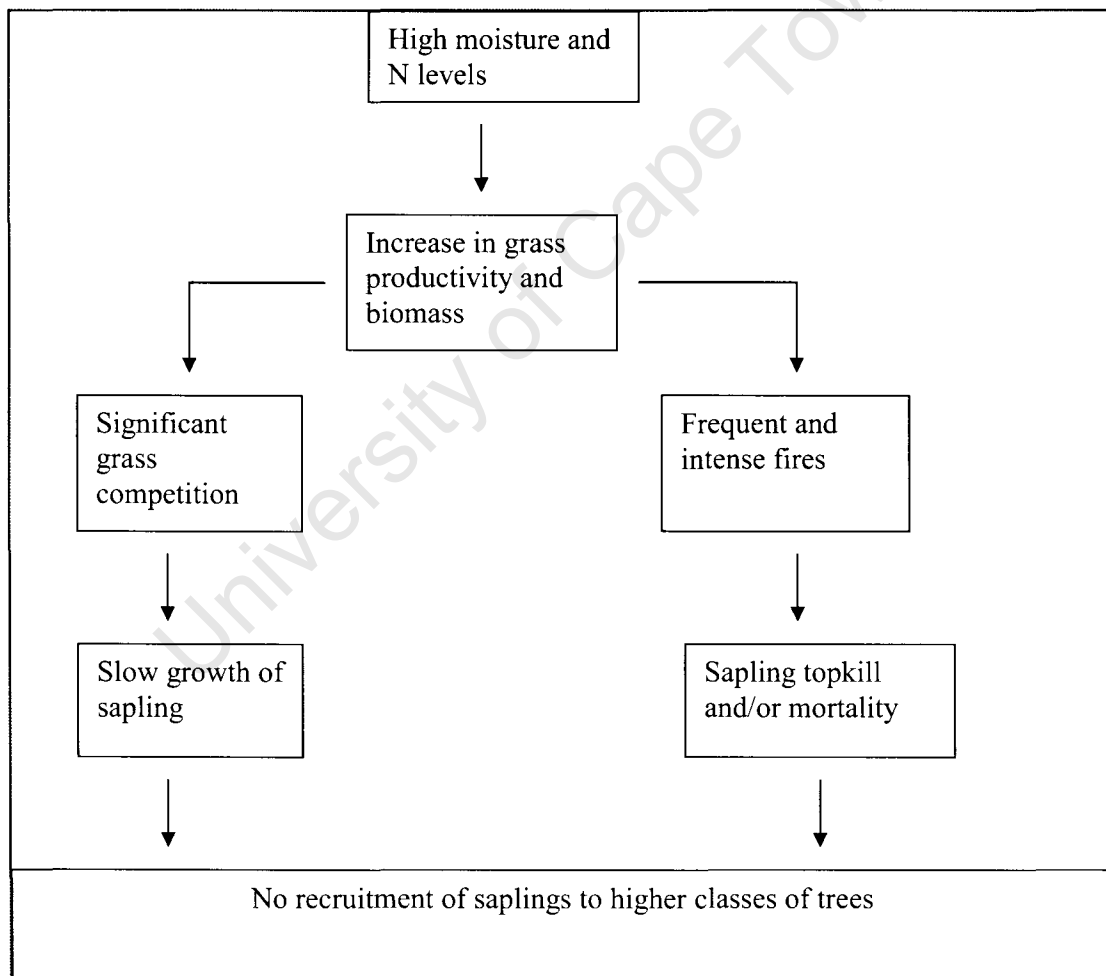


Figure 3.10 Schematic presentation of grass-sapling interaction during wetter periods. Wetter periods are times of high resource abundance which leads to increased grass biomass and associated competition and fire effects on saplings.

