Isotope composition and anion chemistry of soil profiles along the Kalahari Transect

L. Wanga,c,* P. D’Odoricoa G.S. Okinb S.A. Mackoa

a Department of Environmental Sciences, University of Virginia, 291 McCormick Road, Charlottesville, VA 22904, USA
b Department of Geography, 1255 Bunche Hall, University of California, Los Angeles, CA 90095, USA
c Department of Civil and Environmental Engineering, Princeton University, Princeton, NJ 08544, USA

Abstract

Savannas cover about 20% of the Earth’s land area across a wide range of climatic conditions. As an important and distinct biome, savannas produce approximately 29% of global terrestrial net primary productivity. In these ecosystems the distribution of belowground resources remains poorly investigated and the relationship to the climatic conditions remains unclear. In the present study, vertical profiles of soil nutrients (chloride, nitrate, phosphate and sulfate) and nitrogen stable isotopes were analyzed at four sites along the Kalahari mega-transect, where a distinct rainfall gradient exists on a homogeneous soil substrate. The results show clear differences in nutrients and δ^{15}N vertical distributions between wet and dry seasons. The results also show how the formation of “fertility islands” (i.e., the concentration of soil nutrients in the soils beneath tree canopies) is not necessarily coupled with belowground processes in that the distribution of soil nutrients at the surface does not match belowground patterns. The results also indicate that phosphorus may be a limiting nutrient in these savanna ecosystems with seasonal dynamics in its cycling.

© 2008 Elsevier Ltd. All rights reserved.

1. Introduction

Situated in southern Africa, the Kalahari sand sheet covers 2.5 million km² and is one of the largest continuous surfaces of sand in the world (Leistner, 1967). The Kalahari Transect (KT) within the Kalahari sand sheet was identified by the IGBP (International Geosphere–Biosphere Programme) as one of the “mega-transects” for global change studies (Koch et al., 1995). The KT traverses a dramatic aridity gradient (from ~200 mm to more than 1000 mm of mean annual precipitation (MAP), through the Republic of South Africa, Botswana, Namibia and Zambia), on relatively homogenous soils: the deep Kalahari sands (Fig. 1). Thus, with a remarkable rainfall gradient on a homogeneous soil substrate, the KT provides the ideal setting to study carbon, nutrient and vegetation dynamics without confounding soil effects.

Vegetation on the KT is dominated by different types of savannas ranging from the fine-leafed savannas (nutrient-rich) in the south to the broad-leafed savannas (nutrient-poor) in the north. Savannas exhibit a mixture of plant communities with different life forms (mainly trees and grasses) and life histories. The shared dominance between trees and graminoid life forms across vast regions of the world such as the semi-arid tropics and sub-tropics is one of the most fascinating open issues in savanna ecology (Sankaran et al., 2005; Sarmiento, 1984; Scholes and Archer, 1997). Many theories have been put forth regarding the cause of this shared dominance, including mechanisms based on competition–facilitation and disturbance regime. Regardless of the processes underlying tree–grass co-dominance, the belowground distributions of resources (e.g., nutrients) and belowground processes likely play important roles on vegetation dynamics and the composition and structure of vegetation should exhibit the imprints of these distributions and belowground processes.

