Spatial patterns of soil nutrients in two southern African savannas

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[1] Savannas are extensive, seemingly stable mixtures of grasses and trees that are thought to result from a combination of facilitation, competition, and disturbance. Here, we study the spatial distribution in surface soils of soil organic matter and macronutrients at two savanna sites along the Kalahari Transect in southern Africa: a dry site with approximately 350 mm of precipitation annually and a wet site with approximately 950 mm of precipitation annually. The concentrations of total organic carbon, total nitrogen (TN), chloride, sulfate, phosphate, and (nitrate + nitrite) were analyzed in surface soils from these sites using a variety of traditional and geostatistical analyses. Soil nutrient content is generally higher at the wet site (e.g., 0.039% TN versus 0.023% TN, 0.67 μg/g PO_4^{-3} versus 0.30 μg/g PO_4^{-3}, and 3.44 μg/g ($NO_3^- + NO_2^-$) versus 1.79 μg/g ($NO_3^- + NO_2^-$)), though there is considerable variation among sample populations from different vegetation covers. Our results indicate that the dry site is also more spatially heterogeneous than the wet site. At the dry site, where the range of spatial autocorrelation for TN, SO_4^{-2}, PO_4^{-3}, and ($NO_3^- + NO_2^-$) is 8.5 m, 8.5 m, 8.7 m, and 7.3 m, respectively, the spacing of all woody vegetation (both shrubs (woody plants $\leq$ 2 m) and trees (woody plants > 2 m)) contributes to the patterning of soil resources. At the wet site, where the range of spatial autocorrelation for TN, SO_4^{-2}, and PO_4^{-3} is 4.6 m, 6.1 m, and 10.2 m, respectively, only trees contribute to the patterning of soil resources, though ($NO_3^- + NO_2^-$) displays a purely random distribution. We also find weak evidence that nitrogen may not be the, or the only, limiting nutrient in these ecosystems.

1. Introduction

[2] Savannas are extensive, seemingly stable mixtures of grasses and trees that cover 20% of the Earth's surface and 40% of Africa [*Scholes and Walker*, 1993]. They represent an ecological paradox in their shared dominance of herbaceous and woody species. Many theories have been put forth regarding the cause of this shared dominance, but the spatial structuring of vegetation in savannas probably results from a combination of competition-facilitation mechanisms and disturbance regime [*Scholes and Archer*, 1997; *Sankaran et al.*, 2004]. Whatever the cause for their shared dominance, the structure of savanna vegetation likely has a strong imprint on the spatial variability of soils.

Patterns imposed on the soil by vegetation, in turn, may have significant feedbacks on competition and facilitation mechanisms, by strengthening competition through patterns of low resource concentration or aiding facilitation through patterns of high resource concentration. In particular, clustering observed among trees in savannas [*Caylor et al.*, 2003], though sometimes explained by ecohydrological facilitation [*Caylor et al.*, 2004], might also arise in part through spatial patterning of soil resources besides water.

[3] Here, we investigate the relationships between vegetation structure and soil resources in two savanna sites, one dry and the other wet, with particular interest in major macronutrients N, P, and S. We hypothesize that the spatial distribution of these macronutrients at both sites is strongly governed by the distribution of woody species at these sites, rather than herbaceous cover. We further hypothesize that there will be a relationship between the height of woody vegetation (as a proxy for age) and the concentration of these macronutrients in sub-canopy soils.

[4] The importance and origin of spatial variability of soil resources in arid/semiarid regions has been discussed at length in the scientific literature for the past two decades. For instance, *Schlesinger et al.* [1990] proposed that degradation in drylands was accompanied by the development of "fertile islands" centered on woody vegetation. This hypothesis was followed up by a study [*Schlesinger et al.*,

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1996] that showed through the use of variography that the spatial distribution of soil resources changes as desert grasslands are encroached by shrubs. *Ludwig et al.* [2002, 2006, 2007] have suggested that a "leakiness" index of dryland vegetation heterogeneity provides valuable information about a degraded savanna landscape's ability to hold and accumulate soil resources. A recent synthesis by *Peters et al.* [2006] has upheld the importance of spatial redistribution of soil resources in degrading grassland and explained how this mechanism at the plant-interspace scale relates to larger spatial and temporal scales. Most recently, *Li et al.* [2007, 2008] have shown that wind erosion, as a major abiotic transport mechanism in deserts, can create fertile islands in degrading desert grasslands.

