Spatial and competitive responses of tree and grass roots to increased nutrients and water in a semi-arid African savanna.

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ABSTRACT

Savannas show highly significant structural diversity under different bioclimatic conditions and previous studies have attempted to explain the tree-grass coexistence through a combination of resource and disturbance based controls. The competitive strengths between herbaceous C4 grasses and C3 woody tree seedlings and saplings in the rooting zone are significantly impacted by increased resource availability. The lack of adequate understanding of the semi-arid savanna edaphic environment and associated relationships between tree-grass roots prevents predictions of future responses of these ecosystems to rainfall and nutrient changes. Here I show that grasses are strongly favoured with increased resource availability in a semi-arid African savanna. I used $\delta^{13}C$ values of the sampled fine roots and the end member values of the target tree and grass species to determine the relative proportion of tree versus grass roots at each soil depth. Soil water content was determined gravimetrically and total soil and root nitrogen was delivered from isotopic analysis. Bray II and dry-ash methods were used to determine total phosphorous in the soil and roots respectively. Both tree and grass roots were shown to be significantly concentrated in the top 15 cm of the soil and present to a depth of 40cm. This study not only describes the distribution of the soil nutrients and water but also the root nutrient concentrations and the associated responses in fine root biomass, which indicates that the future herbaceous grassy layer will be significantly increased and hold a competitive advantage over the woody tree cover. The African savanna environment is projected to undergo concurrent changes in the climate and anthropogenic nutrient deposition, which will have impacts on these economically and socially significant ecosystems. A decrease in the tree:grass ratio will have highly significant biogeochemical feedback loops to the regional climate and greatly impact our ability to adequately manage these ecosystems. This study significantly contributes to the understanding of the tree-grass coexistence in savannas and has great potential for directing further research.

INTRODUCTION

Savannas are tropical summer rainfall mixed tree-grass systems varying in the density of woody trees that coexist with a continuous matrix of a highly competitive herbaceous grass component (February & Higgins, 2010; Sankaran et al., 2008; van der Waal et al., 2009). Covering around 12% of the land surface, ±17million km^2, savannas are extremely diverse and occur under conditions ranging from climates too arid to support trees to humid climates able to support full canopy forests (Bond & Midgley, 2012; Scholes & Archer, 1997; Staver et al., 2011). Savannas show highly significant structural diversity for which explanations of the tree grass coexistence is exasperatingly complex, intriguing and not fully resolved, despite decades of research (Bond & Midgley, 2012; Favier et al., 2012; Kambatuku et al., 2012).

Savanna tree-grass coexistence is primarily explained via resource or disturbance based hypotheses (February & Higgins, 2010). The former hypothesis explains the co-existence of trees with grasses through the partitioning of rooting niches with trees exclusively accessing deeper resource pools (February et al., 2012; Walker & Noy-Meir, 1982; Walter, 1970, 1971; van Langeveld et al., 2003). The limitations of the root niche hypothesis led to the development of the former hypothesis, which emphasises disturbances such as herbivory, fire and drought as limiting forces on tree recruitment, establishment and successful growth to a disturbance resilient size-class (Gardner, 2006; Higgins et al., 2000; Menaut et al., 1990).

Both hypotheses in their singularity fall short in capturing the vast complexity of savanna tree-grass coexistence (Sankaran et al., 2005) and thus increased attention has been placed into the worked combination of the two theories (February et al., 2012). Water availability is the primary climatic determinant of the potential proportion of trees but disturbance dynamics restricts trees to levels far below this (Cramer et al., 2012; February et al., 2012; Sankaran, et al., 2005; Staver et al., 2011). The shift from predominantly climate to disturbance controlled woody cover occurs around a mean annual precipitation (MAP) of 1000 mm (Bond et al., 2003, 2005; Staver et al., 2011), previously 700mm MAP (Sankaran et al., 2008), yet savannas occur until 2000 mm MAP (Staver et al., 2011). Above 2000mm MAP and ±40% tree cover, fire cannot flourish.

In this intermediate rainfall bracket (1000 mm – 2000 mm MAP), forest and savanna are described as alternative stable states (De Michele et al., 2011; Staver et al., 2011). Disturbance regimes are key in maintaining the savanna state even in the absence of root niche separation (February & Higgins, 2010). Research has suggested that there is significant overlap in the rooting zones of trees and grasses, which leads to intense competition for resources (February et al., 2012). Recently, greater attention has been placed on the significance of the diverse edaphic processes of savanna ecosystems and the resultant root competitive interactions. The tree seedling and gulliver (a

small tree stuck in the browser and grass fire trap (Bond & Van Wilgen, 1996) must establish and grow through an exceptionally strong demographic bottleneck enforced by grass competition, fire and herbivory (Cramer et al., 2007, 2010, 2012). Grasses have a denser root mass and are capable of outcompeting trees for resources and limiting their growth to maturity. Further advancements in realizing the soil nutrient and water distribution relative to tree and grass rooting patterns are essential for furthering our understanding of the complex savanna dynamics.

The global contemporary struggle with bush encroachment across the savanna and grassland ecosystems highlights their sensitivity to environmental change (Sankaran et al., 2005; van der Waal et al., 2009). There have been significant directional changes in climatic and macronutrient patterns of the 21st century, and are set to continue in an ever increasingly anthropogenically affected earth (van der Waal et al., 2009). It is still uncertain how the competitive interactions of trees and grasses in the vulnerable African savannas will respond to these changes (Craine et al., 2008; February & Higgins, 2010; van der Waal et al., 2009, 2011). The deposition of nitrogen and other nutrient into the savannas of the Kruger National Park (KNP) is significant and it is projected to continue and possibly worsen (Dentener et al., 2006; van der Waal et al., 2009). Inter-annual precipitation is projected to increase with climate change (IPCC, 2007) and shifts in intra-annual rainfall dynamics are to become significant. Understanding the responses of trees and grasses to changes in water and nutrient availability has never been more necessary for the management of these ecosystems into the 21st century.

The tree:grass ratio is significant as it affects carbon sequestration capacities, wild and domestic animal behaviour, rates of transpiration, nutrient cycling and primary production, greater impacts on local soil erosion and hydrology, and ultimately affects the biogeochemical feedback loops to the regional climate (Bond & Midgley, 2012; Sankaran et al., 2008; van der Waal et al., 2009). Critical knowledge gaps of savanna ecosystem functioning hampers management practices and the ability to project possible future shifts in response to climate change and associated concurrent changes in local and regional water and nutrient availability (van der Waal et al., 2009).

In this study I aim to investigate the spatial distribution of soil nutrients and water and the relationship of tree versus grass roots down the soil profile in response to increased nutrients and water in a semi-arid savanna where nitrogen, phosphorous and water conditions have been artificially manipulated. It has been reported that nutrients as well as roots are concentrated in the top 20cm of the soil and root distribution is readily responding to nitrogen availability (February & Higgins, 2010). I focus on determining the competitive responses of tree and grass roots to the increased nutrient and water quantities through investigating possible reflected changes in tree versus grass rooting depths, root biomass and root nutrient concentrations. It is still not clear how

the competitive strengths between herbaceous grasses and woody tree seedlings and saplings will change with increased resource availability, furthermore, determining whether the effect of competition in arid and semi-arid savannas on trees and grasses will remain constant, decrease or increase directly impacts management of these ecosystems (Sankaran et al., 2008; van der Waal et al., 2009). My goal, therefore, is to improve the understanding of the semi-arid savanna edaphic environment and how the competitive balance between trees and grasses may shift with the projected concurrent changes in the climate and nutrient deposition rates.

