

BOLUS LIBRARY
C24 0098 0107



The Lazy Root

Will a change in the rainfall regime or increased anthropogenic nitrogen deposition result in an alteration in the competitive balance between trees and grasses in a semi-arid South African savanna?

Wesley Drummond Bell (BLLWES002)

Supervisor: Dr. Edmund February

Dissertation presented in partial fulfilment of the requirements for the degree of Bachelor of Science (Honours) in the Department of Botany at the University of Cape Town, 2012

KD BELL

The copyright of this thesis vests in the author. No quotation from it or information derived from it is to be published without full acknowledgement of the source. The thesis is to be used for private study or non-commercial research purposes only.

Published by the University of Cape Town (UCT) in terms of the non-exclusive license granted to UCT by the author.

Abstract

In an attempt to determine why trees and grasses are able to coexist in savannas, Walter (1971) first proposed the root niche separation model for savannas which suggests that trees and grasses have differential access to water due to spatial differences in their rooting profiles. Subsequent studies in various savannas around the world have found that this is often not the case. In the central region of the Kruger National Park February & Higgins (2010) found that trees and grasses root at the same depths within the soil profile. In this study I determine whether the existence of fine roots in the soil profile necessarily indicates root activity. I also aim to determine the effect of increased water and nitrogen availability on root activity of trees and grasses. Pits of 20 x 20 cm were dug to a depth of 40 cm in plots that were either irrigated with the equivalent of 30 ml of rainfall per month or left without irrigation. This study was performed at the end of the rainfall season. I found that trees and grasses root at the same depths under moist and dry edaphic conditions as well as in plots with increased nitrogen. Tree roots are however, significantly more active than grass roots in non-irrigated plots. Temporal separation in root activity therefore seems to be a factor that allows for the coexistence of trees and grasses in savanna ecosystems.

Introduction

Savanna ecosystems are characterised by the coexistence of two dominant life forms – trees and grasses (Mordelet et al. 1997). The relative distribution of these forms changes considerably across different savanna types, but savannas are typically defined as having a relatively continuous herbaceous layer and a discontinuous distribution of woody plants (shrubs or trees) (Scholes & Archer 1997). Savannas cover over 12% of the global land surface and about half the area of Africa, South America and Australia (Scholes & Archer 1997, Jeltsch et al. 2000). The wide distribution of savannas results in the biome covering a wide range of climatic, edaphic and topographic conditions. How has the general pattern of the savanna biome emerged across such highly variable conditions? The general consensus among savanna ecologists is that there is no universal predictive model to explain why savannas exist (Scholes & Archer 1997). In order to understand, conserve or manage a

particular savanna ecosystem, one has to consider all the factors and processes that prevail in that ecosystem. These factors vary among different savannas and it is therefore important that each factor is understood on its own and in its interactions with other factors (Jeltsch et al 2000).

The relative abundance, productivity and spatial pattern of grasses and woody plants in savannas is determined by complex and dynamic interactions between climate, topography, soils, geomorphology, herbivory and fire (Scholes & Archer 1997). There are two primary hypotheses which attempt to explain tree and grass coexistence in savannas. The first suggests that the coexistence is resource controlled (Walter 1971) and the second suggests that tree and grass coexistence is disturbance controlled (Higgins et al 2000). Most early hypotheses suggest that, although many factors may be influential, the primary determinants of tree/grass dynamics are soil, water and nutrient availability (Frost et al. 1986). Trees and grasses have historically been viewed as competitors for these resources, especially in temperate zones (Scholes & Archer 1997). Competition between trees and grasses has been extensively studied and most hypotheses on competition mechanisms can be grouped into four general models. These are the root-niche separation model; the phenological niche separation model; the balanced-competition model; and the hydrologically driven competition-colonization model (Sankaran et al. 2004). Walter (1971) first proposed the root-niche separation model. This hypothesis assumes that water is the primary limiting factor in savannas and that trees and grasses have differential access to this water due to spatial differences in their rooting profiles (Walter 1971, Walker & Noy-Meier 1982). Grasses may dominate water uptake in the topsoil where both tree and grass roots exist but trees can persist as they can tap into deeper water sources. We could therefore assume that grasses would be able to take advantage of smaller rainfall events while trees would be at an advantage if they are able to source a deeper water supply (Walter 1971).

The root-niche separation model has been widely tested around the world and although some studies support the Walter (1971) hypothesis, root-niche separation cannot be viewed as a general pattern for savannas worldwide (Le Roux et al. 1995; Jackson et al. 1996; Mordelet et al. 1997; Simmons et al. 2007; February & Higgins 2010; Verweij et al. 2011; Xu et al. 2011). The Kruger National Park in South Africa has large expanses of savanna vegetation. Studies in the park have shown that there is no root separation between trees

and grasses (February & Higgins 2010; Verweij et al. 2011). Various authors have found that the majority of both tree and grass roots are located in the upper layers of the soil profile and there is considerable overlap down the profile (February & Higgins 2010, Kulmatiski et al. 2010). These results suggest that belowground competition does exist between trees and grasses and that this competition is not limited to the topsoil. Before this conclusion can be made, however, one needs to consider whether the presence of root mass in the soil necessarily indicates root activity. Kulmatiski et al (2010) found that root mass is in fact a poor indicator of root activity and suggest that precise root activity measurements are needed to test Walter's 1970 two layer hypothesis.

Time partitioning in active growth has been found to reduce competition between two life forms and may allow for tree/grass coexistence in savannas (Menaut et al. 1990). Grasses and trees respond differently to rainfall events. In moist savannas, deciduous trees achieve full leaf expansion before the start of the rainy season and retain their leaves for several weeks after the last rains while grasses only achieve peak leaf area several months after the start of the wet season (Scholes & Walker 1993; Soriano & Sala 1983). Higgins et al. (2011) found the same pattern in a semi-arid, subtropical savanna in Kruger National Park where trees had both an early flushing syndrome as well as a late flushing syndrome while grass leaf flush was found to follow the rain. Trees are hypothesised to use carbohydrates and nutrients carried over from the previous growing season while grass growth is more dependent on current photosynthesis. Trees can therefore dominate resource uptake early and late in the growing season but are reliant on a strongly seasonal climate whereas grasses can take advantage of unpredictable environments with small rainfall events (Rutherford & Panagos 1982; Soriano & Sala 1983).

In this study I will be exploring root niche separation in an arid savanna. I determine the distribution of tree and grass roots down the soil profile at a study site where nitrogen, phosphorus and water have been artificially manipulated. Previous research (February & Higgins 2010) has shown that there should be considerable overlap among tree and grass roots. Using the root material excavated from the different layers of the soil profile I also determine the amount of root activity through a determination of the stable carbon isotope ratios of the respiration of these bulk root samples. The primary objective is to determine the responses of tree and grass roots to additions of nutrients and water and whether or

not these responses reciprocate changes in rooting depth. I specifically ask if increased anthropogenic nitrogen deposition or changes in future rainfall regime may affect the competitive balance between trees and grasses.

Methods

Study site

The study site considered is located approximately 10 kilometres east of Satara Rest Camp in the central section of the Kruger National Park at approximately 31.77°E and 24.40°S (February & Higgins 2010). The climate of the region is typical of summer rainfall regions with hot, wet summers and mild, dry winters. Mean annual precipitation is relatively low at 547 mm while mean monthly maximum and minimum temperatures are 29.8°C and 16°C respectively. Rainfall that falls in the summer months (figure 8) is typically caused by convection storms or the occasional tropical cyclone.