[5] Despite the extensive study and discussion of the role of spatial variation in soil resources in drylands, most studies have considered only disturbed ecosystems. Thus, the resource heterogeneity examined in many studies is essentially a new feature of degraded or disturbed landscapes. There has been very little study of the spatial imprint of vegetation on soil resources in undisturbed areas that are more than a few hundred years old and are not the result of recent land use changes [e.g., *Van Auken*, 2000]. Studies by *Gallardo et al.* [2000, 2006] and *Gallardo and Parama* [2007] from disturbed, but old, savanna-like oak dehesa ecosystems in Spain have supported the hypothesis that woody plants are the most important factors in structuring soil resource distributions in dryland systems. *Moreno Marcos et al.* [2007] have further suggested that the spatial patterning of soil nutrients is critical in establishing patterns of competition and facilitation in oak dehesas. In contrast, *Jackson and Caldwell* [1993] have suggested that in sagebrush steppes, tussock grasses are more responsible for structuring the distribution of soil resources than sagebrush itself and that that root plasticity and active foraging in a heterogeneous soil environment are likely to be important to the nutrient balance of many plants in these ecosystems.

[6] The study of the spatial distribution of soil resources in savannas provides important insight into potential mechanisms of competition and facilitation that are so important in maintaining the shared dominance of herbaceous and woody vegetation that characterizes savanna ecosystems. Because patterns of relatively high soil resources can provide advantages to new recruits [*Bisigato and Bertiller*, 1999], understanding soil resource distribution is also vital in understanding the potential response of savannas to natural or anthropogenic disturbance.

2. Methods

2.1. Site Description

[7] The two sites chosen for this study were located on the wet and dry ends of the Kalahari Transect (Figure 1). The Kalahari Transect is one of a number of International Geosphere-Biosphere Programme transects designated throughout the world and is unique in that it is underlain by homogeneous Kalahari sands [*Koch et al.*, 1995]. Kalahari Transect soils are mainly arenosols (FAO) or psamments/psammids (USDA) with high sand fractions (in excess of 96% by mass [*Joshua*, 1981; *Wang et al.*, 2007a]) in both surface and lower horizons. The soils have an average infiltration rate of 33 cm/hr (ranging from 54.3
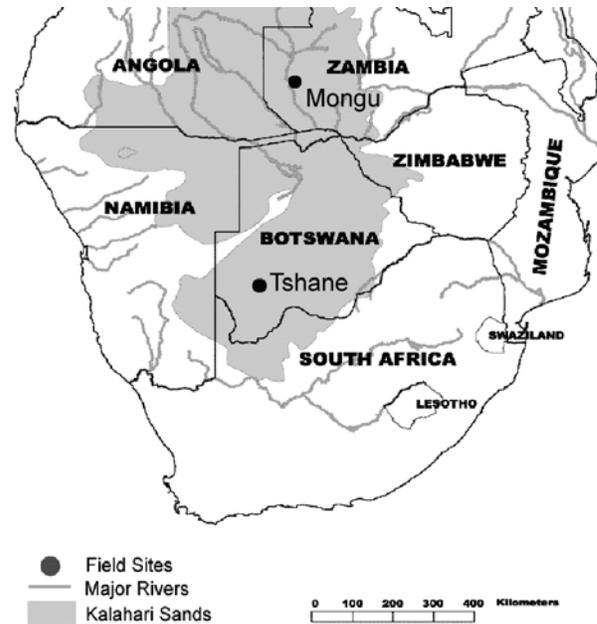
Figure 1. Location of the two research sites, Tshane (dry) and Mongu (wet), within the Kalahari Sands of southern Africa.

to 18.5 cm/hr), a porosity of around 40% [*Scholes et al.*, 2002; *Wang et al.*, 2007a]. Vegetation communities along the Kalahari Transect are characterized by arid shrub savanna in the southwest (southwestern Botswana/northwestern South Africa). In central Botswana, tree savanna predominates and is referred to as the Kalahari tree and bush savanna. Tree savanna extends to the broadleaf mopane belt in northern Botswana that merges northeastward into the dry deciduous Chobe Forest area [*Weare and Yalala*, 1971] with Miombo deciduous woodland further north in Zambia [*White*, 1983]. Land uses vary from mixed wildlife with smallstock grazing in the south to mainly localized land clearing for subsistence and fuelwood/charcoal in the north. Fires are known to be widespread in the region and fire return intervals were reported as 8 years at in the south and 2.7 years at in the north of the Kalahari Transect [*Sankaran et al.*, 2004].

[8] The dry savanna site (located approximately 20 km south of Tshane, Botswana at 24.17°S 21.89°E) receives ~350 mm precipitation annually and is characterized as Kalahari tree and bush savanna. The wet savanna site (located approximately 20 km south of Mongu, Zambia at 15.44°S 23.25°E) receives ~950 mm precipitation annually and is characterized as Miombo woodland. Detailed vegetation composition at the sites has been described by *Scholes et al.* [2002].

