Running title: Nutrient Limitation in the Kalahari

Title: The interactive nutrient and water effects on vegetation biomass at two African savanna sites with different mean annual precipitation

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Abstract

Savannas cover more than 40% of Africa and provide a variety of important ecosystem services. Their productivity is constrained by disturbance and limiting resources. In southern Africa, fine-leaf savannas typical of arid environments are known for being richer in nutrients than broad-leaf mesic savannas. However, despite numerous recent studies on the dynamics of southern African savannas, the interplay among water and nutrient limitations remains poorly investigated in these systems. To better understand the interactions among water, nutrients (N and P in this manuscript) and grazing on the productivity of grasses and trees in fine-leaf savanna ecosystems, a fertilization experiment with controlled grazing was conducted at two sites with different mean annual rainfall in Namibia. The experiment demonstrated that the vegetation at the drier site may not be nutrient limited (N, P or N+P). At the wetter site, however, vegetation showed significant response to nutrient addition. Grasses exhibited N limitation and trees exhibited P limitation. This experiment also showed that grazing reduces the overall grass biomass, but may not modify the response to nutrient treatments. The results indicated a switch from water to nutrient limitation between dry and wet sites and demonstrated different tree and grass responses to nutrient additions.

Keywords: Fertilization, Grazing, Kalahari Transect, Phosphorus, Namibia, Nitrogen, Savanna

Introduction

Savanna ecosystems cover about 20% of the Earth's land area (Scholes and Walker, 1993) and produce approximately 29% of global terrestrial net primary productivity (Grace et al., 2006). Water availability, disturbance (e.g., fire, herbivory) and nutrient availability are considered to be the three major factors determining the structure and function of savanna ecosystems (Walker et al., 1981, Sarmiento, 1984, Scholes and Walker, 1993, Scholes and Archer, 1997, Aranibar et al., 2004, Sankaran et al., 2004, Sankaran et al., 2005, Okin et al., 2008, Wang et al., 2010a). Recent study showed that temperature may also affect tree establishments in cooler savannas (Wakeling et al., 2012). Among these factors, the composition and structure of savanna vegetation and plant-plant interactions are particularly sensitive to soil water availability, which, in turn, depends on rainfall regime and soil properties (Scanlon et al., 2005, D'Odorico et al., 2007).

It is commonly accepted that the so-called "nutrient-poor savannas" existing in semiarid climatic regions of southern Africa, are limited by nitrogen (N) availability (Scholes and Walker, 1993, Ludwig et al., 2001), while savanna vegetation in more arid environments is mainly water limited. However, the Kalahari sands, which cover extensive areas in southern Africa, are highly weathered, mature and highly depleted in primary phosphorous (P) minerals (Wang et al., 2007). Because P is an essential nutrient, its low availability may constrain ecosystem productivity on the Kalahari sands. The likelihood of P limitations is even stronger at the dry end of the Kalahari, due to the dominance of potentially N fixing plants (Wang et al., 2009a). Prior studies in the Kalahari have shown that

grass biomass does not respond to nutrient addition across a major rainfall gradient (Wang et al., 2010b), but less is known about the response of trees to additional nutrient availability. In addition, the nutrient effects on grasses could be affected by grazing and browsing through processes such as physical vegetation removal and dung deposition (e.g., O'Halloran et al., 2010, Wang et al., 2010b) both by livestock and wildlife. Although savannas cover more than 40% of Africa (Scholes and Walker, 1993) and provide extensive rangeland for traditional pastoral societies, only a handful of savanna fertilization experiments have been reported in the literature (e.g., Ludwig et al., 2001, O'Halloran et al., 2010, Wang et al., 2010b). Overall, interactions among water, nutrients and grazing in savannas remain poorly investigated, which significantly hinders our understanding of their response to future environmental and anthropogenic changes.

