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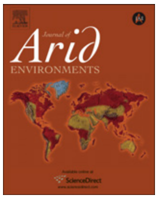

Nutrient limitations on aboveground grass production in four savanna types along the Kalahari Transect

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ABSTRACT

The Kalahari Transect (KT) is an International Geosphere–Biosphere Programme mega-transect designed to examine hydrological and ecological patterns and processes throughout the savannas of southern Africa. The KT traverses a precipitation gradient ranging from ~920 mm rain/year in the north to ~260 mm rain/year in the south. Previous research shows a positive correlation between canopy cover and precipitation suggesting a water limitation on productivity. However, there has been minimal research on other possible sources of limitations, such as soil Nitrogen (N) and/or Phosphorus (P). We used a factorial *in-situ* experimental design to test for increased aboveground grass production (measured as peak season standing stock) under elevated soil P and P + N levels. Four sites along the KT precipitation gradient were used in this study: Mongu (Zambia), Pandamatenga (Botswana), Ghanzi (Botswana) and Tshane (Botswana). Soils at each site were amended with N and P fertilizers during the dry season. We extracted soil samples during the following growing season to analyze for plant available soil P. Vegetation samples were harvested from which we measured foliar P and aboveground grass biomass production. We saw differences in foliar P at the treatment and site level but not for the interaction between treatment and site. There were individual effects from site on biomass but not for any interactions with nutrient treatments. Despite higher levels of foliar P, we did not detect an increase in aboveground biomass. This may be explained by luxury uptake or allocation to belowground resources.

1. Introduction

Approximately one third of southern Africa is occupied by the presence of the Kalahari Sands (Scholes and Parsons, 1997). This sand-filled basin traverses a major north–south precipitation gradient, ranging from ~920 mm/year in the north to ~260 mm/year in the south. The Kalahari is characterized by the continuous presence of mixed life-form plant communities. The savannas found in this region of southern Africa host both trees and grasses with seemingly non-successional persistence, a paradox that has intrigued ecologists for decades. The Kalahari Transect (KT) was identified as an International Geosphere–Biosphere Programme mega-transect research site for ecological and hydrological investigations (Koch et al., 1995) along this dramatic precipitation gradient.

Previous work on savanna ecosystems has highlighted relationships between woody canopy cover and mean annual precipitation (Caylor et al., 2003; Sankaran et al., 2005). The limitations on savanna productivity by precipitation have been documented (e.g., Breman and deWit, 1983; Scanlon et al., 2002; Sankaran et al., 2005) but the role of nutrients at different levels of precipitation is not as clear. Previous work on other precipitation gradients has shown variation in soil nutrients along the gradients (Austin and Vitousek, 1998) but few have connected the interaction between nutrients and precipitation on productivity. Epsteinet al. (2006) put forth hypotheses on the relative effect of limitations by biochemical, light and vegetation constraints across rainfall gradients. They hypothesized that N is equally limiting across precipitation gradients, light is more limiting at high precipitation and plant characteristics are more limiting at low precipitation. Although comprehensive in their review of N, other nutrients that are possibly limiting in sub-tropical savannas, such as P, were not considered.

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Recent studies show that although the soils along the KT are similar in physical parameters such as soil texture, porosity and bulk density, they vary in available soil nutrients such as ammonium and nitrate (Aranibar et al., 2004; Wang et al., 2007). The presence of cyanobacterial soil crusts which can stabilize Kalahari soils may also contribute to this heterogeneity. Cyanobacterial soil crusts can stabilize the sandy soils of the Kalahari, minimizing nutrient loss that may occur as a result of disturbance or leaching (Berkeley et al., 2005). Their presence may be discontinuous and can vary between canopy species (Berkeley et al., 2005), thus contributing to the heterogeneous nature of Kalahari soils, particularly for total N but not phosphate (Thomas and Dougill, 2007).

Other research along the KT has described trends between soil carbon (C) and vegetation structure (Ringrose et al., 1998; Bird et al., 2004) as well as increasing isotopic ^{13}C in C_3 plants with decreasing rainfall. Despite the ubiquity of savannas throughout the earth, the research by Caylor et al. (2003), and thorough characterization of the KT vegetation resulting from the SAFARI 2000 campaign (Global Change Biology Volume 10, 2004), there has been little research on the role of soil nutrients, particularly P, on limitations in plant productivity relative to mean annual rainfall along the transect.

Both N and P are essential nutrients that play critical roles in photosynthesis. Nitrogen is a vital component of rubisco, the enzyme that catalyzes the carboxylation and oxygenation of RuBP in the Calvin cycle. More than half of the N in leaves can be accounted for in such photosynthetic machinery (Lambers et al., 1998). Phosphorus is needed to produce ATP and NADPH in the light reaction which is required to reduce the PGA, to produce triose-P and to regenerate RuBP to sustain the Calvin cycle. It is evident that limitations from N and P availability can therefore limit photosynthesis, the process that generates plant biomass.