2.2. Field Sampling and Vegetation Measurement

[9] Samples were collected in February–March, 2005. Surface soil samples were collected from random locations along a 300-m N-S transect laid out as three 100-m fiberglass measuring tapes. Sample locations were determined from the random number generator in Microsoft Excel prior to fieldwork. We ensured that no two points

were less than 5 cm apart by replacing one of any pairs separated by less than 5 cm with a new random location. Irregular spacing of samples along the transect allowed us to have a large number of pairs that are closely spaced when calculating the variogram, while also allowing the transect to cover a relatively large distance. With the use of a transect, however, our sampling technique was not capable of identifying anisotropy in the distribution of soil nutrients of vegetation.

[10] Soil samples were collected using a trowel from a $\sim$5 cm square area to a depth of $\sim$5 cm. Large debris was removed from the soil surface to facilitate sampling, but no effort was made to clear the top of the mineral soil prior to sampling. Soil samples were air-dried and stored in labeled, sealed plastic bags. 271 samples were collected and analyzed from the Mongu (wet) site. 296 samples were collected and analyzed from the Tshane (dry) site.

[11] A line intercept method was used to characterize herbaceous, shrub (woody cover $\leq$ 2 m), tree (woody cover > 2 m), dead woody, and bare soil cover along the transect. Canopy width and intercanopy distances along the transect were calculated based on line-intercept data. Tree-to-tree distances were calculated as the sum of canopy width and intercanopy distances along the transects. For each soil sample collected, the line-intercept data allowed us to determine what vegetation was immediately above the sampled soil: tree or shrub (Tree/Shrub), Grass, or Tree/Shrub and grass (T/S + G), or whether there was no vegetation above the sample point (Bare).

2.3. Laboratory Analyses

[12] Soil samples were sieved to 2 mm and subsampled using a riffle sample divider. 6-g subsamples were mixed with 30 mL of deionized water in a 50-mL centrifuge tube. The mixture was agitated for 30 min and then was centrifuged for 9 min at 4150 rpm to produce a clear supernatant. The supernatant was decanted and analyzed using a Dionex ICS$^-$2000 ion chromatograph (Dionex Corporation, Sunnyvale, CA) fitted with a 4-μm in-line filter. Nitrite, nitrate, phosphate, sulfate, and chloride concentrations, expressed as μg/g soil, were measured for each sample. Nitrite and nitrate were combined to provide a measure of total anionic inorganic nitrogen.

[13] Subsamples of soils were also analyzed for total organic carbon (TOC) and total nitrogen (TN). These subsamples were oven-dried (at 60°C) in the laboratory, sieved to 2 mm and homogenized using a mortar and pestle. The presence of carbonates was tested by treating the soils with dilute hydrochloric acid (1 M) and no effervesce was observed. TOC and TN, expressed as percent by mass, were measured using an Elemental Analyzer (EA, Carlo Erba, NA1500, Italy) on untreated soil samples.

2.4. Statistical Analyses

[14] Following *Schlesinger et al.* [1990], we calculated the coefficient of variation (CV) for each measured soil analyte as an index of resource island formation. A nonparametric (Kruskal-Wallis) analysis of variance was used to determine differences between concentrations of analytes with different overlying vegetation. A Bonferonni correction was used for these tests with α = 0.05. Pearson's correlation coefficients were calculated between all soil

analytes, plus woody vegetation height, for both sites. Significance was determined using the method of *Sokal and Rohlf* [1981].

[15] All soil analytes were tested for drift by regressing analyte concentration against transect position. No analytes exhibited regression slopes significantly different from zero and, as a result, samples were considered stationary. Analyte concentrations were also log-transformed to reduce outliers and bring the distributions of analyte concentrations to near-normal. Experimental semivariograms were calculated using the jackknife method presented by *Shafer and Varljen* [1990] and discussed by *Huisman et al.* [2003] in a code written in the Interactive Data Language (IDL; ITT Visual Information Solutions, Boulder, CO). All semivariograms were fit to a spherical model using a nonlinear least squares fit employing the Levenberg-Marquardt algorithm, which combines the steepest descent and inverse-Hessian function fitting methods [*Press et al.*, 1992]. Jackknife estimates of variance were employed in the fitting using the method of *Huisman et al.* [2003]. The spherical model semivariance has proven especially useful in the interpretation of soil data [e.g., *Schlesinger et al.*, 1996; *Diekmann et al.*, 2007; *Wang et al.*, 2007b]. The formula for the spherical semivariogram model is:

$$\gamma(h) = \begin{cases} C_o + C\left[\dfrac{3}{2}\dfrac{h}{A_o} - \dfrac{1}{2}\dfrac{h^3}{A_o^3}\right] & h < A_o \\ C_o + C & h \geq A_o \end{cases}$$