The Kalahari Transect (KT) is one of a set of IGBP (International Geosphere-Biosphere Programme) megatransects (Koch et al., 1995, Scholes et al., 2002) identified for global change studies. The KT traverses a dramatic aridity gradient (e.g., 200 mm to 1000 mm in rainfall gradient) on relatively homogenous soils (deep Kalahari sands, Thomas and Shaw, 1991, Thomas et al., 2008), offering an ideal setting to study nutrient and vegetation dynamics under different rainfall regimes without confounding soil effects (Wang et al., 2007). Both modeling results based on remote sensing data (Scanlon and Albertson, 2003) and leaf-level physiological data (Midgley et al., 2004) suggest the existence of two distinct regimes of vegetation productivity-rainfall relationships across the KT, likely mediated by soil biogeochemical variations. In this study, we use two sites along the KT in southern

Africa as representative of relatively dry savannas (mean annual rainfall < 450 mm) under two distinct rainfall regimes. Through a fertilization experiment we directly investigate how the interactions among water and nutrient limitations, and grazing affect the productivity of grasses and trees in dry, fine-leaf and supposedly nutrient rich savannas. Specifically, we ask 1) whether there is a difference in nutrient limitation (N vs. P) at two sites under different levels of mean annual precipitation (MAP), and 2) whether there is a difference in tree and grass response to nutrient additions.

Materials and Methods

Field Sites

Two sites (Okonjoka and Rooibult) from the Kalahari within Namibia were chosen to compare the grass and tree responses to fertilization under different rainfall conditions, with Okonjoka being drier (200-250 mm MAP, the dry site thereafter) and Rooibult (the mesic site thereafter) receiving about 400-450 mm MAP (Fig. 1). However, during the experiment period (November 2008 to May 2009), total rainfall at the dry site (425 mm) was higher than at the mesic site (361 mm), reflecting the strong rainfall interannual variability in drylands. Rainfall at both sites is concentrated between November and April (Fig. 2), corresponding to the growing season of both trees and grasses. Both the dry site (23.48°S, 19.75°E) and the mesic site (21.50°S, 19.18°E) are classified as open savannas dominated by *Acacia* species such as *Acacia erioloba* and *A. mellifera* Benth. Based on the field observations, most grass species found at the dry site were annuals, whereas the grasses at the mesic site were primarily perennials such as *Eragrostis lehmanniana,*

Stipagrostis uniplumis and *Schmidtia kalahariensis*. *A. mellifera* was the most common tree species at the dry site and *A. erioloba* was the most common tree species at the mesic site. Soil properties such as porosity, field capacity, saturated hydraulic conductivity were similar between these two sites and the general pattern of variability of these soil parameters within the Kalahari sand can be found in earlier reports (Wang et al., 2007, Wang et al., 2009a). To summarize, the soils of the Kalahari are sandy (sand content >96%) and acidic (pH ≈ 6); the soil nutrient level is low, with total soil N% ranging from 0.01 to 0.04% (Wang et al., 2007) at the surface (0-10cm); PO_4^{3-} and NO_3^- concentrations range from 1 to 4.5 µg/g, and from 0.5 to 20 µg/g respectively (Wang et al., 2009a), while soil plant available phosphorus (Bray extraction soil P) ranges from 2 to 15 µg/g (O'Halloran et al., 2010).

Fertilization treatment and biomass estimation
Grass fertilization

The experiment consisted of a randomized block design with four 15 m x 15 m plots at each of the two sites along the KT. A fence was installed in 2008 with a total enclosed area of 1800 m^2 (225 x 4 x 2=1800 m^2). Four 15 m x 15 m plots were also set up in an open rangeland at the mesic site to test the interactive effects of grazing and nutrient additions on plant biomass responses. Each 15 m x 15 m plot was divided into four 7 m x 7 m subplots with 1 m buffer zone between each subplot. In this region livestock production relies both on grazers (mainly cattle) and browsers (goats). The dry site was inside the village and subject to heavy grazing while the mesic site was away from the village. At each study site soil

topography and vegetation cover were similar in all the subplots within each block. In October 2008, four treatments (N addition, P addition, N+P addition and control) were randomly applied to the subplots. For the N and N+P treatments, 133 kg N/ha as NH_4NO_3 was evenly applied to each subplot and 33 kg P/ha as $Na_2H_2PO_4$ was evenly applied to the P and N+P subplots, whereas the control subplots were supplied with water only. The applied concentrations of fertilizers were chosen on the basis of data reported by Wang et al. (2010b) for experiments in different locations of the Kalahari savannas. For each treatment plot (49 m^2), the reagents were dissolved in 10 L water. Water was used here as a solvent to homogenize the fertilizer and a sprayer was used to ensure even distribution of the fertilizer solution. The amount of water used for each plot was very small (10 L for 49 m^2), which is equivalent to about 0.2 mm rainfall. This amount of rainfall evaporates almost right way with no substantial impact on vegetation growth. The fertilizer solution was applied to the soil surface and was observed to infiltrate into the soil with only a negligible interception by the sparse canopy of grass leaves. According to Wang et al. (2010b), 40-70% of the foliar N is from the N fertilizer after one growing season. Newly-formed (i.e., post-treatment green tissues) grass biomass was measured by harvesting all grasses from the grass bottom using scissors from the treatment subplots at each site in early June 2009.

