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Review

Biogeochemistry of Kalahari sands

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Abstract

The Kalahari sand sheet, with a 2.5-million ha area, is probably the largest continuous surface of sand in the world. The Kalahari Transect (KT) is one of a set of IGBP "megatransects" identified for global change studies and provides an ideal setting to investigate changes in ecosystem dynamics, vegetation composition and structure, and carbon or nutrient cycles along a spatial precipitation gradient without confounding soil effects. Soil physical properties remain poorly characterized along the KT. The present work provides a review of previous studies on the Kalahari soils combined with new results from recent analyses of physical (mostly hydraulic) and biogeochemical properties of the soil. In summary, the Kalahari soil is acidic, dominated by sand and nutrient poor. Nutrient contents, soil textures and soil hydraulic properties differ under and between canopies. Roots are concentrated in the top 80 cm of the soil, with grass roots more abundant and dominant close to the surface. Moreover, the distribution of tree roots does not exhibit a clear dominance over grasses at deeper soil layers. This review provides important baseline information for this system, as well as insights as to how biochemical processes vary along a rainfall gradient.

Keywords: Biogeochemistry; Hydraulic properties; Kalahari transect; Sand deposits; Stable isotopes

Contents

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1. Introduction

The north–south transect of the Kalahari (known as the Kalahari Transect, KT) is one of a set of International Geosphere–Biosphere Programme (IGBP) ‘‘megatransects’’ (e.g., Koch et al., 1995; Scholes et al., 2002) identified for global change studies. This work focuses on an analysis of the biogeochemistry of the Kalahari sands in order to develop insights as to how biochemical processes vary along the north–south rainfall gradient. The KT provides an ideal setting to investigate changes in ecosystem dynamics, composition and structure of vegetation, and carbon (C) or nutrient cycles along a spatial gradient of precipitation while minimizing the confounding effects of soil heterogeneity.

The Kalahari is essentially a plateau area uplifted following the breakup of Gondwanaland, at least 65 million years ago (Thomas and Shaw, 1991). The plateau edges were uplifted as the continent moved northwards. Both fluvial and dune sediments are believed to have infilled the uplifted basin with mainly sands interbedded with calcrete and silcrete. Areas within the basin have also been shown to comprise weathered material (Haddon, 2000; McFarlane and Eckardt, 2004). Most of the sands have assumed diverse post Gondwana histories including up to 5.0 Ma of weathering, resorting and deposition on previously exposed African surface(s) (Baillieul, 1975; Huntsman-Mapila et al., 2005; Ringrose et al., 2002; Thomas and Shaw, 1991). Most palaeo-environmental work has focused in the central Kalahari Makgadikgadi-Okavango-Zambezi (MOZ) basin area either on Kalahari dune sequences (e.g. Grove, 1969; Lancaster, 1986, 2000; Thomas and Shaw, 2002; Thomas et al., 2003) or on multiple palaeo lake sequences as described in Cooke (1980) and Cooke and Verstappen (1984). Thomas and Shaw (1991, 1993, 2002) and Huntsman-Mapila et al. (2006) attribute wetter (flooding) periods to ca. 40,000 BP or later partially based on ^{14}C ages. Multiple periods of aeolian activity have been age-dated as occurring in the late Pleistocene with optical stimulated luminescence (OSL) ages indicating more arid episodes between 95 and 115, 41 and 46 and 20 and 26 Ka (Stokes et al., 1997).

The present day Kalahari climate ranges from arid to semi-arid/subhumid with relatively strong seasonal and interannual variations in precipitation. Major characteristics are the potential evapotranspiration (PET), which is typically 3 times the annual rainfall; the rainfall variability ranges from less than 200 mm in southwest Botswana to over 1000 mm in the north (i.e., western Zambia). The rainy season (Fig. 1) is typically from October to April during the austral summer months when maximum growth is experienced while dormancy is characteristic of the dry winter months (Shugart et al., 2004).