The relative limitation of N and P on productivity is a function of their availability in the soil and their demand by the vegetation. Consequently, N and P limitations vary spatially and temporally in terrestrial ecosystems. For example, N is often more limiting in early successional ecosystems (temporally) before N has accumulated in the soil and while P derived from parent material is still available (Crews et al., 1995). Because a major source of soil P is from the underlying bedrock, soil P usually is limiting in highly weathered soil, common to tropical forests (Vitousek, 1984). Some studies suggest terrestrial systems such as the Amazon Basin (Swap et al., 1992) receive P deposits from aeolian dust sources but these inputs occur over thousand to million year time scales. At smaller spatial scales, nutrients may vary due to "islands of fertility" (Schlesinger et al., 1996; Okin et al., 2001a, 2001b), the accumulation of nutrients under trees and shrubs.

Phosphorus is removed from the soil during plant uptake, fire, leaching and dust removal. As it is returned to soil via senescent vegetation, fire and dust deposition, P may be partitioned into many forms of which only some are available to plants. Unlike N which can be fixed by N fixing bacteria on plant roots into a plant available form ($N_2 \rightarrow NH_4$) P cannot be sequestered from a gaseous state. Therefore, P would seemingly become limiting in older soils when outputs are greater than inputs.

Previous studies have described savannas as water and N limited (du Preez et al., 1983; Scholes and Walker, 1993; except Wang et al., 2009) but little attention has been focused on potential P limitations. Scholes and Walker (1993) observed high P mineralization rates and a greater abundance of total P in soil than in vegetation suggesting that broad-leaved savannas are not P limited. Fine-leaved savannas have been shown to have higher herbaceous and tree leaf litterfall and larger soil P pools (Scholes and Walker, 1993). Phosphorus pool concentrations are useful for characterizing nutrient distribution in savannas, however, they cannot necessarily be used as an absolute comparison between savannas because of potential confounding effects with edaphic, climatic or biotic differences between savannas.

Walker and Knoop (1987) attempted to address the relative roles of N and P limitations in a *Burkea africana* savanna in Nylsvley (630 mm precipitation/year) by applying N, P and potassium in different combinations to the herbaceous layer. They concluded both aboveground biomass and plant nutrient concentrations of the herbaceous layer increased under fertilized conditions, with the largest response evident in N plots and conflicting responses in P plots (Walker and Knoop, 1987). A similar experiment was conducted in a tropical dry savanna in Tanzania where N and P were added under *Acacia tortilis* trees and in open areas (Ludwig et al., 2001, 2004). Results indicate productivity was higher when P was added to subcanopy grasses but not in open canopy grasses, whereas the opposite was found for the addition of N. A recent study in a woodland savanna in Botswana found end of season aboveground biomass to be higher in plots amended with both N and P, suggesting a nutrient co-limitation (Ries and Shugart, 2008).

There have been limited *in-situ* experiments looking at vegetation productivity to enhance nutrients in the savannas of southern Africa. Given the age of Kalahari Sands, we expect low nutrient availability to constrain vegetation growth. We hypothesize that grasses along the Kalahari to increase biomass production under elevated soil nutrient conditions, particularly in the northern end of the KT where rainfall is higher and water less limiting. Here, we present the results from a regional scale *in-situ* experiment in which we tested the hypothesis that P limits biomass production in the savannas along the KT. We increased the levels of soil P during the dry season and returned the two following wet seasons to measure the resulting biomass production. We also looked at soil P to ascertain the success of our nutrient application technique and foliar P to detect evidence of P uptake.

2. Materials & methods

2.1. Study sites

Four KT sites representing a major portion of the precipitation gradient were used in this study (Table 1). Each site receives a distinct level of mean annual precipitation, ranging from 879 mm rain/year in the north (Mongu) to 365 mm rain/year in the south (Tshane; Scholes et al., 2004). Interannual variability in precipitation is positively correlated with precipitation and decreases from north to south along the KT (Scanlon et al., 2005). For year 1 and year 2 of the experiment, the following rainfall data (3B43 monthly converted to annual) were collected by the Tropical Rainfall Measuring Mission (TRMM) by NASA, from north to south, Year 1: 564 mm/year, 450 mm/year, 362 mm/year, 436 mm/year and Year 2: 914 mm/year, 804 mm/year, 621 mm/year and 597 mm/year (Wang et al., 2009). All sites are at similar elevation between 1084 m and 1115 m, and are characterized by co-existing trees and grasses but support different dominant species (Table 1).

2.2. Nutrient addition

The experimental set-up was a factorial block design at each of the four sites along the KT. We designated four replicate blocks (each 21 m × 13 m) at all sites each containing four 10 m × 6 m fertilizer treatments: phosphorus (P), nitrogen (N), nitrogen and phosphorus (N + P) and control. The 10 m × 6 m plots were bordered by a 1 m wide buffer to limit cross contamination of fertilizer treatments. The results presented here focus on the P limitation portion of the study. Hence, the discussion highlights the effect of the fertilizer treatments (P, N + P and control). The N

Table 1
General site characteristics for sites visited for this study along the Kalahari Transect. Precipitation decreases from north to south. All sites exhibit co-existing trees and grasses although the dominant woody and grass species are not the same.