Tree fertilization

To investigate the effect of P on trees, one representative tree species (*Acacia mellifera* at the dry site and *Acacia erioloba* at the mesic site, both of them are potential nitrogen fixers) was selected at each site. Fertilizer at the same

concentration (10 L water for each tree) as the grass fertilization experiment was applied evenly over an 8 m diameter circle centered at the base of each tree. Three individual trees were used for each treatment (P and control). All the selected trees were within the same age class. The basal diameters of the selected *A. erioloba* trees were 13-26 cm and the heights were 1.7-2.2 m. The canopy diameters of the selected *A. mellifera* were 0.8-2.2 m and the heights were 0.5-1.1 m. Canopy diameter (for *A. mellifera* only), branch length, tree height and basal diameter (for *A. erioloba* only) were measured for all the trees in the subsequent wet season. *A. mellifera* and *A. erioloba* have different growth forms. *A. mellifera* is thorny and has multiple stems. The basal diameters for these trees are very difficult to measure, because their base is difficult to access. Therefore we did not measure basal diameters of *A. mellifera*. The canopy shape of *A.erioloba* is irregular and the canopy diameter cannot be accurately measured even with measurements from multiple directions. For this reason for *A. erioloba* we only measured the basal diameters. We measured canopy diameter in two perpendicular directions and took the average to indicate mean canopy diameter. For branch length measurements, we randomly selected three branches from each tree and marked them. We measured the net growth for these branches and calculated the means for each tree. Relative growth was defined as (basal diameter after fertilization – basal diameter before fertilization)/ basal diameter before fertilization. Relative growth was only estimated for *A. erioloba*, at the mesic site. The experiment was conducted for one season.

Statistical analyses

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To test the grazing and nutrient (N and P) effects on grass biomass response, two-way ANOVA for a randomized block design with grazing and nutrient treatment as two main factors was used to test for differences in grass biomass at Rooibult (SAS v. 9.1 PROC MIX). One-way ANOVA was used for the Okonjoka site since there was no grazed treatment. Mean separations for the treatment effects (e.g., grazing and nutrient fertilization) were achieved using the Tukey *post hoc* test at α = 0.05. To test the P effect on trees, at each site, tree relative growth rate, canopy diameter, tree height and branch length were measured before and after P fertilization and the calculated differences were compared between the P treatment and control using one-way ANOVA at α = 0.05.

Results

The grass biomass at the dry site did not show significant differences among the nutrient treatments (Fig. 3, e.g., N, N+P and P fertilization), though some individual plots showed a large amount of grass biomass for the N+P treatment with a value up to 180 g/m^2. At the mesic site, two-way ANOVA showed a significant grazing effect and a nutrient effect without significant interactions between them (Table 1). Grazing significantly decreased grass biomass from 360.1 g/m^2 to 298.0 g/m^2 (Table 1). For the nutrient effects, the above ground grass biomass showed significant increases at the N and N+P treatments compared with the control treatment (Table 1, Fig. 3). There was no biomass increase for the P only treatment (Table 1, Fig. 3).

Before the nutrient additions, there were no significant differences in the canopy diameter and tree height between control and P fertilization trees at both

sites (p > 0.05). There were no significant differences in the changes of canopy diameter (for *A. mellifera* only), tree height and branch length between the P treatment and the control treatment for *A. mellifera* at the dry site and *A. erioloba* at the mesic site (Table 2). However, the relative growth (basal diameter) of *A. erioloba* at the mesic site significantly increased for P treatment compared with control treatment (Table 2).