Vegetation on the KT is dominated by different types of savannas ranging from the fine-leafed ones (nutrient-rich) in the south to the broad-leafed plants (nutrient-poor) in the north. The distribution of Kalahari vegetation has been investigated through a number of field observations (e.g. Caylor et al., 2003; Privette et al., 2004; Ringrose et al., 1998; Scholes et al., 2002, 2004) and modeling studies (Caylor et al., 2004; Jeltsch et al., 1998, 1999; Privette et al., 2004). Some key findings from these studies include the assessments that (1) woody plant biomass increases from south to north. Above the minimum level of 200 mm MAP, the woody basal area increases at a rate of ca. 2.5 $m^2 ha^{-1}$ per 100 mm MAP. The mean height of the 10% tallest trees also increases along the gradient, reaching 20 m at ca. 800 mm MAP (Scholes et al., 2002); (2) aggregation of plant individuals has

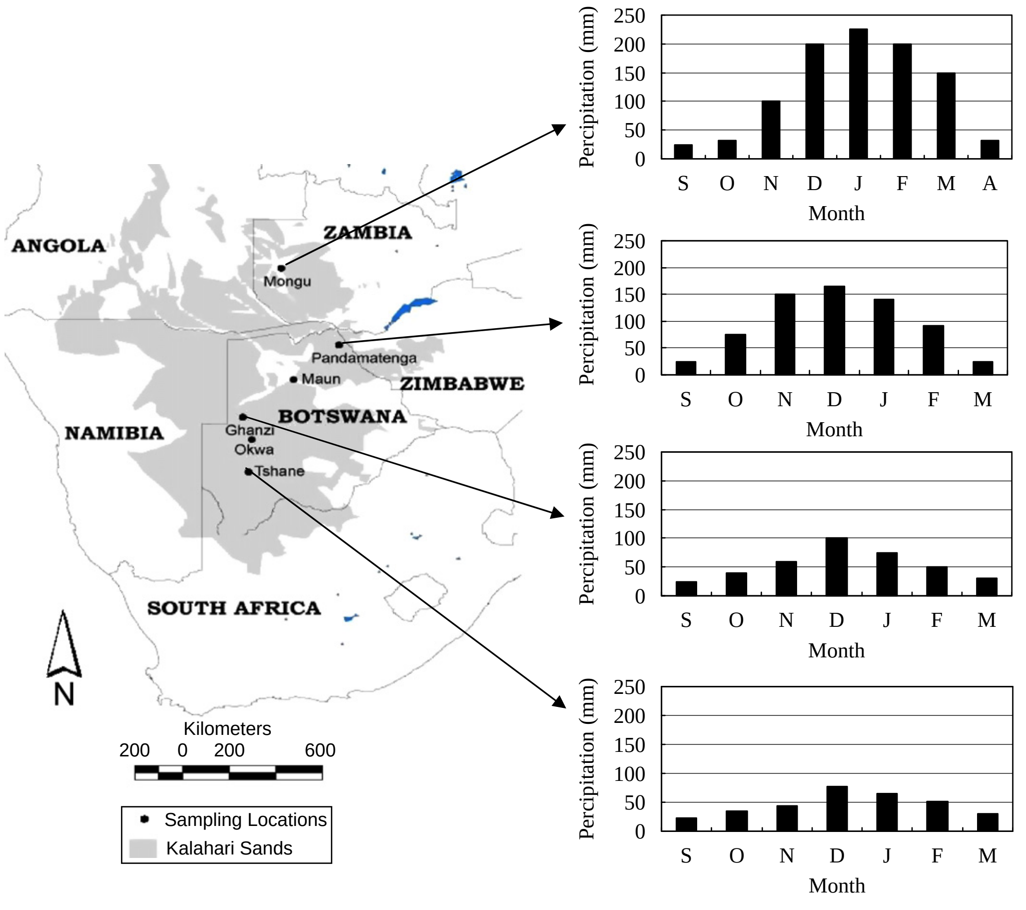

Fig. 1. Location of the field sites established for this study along the Kalahari transect. The bar charts indicate the mean annual cycle of precipitation (1961–1990) at four sampling locations. Modified after Shugart et al. (2004).

been observed in the vegetation communities at most sites, with the exception of the arid southernmost sites. The spatial distribution for the largest 25% of individuals is predominantly random but juveniles tend to cluster around mature individuals (Caylor et al., 2003); (3) interactions among different life forms play a crucial role on vegetation productivity across the rainfall gradient (Caylor et al., 2004).