The study area lies on a narrow strip of sandy soil that runs north to south at the convergence of the Granite and Basalt soils which dominate a large part of the Kruger National Park (Mucina & Rutherford 2006). The vegetation can be described as fine-leaved open savanna or Delagoa Lowveld (as described by Mucina & Rutherford 2006). *Dichrostachys cinerea* is the dominant tree species of the area followed by two *Acacia* species, *A. nigrescens* and *A. tortillis*. *Urochloa mosambicensis* and *Eragrostis rigidior* are the dominant grass species. The growing season generally follows the wet season, starting in late October and ending in early April (du Toit et al. 2003).

Climate analysis

The observed climate figures for Satara as well as projected future climatic conditions were obtained from the Climate System Analysis Group (CSAG) of the University of Cape Town. For the Satara station, rainfall and temperature data was recorded from 1981 to 2006. These values serve as a baseline against which the projected climate of the area is compared. The CSAG use nine Global Climate Models (GCMs) from the CMIP3 archive, which are empirically downscaled through Self Organising Map based Downscaling (SMOD). The climate projections used in this study are for the future period of 2046-2065 and are

forced according to the SRES A2 scenario. The projected climate scenarios are used to predict what possible changes may occur in the savanna matrix.

Experimental design

The experimental area is comprised of sixteen plots each with a diameter of 30 metres, spaced 10 metres apart. Four of the plots were treated with nitrogen, four with Phosphorus, four with both Nitrogen and Phosphorus, and four left untreated. Two of the plots from each treatment were irrigated with the equivalent of 30 mm of rainfall per month for the extent of the growing season. The control area is located adjacent to the experimental area (figure 1).

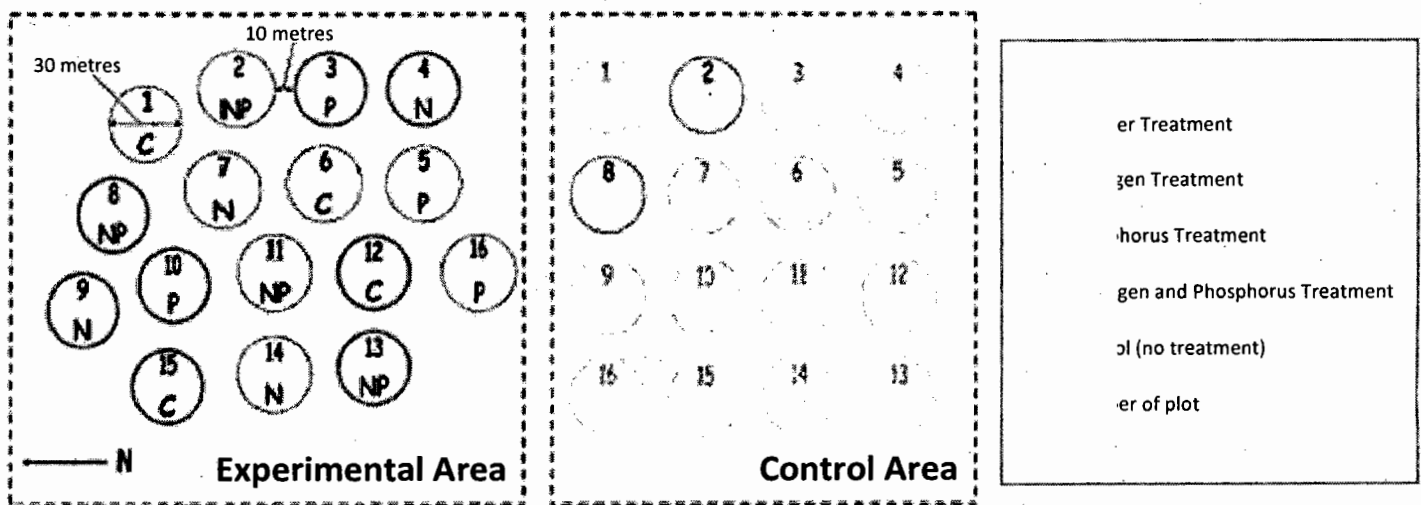


Figure 1. Experimental design of the study site as well as the adjacent control area. Only plots 2 and 8 in the control area were sampled.

Field sampling

Fine roots were sampled as these typify the effective absorbing root surface and are also largely responsible for ion uptake (De Kroon & Visser 2003). Fine roots are defined as having diameters less than 2 mm. At each plot we sampled material from one pit. The pits were dug on the edge of the tree canopy of an *Acacia gulliver* (tree sapling that is trapped within the grass flame zone (Bond & van Wilgen 1996)) so that a true representation of tree and grass roots could be obtained. Due to their high frequency in the study area, *Acacia nilotica* and *Acacia tortillis* were selected for sampling. At each pit, soil was extracted from a 5 cm

deep 20 × 20 cm section every 5 cm for the first 20 cm and then every 10 cm for the next 20 cm. Digging below 40 cm was not possible in most of the plots as the soil became too compact or bedrock was hit. Six individuals of the dominant tree species (three *Acacia nigrescens* and three *Acacia tortillis*) as well as six individuals of the dominant grass species (three *Urochloa mosambicensis* and three *Eragrostis rigidior*) were also excavated and the fine roots removed. The samples were collected towards the end of the wet season at the end of April/ beginning of May during a period of two weeks.

C₃ and C₄ plants have different photosynthetic pathways which ultimately results in these plants having significantly different $\delta^{13}\text{C}$ values. $\delta^{13}\text{C}$ values of plant material can therefore be used to differentiate between trees (C₃, -26.5 ‰) and grasses (C₄, -12.4 ‰) in a savanna. The use of carbon isotope ratios as a means of measuring below-ground biomass due to differences between C₃ and C₄ plants is quite common, particularly in savanna ecosystems (Mordelet et al. 1997; February & Higgins 2010), and has also been used to estimate values for CO₂ respired from roots (Sun et al. 2012). The method uses the $\delta^{13}\text{C}$ value of the dominant trees and grass in a landscape to determine the biomass of each life form in a mixed sample. In this study I apply this method to CO₂ respired from a root sample. Using the mean $\delta^{13}\text{C}$ values for CO₂ respired from both tree and grass roots, I determined what proportion of the CO₂ respired from the entire root sample was tree and what proportion was grass.

The total weight of each soil sample from each plot was determined. Soil gravimetric water content was then worked out and converted to a percentage using the equation,

$$\text{Soil water} = \frac{(\text{Moist soil weight}) - (\text{Dry soil weight})}{(\text{Moist Soil weight})} \times 100$$

Once the entire soil sample was weighed, the fine roots were separated from the soil by wet sieving using an 850 μm sieve. Approximately 0.5 grams of root material was then placed in a glass vacutainer (10 ml, Labotec, United Kingdom) and left in a dark cupboard to respire overnight with the assumption that any CO₂ in the tube at the end of the night would have a $\delta^{13}\text{C}$ value representative of the plants from which the roots were derived. The vacutainer was then placed in the freezer overnight to freeze out any water in the sample. The CO₂ that

was left in the tube was then transferred into a pre-evacuated Exetainer vial (12 ml Borosilicate vial, Labco Ltd, United Kingdom) using a double-sided needle. The CO₂ was then analysed for ¹²C/¹³C ratios using a Thermo Finnigan (Germany) Model II gasbench attached to a Finnigan MAT 252 isotope ratio mass spectrometer (IRMS). The carbon readings are expressed relative to Pee-Dee Belemnite.