METHODS

DESCRIPTION OF THE STUDY SITE

The data for this study was collected at Satara (24.40°S, 31.77°E), central Kruger National Park (KNP), South Africa. Satara is a semi-arid savanna with a long-term mean annual precipitation (MAP) of ~520 mm/year ± 30mm (CSAG, 2012; Buitenwerf et al., 2012; February & Higgins, 2010). The area is characterised by a unimodal summer rainfall season (Fig. 1), which dictates the growing season (~October to April) (Venter et al., 2003) and the rainfall is typically caused by convection storms or tropical cyclones (February & Higgins, 2010). The long-term (1981-2006) mean annual maximum and minimum temperatures (MAT) are 33.5°C; 26.0°C and, 21.0°C; 10.5°C for summer and winter respectively. The KNP is dominated by nutrient poor Granitic soils and relatively fertile Basaltic clay soils (Buitenwerf et al., 2012; Mucina & Rutherford, 2006). The study area was situated within a narrow strip of sandstone soils (north-south) occurring at the convergence of the Granite and Basalt soils that are derived from Karoo sedimentary rocks of the Ecca group and are thus sodium-rich and erosion-prone (du Toi et al., 2003; Mucina & Rutherford, 2006). Satara is a fine-leafed, open savanna (February & Higgins, 2010) with dominant tree species being *Dichrostachys cinera*, *Sclerocarya birrea* and *Acacia nigresens*. The common grass species are *Bothriochloa radicans*, *Themeda triandra*, *Urochloa mosambicensis* and *Chloris virgata* (February & Higgins, 2010; Lane, 2011, pers.comm.; Mucina & Rutherford, 2006).

The study site consisted of 16 plots, each 30 meters in diameter and spaced ±10 meters apart in a random design (Fig. 2). There were two replicates of treatment and control which included phosphorous only (P), nitrogen only (N), water only (W), phosphorous and nitrogen (NP), phosphorous and water (PW), nitrogen and water (NW), phosphorous, nitrogen and water (NPW) and control (C). The experimental plots were treated in 2010 and 2011, which included an annual treatment of 120kg N/ha (urea) and 50kg P/ha (triple-superphosphate) and a water treatment of 30mm/month during the summer rainfall season (October to March). In addition to the 16 experimental plots, two control plots (CC) in the adjacent control area were included in this study.

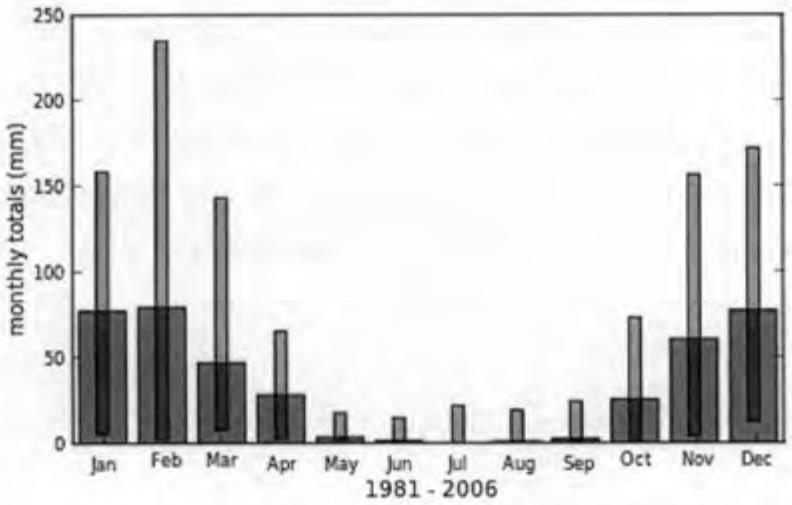


***Figure 1**: Mean monthly rainfall totals for Satara. Historical long-tern data set: 1981-2006. Thick bars represent mean. Thin bars represent 10th-90th percentile interannual range.* (CIP)

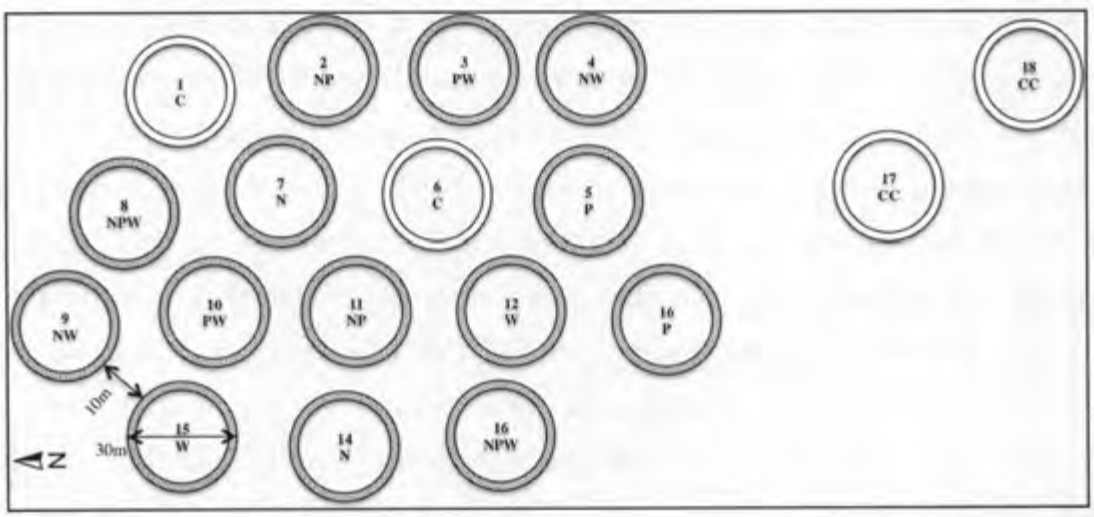


***Figure 2**: Schematic map of the study area and experimental design. Circular plots of 30m: 16 experimental (including 2 control) plus 2 external control plots. Plot numbers and treatment/control indicated inside circle.*

FIELD SAMPLING

Sampling was done at the end of the growing season from April 23 to May 8 2012. Soils and fine roots (≤2mm) were sampled from the 18 plots. The acacia gulliver attributes measured were basal stem diameter (BSD), tree height and the tree branch diameters (where D1 refers to the longest branch diameter and D2 being at a right angle to D1) (Fig. 3). The area within the branch diameters was defined as the gulliver "canopy". Extractions were taken at the end of this canopy of *A. tortilis* or *A. nilotica* gulliver trees within each plot. A trench was cleared along side the gulliver and sample area to allow the extractions to a depth of 40cm. Excavated sample segment dimensions were 20x20cm with varying depths: the top 20cm were sampled in 5cm increments and the last 20 cm were sampled in 10cm increments (6 samples per plot). To minimize evaporation and root isotope fractionation of the samples, the entire volume of soil from each segment (six per plot) was placed into two polyethylene bags (350mm) and sealed. Greater resolution in the upper 20 cm of the soil profile was desired, as the majority of soil nutrients as well as the greatest root biomass have been shown to be present here (February et al., 2012). Fine roots were sampled because they are primarily responsible for plant ion uptake and represent the effective absorbing root surface (February & Higgins, 2010; February et al., 2011). Six samples of the target tree (*Acacia* sp.) and grass (*Urochloa* sp. & *Erogrostis* sp.) roots were excavated for isotopic analysis in order to determine the end member isotopic values to be used for determination of the tree and grass root proportions per segment.