Vegetation distribution and surface soil biogeochemical properties along the KT have been documented by a number of studies (Caylor et al., 2003, 2005; Privette et al., 2004; Ringrose et al., 1998; Scholes et al., 2002, 2004; Wang et al., 2007a; Wang, 2008). The plant–soil interactions along the KT have also been investigated (D’Odorico et al., 2007; Okin et al., 2008). However, most of these studies have been focusing on the aboveground processes, and little is known about the belowground resource distributions and related processes. In fact, only limited data exist on soil profiles in southern Africa in general, as only few published data sets can be found in
the literature (Fritzsche et al., 2007; Hipondoka et al., 2003; Hoffman et al., 1995). The vertical distribution of soil nutrients reflects nutrient inputs, outputs and cycling processes. Plants play an important role in determining the distribution of nutrients through the soil profiles (Jobbágy and Jackson, 2001). Vegetation effects on nutrient profiles depend on the chemical nature of the nutrient and on whether it is a limiting nutrient. For example: phosphorus (P) and nitrogen (N) may limit plant productivity and are expected to be depleted by root uptake. Sulfate and chloride are expected to accumulate below the root depth and have a different profile from N and P (Jobbágy and Jackson, 2001). This lack of information on belowground resource distributions limits the current understanding of the dynamics of savanna ecosystems, particularly the tree–grass interactions and the response of savannas to further climate change. In this paper, soil profile data – including the concentration of major anions and the compositions N isotopes, are reported from four sites each with distinct rainfall regimes (e.g., MAP, rainfall of major anions and the compositions N isotopes, are reported from four sites each with distinct rainfall regimes (e.g., MAP, rainfall depth) (Caylor et al., 2006). A comparison based on samples collected both in a dry and in a wet season is also made. The objectives of this study are to (1) compare the belowground resource distributions between different sites along the KT; (2) compare belowground resources variations for under canopy and between canopy areas; and (3) evaluate the seasonal differences in belowground resource distributions.

2. Materials and methods

2.1. Study sites

Four sites along the KT rainfall gradient (Fig. 1) were selected (from south to north: Tshane, Ghanzi, Pandamatenga and Mongu). The detailed site description including surface soil physical and chemical characteristics can be found in Wang et al. (2007a) and key parameters were reported in Table 1. The major site characteristics are summarized as follows. Three sites were situated in Botswana including Tshane (southernmost site), Ghanzi and Pandamatenga (Fig. 1). The MAP in these three areas ranges from 365 mm to 700 mm, respectively. The Tshane and Ghanzi sites are open savannas dominated by Acacia species such as A. luquerizii Engl. and A. mellifera Benth., and grass species, such as Eragrostis lehmanniana and Schmiddtia pappophoroides. The Pandamatenga site is a woodland savanna dominated by tree species (e.g., Schinziophyton spp.) and grass species such as Panicum maximum and Pogonarthria squarrosa. The northernmost site was situated in Mongu, Zambia, with a MAP of ~880 mm. Vegetation at this site is woodland savanna dominated by the species Brachystegia spicifloris Benth.

2.2. Field sampling

In total, 16 soil pits were dug along the KT, eight in the dry season (August 2004), and eight in the wet season (March 2005). The wet season 2005 was a dry year with precipitation lower than MAP except at Tshane (Table 1). There were occasional rainfall events at Tshane, Ghanzi and Mongu during the 2–3 days of pit digging periods in the 2005 wet season. At Tshane, there was a large storm the night (March 5, 2005) just before soil samplings from the dug pits. Two pits were dug at each site, one under a tree canopy and the other in between canopy areas (usually covered with grasses), for a total of eight soil pits analyzed in each season. Both of the soil pits dug in Ghanzi in March 2005 could be classified as under canopy areas although one was further away from the vegetation thicket. The soil pits were dug to 1 m depth in most cases and soil samples were taken from soil pits along the soil profile at 10 cm intervals. At Tshane, several samples were taken at depths up to 400 cm in the 2005 wet season, using a sand auger at the bottom of the soil pits.

2.3. Chemical analyses

Soil samples were air dried in the field and stored in labeled, sealed plastic bags. The anion concentrations of these soil samples were analyzed using Dionex ICS-2000 ion chromatograph (Dionex, Sunnyvale, CA) with an Ion Pac AS 18 anion exchange column. For these analyses, 6 g subsamples were extracted with 30 mL deionized water (conductivity lower than 1 μS) in a 50 mL centrifuge tube (Okin et al., 2008). The mixture was agitated for 30 min and then centrifuged for 9 min at 4150 rpm to produce a clear supernatant (Okin et al., 2008). Nitrite (NO$_2^-$), nitrate (NO$_3^-$), phosphate (PO$_4^{3-}$), sulfate (SO$_4^{2-}$), and chloride (Cl$^-$) concentrations, expressed as μg/g soil, were measured for each sample. Nitrite and nitrate were combined to provide a measure of total anionic inorganic N and reported as nitrate concentrations.