where γ is the semivariance, h is the lag interval, A_o is the range, C_o is the nugget variance and C is the structural variance. The uncertainty of these parameters (95% confidence) were determined using the variance-covariance method of *Pardo-Iguzquiza and Dowd* [2001]. The nugget (C_o) denotes the y-intercept of the semivariogram and incorporates random or non-spatial errors, as well as errors associated with spatial variability at scales finer than the distance between the closest points [*Rossi et al.*, 1992]. A high nugget variance indicates that high variance occurs over short distances or is due to measurement/locational error. The sill variance is the combination of nugget variance C_o and structural variance C, representing an asymptotic maximum semivariance value. Under stationarity, $C_o + C$ is equal to the data set variance. To estimate the strength of spatial dependence, we calculated the index of $C/(C_o + C)$. As this index approaches one, a greater proportion of the total sample variance is spatially dependent over the distance examined [*Jackson and Caldwell*, 1993; *Schlesinger et al.*, 1996]. The scale of the spatial autocorrelation is indicated by the model range A_o. Samples separated by distances smaller than the range are correlated as a result of their proximity to one another, whereas samples separated by greater distances are effectively independent. Ecologically, the parameters of the semivariogram can be used to describe the patchiness of a spatial pattern.

[16] In addition to calculating variograms of soil analytes, we calculated the variograms of vegetation cover using an indicator approach to the jackknife variogram calculation and model estimation of *Shafer and Varljen* [1990] and *Pardo-Iguzquiza and Dowd* [2001], respectively. For in-

Table 1. Mean Concentration and Coefficient of Variation (CV) for Samples With Different Overlying Vegetation[a]

Site	Cover	TOC, %		TN, %		C/N, unitless		Cl^-, mg/g		SO_4^{-2}, mg/g		PO_4^{-3}, mg/g		$(NO_3^-+NO_2^-)$, mg/g	
		Mean	CV	Mean	CV	Mean	CV	Mean	CV	Mean	CV	Mean	CV	Mean	CV
Tshane (Dry)	All Samples	0.19	0.68	0.023	0.65	8.34	0.10	0.22	5.14	0.45	2.81	0.30	1.17	1.79	2.36
	Tree/Shrub	0.36	0.42	0.044	0.42	8.18	0.12	0.47	2.80	1.15	1.82	0.54	0.59	4.55	1.37
	Grass	0.17	0.41	0.021	0.37	8.35	0.08	0.21	5.63	0.38	2.82	0.24	1.66	1.39	2.27
	Bare	0.16	0.40	0.019	0.45	8.05	0.08	0.11	5.29	0.36	1.12	0.26	0.68	1.24	2.09
	(T/S + G)	0.22	0.69	0.027	0.58	8.67	0.11	0.23	5.10	0.60	1.12	0.36	0.77	2.00	1.81
Mongu (Wet)	All Samples	0.69	0.69	0.039	0.61	17.82	0.10	0.39	2.31	0.49	0.80	0.67	0.71	3.44	1.03
	Tree/Shrub	0.70	0.69	0.041	0.58	17.97	0.11	0.27	3.40	0.46	0.88	0.69	0.69	3.13	1.16
	Grass[b]	0.60	0	0.032	0	18.66	0	0.43	0	0.77	0	0.49	0	10.1	0
	Bare	0.50	0.61	0.028	0.66	17.88	0.09	0.59	1.01	0.32	0.72	0.43	0.50	4.51	0.68
	(T/S + G)	0.53	0.38	0.032	0.33	17.34	0.06	0.14	3.62	0.38	0.59	0.65	0.50	2.65	1.04

[a](T/S + G) refers to samples with both trees or shrubs and grasses.
[b]There was only one sample from Mongu with grass and no overlying tree or shrub, so the CV for this class is zero.

stance, to calculate the jackknife estimate of woody cover, all samples covered by trees or shrubs were given a value of one, and all other points were given a value of zero. The variogram was then calculated, and the parameters estimated, using the same IDL code that was used to calculate variograms and parameters for the soil analytes.

3. Results

3.1. Vegetation Distribution

[17] Woody cover is 20% at the Tshane (dry) site. Here, mean tree canopy width along the transect is 4.5 m and mean tree intercanopy distance is 23.1 m. If both shrubs and trees are considered at Tshane, the mean woody canopy width is 2.8 m and mean woody intercanopy width is 7.0 m. Considered as the sum of canopy width and intercanopy width, mean tree-tree distance at Tshane is 27.6 m and mean woody-woody distance at Tshane is 9.8 m.