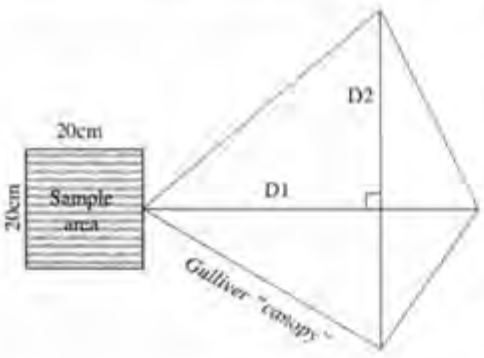


***Figure 3**: Diagram showing an example of plot measurements and the placement of the sample extraction area. D1 refers to the longest tree branch diameter and D2 is the diameter at a right angle to D1. The area of the diameters is referred to the gulliver canopy.*

In the field I prepared the soil and root samples for further analysis at the University of Cape Town, Cape Town. The total soil weight (wet) was determined in grams to one decimal place; and from this a ±50g subsample was weighed out, placed into a small paper bag and into the drying oven at 75°C for a minimum of 24 hours to constant weight. Subsequently the dry sample was re-weighed in order to calculate gravimetric soil water content for each soil segment. The remaining soil was wet sieved through 850 μm to extract all the fine roots. The roots of each sample were placed into a small paper bag, into the drying oven for a minimum of 24 hours to constant weight and weighed.

LAB ANALYSES

Carbon and nitrogen isotopic analysis of both roots and soil was conducted in the Archaeology Department and the total soil P was determined in the Botany Department at the University of Cape Town (UCT). The Institute for Plant Production at Elsenburg, Stellenbosch (Department of Agriculture, Western Cape), conducted total root P analysis.

Prior to analysis for phosphorous, the sample and target species roots were ground into a fine powder using a Retsch MM200 ball bearing mill (Retsch, Haan, Germany) and the soil samples were sieved through a 1mm soil sieve and tray to collect the fine fraction. The total soil phosphorous concentration was extracted via Bray II analysis (Bray & Kurtz, 1945) and determined calorimetrically with photo spectrometry using the Mulitiscan Spectrum (Thermo Fisher Scientific Inc., MA, USA) according to the "UCT Soil P and N extraction and analysis" procedures (see Appendix 1). The percentage of phosphorous of the roots was determined by dry-ashing the root samples at 480°C for eight hours and dissolving with a 1:1 (v/v) of HCl (Kalra, 1998; Power et al., 2010). Assessment of the percentage of P concentration in solution was determined with an inductively coupled plasma atomic emissions spectrometry (Varian Vista MPX, Mulgrave, Australia).

Soil and root samples were analysed for total nitrogen and carbon (%) and $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios using a Flash 2000 organic elemental analyzer connected to a Delta V Plus isotope ratio mass spectrometer (IRMS) via a Conflo IV gas control unit (Thermo Scientific, Bremen, Germany). Three in-house standards were used all of which were calibrated relative to IAEA standards. These IAEA standards are atmospheric nitrogen for nitrogen and Pee-Dee Belemnite for carbon. The results are reported conventionally as the deviation from the standard (δ) expressed as parts per thousand (‰) via the following equation, where n is the heavy isotope of element E and R_i and R_s are ratios of the heavy to the light isotope for the sample and standard respectively:

$$\delta^n E = \left(\frac{R_i}{R_s}\right) x\ 1000$$

DATA AND STATISTICAL ANALYSES

Soil gravimetric water content was determined using the following equation;

$$Soil\ water\ content\ (\%) = \left(\frac{(Total\ soil\ weight) - (Dry\ soil\ weight)}{(Total\ Soil\ weight)}\right) x\ 100$$

The total soil phosphorous concentration (mg/L) was derived from the absorbance values of the Bray II extractions via two standard curves. These values were corrected via the blank/control samples, and then finally corrected via the half method detection limit of 0.025mg/L. The total root biomass was reported as the total fine root weight per m^3 area. The 20x20x5cm samples (four per

plot) had a total area of 0,002m^3 and were thus multiplied by 500 to get to m^3. Similarly, the 20x20x10cm samples (two per plot) had a total area of 0,004m^3 and were thus multiplied by 250.

The basal stem diameter (BSD) represented the most accurate attribute of the gulliver as a proxy for relative belowground root density. Gulliver sizes varied from 20 and 90cm with different amounts of root biomass relative to tree size. Tree height and canopy diameter are not accurate measurements for root biomass but stem diameter is. The biomass, water and nutrient data could not be compared between the different treatments without standardizing the gulliver tree size and as a result I used a worked conversion factor (CF) according to the BSD. Each plot had a unique conversion factor (CF) based on the BSD of the individual tree (i) and the mean BSD. All data was multiplied by their relevant conversion factor:

$$CFi = \frac{BSDi}{mean\ BSD}$$

The fine root $\delta^{13}C$ values of the samples and the target tree and grass species (end member values) were used to determine the proportion of tree and grass fine root material in each sample. This is possible due to the strong difference in heavy isotope discrimination between the C4 and the C3 photosynthetic pathways of the grasses and trees respectively (Scholes & Walker, 1993; Vogel et al., 1978). C3 trees typically have values of -26.5‰ whilst C4 grasses are typically -12.5‰ (February & Higgins, 2010; Vogel et al., 1978). I used the common assumption that the resultant root sample $\delta^{13}C$ value is a combination of the $\delta^{13}C$ values of the grass and tree value (February & Higgins, 2010). Thus, the proportion of tree (p) and grass (1-p) can be calculated via the following equation with G representing the grass, T the tree and S the sample $\delta^{13}C$ values:

$$p = \frac{G - S}{G - T}$$

I ran statistical analyses in the programme Statistica, v.10. (Stat Soft. Inc., 1984-2011) and reported mean results with ±1 standard error. The BSD-converted data (soil N, P and water; root N, P, weight & total biomass; grass and tree fine root biomass) was analysed in a Factorial Analysis of Variance (ANOVA). This was used to test for significant differences between the treatment and soil depth effects as well as to test for significant difference between the upper and lower soil layers. Following these tests I ran the Tukey HSD posthoc tests for all data (Yandel, 1997). A Student's T-test for a single sample was run to test for significant differences between the mean tree:grass root ratios of each plot. I created 2D scatterplots to test for relationships between soil and root N, as well as the tree:grass root ratios with the root N and P status and soil water content. A Student's T test was performed to test significant differences between the observed and future projected minimum and maximum temperatures. All additional data analyses and graph construction were done through Microsoft Excel for Mac 2011, v.14.1.0 (Microsoft Corporation, 2010).