After extracting the CO₂, the remaining roots were then dried to constant mass in a drying oven (set at 70°C). After grinding, using a Retsch MM200 ball bearing mill (Retsch, Haan, Germany), the samples were then combusted in a Flash 2000 organic elemental analyzer and the gases were passed to a Delta plus isotope mass spectrometer (IRMS) via a ConFlo IV gas control unit (Thermo Scientific, Bremen, Germany). The in-house standards used were: Sucrose (Australian National University); Merck Gel (Merck) and Acacia (*Acacia saligna* leaves, Glencairn). All in-house standards are calibrated against the IAEA (International Atomic Energy Agency) standards. Carbon readings are expressed relative to Pee-Dee Belemnite.

Stable isotope values are given as:

$$\delta(\text{‰}) = \left[\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right] \times 1000,$$

where R is the ratio of the heavy to the light isotope (¹³C/¹²C). The values are expressed relative to the globally accepted standard for Carbon, Vienna Pee Dee Belemnite. The deviation from the standard is denoted by δ and the results expressed in parts per thousand (‰). Higher δ values indicate enrichment relative to the heavier isotope (¹³C).

The mean values for trees and grasses were used as end members for the equation below. We assume that the isotopic signal of the entire root sample (S) is a simple mixture of the isotopic signatures of the tree (T) and grass (G) material in the sample. A mixing equation to represent this assumption is

$$S = pT + (1 - p)G$$

where p is the proportion of the sample that is tree root and $1 - p$ is the proportion of the sample that is grass root. The only unknown in the equation is p which can be calculated as:

$p = (G - S)/(G - W)$ (February & Higgins 2010). The same method was used to determine the proportional contributions of trees and grasses to the overall $\delta^{13}\text{C}$ value of the gas respired from the root samples.

Data analysis

The Morisita index of niche overlap was used to quantify the level of overlap between grass and tree roots (Mueller & Altenberg 1985). The Morisita index has a range from 0 to 1. A value of 1 means that there are equal densities of tree and grass roots down the profile while a value of 0 means there is no overlap at all. The Morisita index was calculated for root biomass obtained from the $\delta^{13}\text{C}$ values of root material as well as the $\delta^{13}\text{C}$ values of gas respired from the root samples.

Factorial analysis of variance (ANOVA) tests were used to test for differences in rooting depth and root activity. One-way ANOVAs were used to test for differences in soil moisture content down the soil profile. If significant differences were obtained from the ANOVA tests, Post-hoc Tukey tests were used to determine the specific relationships where significant differences existed. In the results mean values of measured variables are reported ± 1 standard error.

Results

The mean end member values were determined for fine roots of six grass tussocks (three *Urochloa mosambicensis* tussocks and three *Eragrostis rigidior* tussocks) and six gullivers (three *Acacia nigrescens* and three *Acacia tortillis*). The mean $\delta^{13}\text{C}$ value for tree root biomass was $-23.87 \pm 0.03\text{‰}$ and the mean for grasses was $-12.93 \pm 0.14\text{‰}$. The mean tree value was significantly higher than the mean grass value allowing for these means to be used as end member values for the mixing equation ($F_{1, 10} = 6108.5$ $p < 0.001$). The values for CO_2 respired from the roots were slightly higher for trees ($-22.33 \pm 0.17\text{‰}$) and lower for grasses ($-14.68 \pm 0.10\text{‰}$) compared to the values for actual root biomass (table 1). The tree respiration values were again significantly higher than the grass values allowing for use in the mixing equation ($F_{1, 10} = 934.78$ $p < 0.001$). These values fall in the ranges that have been found for C_3 trees and C_4 grasses in the literature (Vogel et al. 1978; Cerling et al. 1997; February & Higgins 2010).

Table 1. Individuals sampled for the end member determination of the $\delta^{13}\text{C}$ values (‰) of grass and tree roots.

Species	Root Biomass	Respiration
<i>Acacia nigrescens</i>	-23.99	-21.44
<i>Acacia nigrescens</i>	-23.84	-22.42
<i>Acacia nigrescens</i>	-23.87	-22.01
<i>Acacia tortillis</i>	-23.75	-22.85
<i>Acacia tortillis</i>	-23.86	-23.06
<i>Acacia tortillis</i>	-23.88	-22.52
<i>Eragrostis rigidior</i>	-12.55	-14.86
<i>Eragrostis rigidior</i>	-12.65	-14.46
<i>Eragrostis rigidior</i>	-12.69	-14.62
<i>Urochloa mosambicensis</i>	-13.32	-14.47
<i>Urochloa mosambicensis</i>	-13.19	-14.92
<i>Urochloa mosambicensis</i>	-13.17	-14.68

Mean root biomass for the entire root sample was highest in the top 10 cm of the soil profile and decreased significantly with depth ($F_{5, 102} = 22.09$ $p < 0.001$). The end member values obtained for root biomass (table 1) were used to calculate the proportion of tree and grass root material in each root sample and these proportions were used to determine the tree and grass root biomass in each sample (figure 2). Both tree and grass root material decreased significantly with depth ($F_{5,204} = 31.87$ $p < 0.001$) but there was no significant difference between tree and grass material at any given depth ($F_{5,204} = 0.69$ $p = 0.629$). Trees and grasses have therefore been found to root at the same depths at this particular study site.

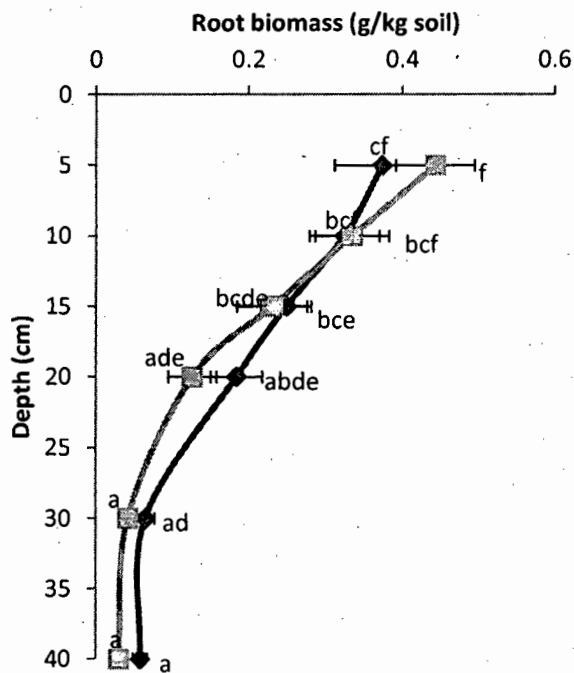


Figure 2. Distribution of tree (◆) and grass (■) root biomass in the top 40 cm of the soil profile. Different letters denote a significant difference between values; error bars show positive and negative standard error.

The Morisita index of niche overlap was used as another measure of overlap within the rooting zone. The mean Morisita index of all root material samples down the soil profile was 0.74 and the 95% confidence intervals were 0.62 and 0.85. This data suggests that there is a greater degree of niche overlap than niche separation at the Satara study site.