For N isotope analyses, the soil samples were further oven dried at 60 °C for 72 h in the laboratory. After drying, they were sieved and homogenized by mortar and pestle. Stable N isotope analyses were accomplished using a Micromass Optima Isotope Ratio Mass Spectrometer (IRMS) connected to an elemental analyzer (EA; GV/Micromass, Manchester, UK). The stable isotope compositions are reported in the conventional form:
surface using plant root systems as a conduit (Caldwell et al., 1998), movement from the relatively moist deep layers to the dry soil under canopy and between canopy soils, may also result from water (Okin et al., 2008). The differences in vertical distribution between two periods. The more elevated chloride concentrations in the under canopy soils (Fig. 2) decrease with depth (Jobbágy and Jackson, 2001). With the exception of Tshane, sulfate tends to accumulate more in the surface soils (0–20 cm) under trees/shrubs than in the between canopy areas. This pattern is observed both in the wet and in the dry seasons. Moreover, sulfate concentrations are higher in the dry end of the transect (Tshane and Ghanzi, Figs. 2 and 3). The high sulfate concentrations at the dry sites is possibly due to (1) sulfate from salt pans located closer to the southern sites, and (2) the proximity to South Africa industrial sources, as evidenced by the higher sulfate concentrations in rainfall in these sites (Tshane = 5.01 ppm, Ghanzi = 3.95 ppm, Pandamatenga = 2.3 ppm, Kasane (~ 100 km north of Pandamatenga) = 0.3 ppm based on rainfall events in the 2006 wet season). The sulfate distributions below the top 20 cm remain constant with depth in both seasons and at all sites except Tshane (Figs. 2 and 3). These patterns are different from the global pattern of sulfate distribution, which clearly show sulfate concentration increase with depth (Jobbágy and Jackson, 2001). The relatively high concentration of sulfate at depth that is observed at Tshane is quite different from all other sites (Figs. 2 and 3).

Phosphate is primarily mineral-derived and occurs in low concentrations in geological formations. The available inorganic phosphorus is limited in supply in the highly weathered soils of the tropics and therefore is often considered to be a limiting nutrient to ecosystem productivity in the tropics (Vitousek and Sanford, 1986; Walker and Syers, 1976). In the mineralogical mature Kalahari sands, which are composed of nearly pure quartz (Wang et al., 2007a), P-bearing minerals are largely absent, suggesting that these plants on the Kalahari sands may be P-limited. In the dry season, phosphate rich soils were found to accumulate under trees/shrubs (0–20 cm). Moreover, the phosphate levels are slightly higher at the dry end of the transect (Ghanzi and Tshane) for soils both under the canopy and in between canopy areas (Fig. 2). Unlike the surface soils, below the top 20 cm, the vertical distributions of phosphate are the same beneath and between canopies. During the wet season, however, the concentration of phosphate in the top 20 cm of soil is the same between and beneath canopies. The wet season subsurface (below 20 cm) concentrations of phosphate beneath canopies are higher at the drier sites (Tshane and Ghanzi) than at the two wetter sites (Pandamatenga and Mongu). During the wet season, the phosphate concentration below 40 cm beneath canopies is elevated compared to the dry season. In the wet season, the subsurface (below 20 cm) phosphate concentrations at Tshane and Ghanzi under canopy are also higher than in the soils from between canopy areas (Fig. 3). These differences do not exist in the two wetter sites (Pandamatenga and Mongu). If phosphate is one of the limiting nutrients in these savanna ecosystems, biological cycling has to play an important role in nutrient profile distributions. Unlike leaching, biological cycling generally moves nutrients upwards because some proportion of the nutrients absorbed by