CLIMATE ANALYSIS

The local historically-observed and the future-projected climate was gained via the Climate Information Portal (CIP) of the Climate Systems Analysis Group (CSAG, 2012) of UCT. From the Satara weather station, climate data was reported from 1981 to 2006. The CSAG CIP uses nine Global Climate Models (GCMs) from the CMIP3 archive, which are empirically downscaled via statistical methodology through SMOD (Self Organising Map based Downscaling). The climate projections used in this study are for the future period of 2046-2065 and are forced according to the SRES A2 Scenario, a future with moderately high emissions in a differentiated world (IPCC, 2001) (Hewitson et al., 2009). The signal of climate change (if any) would likely be detectable from the natural inherent climatic variation by the projected period of 2046-2065 (mid-century) (Hewitson et al., 2009). The models deliver climatic envelopes of probability and the level of agreement between models can be assessed via the mean and range of projection.

RESULTS

The total bulk fine root biomass decreased significantly down the profile ($F=12.913$; $p<0.0001$). The first 15cm held a significantly higher root biomass than the bottom 16-40cm ($F=43.85$; $p<0.0001$) which increased relative to the control with an increase in nutrients and water (except for P-only treatment) (Fig. 4). *Soil* nitrogen (%) differs significantly between the treatments ($F=4.21$; $p < 0.001$) but not down the soil profile ($F=0.3743$; $p= 0.864$). Soil N was significantly higher in the N-only treatment than in any other treatments (Fig. 5a). *Root* percentage nitrogen also differs significantly between the treatments ($F=7.62$; $p < 0.0001$) but not down the soil profile ($F=0.20$; $p= 0.960$) (Fig. 7a). I test for toot uptake of added nutrients via correlation and root %N shows a significant linear relationship with soil %N ($r^2= 0.86$; Fig. 8). *Soil* phosphorous concentration ([P]) is significantly greater with P treatment but only in the first 5cm of the soil profile ($F=6.62$; $p<0.0001$) (Fig. 6). [P] is greater when coupled with water, although non-significantly. *Root* percentage P does not differ significantly down the soil profile ($F=0.33$; $p=0.892$) but it does differ significantly between treatments ($F=3.96$; $p<0.0001$) (Fig. 7b). Soil gravimetric moisture content (%) is significantly different with the treatments ($F=4.19$; $p<0.001$) and, similarly to soil [P], is greatest when coupled with P treatment (Fig. 5b). Percent water decreased down the profile, although these results were not significant ($F= 0.79$; $p=0.561$).

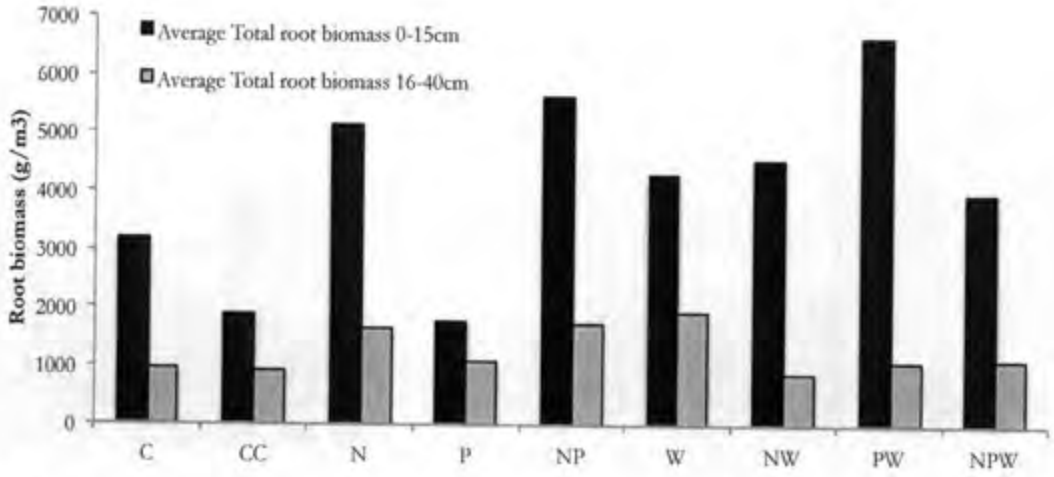


***Figure 4**. Total mean root biomass across treatments, of the two significant verticle layers: 0-15cm (Black) and 15-40cm (Grey). Graphs derived in Excel.*

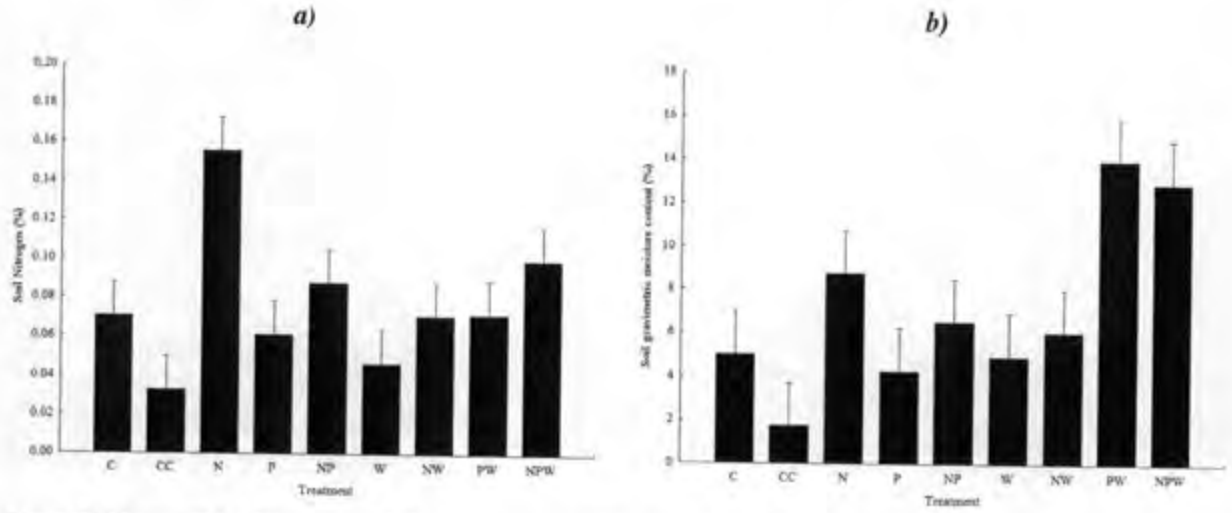


***Figure 5**. Mean soil (a) Nitrogen and (b) Water content in response to the artificially added treatment of N and water. Bars represent standard error. Graphs derived from Factorial ANOVA, Statistica.*