[18] Woody cover is 78% at the Mongu (wet) site. Here, mean tree canopy width is 3.1 m and mean tree intercanopy distance is 1.5 m. If both shrubs and trees are considered at Mongu, the mean woody canopy width is 1.3 m and mean woody intercanopy width is 0.6 m. Mean tree-tree distance at the wet savanna site is 4.6 m and mean woody-woody distance is 1.9 m.

[19] Grass cover from line-intercept data indicates strong competitive relationships between woody vegetation and grass at the dry savanna site. Specifically, we find a significant negative correlation between the woody vegetation and grass cover at this site, whereas no significant relationship between grass and woody vegetation cover exists at the wet savanna site. This confirms the identification of competition between grass and woody species along the Kalahari Transect, at least for the Tshane (dry) site [e.g., Hipondoka et al., 2003].

3.2. Soil Chemical Analyses

[20] In general, the concentrations of soil analytes were higher at the Mongu (wet) site than the Tshane (dry) site, though there is considerable variation among sample populations from different vegetation covers (Table 1). The CVs of TOC, TN and C/N are similar at both sites, but CVs of anionic species are higher at Tshane relative to Mongu.

[21] At both sites, nonparametric analysis of variance reveals that many analytes can be elevated beneath trees, or in places where trees and grasses are both present, though this patterns is much stronger at the Tshane (dry) site than the Mongu (wet) site (Table 2). At Mongu, it is only true in direct comparisons of samples from trees versus bare areas and only for TOC, TN, and PO_4^{-3}. At Tshane, it is true for all analytes in direct comparisons of samples covered by trees (or trees and grass) with samples covered by other vegetation cover. Comparisons between samples with no vegetation cover and samples with grass cover do not reveal any significant differences for any analyte at either site.

[22] There are significant correlations at both sites between most analytes (Table 3). The only cases in which no significant correlation exists is between $(NO_3^- + NO_2^-)$ and TOC or TN at the Mongu (wet) site. The strongest correlations are between TOC and TN ($\rho = 0.98$) at both sites. Strong correlations are also observed between PO_4^{-3} and TOC/TN at both sites, as well as between SO_4^{-2} and $PO_4^{-3}/(NO_3^- + NO_2^-)$ at Tshane. Significant correlations between woody vegetation height and TOC/TN are observed at Tshane, but no significant correlations between woody height and any analyte is observed at Mongu. Although correlations between TOC and anionic species are significant, they are not high. Indeed, variation in TOC explains at most 34% (calculated as the square of the correlation coefficient) of the variability in any anionic species. Because organic compounds are likely the predominant source of anion exchange capacity in these slightly acidic sandy soil [Wang et al., 2007a], we conclude that differences in the abundance anionic species cannot be due simply to differences in anion exchange capacity.

3.3. Variogram Analysis

[23] The jackknife estimate of the range of spatial autocorrelation at the Tshane (dry) site is between 7.27 m and 9.08 m for all analytes except Cl^-, which has a range of 17.4 m. Jackknife estimates of $C/(C_o + C)$ vary from 0.59 to 0.99 for all analytes at Tshane with TOC and TN exhibiting the highest values and Cl^- exhibiting the lowest value. Jackknife range estimates from vegetation cover indicator variograms at Tshane are 8.43, 3.02, and 14.60 m for woody, grass, and bare cover, respectively.

Table 2. Results of Nonparametric (Kruskal-Wallis) Analysis of Variance for Samples Collected With Different Overlying Vegetation[a]

Site	Cover	TOC	TN	C/N	Cl^-	SO_4^{-2}	PO_4^{-3}	$(NO_3^-+NO_2^-)$
Tshane (Dry)	Woody versus Grass	Woody	Woody			Woody	Woody	Woody
	Woody versus Bare	Woody	Woody		Woody	Woody	Woody	Woody
	Woody versus (W+G)	Woody	Woody			Woody		
	Grass versus Bare							
	Grass versus (W+G)	(W+G)	(W+G)				(W+G)	
	Bare versus (W+G)	(W+G)	(W+G)	(W+G)				
Mongu (Wet)	Woody versus Grass							
	Woody versus Bare	Woody	Woody				Woody	
	Woody versus (W+G)							
	Grass versus Bare							
	Grass versus (W+G)							
	Bare versus (W+G)							

[a](W+G) refers to samples with both trees/shrubs and grasses. Entries indicate which samples had higher concentrations. Significance was determined by a Bonferonni correction to an overall a = 0.05.