Site	Latitude, longitude	Altitude (m)	Mean annual precip (mm)	Savanna type	Dominant woody species	Dominant grass species
Mongu (Zambia)	15.44 S, 23.25 E	1084	879	Miombo woodland (broad-leaf)	*Brachystegia spiciformis*	*unknown #3*
Pandamatenga (Botswana)	18.66 S, 25.50 E	1065	698	Dry Kalahari woodland (broad-leaf)	*Kirkia acumunata, Baikiaea plurijuga*	*Panicum maximum*
Ghanzi (Botswana)	22.41 S, 21.71 E	1089	424	Open Acacia savanna (fine-leaf)	*Acacia mellifera, Grewia flava*	*Schmidtia pappaphoroides*
Tshane (Botswana)	24.17 S, 21.89 E	1115	365	Open Acacia shrubland (fine-leaf)	*Acacia mellifera, Acacia luederitzii*	*Erogrostis lehmanniana*

treatment was only used to assess limitations on aboveground biomass production.

Mean annual P inputs from litterfall (herbaceous and woody) are 0.22 g P/m^2/year for broad-leaf savannas and 0.73 g P/m^2/year for fine-leaf savannas (Scholes and Walker, 1993). We applied P at a loading rate of 3.30 g P/m^2/year, which exceeds the annual input from litterfall. Calcium nitrate and single super phosphate fertilizers were applied in the 2004 and 2005 dry season (late July/early August). A solution of 1.75 kg $Ca(H_2PO_4)_2$ (10.5% P) and 10 L water was applied to each P plot using a SHURflo ProPack™. The N + P plot received the same P treatment plus 4.7 kg $Ca(NO_3)_2$ and 10 L water with a SHURflo ProPack™ electric backpack sprayer. The control treatment received only 10 L water. We are confident that the signature from the water addition in each plot was diminished by the onset of the rainy season. Based on Kalahari potential evaporation rates, 0.01–2.09 mm/day (Obakeng and Lubczynski, 2004), the water applied in the treatments (10 L/60 m^2, equivalent to 0.003 mm), would evaporate within a day.

2.3. Vegetation and soil sampling and analyses

Vegetation and soil samples were taken during two consecutive growing seasons proceeding nutrient application. Henceforth, we refer to the 2005 growing season as "Year 1" and the 2006 growing season as "Year 2." Sites were visited from south to north during the wet season in January/February 2005 and 2006. At each site we selected five random sampling points within each treatment in each of the four replicate blocks. This provided a total of 20 sampling points for each fertilization treatment and a total of 80 sampling points per site. At each sampling point we used a 1-m quadrat from which all aboveground grass biomass within the quadrat was harvested by species. The wet weight was recorded and grass samples were stored in paper bags, air dried in the field, weighed for dry weight and returned to the laboratory where they were stored for foliar nutrient analysis. Additionally, one soil sample was removed at each sampling point using a stainless steel soil auger from 0–15 cm deep. Soil samples were stored in zip-lock bags, allowed to air dry in the field and stored until laboratory analysis.

After returning to the University of Virginia laboratory, vegetation samples were dried at 50 °C to constant weight. Vegetation was ground in a Wiley mill (#20 sieve) and stored in paper envelopes until ready for nutrient extraction. Soils that were dried in the field were sieved with a 2 mm sieve and stored until ready for nutrient extraction. Vegetation and soil samples were processed in the laboratory for plant available P using the Bray technique (Bray and Kurtz, 1945). The Bray extraction reagent was a 0.03 N ammonium fluoride and 0.025 N hydrochloric acid solution used for 2 ± 0.003 grams of soil. Phosphorus extracted from the soil samples was measured using an Alpkem Autoanalyzer as described in Ries and Shugart (2008).

Data were analyzed to compare the effects of fertilizer on plant available P, foliar P and grass biomass production within and

Table 2
Statistical data for all fixed effects (site and treatment) and the interaction effect between site and treatment on plant available phosphorus, foliar phosphorus and aboveground grass biomass. Year 1 (2005) and year 2 (2006) of the experiment data are presented.

Source	Plant-available P 2005*				Plant-available P 2006*			
	Num DF	Den DF	F	*p*	Num DF	Den DF	F	*p*
Site	3	168	33	<0.0001	3	94	29.5	<0.0001
Treatment	2	168	35.28	<0.0001	2	94	5.23	0.007
Site*Treatment	6	168	3.66	0.0019	6	94	2.6	0.0224
	*Data were log transformed				*Data were log transformed			

Source	Foliar P 2005*				Foliar P 2006*			
	Num DF	Den DF	F	p	Num DF	Den DF	F	p
Site	3	33	18.81	<0.0001	2	20	21.33	<0.0001
Treatment	2	33	10.78	0.0002	2	20	8.7	0.0019
Site*Treatment	6	33	1	0.4417	4	20	1.08	0.395
	*Data were log transformed				*Data were log transformed			