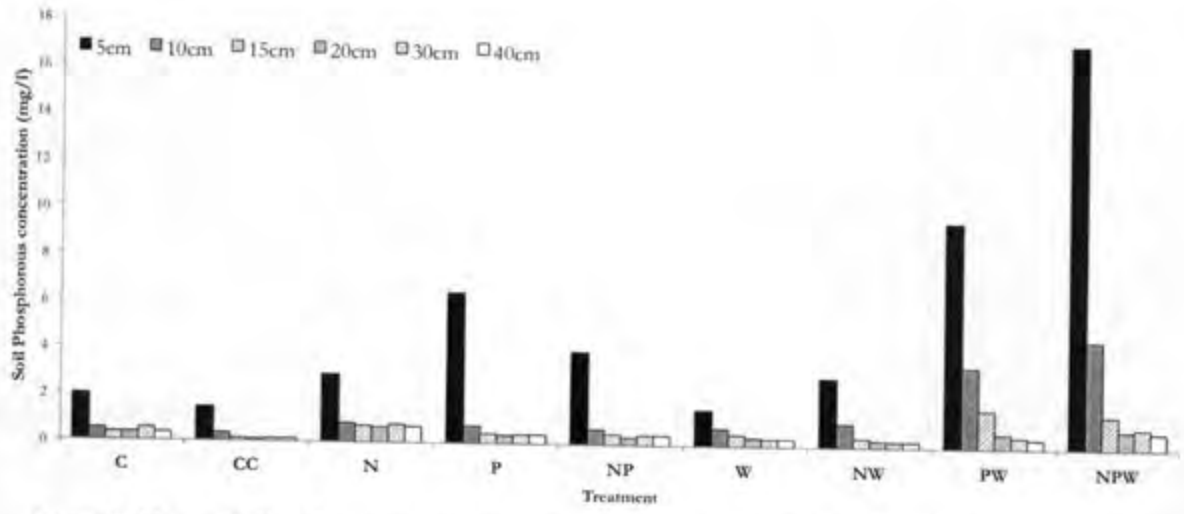


***Figure 6**. Mean soil Phosphorous concentration for each treatment & at different soil depths in response to artificially added P. Graph constructed in Excel.*

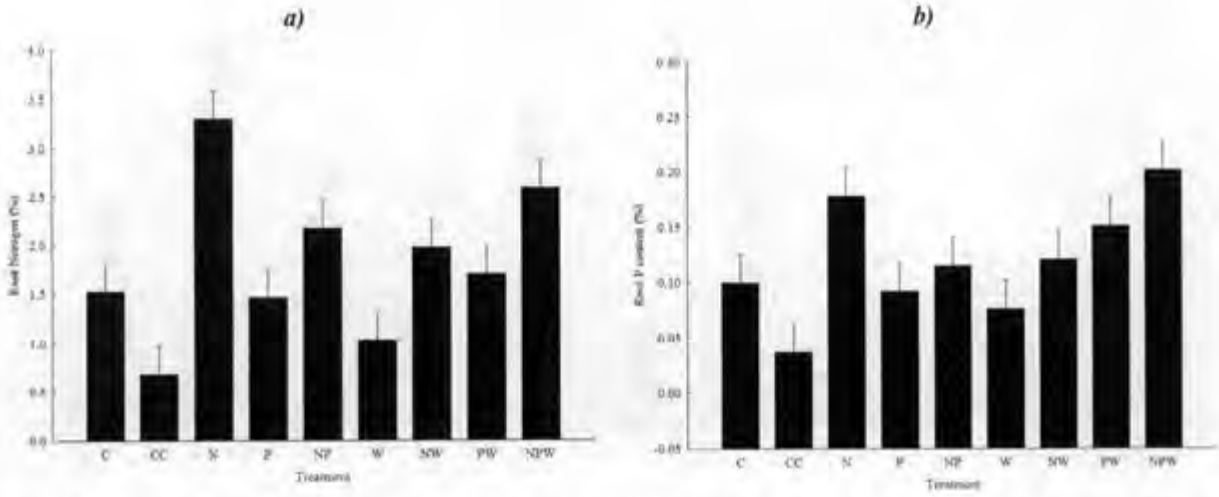


Figure 7. *Root mean a) Nitrogen and b) Phosphorous content in response to the artificially added treatment of N and P. Bars represent standard error. Graphs derived from Factorial ANOVA, Statistica.*

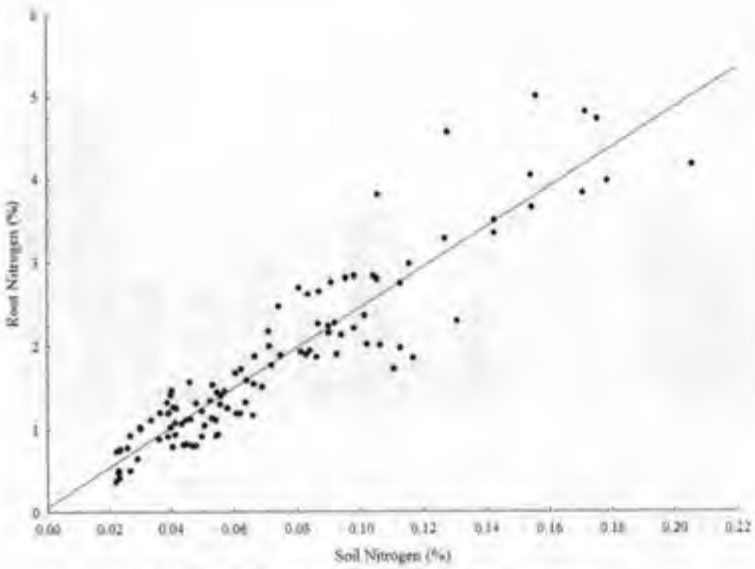


Figure 8: *Root versus Soil nitrogen content. Linear trend line: y= 24,0734x + 0,056. r^2= 0,86.*

Mean fine root $\delta^{13}C$ values decreased significantly down the soil profile ($F_{5,45}$=5.61, P<0.001). The target (end member) tree and grass species' mean $\delta^{13}C$ values were -23.86‰ ± 0.08 and -12.93‰ ± 0.33 respectively (n=6). The $\delta^{13}C$ value of -23.86‰ is not viable for an Acacia tree $\delta^{13}C$ value and thus it was replaced by -27.07‰, as this was the mean value of the dominant acacia $\delta^{13}C$ value (*A. nigresens*, n=5) as reported in previous studies at Satara (February & Higgins, 2010; Shadwell, 2011, pers.comm.). The tree and grass $\delta^{13}C$ values were used to calculate the proportion of tree versus grass fine root material in each sample and from this the fine root biomass of both tree and grass in each sample. The tree and grass fine roots are both present throughout the profile and significantly decrease with depth (Tree: F=7.79; p<0.0001, Grass: F=15.57; p<0.0001) (Fig. 9). The tree and grass fine roots were both significantly greater in the top 15cm of the soil (Tree: F=29.58, p<0.0001, Grass: F=49.97; p<0.0001). Relative to the controls, the addition of nutrients and water favoured the grasses rather than the trees as grass fine roots increase significantly with treatment (F=2.98; p<0.01) whilst tree fine roots did not (F= 1.63; p=0.137) (Fig. 15) and the tree:grass root ratio significantly decreased with treatment (F=7.93; p<0.001) (Fig. 10).

I used the tree:grass root ratio as an indicator of the equality or dominance of the tree and grass fine roots. The water treatments (W, NW, PW, NPW) saw the greatest increase in grass root biomass and the lowest tree:grass root ratios (Fig. 10 & 11). There is a negative relationship between the nutrients in the roots and water in the soil with the tree:grass root ratio (Fig. 12) which further indicate the favouring of grass roots with increased nutrient and water availability.