### Table 1

<table>
<thead>
<tr>
<th>Location</th>
<th>Elevation (m)</th>
<th>MAP (mm/yr)</th>
<th>2005 wet season rainfall (mm)</th>
<th>Mean rainfall depth (mm)</th>
<th>Mean rainfall frequency (day⁻¹)</th>
<th>Woody cover (%)</th>
<th>Bulk density (g cm⁻³)</th>
<th>Soil texture</th>
<th>pH</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tshane</td>
<td>24.17 S</td>
<td>1115</td>
<td>365</td>
<td>436</td>
<td>10</td>
<td>0.150</td>
<td>14</td>
<td>3.70</td>
<td>0.47⁹, 1.41⁸, 1.47⁸</td>
</tr>
<tr>
<td>Ghanzi</td>
<td>21.89 E</td>
<td>1125</td>
<td>424</td>
<td>362</td>
<td>10</td>
<td>0.175</td>
<td>20</td>
<td>5.09⁹, 1.34⁸, 1.42⁸</td>
<td>96.0 – 6.12⁴, 6.16⁵</td>
</tr>
<tr>
<td>Pandamatenga</td>
<td>18.66 S</td>
<td>1082</td>
<td>698</td>
<td>450</td>
<td>10</td>
<td>0.290</td>
<td>40</td>
<td>4.05⁹, 1.46⁸, 1.51⁸</td>
<td>96.8 – 5.62⁴, 6.10⁵</td>
</tr>
<tr>
<td>Mongu</td>
<td>25.50 E</td>
<td>1076</td>
<td>879</td>
<td>564</td>
<td>10</td>
<td>0.380</td>
<td>65</td>
<td>4.44⁹, 1.47⁸, 1.50⁸</td>
<td>97.5 – 5.02⁴, 5.11⁵</td>
</tr>
</tbody>
</table>

MAP: mean annual precipitation.

The superscript letters “a” and “b” denote under canopy and between canopy, respectively.

The data are adopted from Wang et al. (2007a), Wang (2008) and Caylor et al. (2006).

c Sand–silt–clay ratio.

\[ \delta^{15}N(\text{sample}) = \left( \frac{^{15}N/^{14}N}_{\text{sample}} / ^{15}N/^{14}N_{\text{standard}} - 1 \right) \times 1000 \]

where \( ^{15}N/^{14}N_{\text{sample}} \) is the ratio of the N isotopes in a sample, and \( ^{15}N/^{14}N_{\text{standard}} \) is the ratio of the N isotopes of the standard material, atmospheric molecular N\(_2\) (AIR). Reproducibility of these measurements is approximately 0.2\(^{\circ}\)

3. Results and discussion

#### 3.1. Anion distribution

Chloride does not generally constrain plant growth (Jobbágy and Jackson, 2001). The patterns of chloride in soils most likely result from physical mechanisms (Schlesinger et al., 1996). In arid soils, chloride is a relatively mobile element. Because the amount of water that leaches salts decreases dramatically with depth owing to root water uptake, soil chloride levels usually increase with depth, being greatest at the maximum rooting depth (Jobbágy and Jackson, 2001). In the African savanna ecosystems considered in this study, surface chloride concentrations (0–20 cm) are higher for the under canopy soils both in the wet and the dry seasons with higher differences between “under canopy” and “between canopy” soils occurring in the wet season (Figs. 2 and 3). In the wet season, except the under canopy soil of Tshane, chloride concentrations below the top 20 cm of soil tend to be constant for both under canopy and between canopy soils (Fig. 3). The maximum chloride concentrations could take place below 100 cm for all the sites in the wet season (Fig. 3). This depth corresponds to the rooting depth reported for the drier sites (the rooting depths in the drier sites are based on Hipondoka et al., 2003; Wang et al., 2007a). In the dry season, the chloride concentrations remain almost constant with depth in the between canopy soils for nearly all sites; at all sites, the chloride concentrations in the under canopy soils (Fig. 2) decrease with depth to reach minimum values at 40–60 cm and then increase until reaching the soil pit bottom (100 cm). The obvious differences in chloride distributions between wet and dry seasons are probably influenced by the differences in water availability between two periods. The more elevated chloride concentrations in the surface soils beneath woody vegetation are presumably caused by physical mechanisms such as canopy interception and stemflow (Okin et al., 2008). The differences in vertical distribution between under canopy and between canopy soils, may also result from water movement from the relatively moist deep layers to the dry soil surface using plant root systems as a conduit (Caldwell et al., 1998); a process known as “hydraulic lift” (Richards and Caldwell, 1987), which is relatively common in arid environments.
Plants are transported aboveground and then recycled to the soil surface through litterfall, resupplying the nutrients to the soil surface (Trudgill, 1988). These results clearly show a strong concentration of phosphate near the surface, consistent with active P cycling in similar ecosystems (Jobbágy and Jackson, 2001). During the dry season this effect is strongest beneath tree canopies, but an increase in near-surface phosphate is observed in all of our data. Decomposition of P-bearing litter and the related mineralization of P at the surface when water becomes available may explain the increase in phosphate between canopies during the wet season. The uptake of mineralized P by plants during the wet season may explain the relatively low concentration of phosphate near the surface during the dry season; all of the P is in plant tissue and litter, and there is not sufficient moisture to allow the microbial remineralization of P. This tight seasonal coupling of plant growth and phosphate in the surface soils argues strongly for P-limitation or low nutrient adaptation, at least among the grasses found between tree canopies. The P-limitation is also supported by the observed high foliar N/P ratios (N/P = 20–30) for C3 plants at the drier Kalahari sites in a wet year (Aranibar et al., 2003).