Respired CO₂

The end member values for respiration (table 1) were used to determine the proportion contribution of trees and grasses to the sample $\delta^{13}\text{C}$ values. These proportions were multiplied by the total root mass for each level in the soil profile (figure 3). Although there seems to be a separation between trees and grasses in the top 5 cm, as well as down the soil profile, this is not significant ($F_{5, 204} = 2.02$ $p = 0.077$). Both trees and grasses follow the same general trend that is observed in figure 2 in that there is a decrease in root material with depth ($F_{5, 204} = 18.44$ $p < 0.001$) but there is no significant separation in root activity down the soil profile (figure 3).

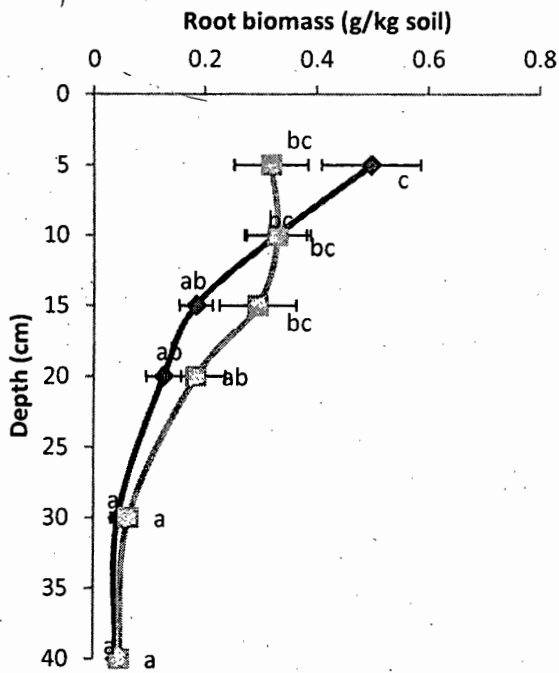


Figure 3. Relative respiration of tree (◆) and grass (■) root biomass in the top 40 cm of the soil profile. Different letters denote a significant difference between values, error bars show positive and negative standard error.

The Morisita index of niche overlap was used on the respiration data. The mean Morisita index of all the samples down the soil profile was 0.43 and the 95% confidence intervals were 0.54 and 0.32. The Morisita index for the respiration samples was significantly lower than that for the root samples ($F_{1,10} = 13.72$ $p < 0.05$). This suggests that there is greater niche separation with regards to respiration than niche overlap. The Morisita Index in this case suggests that there may be a separation in root activity that has not been picked up by the ANOVA tests.

Effect of water

Half of the plots in the experimental area were irrigated during the time that the field work was completed (figure 1). Percentage water content was significantly higher overall in the irrigated plots than in the non-irrigated plots ($F_{1,96} = 39.75$ $p < 0.001$). This difference was only significant in the top 10 cm of the soil profile with no significant difference in water content between irrigated and non-irrigated plots below this depth ($p > 0.05$). For the irrigated plots, water content was highest in the top 10 cm of the soil profile and decreased

significantly thereafter ($p < 0.05$). Water content was consistently low in the non-irrigated plots with no significant change down the soil profile ($F_{5, 54} = 0.58$ $p = 0.72$) (figure 4).

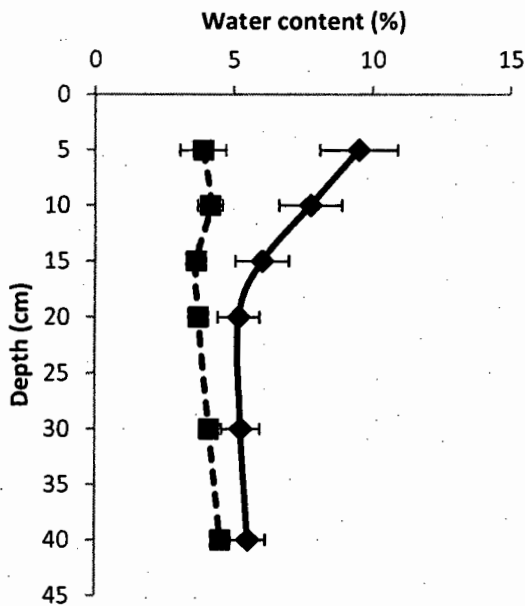


Figure 4. Mean percentage water content down the soil profile of irrigated (♦) and non-irrigated plots (■).

When only the irrigated plots are considered, grass roots are more abundant than tree roots in the top 10 cm of the soil, although this is not significant ($p = 0.09$, figure 5A). Down the profile, tree and grass roots are equally abundant in the irrigated plots (figure 5A). In the non-irrigated plots, tree roots appear to be more abundant down the entire soil profile but this difference is not significant ($F_{5, 108} = 0.268$ $p = 0.930$) (figure 5B). The Morisita Indices of niche overlap were determined for root biomass at each depth in both the irrigated and non-irrigated plots (table 2). These values are relatively high for both irrigated and non-irrigated plots suggesting greater niche overlap than niche separation.

Table 2. Mean Morisita Index's for respiration and root biomass $\delta^{13}C$ values from irrigated and non-irrigated plots.

Depth	Irrigated		Non-irrigated	
	Root Biomass	Respiration	Root Biomass	Respiration
5	0.87	0.83	0.91	0.29
10	0.79	0.57	0.85	0.72
15	0.89	0.34	0.80	0.65
20	0.79	0.09	0.41	0.50
30	0.72	0.32	0.37	0.41
40	0.84	0.36	0.60	0.46

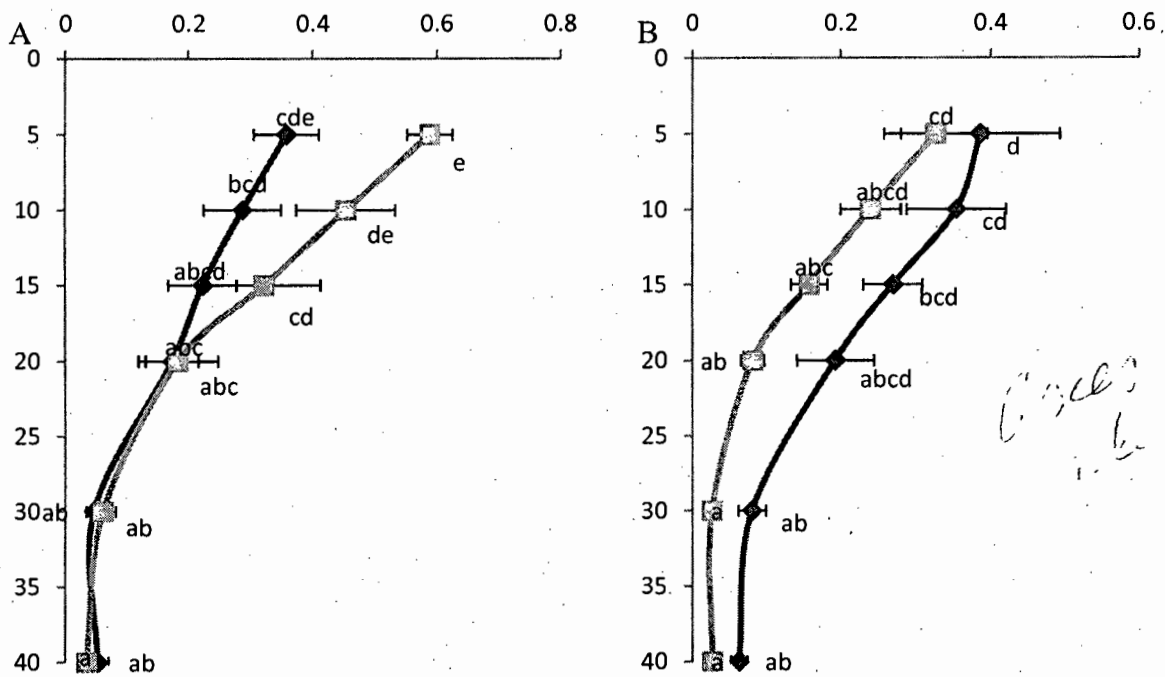


Figure 5. Distribution of tree (♦) and grass (■) root biomass in the top 40 cm of the soil profile in (A) irrigated plots and (B) non-irrigated plots. Different letters denote a significant difference between values, error bars show positive and negative standard error.