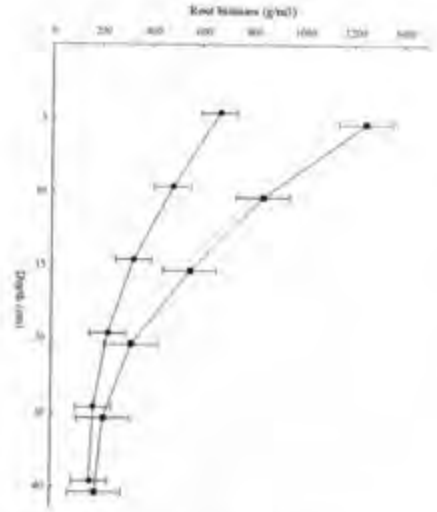


***Figure 9**. Mean Tree (circle) and Grass (square) root biomass down the soil profile. Verticle bars represent standard error. Graphs derived from Factorial ANOVA, Statistica*

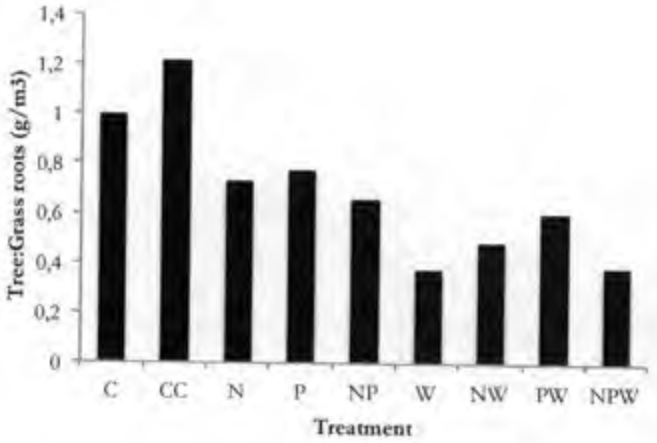


***Figure 10**: Tree:Grass root biomass ratio mean across the treatments. 1 indicates equal tree roots to grass, <1 indicates grass root dominance, and conversely for >1. Graph from Excel.*

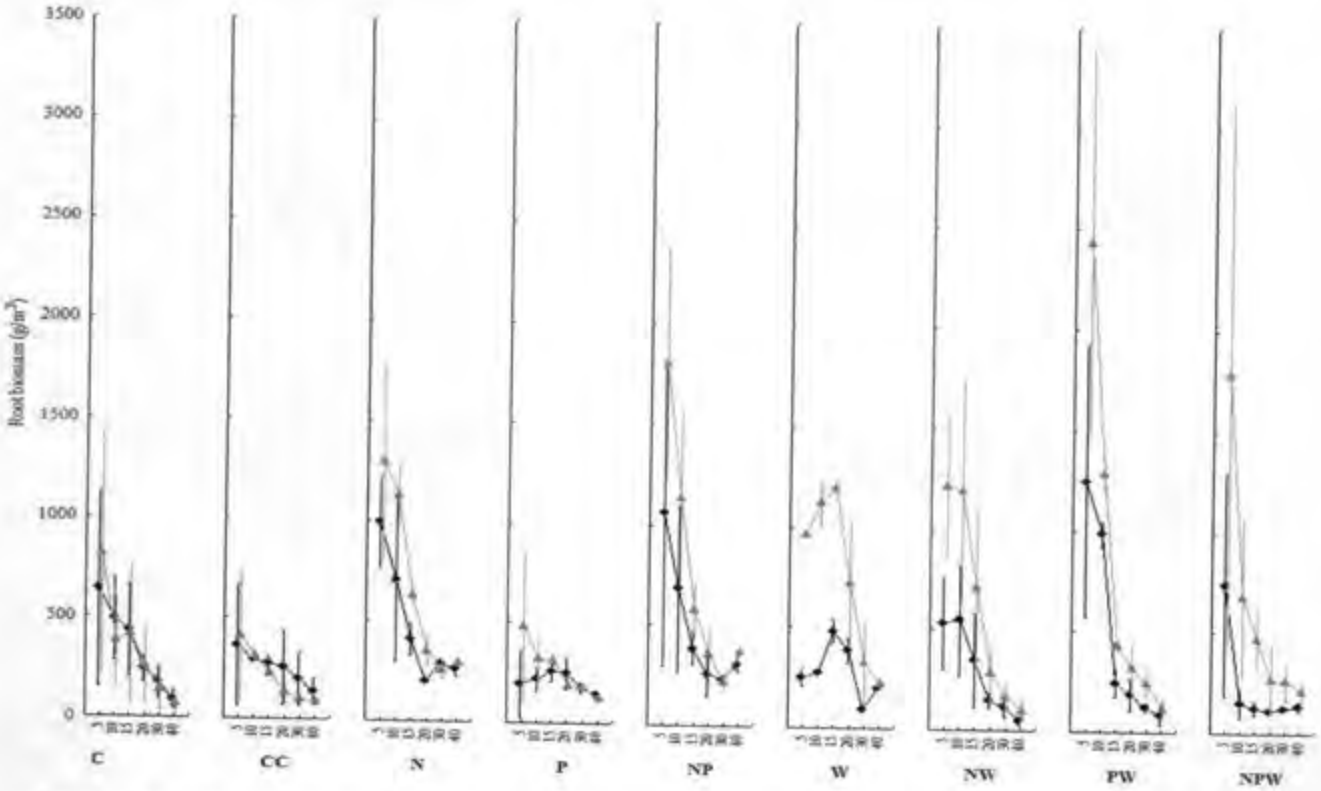
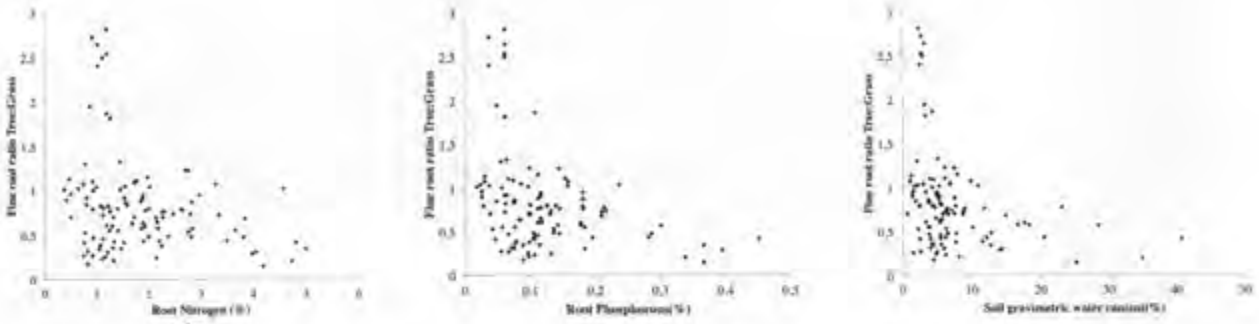


***Figure 11**. Mean Tree (black circles) and Grass (grey triangles) fine root biomass down the soil profile in response to the treatments. Verticle bars represent standard error. Graphs derived from Factorial ANOVA, Statistica*



a) b) c)

Figure 12. *Ratio of Tree:Grass fine root biomass against (a) Root N, (b) Root P and (c) Soil water content.*

CLIMATE ANALYSIS

Satara experiences a unimodal summer rainfall with a long-term MAP of ±530mm/year with a highly significant 10^{th}-90^{th} percentile interannual variation (see Fig. 1). The model NCEP downscaled re-analysis of the past climate is used to test the viability of the models and are shown to have captured the unimodal summer rainfall pattern adequately but the model underestimate the mean and interannual range of rainfall received by ±30mm and ±80mm respectively (CSAG, 2012). Satara is projected to experience an increase in monthly rainfall totals (Fig. 13) and a consequent decrease in the dryspell-duration/drought length (Fig. 14). The models are projecting the summer rainfall to shift earlier as early summer is getting wetter whilst late summer is getting dryer (Fig. 13 & 15). The maximum and minimum temperatures are projected to significantly increase ($p<0,0537$; Observed mean: 29,99°C, Projected mean: 32,19°C).