[24] Pure nugget variograms exist for C/N, $(NO_3^-+NO_2^-)$ and grass at the Mongu (wet) site, indicating that there is no pattern at the scale of measurement. For analytes that exhibited spatial patterning, jackknife estimates of range vary from 4.61 to 10.20 m. The estimate of $C/(C_o + C)$ for TOC and TN at Mongu is lower than at Tshane, but estimates of $C/(C_o + C)$ for all other analytes are similar where spatial patterning exists. Jackknife range estimates for woody cover and bare cover are 15.6 and 17.1 m, respectively.

4. Discussion

[25] In addition to having lower MAP, the Tshane (dry) site also appears to have lower soil organic matter (SOM) and macronutrient concentrations than the Mongu (wet) site. However, the differences within a site, stratified by vegetation cover, are greater than the differences between sites. Although nutrient concentrations are higher at Mongu, the quality of SOM appears to be higher at Tshane, i.e., the C/N ratio is lower. There are two possible explanations for this: First, it could results from the different sources of SOM at the two sites, at least for the surface soil samples analyzed in this study. At Mongu, there is significantly more woody vegetation cover, and less grass cover, than at Tshane. Therefore, the contribution of low-quality, high C/N woody litter, comprising both leaves and twigs, to the surface soils could be more important at Mongu, leading to lower overall SOM quality at this site relative to Tshane, where more of the litter comes from grass with higher C/N. Alternatively, the litter itself may start out with different quality. At

Tshane, the dominant trees belong to the leguminous genus *Acacia* (*A. luederitzii* and *A. mellifera*) and vegetation at this site has high foliar N contents [*Scholes and Walker*, 1993]. This could lead directly to litter and SOM with lower C/N and higher quality. The fact that the analysis of variance (Table 2) showed no difference in C/N for samples beneath different vegetation types supports the second hypothesis, that the litter N content contributes to the difference in C/N between the two sites.

[26] The development of fertile islands appears to be much stronger at Tshane than at Mongu. This is reflected in higher CVs for anionic analytes at Tshane relative to Mongu. It is also reflected in the results of our nonparametric analysis of variance. At Tshane, we found significant differences between woody plant samples and samples from grass or bare ground for most analytes, including TOC and TN. No similar pattern was observed at Mongu. At Mongu, only significant differences between bare ground samples and woody samples were observed for TOC, TN, and PO_4^{-3}. In general, non-parametric tests confirm the hypothesis that woody vegetation is primarily responsible for the creation and maintenance of islands of fertility in these largely undisturbed savanna ecosystems. Furthermore, statistically significant correlations between woody height and TOC/TN at Tshane seem to suggest the accumulation of SOM beneath a woody plant is a function of age (as inferred by its proxy, height).

[27] Variogram results also corroborate the importance of woody vegetation determining the spatial heterogeneity of SOM and macronutrients at Tshane. At this site, the range

Table 3. Statistically Significant (95% Confidence) Correlations Between Soil Analytes at Tshane (Dry) and Mongu (Wet)[a]

	TOC	TN	Cl^-	SO_4^{-2}	PO_4^{-3}	$(NO_3^- + NO_2^-)$	Woody Height
TOC		0.98[b]	0.23[b]	0.20[b]	0.49[b]		
TN	0.98[c]		0.25[b]	0.23[b]	0.53[b]		
Cl^-	0.30[c]	0.27[c]		0.26[b]	0.17[b]	−0.15[b]	
SO_4^{-2}	0.58[c]	0.62[c]	0.41[c]		0.38[b]	0.72[b]	
PO_4^{-3}	0.49[c]	0.50[c]	0.24[c]	0.48[c]		0.19[b]	
$(NO_3^- + NO_2^-)$	0.43[c]	0.46[c]	0.33[c]	0.57[c]	0.46[c]		
Woody Height	0.73[c]	0.72[c]					

[a]Concentrations were log-transformed prior to calculation of correlation coefficient.
[b]Wet.
[c]Dry.

of the indicator variogram for woody vegetation is 8.43 m, which is close to the average distance between woody plants along the transect, 9.8 m. All analytes at Tshane, except Cl^-, have ranges similar to that of woody vegetation, suggesting that woody vegetation is responsible for the spatial distribution of the major macronutrients and SOM. The distance between trees (woody plants > 2 m) at Tshane is 27.6 m, and no analyte, not even Cl^-, has a range close to this value. Thus, we do see evidence that the size (and presumably age) of a woody plant is related to the strength of its fertile island; however, the largest individuals (e.g., trees) are not primarily responsible for the spatial heterogeneity of soil macronutrients and the development of fertile islands at Tshane. Both trees and shrubs appear to have significant impacts on the scale and pattern of soil heterogeneity at this site.