Nitrogen is another potential factor that limits plant productivity in part of tropical savannas with higher water availability (Scanlon and Albertson, 2003) although recent studies show that in the KT N limitations are less important than water limitation (Wang, 2008). With the exception of Tshane, soil surface (top 20 cm) nitrate concentrations are much higher in the under canopy areas than the between canopy areas in the dry season but are similar in the wet season. Except Tshane, nitrate subsurface (>20 cm) profiles are not very different between the wet season and the dry season, nor under canopy or between canopies. Since nitrate is a mobile nutrient, the

Fig. 2. The anion concentrations along the soil profiles in the dry season 2004: chloride, under tree/shrub canopy (A); chloride, between canopy (B); sulfate, under tree/shrub canopy (C); sulfate, between canopy (D); phosphate, under tree/shrub canopy (E); phosphate, between canopy (F); nitrate, under tree/shrub canopy (G); and nitrate, between canopy (H).
belowground nitrate distribution is expected to be influenced by aboveground distribution, especially for the sandy soil of the Kalahari. However, the nitrate subsurface profile distributions are different from the surface “fertility island” patterns found in the same region (Okin et al., 2008). The very high concentration of nitrate beneath trees during the wet season at Tshane probably results from N fixation by leguminous Acacia species at this site. This point is supported by the observation that soil δ15N values are lower in the soil profiles under canopy compared to the between canopy soil (Fig. SC, D), consistently with the fact that N fixation is expected to lower δ15N values in these soils. Although Acacia species are also found at the Ghanzi site, the under canopy pit was actually located beneath Terminalia species, possibly explaining low nitrate concentration beneath the canopy at the Ghanzi site. During the dry season, the occasional increase in nitrate below 80 cm may result from leaching of nitrate, particularly at the wetter sites, Pandamatenga and Mongu.

The nitrate, chloride and sulfate profiles at Tshane exhibit much higher concentrations than the other three sites. The abnormal high values of soil moisture measured at Tshane in the 2005 wet season must have played an important role in determining these high concentrations of chloride, nitrate, and sulfate. In fact, these three anions are mobile and the pattern of their profiles matches the profile of average seasonal soil moisture (Fig. 4). The single storm event, on the other hand, is not expected to affect the distributions of these mobile nutrients to a great extent. For example, there was a relatively large storm occurred at Tshane the night before soil sampling; however, the wetting front reached only a depth of about 10 cm.

![Fig. 3. The anion concentrations along the soil profiles in the wet season 2005: chloride, under tree/shrub canopy (A); chloride, between canopy (B); sulfate, under tree/shrub canopy (C); sulfate, between canopy (D); phosphate, under tree/shrub canopy (E); phosphate, between canopy (F); nitrate, under tree/shrub canopy (G); and nitrate, between canopy (H).]
3.2. $^{15}$N distributions