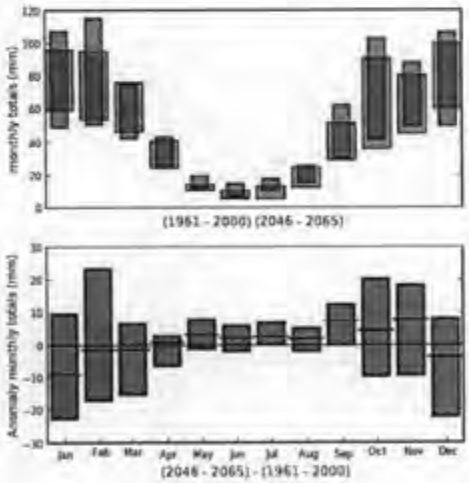


Figure 13. Top Panel: *Rainfall monthly totals 10^{th}-90^{th} percentile multi-model range of the projected period (thin bar) overlaid on the downscaled 20^{th} Century simulation period (thick bar).* ***Bottom panel:*** *10^{th}-90^{th} percentile multi-model anomaly range between the future simulation period and the 20^{th} Century simulation period.* (CSAG, 2012)

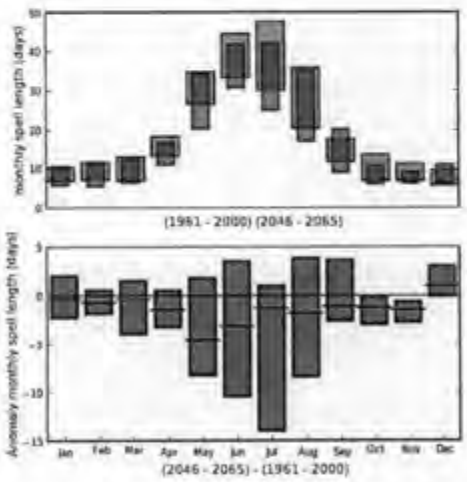


Figure 14. Top Panel: *Rainfall monthly dry-spell duration 10^{th}-90^{th} percentile multi-model range of the projected period (thin bar) overlain on the downscaled 20^{th} Century simulation period (thick bar).* ***Bottom panel:*** *10^{th}-90^{th} percentile multi-model anomaly range between the future simulation period and the 20^{th} Century simulation period.* (CSAG, 2012)

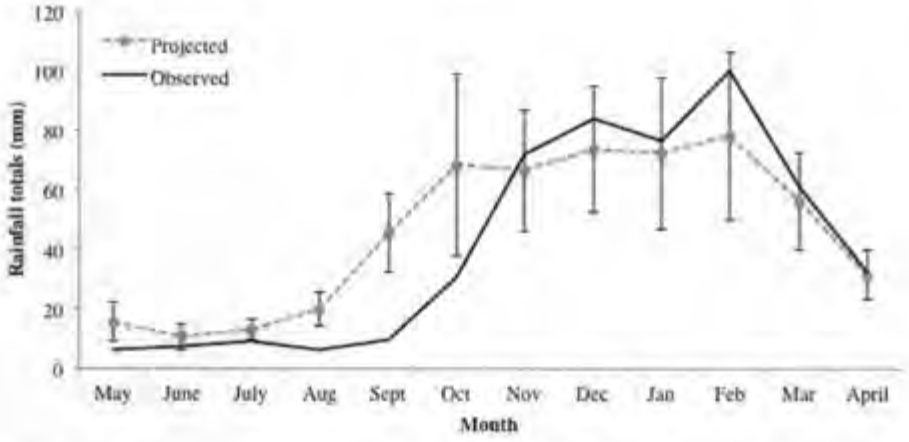


***Figure 15**. Rainfall monthly totals of the observed 20th Century period (black solid line) with the mean (±stdev) projected rainfall monthly totals from the multi-model projections. Graph restructured from May to April, showing the unimodal summer rainfall. Raw data:* (CSAG, 2012)

DISCUSSION

My results show that the distribution of tree and grass fine roots within the soil horizons of the semi-arid savanna study site have a positive relationship with the distribution of available resources (N, P, water). The roots are actively taking up the nutrients where they are highest as the tree and grass roots were both concentrated in the top 15cm of the soil, which increased with increasing nutrients and water relative to the controls. With the positive correlations between the soil and root nitrogen percentages (Fig. 8) and the presence of both tree and grass roots in the same soil horizons, the roots are likely significantly competing for nutrients and space. This is hypothesized for the gulliver trees however, this phenomenon has also been found in studies with mature trees (February & Higgins, 2010; Shadwell, 2011, pers.comm.; Verweij et al., 2011). In addition, isotopic analysis indicated that gulliver and grass roots are shown to be actively respiring at the same depths (Bell, 2012, pers.comm.) which further indicate significant competition for resources between the gulliver and grass fine roots.

This study showed specifically that grass fine root biomass was significantly increased with increased moisture availability whilst Acacia gulliver fine root biomass was not. The climate projections for the study area project an increase in rainfall. The models (SRES A2) indicate an early summer season wetting and a late summer season drying due to predicted shifting rainfall patterns by mid-century. Climate change impacts on intra-annual rainfall patterns are highly significant for plant phenology (Lohman et al., 2012). The mean (± stdev) rainfall of the CIP baseline period (1982-2005) was 480 mm/year (±200mm) and this is expected to increase to a mean (± stdev) of 550 mm/year (±81mm) for the projection period of 2046-2065 (CSAG, 2012). The

winter drought length will be shortened and the inter-annual minimum and maximum rainfall expected to increase. The growth of the gulliver tree roots below and shoots above ground was retarded due to the increased competitiveness of the grassy root matrix and the grass shoots with increased water. Grasses will be favoured by the potential shifting of summer rains earlier as trees will no longer have the advantage of an early summer season flush due to their possible access to deeper water resources (February et al., 2012). Grasses would be vulnerable to extended drought and the dehydration of the upper soil layers, therefore grasses will again be favoured considering the projected decrease in the dry-spell duration. Semi-arid savanna tree densities are climatically controlled, but an increase in water availability will most likely result in a possible shift towards a grass dominant ecosystem, as grasses will have the competitive advantage over trees.