Discussion

Grass response to fertilization

The grass biomass at the drier site (Okonjoka) did not show significant differences between the nutrient treatments, indicating that the drier site may not be nutrient limited. The grass biomass at the dry site was significantly lower than that at the mesic site (Fig. 2). This was not only caused by lower mean annual rainfall, but also vegetation composition and temporal patterns of rainfall. Based on communications with Okonjoka residents, even though the total rainfall was high for this particular year, it came as intensive infrequent storms. Thus grass seedlings died between major rainfall events. Furthermore, the only grass species found in our plots at the dry site was an annual, whereas the grasses at the mesic site were primarily perennials. Due to their ability to survive dry periods between storms and their deeper rooting systems, perennials are more amenable to exhibit differences in growth in experiments like ours (Wang et al., 2006). In addition, the significant spatial variability observed in grass responses at the drier site - which were likely caused by the uneven soil moisture distribution due to the presence of trees (D'Odorico et al., 2007, Wang et al., 2009b) - contributed considerably to the

variability in biomass among plots. Prior livestock impacts at the dry site may also have contributed to the high variability in biomass production. In fact, the dry site is located within 1 km from a borehole and is therefore exposed to significant livestock impacts. Although obvious indicators of differential animal impacts were avoided when placing our experimental plots, earlier activity by grazers and browsers, including differential effects of fecal matter could have contributed to the heterogeneity observed in our experiment (e.g., Li et al., 2010). Moreover, the heterogeneity was likely enhanced by aeolian processes (e.g., sand saltation and wind-induced nutrient redistribution) acting on a heterogeneous vegetation cover (e.g., Ravi et al., 2009).

The significant increase in grass biomass for N and N+P treatment at the wetter site (Rooibult; Fig. 2) indicate that the grasses at the wetter site are limited not by P, but by N. Grazing decreased overall grass biomass, but did not change the grass response to nutrient additions (Table 1, Fig. 3). An earlier fertilization experiment in the Botswana's Kalahari showed that nitrogen additions did not result in increased plant nitrogen content (Wang et al., 2010b), e.g., no increase in grass palatability (a function of N content). This could explain why grazing did not affect the results of nutrient treatments (Fig. 3). It is possible that after fertilization leaching of NO_3^- occurs both at the dry and at the mesic sites. However, since in these environments soil moisture seldom reaches field capacity, the rates of NO_3^- leaching are expected to be low especially in relatively well vegetated areas (the vegetation cover at the two sites was larger than 80%), though in areas denuded of vegetation leaching may occur (Aranibar et al., 2011). An earlier experiment on

Kalahari sands using ^{15}N as a tracer, Wang et al. (2010b) showed that 40-70% of the foliar N was from the N fertilizer after one growing season. Thus we expect the effect of NO_3^- leaching to be minimal when compared to plant uptake.

The limitation of grass productivity by N observed at the mesic site contrasts with results from a previous field experiment in the Botswana Kalahari (Wang et al., 2010b) where the grass biomass did not respond to N and P additions. However, the experiment by Ludwig et al. (2001) in the dry savannas of Tanzania showed that grass production was limited by N availability. Nitrogen limitation is expected to exist especially in the more mesic areas, where soils are weathered or depleted in N. The diversity of results from these three experiments (from Botswana, Tanzania and Namibia) demonstrates the complexity of nutrient and water interactions in dry savannas: water availability affects plant photosynthesis, plant nutrient uptake and soil microorganism activity (e.g., mycorrhiza P transfer and symbiotic N fixation); these processes, in turn, affect plant photosynthesis. Moreover, the complexity also arises from the interactions among different nutrients. For example, micronutrients such as Mo could limit N fixation (Barron et al., 2009), while N and P could co-limit N fixation. These complex interactions suggest that some of the responses to nutrient additions could be transient and/or region-specific.

Tree response to fertilization

The significant differences in relative growth (calculated from basal diameter changes) of *A. erioloba* before and after P fertilization at the mesic site demonstrate that at the wetter site, P limits tree growth rates. These results also indicate that differences in changes of canopy diameter, tree height and branch length before and

after P fertilization may not be sensitive indicators to assess tree responses to nutrient fertilization. The fact that *A. mellifera* has multiple stems made it difficult to repeatedly measure basal diameter, and thus it is unclear whether *A. mellifera* at the drier site (Okonjoka) is limited by P or not.