Source	AG Grass Biomass 2005				AG Grass Biomass 2006			
	Num DF	Den DF	F	*p*	Num DF	Den DF	F	*p*
Site	3	32	28.64	<0.0001	3	32	142.5	<0.0001
N	1	32	0.25	0.6195	1	32	0.61	0.439
P	1	32	1.69	0.203	1	32	0.19	0.6688
N*P	1	32	0.01	0.9401	1	32	3.95	0.0553
Site*N	3	32	0.06	0.9793	3	32	0.44	0.7237
Site*P	3	32	0.09	0.9628	3	32	0.08	0.9694
Site*N*P	4	32	0.13	0.9991	4	32	5.42	0.002

between sites along the KT precipitation gradient. Data were analyzed with a two-way ANOVA using SAS (v. 9.1, PROC MIX). All response variables (plant-available P, foliar P, aboveground grass biomass) were analyzed for a treatment defined by classes: P, N + P and control and site. A post-hoc Tukey test ($\alpha = 0.05$) was used to assess significant differences, denoted by different letters in the figures, between P, N + P and the control for all response variables.

3. Results

3.1. Plant available soil P

Site, treatment, and the interaction between site and treatment all had significant effects on plant available P for 2005 (year 1) and 2006 (year 2; Table 2). In year 1, site had a strong significant effect ($F = 33.0$, $p < 0.0001$) on plant available P. Results from Tukey comparison between sites show us that plant available P was lowest in Mongu (0.005 mg/g ±0.001), the wettest end of the transect and was highest in Ghanzi (0.02 mg/g ±0.001; Fig. 1). Tshane (0.008 mg/g ±0.001) and Pandamatenga (0.009 mg/g ±0.001) did not differ significantly from each other but were significantly lower in plant available P than Ghanzi. In year 2, there was also a site effect ($F = 29.5$, $p < 0.0001$). We found the greatest amount of plant available soil P in the middle of the transect at Ghanzi (0.015 mg/g ±0.001) and Pandamatenga (0.011 mg/g ±0.001), which were not significantly different from each other. Tshane (0.004 mg/g 0.002) and Mongu (0.002 mg/g 0.002) were not significantly different from each other but were significantly lower than Ghanzi and Pandamatenga.

There was a significant treatment effect ($F = 35.28$, $p < 0.0001$; Table 2) during year 1 of the experiment on plant available P. Both of the phosphorus treatments, P (0.013 mg/g ±0.001) and N + P (0.013 mg/g ±0.001), had higher levels of plant available P than the control treatment (0.006 mg/g ±0.001; Fig. 2). The P and N + P treatments had over 100% greater plant available soil P than the control treatment. During the second year, soil plant available P was significantly higher in the P treatment (0.010 mg/g ±0.001) and N + P treatment (0.010 mg/g ±0.002) than the control treatment (0.005 mg/g ±0.001).

There was a significant interaction effect between site and treatment on plant available P in year 1 of the experiment ($F = 3.66$, $p = 0.0019$) and year 2 ($F = 2.60$, $p = 0.0224$; Table 2). In year 1 there was a positive P treatment effect on plant available P at Tshane (154% increase), Ghanzi (64% increase), Pandamatenga (200% increase) and Mongu (213% increase) relative to the control treatments at each of those sites (Fig. 2a). Similar increases in plant available P were also seen for the N + P treatment at each site relative to the control: Tshane (145% increase), Ghanzi (57% increase), Pandamatenga (211 %) and Mongu (576%) (Fig. 2a). During year 2 the P treatment significantly increased plant available P relative to the control treatments for three of the sites Tshane (81 %), Ghanzi, (85%) and Pandamatenga (198%) but there was no significant change in Mongu (Fig. 2b). The N + P treatment

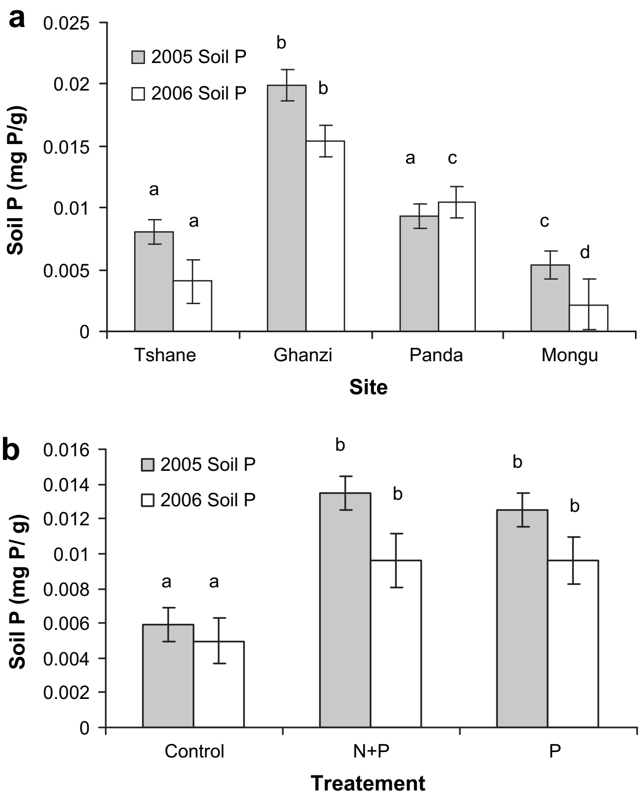

Fig. 1. Soil plant available phosphorus least square means for site effects (a) and treatment effects (b). Data are presented for year 1 (grey) and year 2 (white). Sites vary in mean annual precipitation (Mongu = 879 mm, Pandamatenga = 698 mm, Ghanzi = 424 mm, Tshane = 365 mm). Nutrient treatments include increased phosphorus (P), increased nitrogen and phosphorus (N + P) and a control where no nutrients were added. Letters in both (a) and (b) denote significant Tukey Kramer adjusted differences between site and treatment means, not between years.