The contributions to respiration were not significantly different for trees and grasses in the irrigated plots ($F_{5, 84} = 0.58$ $p = 0.711$) (figure 6A) although there seems to be a higher

contribution by grasses throughout the soil profile. This observation is supported by the Morisita Indices down the soil profile which suggest greater niche separation than niche overlap below 10 cm (table 2). In the top 5 cm of the non-irrigated plots, trees contribute significantly more CO₂ than grasses, suggesting greater root activity by trees ($p < 0.001$) (figure 6B). The Morisita index for the top 5 cm of non-irrigated plots was 0.29 which indicates greater niche separation than niche overlap and supports the suggestion that tree roots are more active in the top 5 cm of the soil profile during a dry period.

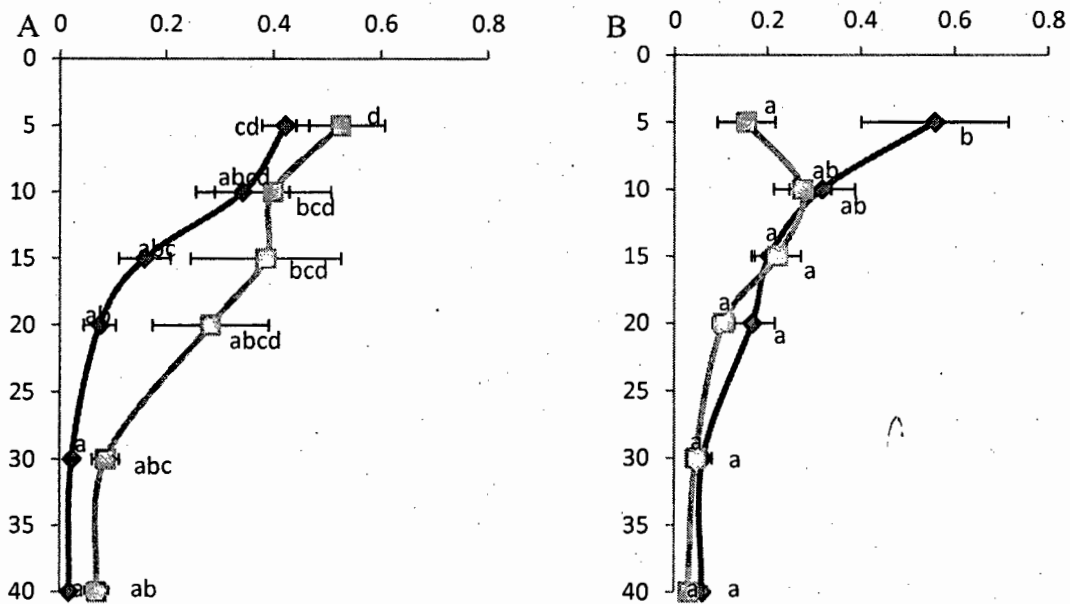


Figure 6. Relative respiration of tree (◆) and grass (▣) root biomass in the top 40 cm of the soil profile in (A) watered plots and (B) non-watered plots. Different letters denote a significant difference between values, error bars show positive and negative standard error.

Effect of nutrients

Tree and grass root biomass are not significantly different at any depth in the soil profile in the Nitrogen-treated plots ($F_{(5, 12)} = 0.143$, $p = 0.98$). Although figure 7A suggests that tree roots are more abundant in the top 5 cm of the profile, this is not statistically significant ($p = 0.99$). Tree and grass root biomass is not significantly different for plots treated with nitrogen and water either ($F_{(5, 12)} = 0.459$, $p = 0.80$), although the observed pattern from

figure 7A is reversed with grasses appearing more active in the top 5 cm, but insignificantly so ($p = 0.89$) (figure 7B).

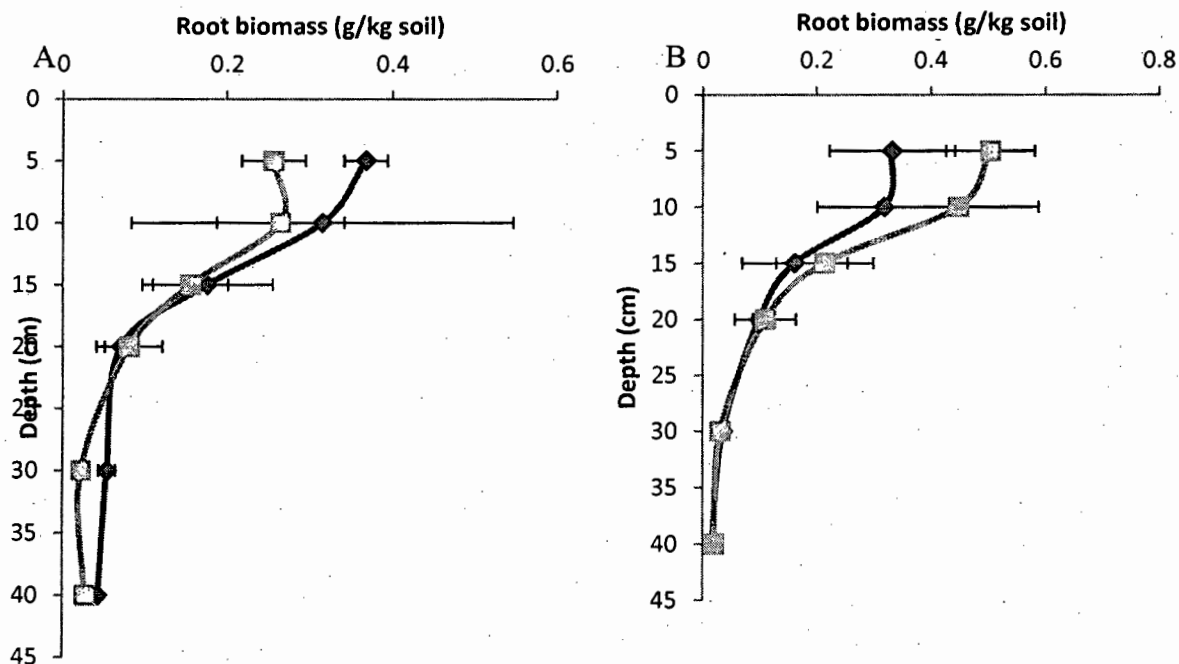


Figure 7. Distribution of tree (◆) and grass (■) root biomass in the top 40 cm of the soil profile in (A) nitrogen-treated plots and (B) plots treated with water and nitrogen.