Tree responses to nutrient additions were different than the responses of grasses. In our experiments, N was not added to trees, so we cannot rule out the possibility that trees are limited by N as well. However, *A. erioloba* and *A. mellifera* are reported to fix N in southern African savannas (Schulze et al., 1991), though anther study showed that the growth of N-fixing trees was constrained by grass competition (Cramer et al., 2010). Using foliar $\delta^{13}C$ and $\delta^{15}N$ data of trees and grasses in southern African savannas, Wang et al. (2010a) implied that, trees are not likely limited by N, even if grasses are superior competitors for soil N. In our results, it is clear that P limits tree growth and not grass growth, at least at the wetter site. The difference in response to P addition between trees and grasses are likely based on their physiological traits. As N fixers are typically limited by P or micronutrients (Vitousek et al., 2002), it is not surprising to see the different response to P addition between trees and grasses. Indeed, the different usage of N and P between trees and grasses may contribute to the co-existence of these two plant functional types (Swap et al., 2004, Aranibar et al., 2008, Wang et al., 2010a). Only limited data exist on tree response to nutrient addition in tropical savannas. A recent report for tropical forests showed that the relative growth rate of trees increased with N and P combination but not P alone (Santiago et al., 2011). Our results differ from this study in that P alone increased relative growth. Notice that

in this experiment, grass treatments were at the community level and tree treatments at the individual level. However, since the tree species selected are the most common species at these sites, our results may capture trees' response at these locations. Nevertheless, these results refer to only one growing season; the long-term response still need to be assessed by future experiments.

The results from our multiple-site fertilization experiment have important implications for the management of savanna ecosystems. These results indicate that in the south-western Kalahari the grass biomass of arid rangelands (MAP $\approx$ 200 mm) is strongly controlled by interannual variations in rainfall and soil moisture (Scanlon et al., 2005), while no significant dependence on nutrient availability (either N or P) is detected. The lack of nutrient response was further supported by the fact that the experimental year was particularly wet at the dry site: despite these anomalous wet conditions we still did not see the effect of nutrient additions. It is worth noticing, however, that because of the structure of multi-stem trees, we were not able to measure the relative growth at the dry site. In addition, we did not measure belowground biomass; thus, the belowbrwound biomass response to N and P addition is not known. Since in these environments rainfall is the main determinant of ecosystem productivity, adequate rangeland management should focus mainly on the hydrologic conditions and their interannual variability. Conversely, the more mesic site (i.e., MAP $\approx$ 400 mm) in north-eastern Namibia is limited by nutrients: grasses appear to be N limited while *A. erioloba* trees are P limited. At the same time, past modeling study showed that soil moisture and rainfall have a strong control on soil nutrients in the Kalahari even under wetter

rainfall regimes (Wang et al., 2009a). Together these results contribute to the understanding of the water and nutrient interactions, which is fundamental to better manage rangeland productivity.

Summary

To summarize the findings, this experiment demonstrates that a site on Kalahari sands in Namibia with 400 mm MAP is limited by nutrients, with grasses appearing to be N limited while the tree *A. erioloba* is P limited. The different tree and grass responses are likely due to N-fixation of trees. At a drier site, with only 200 mm MAP, our experiments did not show nutrient limitation, through high variability in rainfall timing and grass growth, and difficulty measuring basal diameter for the multistemmed *A. mellifera* may have contributed to the lack of a significant treatment effect.

Acknowledgements

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Table 1. Results of two-way ANOVA and *post hoc* Tukey test of grass biomass responses to grazing and nutrient treatments at Rooibult site (mesic site). The different capital letters indicate differences between treatments for Tukey test.

Source	df	F-value	p	
Grazing	1	4.28	0.05	
Nutrients	3	5.08	0.007	
Grazing x Nutrients	3	0.47	0.71	
Residual	24			
Mean biomasses at different grazing treatments (g/m^2)	Grazed	Ungrazed		
	298.0^A	360.1^B		
Mean biomasses at different nutrient treatments (g/m^2)	N	P	N+P	Control
	386.0^{AC}	275.9^{BC}	389.0^{AC}	265.3^B

Table 2. Differences between control treatment and phosphorus treatment for tree species at two sites with distinct rainfall regimes. The parameters monitored include relative growth, changes in canopy diameter, height and branch length. The numbers in parentheses are standard deviations. The different capital letters indicate differences between treatments.