Globally, the percent of natural ecosystems affected by artificially enhanced atmospheric nitrogen deposition, beyond the critical threshold of 1g N/m/y, is expected to increase from 10% to 25% by the year 2030 (SRES A2) (Dentener et al., 2006). This can be attributed to anthropogenic activities such as farming, mining and fossil fuel burning (Dentener et al., 2006). Artificial N deposition is significantly occurring in the KNP of South Africa (Dentener et al., 2006; Sheffield & Wood, 2008; van der Waal et al., 2009). An increase in nutrients is predicted to negatively affect woody trees due to the intensification of grass competition with tree seedlings and saplings (van der Waal et al., 2009). This was supported in my study as it showed that tree and grass fine root biomass had a positive relationship with increased nitrogen and phosphorous and the grass fine root biomass increased to a greater degree than that of the tree fine roots. An increase in P-only did not elicit a significant response from the tree or grass roots, but when coupled with water, nitrogen or both, tree and grass roots showed an increase in biomass, with grasses dominating. The grass root biomass increase seen with N-only treatment was less than that seen when coupled with P, or P and water. This supports the growing evidence of N and P being co-limited in South African grassland ecosystems (Craine, Morrow, & Stock, 2008). Semi-arid and arid savanna ecosystems are particularly susceptible to nitrogen limitation, in addition to water limitation (Kambatuku et al., 2012), and my results possibly agree and suggest Satara to be more nitrogen and water limited than phosphorous limited. Tree densities are most likely to decrease in a future with increased soil nitrogen. This response will be heightened if phosphorous increases concurrently.

The Future Satara

Under control conditions the tree and grass fine roots are of near equal proportions, i.e. the tree:grass ratio is ≈1. This ratio is significantly decreased with increased water and nutrients as the grasses are responding with exceptional growth to the added resources. The competitiveness of the grasses was heightened significantly and the gullivers were not able to compete and significantly

grow. Despite the ability of the Acacia gullivers to biologically fix nitrogen, the nitrogen treatment does not relieve the competitive pressure for N; a result also found in other studies (Cramer et al., 2012; Kambatuku et al., 2012). The results from this study indicate an altered future for the semi-arid savanna of Satara. The future herbaceous grassy layer will be significantly increased and hold a competitive advantage over the woody tree cover (currently ±20-25%) due to the predicted concurrent increases in nutrients and water availability. Tree densities will decrease as seedling establishment, sapling and gulliver growth will be greatly reduced and mature trees over time will naturally senesce and die.

A rapid increase in temperature will favour grass survival (Higgins & Scheiter, 2012). In addition to resource changes, Satara will experience a 2°C increase in minimum and maximum temperatures, as well as an increase in wind by mid-century (SRES A2) (CSAG, 2012). These conditions may increase the fire potential of the fire prone savanna ecosystem in combination with the increased grass fuel load. Gulliver trees are stuck in the fire and browser trap and may exist in this state for decades (Bond, 2008) affecting the future generation of established mature trees. To better understand the competitive interactions between the grasses and the trees and whether it is predominantly for water or nutrients, research needs to include the temporal distribution of nutrients and water and the uptake of these nutrients (February & Higgins, 2010) as my results are only a snapshot in time of the tree and grass interactions. Further research will help determine whether tree and grass co-existence is mutually beneficial or competitively exclusive (February et al., 2012).

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Appendix 1: UCT soil P and N extraction and analysis procedures

Soil Exchangeable Phosphate Extractions: Bray II method

This method yields so-called plant-available phosphate in soil. Since it is a commonly used standard method it is useful to use Bray II versus other methods. Also Bray II yields similar results to extraction with resin bags and/or 100 mM citric acid (Heidi Hawkins, 2007 pers comm.).

- NH4F – Solution: Dissolve 93 g NH4F in 2.5 L dH2O
- Bray II extracting solution: Place 300 ml NH4F solution in a 10 L tank. Add 5 L dH2O. Add 100 ml concentrated HCl (AR). Make up to 10 L volume and mix well.

Adjust volume of above depending on number of samples, e.g. need total of 7.5 L for 300 soil samples.

Place 3,3 g soil in an extraction bottle and add 25 ml Bray 2 solution. Shake for 40 sec by hand and filter. Analyze the filtrate for P with the ICP or colorimetrically (e.g. Molybdate Blue or Malachite Green). Colorimetric methods are more sensitive for P than ICP.

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Molybdenum Blue Method

Sulphuric Acid:

5N concentrated sulphuric acid. Dilute 70mL of concentrated H2SO4 to 500mL with milli-Q water.

Ammonium Molybdate:

Dissolve 20g Ammonium molybdate tetrahydrate [(NH4)6Mo7O24.4H2O] in 500mL Milli-Q water.

Ascorbic Acid (0.1M):

Dissolve 1.32g of ascorbic acid in 75mL milli-Q water. PREPARE DAY OF ANALYSIS BECAUSE QUICKLY OXIDIZES!

Potassium antimonyl tartrate (1mgSb/mL):

Dissolve 0.2743g potassium antimonyl tartrate in milli-Q water and dilute to 100mL.

Mixed Reagent:

Mix thoroughly 125mL of 5N sulphuric acid and 37.5mL of ammonium molybdate. Add 75mL of ascorbic acid solution and 12.5mL potassium antimonyl tartrate solution. DO NOT STORE FOR MORE THAN 24 HOURS!

Stock Phosphate Solution (100mg/L) (store in refrigerator up to 2 weeks):

0.219674g monopotassium phosphate (KH2PO4) or potassium dihydrogen orthophosphate 500mL Milli-Q water

Bray 2 Extract Matrix

Materials:

- ~ 250mL of Matrix solution (0.5M $NaHCO_3$)
- Mixed Reagent (MADE DAY OF ANALYSIS)
- Stock phosphate solution (100 mg/L) (made fresh every 2 weeks)
- 96-well microplates and lids – sterile
- Micropipettes and tips
- Pipetting basins
- 1.5mL Eppendorf microfuge tubes

Procedure:

Make a Standard Ladder –

1) Dilute the 100 mg/L stock phosphate solution into a 1.5mL Eppendorf tube: High Concentration: 150µL stock solution in 1350µL 2M KCl matrix solution (for 1.5 mL volume of a 10 mg/L solution). Low Concentration: 15µL stock solution in 1485µL 2M KCl matrix solution (for 1.5mL volume of 1 mg/L solution).

2) Using the diluted stock solution made in #1 (dependent on whether you want the "high" 1-10 mg/L range or "low" 0-1 mg/L range), create the following standard curves in 6 Eppendorf tubes.

STANDARD LADDER			
Low Concentration (mg/L)	High Concentration (mg/L)	µL 10 mg/L stock solution	µL matrix solution
0.00	0.0	0	1000
0.05	0.5	50	950
0.10	1.0	100	900
0.20	2.0	200	800
0.50	5.0	500	500
1.00	10.0	1000	0

Load the Plate –

3) Add the following to each well of a 96-well microplate (load ALL samples FIRST before adding the reagent): High Concentration: 100µL ladder solution and sample 20µL Mixed Reagent. 5 µL Milli-Q water (optional-used to dilute sample to a larger volume) NOTE: Absolute amounts of sample and reagent do not matter as long as the proportion remains 10 : 2 : 0.5 (optional).

4) Incubate for 30 minutes until an intense bluish-purple color develops. Remains stable for up to 24 hours.

5) Read the plate at 882nm. Detection limit <0.05 mg/L.