Root activity of trees and grasses is not significantly different in nitrogen-treated plots ($F_{(5, 12)} = 0.706$, $p = 0.63$) as both tree and grass roots seem to be equally active down the soil profile (figure 8A). Root activity is equally insignificant in plots treated with nitrogen and water ($F_{(5, 12)} = 0.14$, $p = 0.98$). Figures 7 and 8 were obtained from only two replicate plots but when all plots where Nitrogen was added (including nitrogen; nitrogen and water; nitrogen, phosphorus and Nitrogen) are considered the pattern is very similar. There is no significant difference in either root biomass ($F_{(5, 84)} = 0.405$, $p = 0.844$) or root activity ($F_{(5, 84)} = 0.436$, $p = 0.82$) between tree and grass roots down the soil profile.

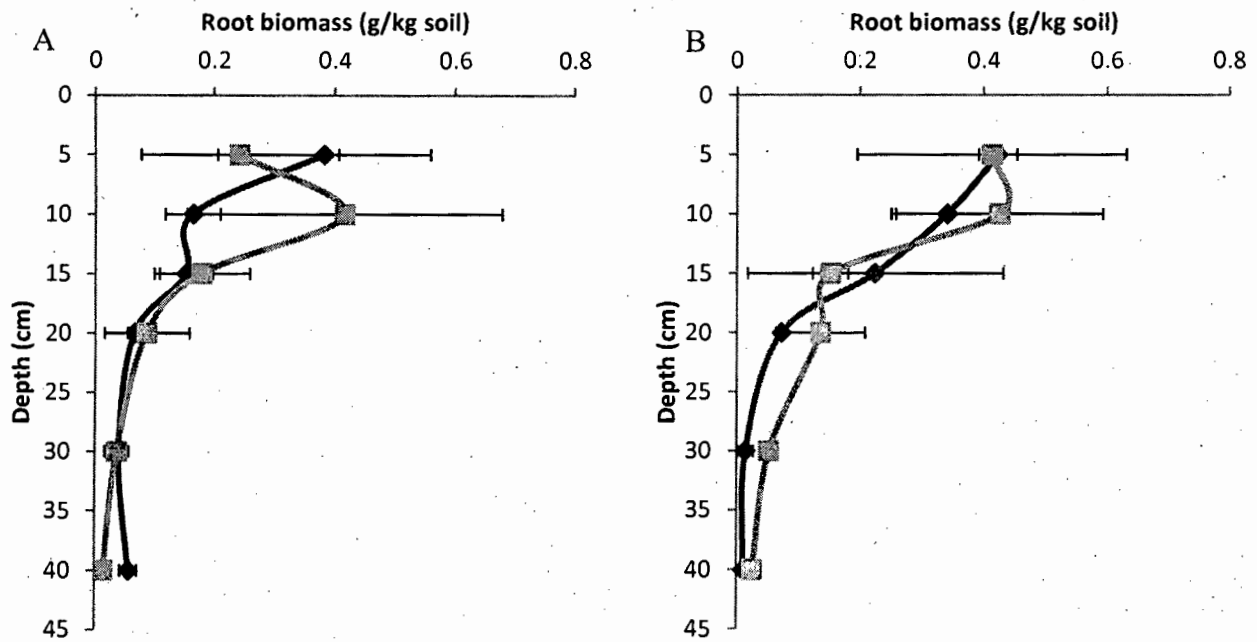


Figure 8. Relative respiration of tree (◆) and grass (■) root biomass in the top 40 cm of the soil profile in (A) nitrogen-treated plots and (B) plots treated with water and nitrogen.

Climate

The climate of the region is typical of summer rainfall zones with peaks in rainfall from November to February and extensive dry periods during the winter months during which time little to no rain falls (figure 9). This pattern is predicted to change somewhat as a result of global climate change. Satara is projected to receive an increase in total annual rainfall with a possible shift in rainfall patterns. Projections suggest that the rainfall season may commence earlier in the year with more rainfall in September and October than is currently experienced (figure 10A). Temperatures are also expected to increase at Satara throughout the year with an average increase of 2 - 2.5°C throughout the year (figure 10B).

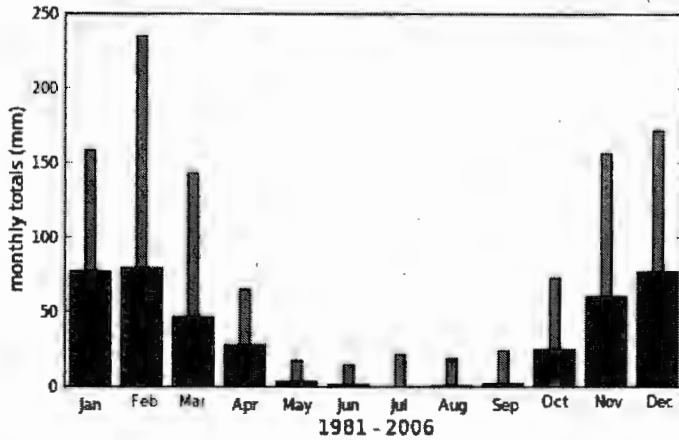


Figure 9. Annual cycle of monthly rainfall (mm) for Satara station. Wide bars indicate the median monthly rainfall from 1981-2006. Narrow bars indicate the 10th to 90th percentile range of monthly rainfall for each month during the climate period (CSAG).