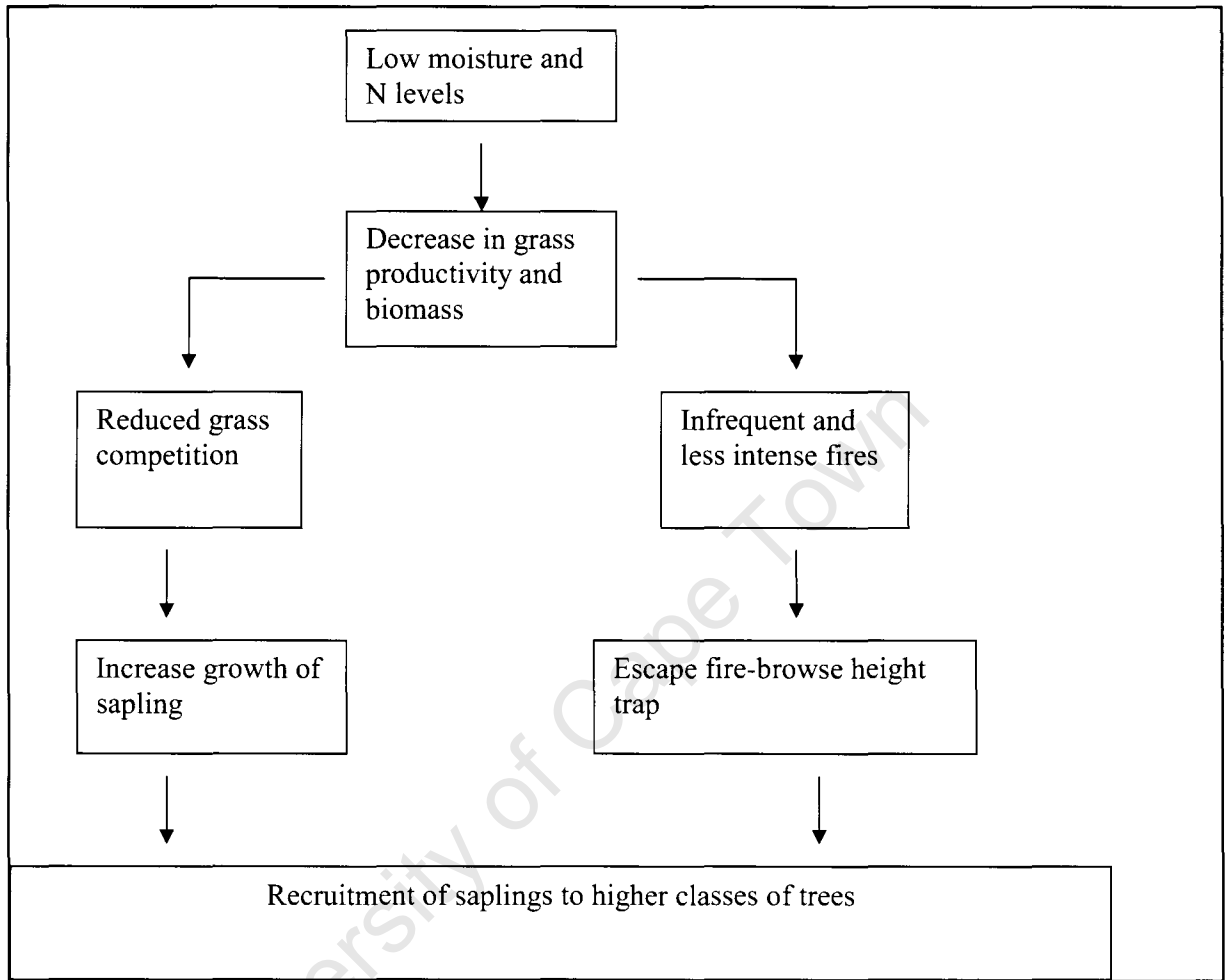


Figure 3.11 Schematic presentation of grass-sapling interactions during dry periods. Lower resource availability reduce grass competition and allow saplings to grow and escape fire-browse trap.

CHAPTER 4: Synthesis and applications

Summary

This study was initiated to determine the relationship between available water, available nitrogen and the structure of savanna systems. Most studies have focused on the role of rainfall and available water while neglecting the interaction with nutrient cycling, especially N mineralization (Walter 1971; Sankaran *et al.* 2005; February *et al.* 2007). Here I propose that it is not only rainfall amount that is driving tree-grass balance in savannas, but the combined effects of water and available N.