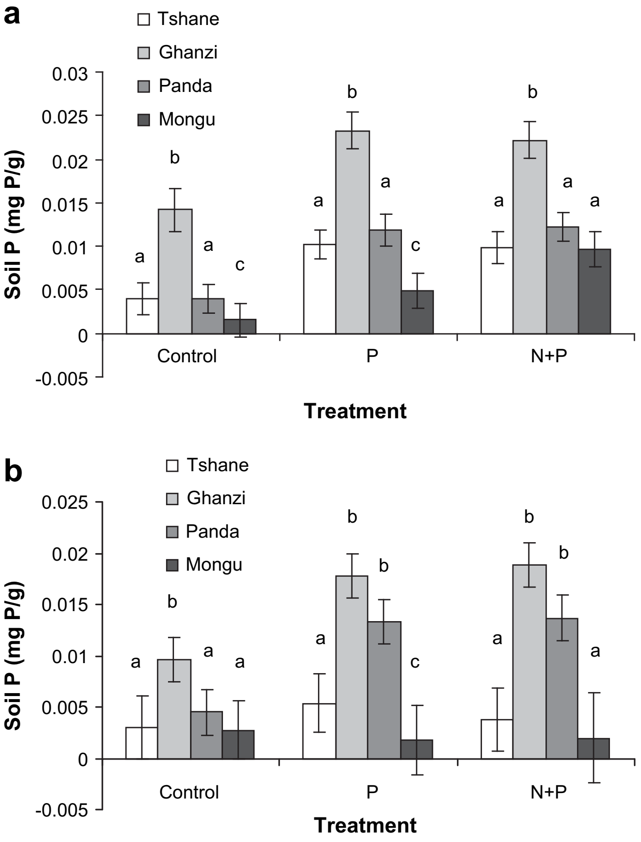

Fig. 2. Soil plant available phosphorus least square means at each site for each treatment (site by treatment interaction). Data are presented for year 1 (a) and year 2 (b). Sites vary in mean annual precipitation (Mongu = 879 mm, Pandamatenga = 698 mm, Ghanzi = 424 mm, Tshane = 365 mm). Nutrient treatments include increased phosphorus (P), increased nitrogen and phosphorus (N + P) and a control where no nutrients were added. Letters in both (a) and (b) denote significant Tukey Kramer adjusted differences between site means for each treatment.

significantly increased plant available P at Tshane (80 %), Ghanzi (82 %) and Pandamatenga (201 %). There were no significant treatment effects on plant available P in Mongu (Fig. 2b).

3.2. Foliar P

Site had a significant effect ($F = 18.81$, $p < 0.0001$) on foliar P during year 1 of the experiment. Mongu exhibited the lowest foliar P (0.88 mg/g ±0.08; Fig. 3a). Pandamatenga (1.46 mg/g ±0.09) and Ghanzi (1.70 mg/g ±0.08), had the highest levels of foliar P and were not significantly different from each other (Fig. 3a). Tshane (1.07 mg/g ±0.08) exhibited foliar P levels between those found at Ghanzi and Mongu (Fig. 3a). During the second year of the experiment, there were different trends along the KT. Foliar P decreased from Pandamatenga in the north (3.72 mg/g 0.23), to Ghanzi (2.43 mg/g 0.21) to the lowest P in Tshane (1.48 mg/g 0.23; Fig. 3a). There are no data available from Mongu for year 2.

There was a significant treatment effect ($F = 10.78$, $p = 0.0002$, Table 2) on foliar P in year 1. Both the P treatment (1.345 mg P/g ±0.08) and the N + P treatment (1.489 mg P/g ±0.08) significantly increased foliar P in comparison to the control treatment foliar P levels (Fig. 3b). In year 2 there was also a significant treatment effect ($F = 10.27$, $p = 0.0009$) on foliar P. As in the first year, the P (3.03 mg P/g ±0.23) and N + P (2.79 mg P/g ±0.22) treatments did not differ from each other but were significantly higher in foliar P than the control (1.81 mg P/g ±0.22) treatment.

There were no significant interaction effects between site and treatment ($F = 1.0$, $p = 0.4417$) during year 1 (Fig. 4a) or year 2 (Fig. 4b).