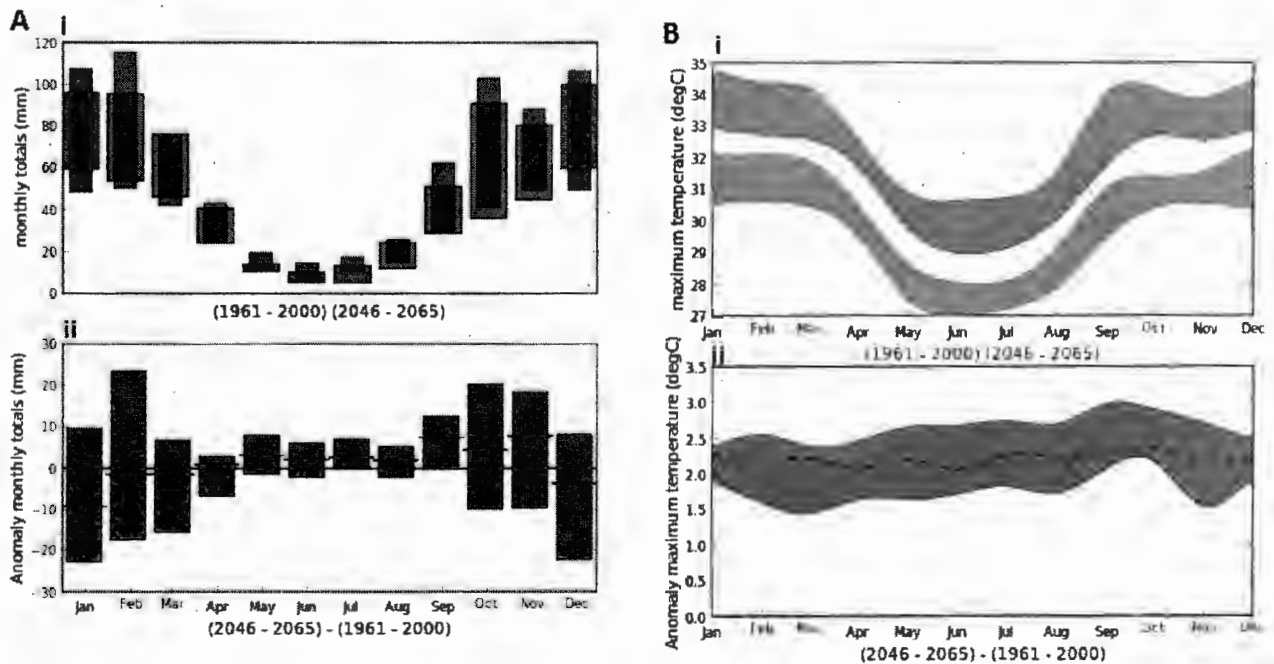


Figure 10. Change in monthly total rainfall for Satara station. Wide bars (Ai) represent 10th to 90th percentile range of the control period multi-model climatologies (1961-2000). Narrow bars (Ai) represent 10th and 90th percentile range for the future period multi-model projections (2046-2065). Aii shows 10th to 90th percentile ranges of future minus present anomalies with median change marked as a solid black line. The bottom band (Bi) represents 10th to 90th percentile range of the control period multi-model climatologies (1961-2000). Top band represents the same but for the future period multi-model projections (2046-2065). Bii represents the 10th to 90th percentile range of anomalies with the median anomaly as a dashed line (CSAG).

Discussion

Climate

In order to best manage and conserve areas of interest, we need to understand how these ecosystems and landscapes will respond to changes in the environment (Lohmann et al. 2012). In Satara, climatic changes as well as increased anthropogenic nitrogen deposition are expected to impact on the semi-arid savanna of the region. Satara has historically experienced strongly seasonal climatic conditions with hot, wet summers and mild, dry winters (figures 9 & 10Bi). Although this general pattern is expected to persist, changes in temperature and rainfall as well as changes in the duration and timing of the rainfall season have been projected by climate models. Temperatures throughout the year are expected to increase by an average of 2-2.5°C (figure 10Bii). Annual rainfall is also expected to increase over the region, accompanied by shifts in the rainfall season (Davis 2010). It has been projected that the historically wet months of December and January will receive less rainfall, while autumn and winter months will receive slightly more rainfall in the future. The spring months from September to November are expected to receive considerably more rainfall than they do at present (figure 10Aii). This will not only result in slightly wetter winters, but also an earlier rainfall season that could possibly commence in September and end in December or January (CSAG). Increased mean annual precipitation has been found to correlate well with increased woody cover in arid and semi-arid African savannas (Sankaran et al. 2005) and we therefore predict that tree root activity will be greater than grass root activity in irrigated plots.

Nitrogen Deposition

Mining constitutes a large percentage of the economic activity in the surrounding areas of Kruger National Park as well as large parts of the interior plateau of South Africa (Wigley et al. 2010). Of the many impacts that mining has on natural systems, anthropogenic nitrogen deposition is one of the most far reaching (Fenn et al. 2003). The burning of fossil fuels results in increased atmospheric nitrogen and therefore increases the amount of fixed nitrogen available to plants. The direct effect of nitrogen deposition on tree/grass dynamics has not yet been fully studied (Wigley et al. 2010) but the expectation is that grasses will

respond more rapidly than trees to nutrient additions (Belsky 1994). Van der Waal et al. (2009) propose that the more rapid response of grasses to increased nutrient availability leads to a faster depletion of soil water, which causes increased water stress in tree saplings if dry spells are more drawn out. The suggestion is that the effect of increased nitrogen deposition is reliant on water availability and grasses will only benefit when water is limiting (van der Waal et al. 2009).

Effect of increased water availability

The irrigated plots in this experiment represent areas that have received increased rainfall over the wet season and can therefore be used to demonstrate what future changes may occur in this savanna under projected climatic conditions. Non-irrigated plots represent normal conditions for the end of the rainfall season (the period the plots were sampled). When all the plots are considered together, there is no significant difference in either rooting depth or root activity between trees and grasses down the soil profile (figures 2 & 3). This pattern is repeated under increased rainfall conditions with no difference between trees and grasses (figures 5A & 6A). My results therefore do not support the hypothesis that trees would be favoured under increased rainfall conditions. However, as the treatments have only been applied since 2010, the observed pattern may simply represent conditions during the rainfall season and a trend may not have yet developed. We would therefore expect that both life-forms would be actively growing (Scholes & Archer 1997; Higgins et al. 2011). Root biomass was not significantly different for trees and grasses in non-irrigated plots (figure 5B), but tree roots were significantly more active than grass roots in the top 5 cm of the soil profile of non-irrigated plots (figure 6B). Scholes & Walker (1993) proposed that a temporal niche separation in root activity may ameliorate the effects of tree/grass competition. This hypothesis suggests that trees become active earlier in the growing season allowing trees a period of growth when grass competition is reduced (Scholes & Walker 1993). More recently, Higgins et al. (2011) have suggested that temporal niche separation may be more pronounced at the end of the growing season. Trees therefore seem to rely on a more predictable rainfall regime but it is still unclear what resource triggers trees to begin growing and continue to grow for a period after the wet season has ended (Higgins et al. 2011). The availability of some or other resource must be the axis upon which tree activity relies upon. More rainfall as well as a shift in the rainfall regime will allow

trees to remain active for a longer time period but, according to my results, my not benefit either life-form.

Effect of increased Nitrogen deposition

If the Belsky (1994) hypothesis is correct then grass roots should be more active than tree roots in nitrogen-treated plots and this difference should be magnified in the nitrogen-treated plots that have not been irrigated. Tree and grass roots were found at the same depths in the soil profile in nitrogen-treated plots (figure 7A) suggesting that neither life-form is favoured by increased nitrogen availability. There is a trend for increased tree root abundance in the top 10 centimetres of the soil in nitrogen-treated plots, but this difference is not significant. Nitrogen-treated plots that were irrigated as well showed similar results to purely nitrogen-treated plots. Root activity of trees and grasses down the soil profile was similar whether the plots were irrigated or not (figures 8A & 8B), suggesting that neither trees nor grasses benefit from nitrogen addition. The data therefore does not support the hypothesis that grasses take advantage of increased nitrogen availability and suppress tree growth. In order to appropriately measure the effect of increased nitrogen on tree/grass dynamics, the area would have to be sampled over the entire growing season as the observed results are merely a snapshot of a dynamic process. Van der Waal et al. (2009) suggest that the frequency and span of drought periods is important to nutrient acquisition and therefore the plots would have to be sampled during the dry season in order to properly assess the effects of increased nitrogen deposition.

Conclusions

The interactions between trees and grasses are dynamic and complex and are reliant on factors other than water and nutrients. I have found that the mere presence of root biomass at any given depth in the soil profile does not necessarily indicate root activity. Although tree and grass roots were present and active at the same depths in the soil profile under most environmental conditions, there was one significant exception. Tree roots were more active in the top 5 cm of the soil profile in non-irrigated plots, stressing the importance of temporal niche separation for tree/grass dynamics. The importance of the timing of rainfall

and fire events is also demonstrated as fire intensity may depend on the amount of grass growth which is in turn dependent on the length of the rainfall season. The predicted longer rainfall season may allow for more grass growth which will result in a more intense fire that impedes tree growth allowing for a shift to a more grassland state. In order to better understand the dynamics of this particular ecosystem however, data should be collected throughout the year for as many seasons as possible as my data represents only a snapshot of a dynamic process. It would also be beneficial if more replicates of nitrogen addition were available as the data for the impact of added nitrogen is sparse. Lastly, this paper demonstrates the value and potential of using respired CO₂ δ¹³C values as a proxy for root activity as well as demonstrating the possible flaws in using root biomass alone as a measure of tree/grass interactions.