The first part of the study examined the effects of rainfall seasonality, available water and vegetation cover on N mineralization rates. The results for this part of the study show that N mineralization rates increases with an increase in available water. The reason for this is that soil microorganisms responsible for N mineralization are drought sensitive, and reliant on available water and warm temperatures (Binkley and Vitousek, 1989; Scholes *et al.* 2003). My study shows that these soil microbes only become increasingly active when monthly summer rainfall increases to above 50 mm, as evidenced by the surge/pulse in N mineralization rates. These results show the importance of rainfall amount in determining available N (Scholes and Walker 1993; Feig 2004).

Nitrogen mineralization rates were also affected by the seasonality of rainfall as low rainfall amounts in winter led to low N mineralization rates. Low temperatures and lack of moisture in winter constrained microbial activity, resulting in slow N turnover (Fierer and Schimel 2002; Austin *et al.* 2004). When rainfall amounts increase above 50 mm in summer, there is a pulse in N mineralization rates after which mineralization rates decrease to the end of the wet season even though rainfall amounts are high. This reduction in available N can be attributed to the depletion of the labile organic substrate (Fierer and Schimel 2004), immobilization of N by microorganisms (Mikha *et al.* 2005), and an increase in plant uptake (James and Richards 2004). The results is that nitrogen availability is limited by water in the dry season, stimulated by first rainfall events in the

early wet season, and limited by substrate availability, increased plant uptake and microbial immobilization in the late wet season (Cui and Chadwell 1997).

Chapter 2 also shows an increase in available water and N in grassy patches, and a decline in bare ground patch. Plant cover is therefore an important regulating influence on soil moisture and N mineralization rates. The increase in runoff and evaporation associated with bare soils, and the increase in water infiltration and retention found in grassy patches has an important influence on N mineralization rates (Scholes and Walker 1993). Trees are not able to establish in savannas because of competition with grasses for light, nutrients, and water in the establishment phase but also because bare patches between grasses do not have enough available resources.

Having established the relationship between available water and N mineralization rates, the second part of the study focused on the relationship between available water, (available N), and competition for resources between trees and grasses. The results for the second part of the study show that the growth of saplings was suppressed by grass presence, especially in wet treatments where there was high moisture and N availability. Sapling growth improved under dry conditions, with lower grass productivity, however, sapling growth was highest in the treatments where grass was removed. The results show that tree growth benefited more from complete grass removal, than in treatments where there was less grass growth even though N mineralization rates in these treatments were lower. These results show that grasses are able to out-compete trees for resources. Trees are only able to establish when grass biomass is reduced through drought, below average rainfall and/or grazing. This disturbance on grass reduces competition intensity opening an opportunity for sapling to grow and recruit to adult classes.

These results do not support the proposal that trees and grasses root in different layers of the soil, and that trees dominate in wet years, as more water is able to filter through to deeper layers, while grass dominates in dry years with no or little water infiltration (Walter 1971). Contrary to this prediction, my results show that grass competition is more important in limiting recruitment of saplings to adult size classes. The effects of grass competition on saplings are regulated by rainfall amounts, with wet years having

intense competition and dry years having less competition. The slow growth of saplings coupled with high grass biomass in wet treatments shows that in wet years, sapling recruitment to adult classes will be limited not only by intense competition from grass, but also by an increase in fire frequency and intensity because of the high availability of fuel (Govender *et al.* 2006). High grass biomass cause intense fires that cause topkill of saplings, whereas the slow growth rates which are caused by grass competition means the saplings will not grow to reach fire resistant sizes (Higgins *et al.* 2000; Govender *et al.* 2007; Higgins *et al.* 2007). In dry and below average rainfall years, reduced grass productivity and competition, as well as longer fire return intervals and low fire intensities provide an opportunity for saplings to recruit to adult classes (Higgins *et al.* 2000; Govender *et al.* 2006; Higgins *et al.* 2007).

My study concludes that N mineralization rates, facilitated by fluctuating moisture levels has a profound influence on grass biomass and consequently on savanna structure. Fluctuations in rainfall amount results in fluctuations in microbial activity and N mineralization rates. Plants respond by competing for available nitrogen and water. Grasses are stronger competitors for these resources increasing in biomass and out-competing trees when rainfall and N mineralization rates are high. When N mineralization rates are low with subsequent decrease in grass biomass trees are able to establish. In general, drier rainfall cycles will favour trees, while wetter rainfall cycles will favor grass. I conclude that savanna structure can vary between an open savanna dominated by grass to a close savanna dominated by trees because of the interaction between rainfall, nitrogen availability and fire.