[28] At Mongu, the range of the indicator variogram for woody vegetation is 15.6 m, which is not close to either the tree-tree distance or the woody-woody distance at this site. The tree-tree distance at Mongu, nonetheless, falls within the 95% confidence intervals of both TOC and TN, whereas the woody-woody distance is significantly lower. These results provide evidence at Mongu that trees alone are responsible for spatial structuring of surface SOM. This is in stark contrast to Tshane where both shrubs and trees contribute to the spatial structuring of surface macronutrients and SOM. We believe that this difference could arise from differences in woody growth rates between these two sites. At Tshane, on the dry side of the Kalahari Transect, the rate of woody growth is likely slower than at Mongu, on the wet side of the Kalahari Transect. A shrub at Tshane may, therefore, be older than a shrub of the same size at Mongu. Due to their relatively slow growth and corresponding old age, shrubs at Tshane may have been present long enough to impact their soil environment. In contrast, shrubs at Mongu may not have been present long enough to significantly impact their soil environment, whereas the trees have. At neither site does grass appear to have a significant impact on the spatial patterning SOM, or other analytes, in soils.

[29] The results also provide some interesting suggestions about which macronutrients may be cycled conservatively, that is with little loss, within the savanna ecosystems studied here. Cl^- is often used as an index element because it is not actively taken up by plant roots, though it is often taken up to balance charge, and patterns of Cl^- in soils therefore mostly result from physical mechanisms [e.g., *Schlesinger et al.*, 1996]. Ions that behave spatially in a manner similar to Cl^- are thus thought to be dominated by abiotic rather than biotic processes. Our analysis of variance at Mongu shows that there is no relationship between the either Cl^- and SO_4^{-2} and different vegetation covers. Among anionic species, only PO_4^{-3} shows any relationship with vegetation cover at Mongu. Thus, at this site, we suspect that the distribution of Cl^- and SO_4^{-2} is dominated by physical factors. At Tshane, Cl^- is slightly elevated beneath woody vegetation relative to bare soils, indicating concentration of Cl^- by stemflow or some other physical mechanism. At this site, SO_4^{-2}, PO_4^{-3} and $(NO_3^- + NO_2^-)$ show some concentration beneath trees relative to other vegetation covers beyond that exhibited by Cl^-. This pattern is exhibited perhaps most clearly by PO_4^{-3}, which shows higher concentrations for samples beneath woody vegetation or woody vegetation + grass than for samples beneath grass alone. Thus, at Tshane, SO_4^{-2}, PO_4^{-3} and $(NO_3^- + NO_2^-)$ all exhibit patterning beyond that explained by purely physical processes.

[30] A similar pattern is seen in the correlation results (Table 3). At Mongu, among anionic species taken up by organisms, PO_4^{-3} has the highest correlation with TOC, its ultimate source in these highly weathered soils. The correlation between PO_4^{-3} and TOC is more than twice that of Cl^- and TOC. At Tshane, SO_4^{-2}, PO_4^{-3} and $(NO_3^- + NO_2^-)$ all exhibit correlation coefficients with TOC that exceed that of Cl^-. Indeed, even our variogram results provide a similar picture. At Mongu, the range of PO_4^{-3} approaches

Table 4. Range and Proportion of Spatially Structured Variance ($C/(C_o + C)$) for Spherical Models of Variograms From Both Sites[a]

Site		Analyte or Cover	Range, m			$C/(C_o + C)$		
			M	L	U	M	L	U
TSHANE (Dry)	Canopy Width =	TOC	9.08	8.96	9.20	0.96	0.94	0.98
	4.5 m Tree-Tree	TN	8.48	8.36	8.60	0.99	0.97	1.00
	Distance = 27.6 m	C/N	8.27	8.00	8.54	0.57	0.54	0.60
	Woody-Woody	Cl^-	17.40	17.02	17.78	0.59	0.56	0.63
	Distance = 9.8 m	SO_4^{-2}	8.46	8.23	8.69	0.77	0.73	0.81
		PO_4^{-3}	8.69	8.44	8.94	0.67	0.63	0.71
		$(NO_3^- + NO_2^-)$	7.27	7.03	7.51	0.68	0.63	0.72
		Woody	8.43	8.17	8.69	0.88	0.85	0.91
		Grass	3.02	2.92	3.12	0.99	0.95	1.00
		Bare	14.60	12.89	16.31	0.60	0.48	0.71
MONGU (Wet)	Canopy Width =	TOC	4.77	4.59	4.95	0.64	0.61	0.67
	3.1 m Tree-Tree	TN	4.61	4.43	4.79	0.64	0.61	0.67
	Distance = 4.6 m	C/N			NUGGET			
	Woody-Woody	Cl^-	7.55	7.31	7.79	0.71	0.67	0.76
	Distance = 1.9 m	SO_4^{-2}	6.11	5.80	6.42	0.62	0.56	0.67
		PO_4^{-3}	10.20	9.91	10.49	0.62	0.59	0.65
		$(NO_3^- + NO_2^-)$			NUGGET			
		Woody	15.60	15.18	16.02	0.58	0.54	0.62
		Grass			NUGGET			
		Bare	17.10	16.62	17.58	0.57	0.53	0.60