3.3. Aboveground grass biomass

There was a significant site effect ($F = 28.65$, $p < 0.0001$; Table 2) on aboveground grass biomass (AGB) during the first year of the experiment. Aboveground grass biomass was not significantly different between Mongu (8.90 g/m^2 ±4.075), Pandamatenga (12.64 g/m^2 ±4.32) and Ghanzi (16.30 g/m^2 ±4.07), and for year 1 (Fig. 5a). Tshane (56.01 g/m^2 ±4.075) produced significantly higher AGB than the other sites. During year 2, there was also a significant site effect ($F = 40.45$, $p < 0.0001$; Table 2) on AGB. In contrast to year 1, Mongu (1.99 g/m^2 ±3.18) had a significantly lower AGB than the other three sites. Pandamatenga (76.76 g/m^2 ±3.18) produced the greatest AGB while the two southern sites, Ghanzi (5.56 g/m^2 ±3.18) and Tshane (7.49 g/m^2 ±3.18) had significantly lower yet similar levels of AGB (Fig. 5a).

There were no significant effects from N ($F = 0.25$, $p = 0.6195$), P ($F = 1.69$, $p = 0.203$), N*P ($F = 0.01$, $p = 0.203$), Site*N ($F = 0.06$, $p = 0.979$), Site*P ($F = 0.09$, $p = 0.963$) or Site*N*P ($F = 0.13$, $p = 0.9991$; Fig. 6a) on AGB during year 1 (Table 2). In year 2 there were no significant effects from N ($F = 0.61$, $p = 0.439$), P ($F = 0.19$, $p = 0.669$), N*P ($F = 3.95$, $p = 0.055$), Site*N ($F = 0.44$, $p = 0.724$) or Site*P ($F = 0.08$, $p = 0.969$). The interaction effect, Site*N*P, had

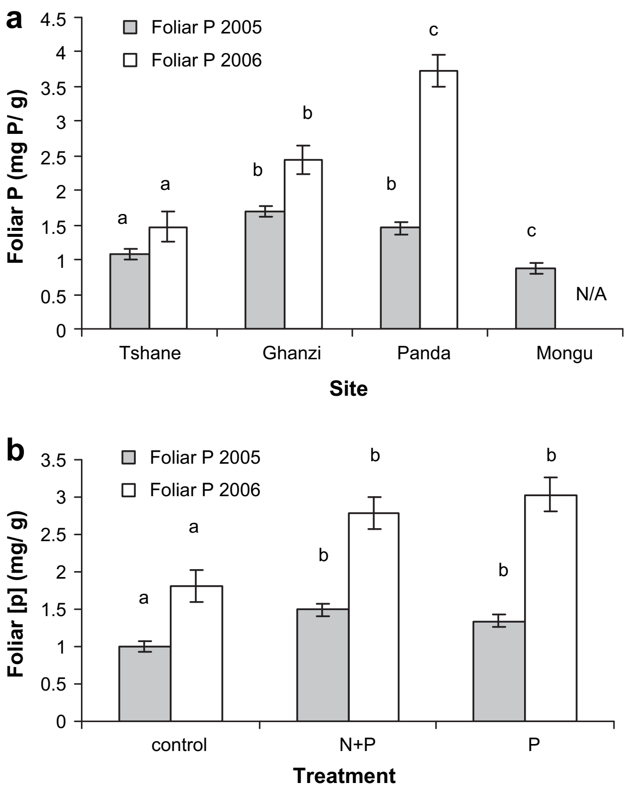

Fig. 3. Foliar grass phosphorus concentrations (mg P/g) least square means for year site effects (a) and treatment effects (b). Data are presented for year 1 (grey) and year 2 (white). Sites vary in mean annual precipitation (Mongu = 879 mm, Pandamatenga = 698 mm, Ghanzi = 424 mm, Tshane = 365 mm). Nutrient treatments include increased phosphorus (P), increased nitrogen and phosphorus (N + P) and a control where no nutrients were added. Letters in both (a) and (b) denote significant Tukey Kramer adjusted differences between site (Fig. a) and treatment (Fig. b) means . Data are unavailable for Mongu during year 2.