RELEVANCE TO KNP RESEARCH OBJECTIVES

Research and monitoring in KNP is guided by a “learning-by-doing” framework known as strategic adaptive management (SAM). This framework integrates research, planning, and management in repeated cycle of learning to achieve and improve objectives (Biggs and Rogers, 2003; Pollard and du Toit, 2005). These research objectives are measured through monitoring end points called “threshold of potential concern” (TPC). Threshold

of potential concern are upper and lower levels of change in a selected biodiversity indicator in an ecosystem (Biggs and Rogers, 2003; Pollard and du Toit, 2005).

Research on the role of nutrients in the KNP falls under the nutrient distribution and movement objective (Figure 4.1) which seeks “to understand the relationship between nutrients in the ecosystem, functional diversity and biodiversity” (KNP management objectives, 2006). This objective has two main sub-objectives that were relevant to my study. The first one, which was “to understand processes that increase N availability to plants”, was covered in Chapter 2. The second one which focuses on “the influence of nutrient availability on plant structure”, was addressed in Chapter 3.

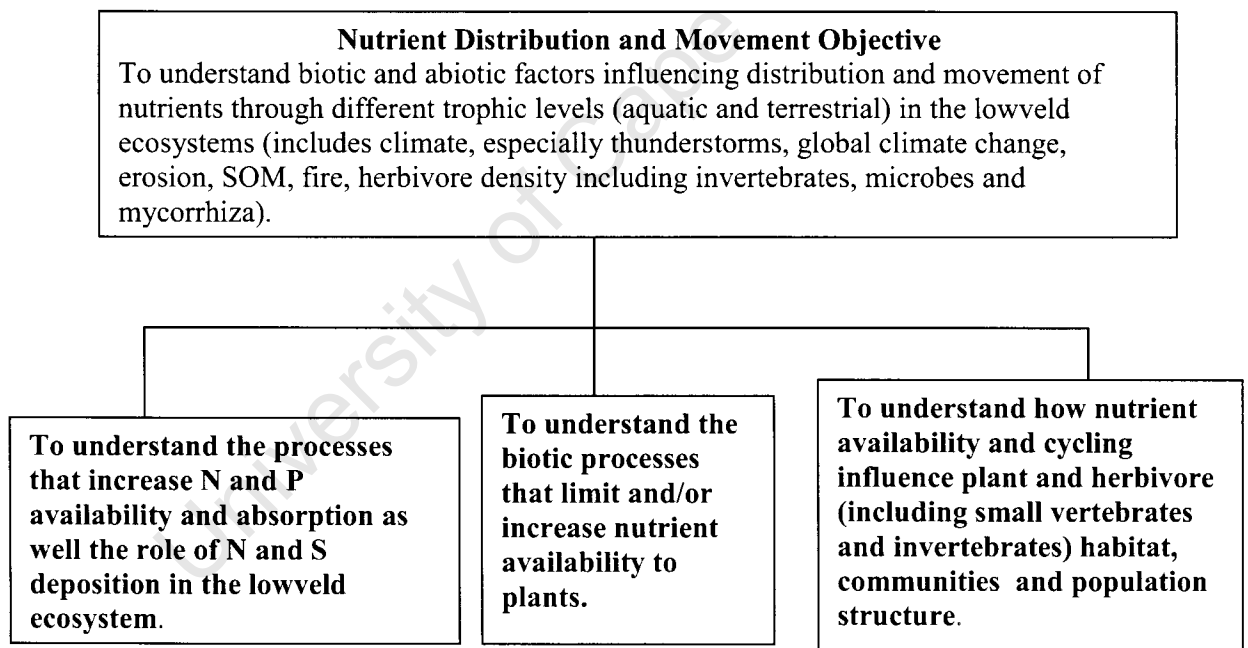


Figure 4.1 Nutrient research objectives and sub-objectives relevant to this study. These objectives are obtained from the Kruger National Park Management Plan October 2006.

Sub-objective 1: Understanding the processes that limit and/or increase nutrient availability to plants.