References

- Belsky AJ (1994). Influences of trees on savanna productivity: Tests of shade, nutrients, and tree-grass competition. *Ecology* 75 (4): 922-932
- Bond WJ & van Wilgen BW (1996). *Fire and plants*. Chapman & Hall, London, UK
- Cerling TE, Harris JM, MacFadden BJ, Leakey MG, Quade J, Eisenmann V & Ehleringer JR (1997). Global vegetation change through the Miocene-Pliocene boundary. *Nature* 389: 153-158
- CSAG. (n.d.). *Satara Station Climate Records*. Retrieved 10 2012, from Climate Information Portal: [http://cip.csag.uct.ac.za/webclient/map/South%20Africa%20\(stations\)#title=station-observed&folder_id=27&extent_id=48119](http://cip.csag.uct.ac.za/webclient/map/South%20Africa%20(stations)#title=station-observed&folder_id=27&extent_id=48119)
- Davis C (ed). 2010. A Climate Change Handbook for North-Eastern South Africa. Council for Scientific and Industrial Research (CSIR).
- De Kroon H & Visser EL (2003). *Root Ecology*. Springer, Berlin, Heidelberg, New York.
- du Toit JT, Rogers KH and Biggs HC (eds.) (2003). *The Kruger Experience: Ecology and Management of Savanna Heterogeneity*. Island Press, Washington. pp 83-129, pp 292-309.

February EC & Higgins SI (2010). The distribution of tree and grass roots in savannas in relation to soil nitrogen and water. *South African Journal of Botany* 76: 517-523

Fenn ME, Baron JS, Allen EB, Rueth HM, Nydick KR, Geiser L et al. (2003). Ecological effects of nitrogen deposition in the Western United States. *BioScience* 53 (4): 404-420

Frost PG, Medina E, Menaut J-C, Solbrig O, Swift M & Walker BH (eds). 1986. Response of savannas to stress and disturbance. *Biology International Special Issue 10*, IUBS, Paris.

Higgins SI, Bond WJ & Trollope SW (2000). Fire, resprouting and variability: A recipe for grass-tree coexistence in savanna. *Journal of Ecology* 88 (2): 213-229

Higgins SI, Delgado-Cartay MD, February EC & Combrink HJ (2011). Is there a temporal niche separation in leaf phenology of savanna trees and grasses? *Journal of Biogeography* 38: 2165-2175

Jackson RB, Canadell J, Ehleringer JR, Mooney HA, Sala OE & Schultz ED (1996). A global analysis of root distributions for terrestrial biomes. *Oecologia* 108: 389-411

Jeltsch F, Weber GE & Grimm V (2000). Ecological Buffering Mechanisms in Savannas: A Unifying Theory of Long-Term Tree-Grass Coexistence. *Plant Ecology* 150 (1/2): 161-171

Kulmatiski A, Beard KH, Verweij RJT & February EC (2010). A depth-controlled tracer technique measures vertical, horizontal and temporal patterns of water use by trees and grasses in a subtropical savanna. *New Phytologist* 188: 199-209

Le Roux X, Bariac T & Mariotti A (1995). Spatial partitioning of the soil water resource between grass and shrub components in a West African humid savanna. *Oecologia* 104: 147-155

Lohmann D, Tietjen B, Blaum N, Joubert DF & Jeltsch F (2012). Shifting thresholds and changing degradation patterns: climate change effects on the simulated long-term response of a semi-arid savanna to grazing. *Journal of Applied Ecology* 49 (4): 814-823

Menaut J-C, Gignoux J, Prado C & Clober J (1990). Tree community dynamics in a humid savanna of the Cote d'Ivoire: modelling the effects of fire and competition with grass and neighbours. *Journal of Biogeography* 17: 471-481

- Meuller LD & Altenberg L (1985). Statistical Inference on Measures of Niche Overlap. *Ecology* 66 (4): 1204-1210
- Mordelet P, Menaut J-C & Mariotti A (1997). Tree and grass Rooting Patterns in an African Humid Savanna. *Journal of Vegetation Science* 8 (1): 65-70
- Mucina L and Rutherford MC (2006). The vegetation of South Africa, Lesotho and Swaziland. South African National Biodiversity Institute, Pretoria. pp 439-459, pp 493
- Rutherford MC & Panagos MD (1982). Seasonal woody plant growth in *Burkea africana*-*Ochna pulchra* savanna. *South African Journal of Botany* 1: 104-116
- Sankaran, M., Ratnam, J. & Hanan, N.P. (2004). Tree-grass interactions in savannas revisited – insights from an examination of assumptions and mechanisms invoked in existing models. *Ecology Letters* 7: 480-490
- Sankaran M, Hanan NP, Scholes RJ, Ratnam J, Augustine DJ, Cade BJ et al. (2005). Determinants of woody cover in African savannas. *Nature* 438 (8): 846-849
- Scholes RJ & Walker BH (1993). An African savanna: synthesis of the Nylsvley Study. Cambridge, UK: Cambridge University Press.
- Scholes RJ & Archer SR (1997). Tree-Grass Interactions in Savannas. *Annual Review of Ecology and Systematics* 28: 517-544
- Simmons MT, Archer SR, James Ansley R & Teague WR (2007). Grass effects on tree (*Prosopis glandulosa*) growth in a temperate savanna. *Journal of Arid Environments* 69: 212-227
- Soriano A & Sala O (1983). Ecological strategies on a Patagonian arid steppe. *Vegetatio* 56: 9-15
- Sun W, Resco V & Williams DG (2012). Environmental and physiological controls on the carbon isotope composition of CO₂ respired by leaves and roots of a C₃ woody legume (*Prosopis velutina*) and a C₄ perennial grass (*Sporobolus wrightii*). *Plant, Cell and Environment* 35: 567-577

Van der Waal C, de Kroon H, de Boer WF, Heitkonig IMA, Skidmore AK, de Knegt HJ et al. (2009). Water and nutrients alter herbaceous competitive effects on tree seedlings in a semi-arid savanna. *Journal of Ecology* 97: 430-439

Verweij RJT, Higgins SI, Bond WJ & February EC (2011). Water sourcing by trees in a mesic savanna: Responses to severing deep and shallow roots. *Environmental and Experimental Botany* 74: 229-236

Vogel JC, Fuls A & Ellis RP (1978). The geographical distribution of krrtz grasses in South Africa. *South African Journal of Science* 74: 209-215

Walker BH & Noy-Meir I (1982). Aspects of stability and resilience of savanna ecosystems. In *Ecology of Tropical Savannas*, ed. Huntley BJ & Walker BH, pp. 577-590. Berlin: Springer-Verlag

Walter H (1971). *Ecology of Tropical and Subtropical Vegetation*. Edinburgh, UK: Oliver & Boyd.

Wigley BJ, Bond WJ & Hoffman MT (2010). Thicket expansion in a South African savanna under divergent land use: local vs. global drivers? *Global Change Biology* 16 (3): 964-976

Xu C, Liu M, Zhang M, Chen B, Huang Z, Uriankhai T & Sheng S (2011). The spatial pattern of grasses in relation to tree effects in an arid savanna community: Inferring the relative importance of canopy and root effect. *Journal of Arid Environments* 75: 953-959