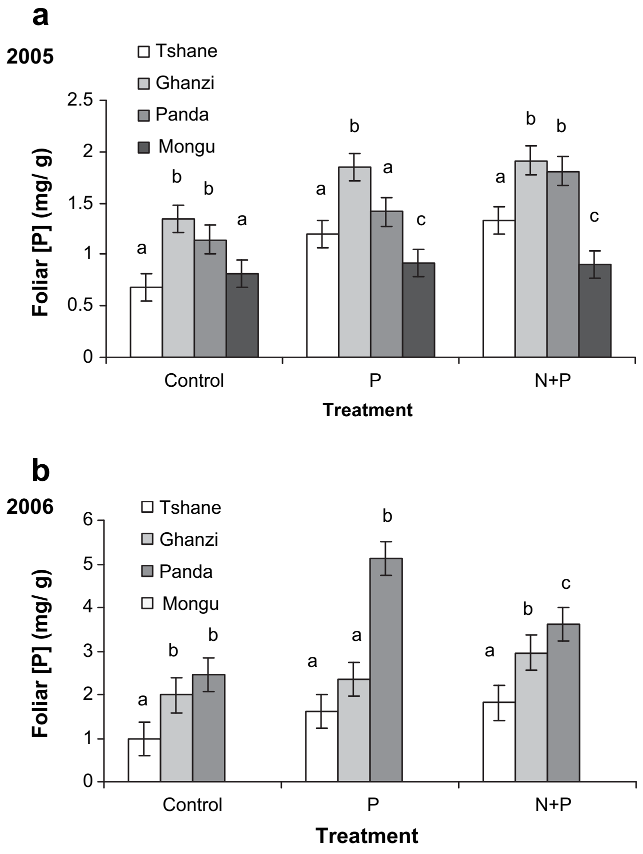

Fig. 4. Grass foliar phosphorus least square means at each site for each treatment (site by treatment interaction). Data are presented for year 1 (a) and year 2 (b). Sites vary in mean annual precipitation (Mongu = 879 mm, Pandamatenga = 698 mm, Ghanzi = 424 mm, Tshane = 365 mm). Nutrient treatments include increased phosphorus (P), increased nitrogen and phosphorus (N + P) and a control where no nutrients were added. Letters in both (a) and (b) denote significant Tukey Kramer adjusted differences between site means for each treatment. Data are missing for Mongu during year 2.

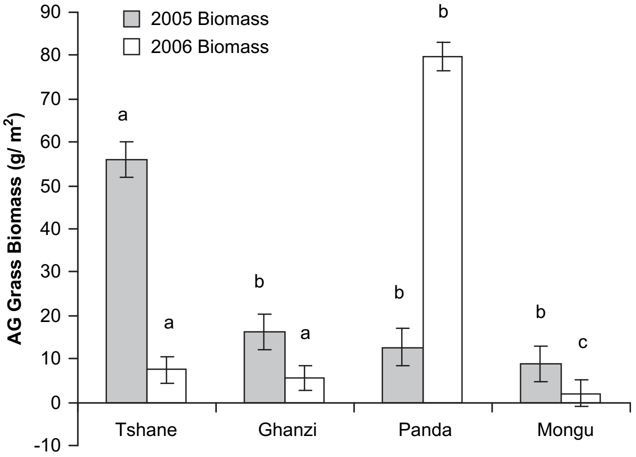

Fig. 5. Aboveground grass biomass (g/m^2) means for all sites regardless of treatment. Data for year 1 (2005) and year 2 (2005) are presented. Sites vary in mean annual precipitation (Mongu = 879 mm, Pandamatenga = 698 mm, Ghanzi = 424 mm, Tshane = 365 mm). Site had a significant effect on year 1 biomass ($F = 28.64$, $p < 0.0001$) and year 2 biomass ($F = 142.5$, $p < 0.0001$). Letters denote significant differences between site means for the same year. In year 1, Tshane produced the highest biomass (g/m^2) while Pandamatenga produced the highest biomass (g/m^2) in year 2.

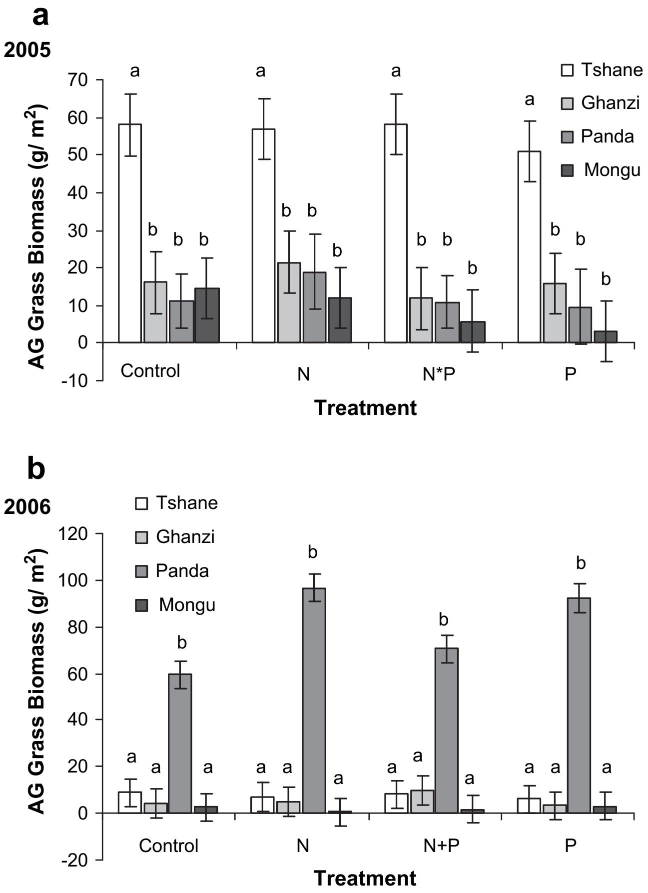

Fig. 6. Aboveground grass biomass (g/m^2) least square means at each site for each treatment (site by treatment interaction). Data are presented for year 1 (a) and year 2 (b). Sites vary in mean annual precipitation (Mongu = 879 mm, Panda = 698 mm, Ghanzi = 424 mm, Tshane = 365 mm). Nutrient treatments include increased phosphorus (P), increased nitrogen and phosphorus (N + P) and a control where no nutrients were added. Letters in both (a) and (b) denote significant Tukey Kramer adjusted differences between site means for each treatment.

a significant effect on AGB ($F = 5.42$, $p = 0.002$; Fig. 6b) in year 2. Fig. 6b shows significant differences between sites. Relative to the control treatment, the N treatment showed significantly lower biomass production in Mongu.