		Relative growth[a]	Changes in canopy diameter (m)	Changes in height (m)	Changes in branch length (m)
Okonjoka (*Acacia mellifera*)	**Control**	\	5.5 (2.4)^A	-1.4 (2.9)^A	11.8 (3.5)^A
	P	\	6.2 (7.3)^A	1.5 (1.9)^A	10.1 (2.7)^A
Rooibult (*Acacia erioloba*)	**Control**	0.08 (0.07)^A	\	0.29 (0.13)^A	67.1 (20.2)^A
	P	0.35 (0.20)^B	\	0.36 (0.28)^A	66.1 (16.7)^A

[a]: Relative growth = (basal diameter one growing season after the treatments–initial basal diameter)/initial basal diameter

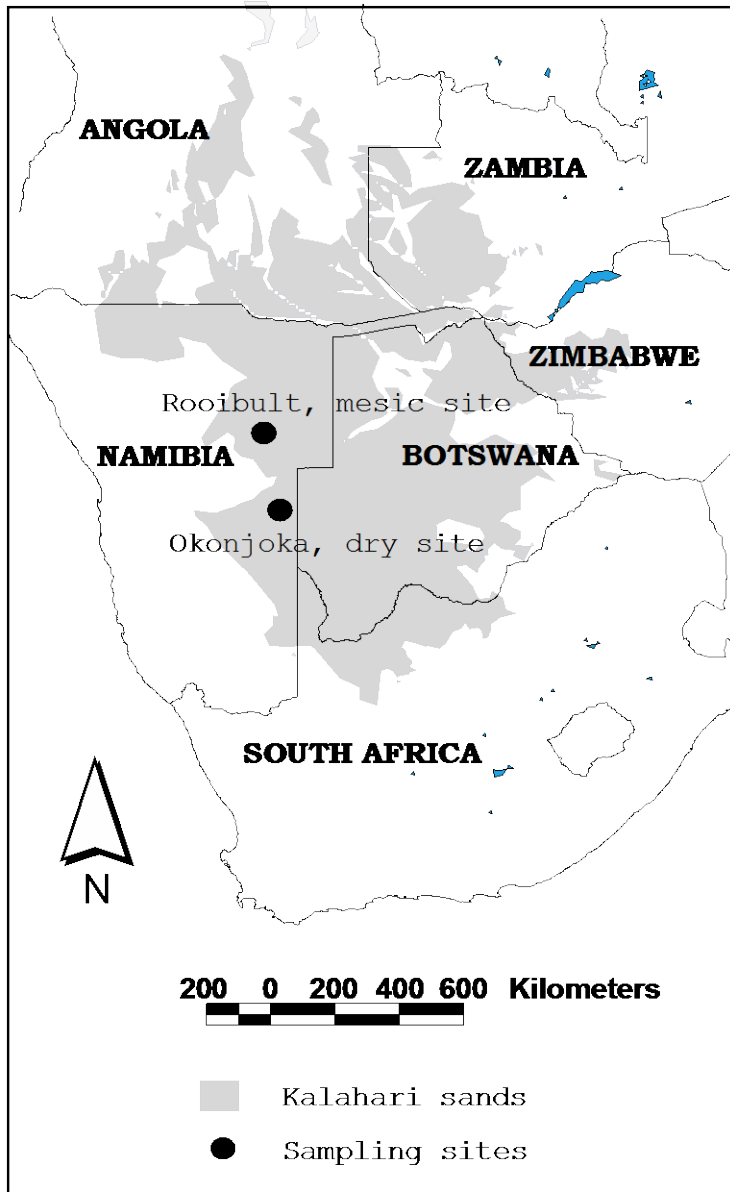Figure 1. Sampling locations within the Kalahari desert.