[a]"M" denotes the mean jackknife estimate. "L" and "U" denote the lower and upper bounds of the 95% confidence estimates, respectively.

that of woody vegetation and is considerably different from that of Cl^- and SO_4^{-2}. At Tshane, the range of SO_4^{-2}, PO_4^{-3} and $(NO_3^- + NO_2^-)$ are all similar to that of woody vegetation and TOC, but appreciably different from that of Cl^- (Table 4).

[31] The relationship between woody vegetation or TOC and PO_4^{-3} at Mongu and SO_4^{-2}, PO_4^{-3} and $(NO_3^- + NO_2^-)$ at Tshane from analysis of variance, correlation analysis, and variogram analysis suggests that these elements are cycled conservatively within their respective sites. We argue that, in order for these relationships to exist, little time can pass between mineralization of these elements and their subsequent uptake/immobilization. If uptake/immobilization were to lag significantly behind mineralization, we believe that physical processes, such as those that govern the distribution of Cl^-, would lead to weakened relationships between woody vegetation or TOC and mineralized anionic forms of S, P, and N.

[32] Although arguments of this sort do not constitute evidence of nutrient limitation by these elements, it does suggest reevaluation of the role that these elements play in these ecosystems. There are sound pedological reasons for reconsidering the importance of mineral-derived nutrients (e.g., P) in the Kalahari. The Kalahari Sands are mineralogically mature, meaning that they are primarily quartz and are depleted in P-bearing minerals. As a result, these sands may be P-poor, while also having a large number of N-fixing plants, particularly in the south. On the basis of this, the savannas of the Kalahari might be considered candidates for non-tropical forest ecosystems that are limited by P rather than N. P-limitation would explain the strong spatial relationships between woody vegetation and PO_4^{-3} because under conditions of P-limitation, PO_4^{-3} would have a short lifetime in the soil due to active scavenging by roots [Jackson and Caldwell, 1993]. A likely explanation for correlations between woody vegetation or TOC and SO_4^{-2} is more difficult than that for PO_4^{-3}, particularly in light of significant S deposition from industrial sources in South Africa [Zunkel et al., 2000], but on the basis of the evidence presented here, we believe that further investigation of the role of S in Kalahari savanna ecosystems may be a fruitful avenue of research.

5. Summary and Conclusions

[33] The purpose of this study is to determine how vegetation structure impacts the heterogeneity of macronutrients (N, P, and S) at two savanna sites along the Kalahari Transect that differ only in the amount of precipitation and the vegetation that results. On the basis of our analysis, it is clear that there is significantly stronger heterogeneity at the dry savanna site (Tshane) compared to the wet savanna site (Mongu). Patterns of soil resource distribution are largely determined by the location of woody vegetation at both sites. However, shrubs (i.e., woody plants $\leq$ 2 m in height) are more important in determining the spatial heterogeneity of soils in the southern dry site compared to the northern wet site. We hypothesize that the difference in the importance of shrubs arises from the slower rate of growth, and therefore the greater age of shrubs, in the dry southern site.

[34] Theories of facilitation and competition are common among explanations for the shared dominance of herbaceous and woody vegetation that characterizes savannas [Scholes and Archer, 1997; Sankaran et al., 2004]. Owing to the fact that savannas are water-limited ecosystems, explanations of competition and facilitation often involve competition for water and facilitation that eases water stress [e.g., Caylor et al., 2004, 2006]. Insofar as areas near woody vegetation in savannas tend to have higher SOM as well as higher macronutrient concentrations, however, these might also be areas where facilitation occurs as a result of the higher concentration of these soil resources. Further evidence is required to show that facilitation can take place as a result of chemical, rather than ecohydrological, factors, but relatively simple experiments could be devised. For instance, the emergence and survival of woody seedlings could be measured in pots with soil from different locations on the landscape under identical water and light conditions.

[35] Our analysis also suggests that Kalahari savanna ecosystems might be limited by nutrients other than N, in particular, P. This possibility is reasonable mineralogically, due to the composition of Kalahari Sands, and floristically, due to the abundance of leguminous woody species, but further evidence is required to show definitively that these systems are not N-limited. Because most ecosystems are considered N-limiting outside of tropical forests with highly weathered Ultisols or Oxisols, this finding would be significant in that it would show that other ecoregions and soil types can exhibit limitation by rock-derived nutrients.

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