My study has shown that rainfall plays an important role in creating suitable conditions for microorganisms which are responsible for N mineralization. Wet years have high mineralization rates and high grass productivity compared to dry years. These

fluctuations in rainfall amount over the years affect N mineralization rates. However, this fluctuation in rainfall facilitates tree-grass coexistence and affect the savanna structure. Further-more, my study showed that the seasonality of rainfall in savannas, with more rainfall in summer and less or no rainfall in winter, also plays a role in the availability of N as N mineralization rates are correlated with water availability. In addition, the influence of rainfall on microbial processes in the soil is controlled by plant cover, especially the presence/absence of grass. This is important as cover heterogeneity in savannas varies in space and time.

Sub-objective 2: Understanding how nutrient availability and cycling influence plant habitat, communities and population structure.

The change in savanna structure is largely depended on saplings ability to grow and reach adult stages (Bond *et al.* 2003). My study showed that when available N increases with increases in available water, grass productivity also increases limiting the growth rates of saplings. As a result, the establishment of trees is limited when rainfall increases. Increases in grass biomass also increases fire intensities which prevents trees from reaching adult size classes (Higgins *et al.* 2000). Saplings grew better in treatments where grass was removed. The absence and low grass biomass also lead to less frequent and less intense fires, which reduces the impact of fire on saplings (Higgins *et al.* 2000). Increased growth rate by saplings under these conditions grant them an opportunity to grow beyond the heights where they are vulnerable to both fire and herbivory.

MANAGEMENT IMPLICATIONS

Management actions are based on knowledge which is provided by both science and monitoring. Science, monitoring and management act together as a three-part unit to meet the set objectives (Biggs and Rogers, 2003). Managers and scientists in South African National Parks (SANParks) have moved away from stable equilibrium concepts, and are managing to enhance heterogeneity and biodiversity (Rogers 2003; Govender *et al.* 2006).

Rogers (2003) suggest that managers should focus on key agents of change that they can manipulate when implementing research outcomes. In the Pretoriuskop area of the KNP, fire is the preferred change-agent and management tool because of the high grass biomass associated with high annual rainfall (750 mm). Sankaran *et al.* (2005) has proposed that in areas with mean annual precipitation (MAP) of > 650 mm fire is the main agent limiting tree proliferation in savannas. The impact of grazing on the Pretoriuskop system is negligible because of high grass biomass, resulting in available fuel for fire.

Govender *et al.* (2006) showed that managers can control the intensity but not the frequency of fire. They showed that fire frequency is directly control by rainfall amount. However, fire intensity can be manipulated by burning in different seasons. Their study showed that fire intensities were lower in summer and autumn, but high in winter. Burning during the summer and autumn season will result in cooler fires which can eliminate and/or reduce grass competition while having minimal impacts on the saplings (not causing topkill). These cooler fires will therefore enhance the chances of saplings to recruit into adult stages. However, if a more open savanna is desired, managers can put in fires in late winter season to effect hot fires which will cause topkill of saplings. Fire can only be used to affect the structure but not the density of plant communities because of the resilient nature of saplings which resprout from the ground after being burned (Higgins *et al.* 2007).

FUTURE RESEARCH

Information on the role of nutrients as drivers of savanna is still unclear and equivocal. More research and synthetic evaluation of the literature is needed to understand the bottom-up control of nutrients in savannas. Quantitative information is required to ascertain the ecological importance of the surge in N mineralization rate that occurs after the first rainfall events on tree-grass interactions. We need to test whether this surge in N mineralization rate can create a temporal resource partitioning between trees and grasses, with trees being the primary benefactor during the N mineralization surge, and grass benefiting from smaller rates of N mineralization throughout the growing season.

Another way of understanding the role of available N in tree-grass dynamics is to test whether trees and grass use the same type of inorganic N (e.g, nitrate or ammonium).

Higher rates of N deposition have been recorded for KNP savannas (Scholes *et al.* 2003). We need to test how this elevated N affect tree-grass interactions, and whether KNP savannas are N saturated and P limited. All these factors need to be understood in context of the predicted changes in the climate. We need to understand how global climate change will affect soil nutrient cycling and tree-grass dynamics.

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CHAPTER 5: References

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