Surface soil $^{15}$N can vary with aridity (Aranibar et al., 2004; Swap et al., 2004), rainfall (Austin and Vitousek, 1998), soil age (Brenner et al., 2001), successional age (Wang et al., 2007b) and soil crust density in arid environments (e.g., Aranibar et al., 2003; Berkeley et al., 2005) since cyanobacterial crusts are capable of fixing atmospheric N$_2$. Soil $^{15}$N variations with depth are more complex and are affected by multiple factors, which include N transport processes, depth-dependent plant N inputs, and multiple N pools other than those from plant tissues (e.g., microbial biomass) (Amundson et al., 2003). Depending on climate conditions, the vertical profile of soil $^{15}$N can either exhibit random distributions like in gravelly desert soil, little variation as in montane environments or, most commonly, a consistent (exponential) increase with depth, commonly found in grasslands (Amundson et al., 2003). Despite the presence of fluctuations in the vertical profile of dry season soil $^{15}$N (Fig. 5), similar to those observed in gravelly desert soils (Brenner et al., 2001), the $^{15}$N in the Kalahari increases with depth through the major portion of the root zone (top 50 cm based on Wang et al., 2007a) to a maximum value; at greater depths it exhibits larger fluctuations. This pattern is observed both in between canopy and under canopy areas for the dry season (Fig. 5). During the wet season, the $^{15}$N values generally show similar patterns. However, in the wet season $^{15}$N values are more enriched at all sites and the depths with maximum $^{15}$N values are deeper (top 60 cm) when compared to those in the dry season (Fig. 5). The seasonal differences in $^{15}$N distributions are presumably caused by the higher levels of microbial activity (e.g., denitrification and mineralization) during the wet season, which results in $^{15}$N enriched residual substrate (Robinson, 2001; Swap et al., 2004). At depths greater than 10 cm, similar patterns in the distributions of $^{15}$N exist for under canopy and between canopy locations. This is presumably the result of the interactions of tree-grass roots at the subsurface (e.g., N uptake competition, N source

Fig. 4. Soil moisture profiles from wet season 2005 (October–April) for under canopy (A) and between canopy (B) soils. The data are based on D’Odorico et al. (2007).

Fig. 5. Soil $^{15}$N distributions for under tree/shrub canopy (A) and between canopy (B) soils in dry season 2004, and for under tree/shrub canopy (C) and between canopy (D) soils in wet season 2005.
differentiation and plant N input). These similarities were not observed in the surface soils, where soils are richer in nutrients under the tree canopies, a phenomenon known as the “fertility island”, as found in Wang et al. (2007a) and Okin et al. (2008) in the same region. In addition, a pattern of increasing $^{31}$P with increasing aridity can be observed along the KT rainfall gradient both in aboveground plant biomass (Aranibar et al., 2004; Swap et al., 2004; Wang et al., in press) and in surface soils (Wang et al., 2007a, in press). However, similar to nitrate distribution, the distributions of belowground $^{31}$P do not follow the aboveground trends, indicating different mechanisms governing N processes belowground.

4. Summary

Nutrient and N isotope profiles analyzed at four sites along the KT rainfall gradient, provided valuable and timely information on the belowground distribution of resources in savannas of southern Africa. This information fills in an important knowledge gap in the study of soil biogeochemistry in this region and will enhance the understanding and prediction of aboveground vegetation structure, tree/grass ratios and nutrient dynamics. However, because the digging of soil pits was time and labor intensive, no replicates were available. This lack of replication places constraints on the generalization for these findings. The results do show clear differences in nutrients and $^{15}$N vertical distributions between wet and dry seasons. The results also show that the aboveground nutrient “fertility islands” do not necessarily match the belowground patterns. Moreover, the results show the importance of soil moisture profiles in determining the patterns of mobile nutrients (e.g., chloride, sulfate and nitrate) distributions especially at the drier sites. Together with other evidence, the belowground P profiles also indicate that phosphorus may be a limiting nutrient in these savanna ecosystems and that there are seasonal dynamics in the cycling of P.

Acknowledgements

The project was supported by NASA-IDS2 (NNG-04-GM71G) and Moore Research Award to LW from Department of Environmental Sciences at University of Virginia. We greatly appreciate the teamwork and field assistance from Natalie Mladenov, Todd Scanlon, Ian McElynn (University of Virginia), Kelly Cairyl (Princeton University), Billy Mogojwa, Dikitoso Kolokoze, O.G.S.O. Kgosidintsi and Thoralifier (University of Botswana), Kebonyethata Dintwe (Department of Agriculture, Botswana). We thank Junran Li for his help with the laboratory instrumentation. The clarity and strength of the paper were improved by the comments of three anonymous reviewers to whom we are grateful.

References