Figure 1

Figure 2. The monthly rainfall at Okonjoka (dry site) and Rooibult (mesic site) between November 2008 and May 2009. The mean annual precipitation (MAP) of each site was shown in the legend.
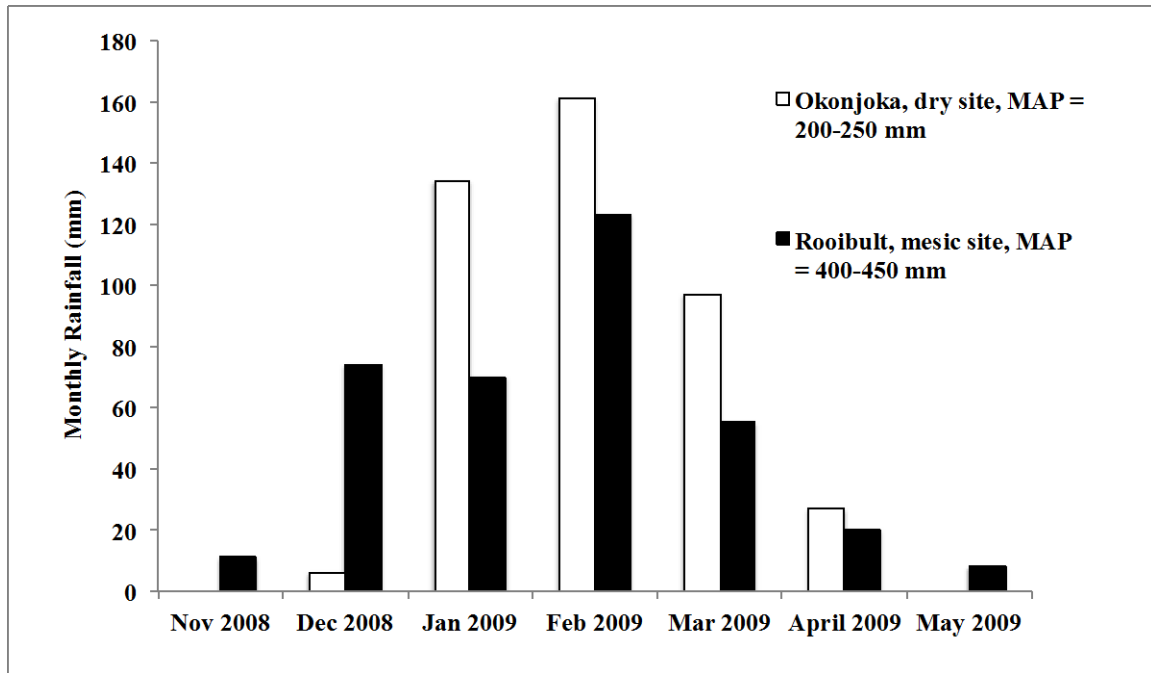

Figure 2

Figure 3. Grass biomass response to fertilization and grazing exclusion at Okonjoka (dry site) and Rooibult (mesic site). Two-way ANOVA for a randomized block design was used for Roobibult site and one-way ANOVA was used for Okonjoka site. The error bars represent standard errors.
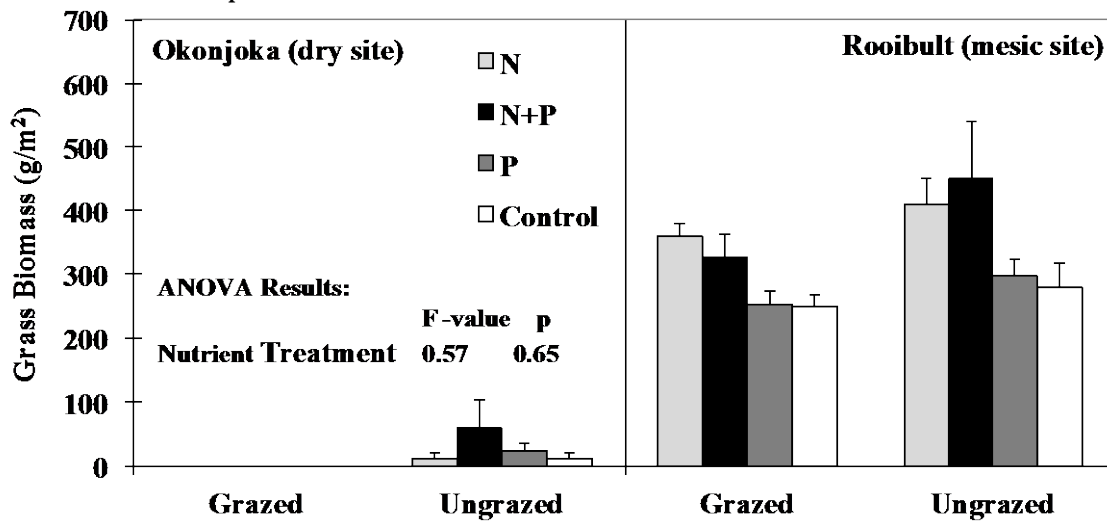

Figure 3.