4. Discussion

The methods employed to increase plant available P were successful in that both the P treatment and the N + P treatment plots contained nearly twice as much plant available P as the control plots. The results on plant available P clearly suggest that there are differences in ambient levels (i.e. control treatment) of soil plant available P along the KT. With the exception of the most southern site, Tshane, there is a general increase in plant available P from north to south along the KT. These data agree with general hypotheses that open fine-leaf savannas, as seen in the southern portion of the KT, are relatively eutrophic while broad-leaf savanna woodlands, as seen in the northern portion of the KT, are more dystrophic (Scholes and Walker, 1993). The values found in the *Acacia* dominated dry end of the KT (0.004–0.014 mg P/g), are higher than those values (0.0005–0.0013 mg P/g) found in an *Acacia* dominated savanna in Tanzania (4° S, 37° E, 650 mm rain/year; Ludwig et al., 2004). However they are very similar to those values (0.0046 mg P/g) found in the Chihuahuan Desert, NM (32° N, 106° W) which receives comparable mean annual rainfall (Whitford et al., 1997), emphasizing the link between plant available P and precipitation.

When we look at the trend in plant available P across the KT regardless of treatment (i.e. site effect only) the values of plant available P are greater than looking at the site effect alone (because they include all treatment types) but still follow the same pattern of decreasing plant available P with the exception of Tshane. The interaction term, site*N*P highlights that plant available P differed significantly across the transect and nutrient treatments relative to the control treatments. A similar correlation between decreasing precipitation and increasing P was also seen along a rainfall gradient in Hawai'i (Austin and Vitousek, 1998).

Differences in foliar P were only apparent when all sites were analyzed together (i.e. treatment effect). There was indeed a significant increase in foliar P after nutrients were added to the soil as compared to the levels of foliar P in the control treatment. The interaction effect between site and treatment provides us with the most information on the relative uptake of nutrients along the KT. There was not a significant effect from the interaction of these two terms, suggesting that there is no difference in the rate of uptake between sites. However, an increase in foliar P in the absence of an increase in biomass suggests a possible luxury uptake of nutrients. A more comprehensive analysis of P allocation throughout the growing season and during leaf senescence would provide evidence for the physiological purpose of this potential luxury uptake. Further investigation of below and aboveground nutrient allocation might also provide explanation of increased foliar P. Perennial grasses such as those seen along the KT, may store nutrients to be used when co-limiting factors, such as precipitation, become more available.

Regardless of nutrient treatment, we did see a difference between sites in AGB. Tshane produced a higher AGB than the other sites during the first year and Pandamatenga produced a similarly high amount of AGB in the second year of the experiment. These interannual differences in biomass production are much greater than the differences between treatments, emphasizing limitation by water as a dominant ecosystem control on production. This is supported by the fact that mean annual rainfall was greater at all sites during the second year of the experiment (see Methods) when biomass production increased across all sites. The greatest relative increase of rainfall between years was at the Pandamatenga site from 450 mm/year to 804 mm/year, where aboveground biomass also had the greatest relative increase. Dramatic differences in grass production in Pandamatenga agree with high levels of interannual variability for modeled grass production (Scanlon et al., 2002). Additionally, other factors affecting production such as fire could be affecting biomass production at each site. Depending on time and intensity of fire, burning can increase fuel load from one year to the next (e.g., Frost and Robertson 1985). For example, fuel load increased from 2964 kg/ha to 3972 kg/ha in a South African savanna fire experiment after burning (Govender et al., 2006).

Overall, we see increases in grass foliar nutrient concentrations when additional nutrients are made available in the soil. However, this uptake does not result in relative increases in biomass between sites, even in wetter years when water would seemingly be less limiting. This suggests that AGB is not limited by soil P or N within each site along the highly weathered soils of the Kalahari. This is in contrast to other studies that suggest that systems with old soils (e.g., tropical soils) are limited by P due to excessive weathering (Vitousek, 1984). However such tropical soils may differ in their mineralogy. The soils of the Kalahari sands are comprised of predominantly quartz (Wang et al., 2007) which may lack P-bearing minerals that are found in tropical soils and consequently host species that do not demand or are unable to utilize higher levels of soil P. Plants do exhibit luxury uptake of nutrients to be used during times when they are less available or they may be allocating nutrients belowground. This, however, would seemingly lead to an increase in AGB which we did not see. A dramatic difference between AGB between years suggests another type of limitation is dominant such as precipitation or other processes affecting nutrient cycling such as fire (Frost and Robertson, 1987; Govender et al., 2006), herbivory (Milchunas and Lauenroth, 1993) or a combination of these factors that vary interannually.

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