Despite the relevance of the KT to regional and global change studies, the soil physical properties remain poorly characterized (cf. Joshua, 1981). This is a major limitation as the response of arid and semiarid ecosystems to changes in rainfall regime is mediated by variations in the soil moisture dynamics, which, in turn, depend on the soil hydraulic properties. In contrast, a few studies have investigated the biogeochemical properties of the Kalahari sands (Aranibar et al., 2004; Bird et al., 2004; Dougill et al., 1998; Feral et al., 2003; Hudak et al., 2003; Pardo et al., 2003; Skarpe and Bergstrom, 1986), although a comprehensive synthesis of the main results remains to be accomplished. This paper provides a brief review of previous studies on the sandy Kalahari soils (hereafter called the Kalahari sands) combined with previously unpublished results from recent analyses of the soil physical (mostly hydraulic) and biogeochemical properties.

2. Materials and methods

2.1. Field sampling

The new results presented in this review were obtained from soil samples collected at four locations (Tshane, Ghanzi, Pandamatenga and Mongu) along the Kalahari transect during the dry season (August) of 2004 (Fig. 1). The climate and vegetation characteristics of these field sites are reported in Table 1. At each site, soil samples were collected (in five replicates) from both beneath tree canopies and in open areas. Two 1-m-deep soil pits were dug from each of the four locations: one in an open area and the other under a tree canopy. The soil pits were used to establish the soil profile at different depths (at 10 cm intervals). All soil samples were air-dried in the field and stored in plastic bags. In the wet season of 2006, 2–3 soil pits were dug from each location and soil samples from every 10 cm interval were collected for soil particle analysis, soil color and soil scanning electron microscope (SEM) analysis.

Table 1
Location and general characteristic of four sampling sites along the Kalahari transect

	Location	Elevation (m)	Rainfall (mm year)[a]	Vegetation type	Woody cover[a]
Tshane	24.17°S 21.89°E	1115	365	Open *Acacia* savanna	14
Ghanzi	21.65°S 21.81°E	1125	400	*Acacia–Terminalia* woodland	20
Pandamatenga	18.66°S 25.50°E	1082	698	Baikea woodland	40
Mongu	15.44°S 23.25°E	1076	879	Miombio woodland	65

[a]Rainfall, woody cover data are from Caylor et al. (2006).

2.2. Measurement of physical/hydraulic properties

Soil physical properties were measured on composite samples obtained by mixing five soil samples collected at each site, either from intercanopy or from subcanopy soils. The size of soil grains was expressed using phi (ϕ) units defined as $\phi = -\log_2(D_{mm}/1_{mm})$, where D_{mm} is the grain diameter in mm. Soil samples were dry-sieved at 1 and 0.5ϕ intervals (cf. Lancaster, 1986) after passing through a sample splitter. Sieving took place using nested sieves (2.0–0.063 μm or −1 to 4ϕ) on an automatic Retsch shaker whereby 100 g of loose sand was sieved for 15 min. Size analysis followed procedures devised by Folk and Ward (1957) as updated in Tucker (2001). The saturated hydraulic conductivity (K_s) was measured using a falling-head permeameter on composite samples (~300 g) from sub-canopy and inter-canopy soils at each site. Five or six measurements were made for each sample and averaged (Table 2). One-way ANOVA was used to compare the difference (at 0.05 significance level) in K_s between intercanopy and subcanopy soils at each sampling location.

The bulk density, ρ_b was calculated at each site for both subcanopy and intercanopy soils by determining the weight of 40 ml of oven-dried samples (105 °C for 48 h). Soil porosity, n, was estimated as $n = 1-\rho_b/\rho_s$, assuming a value of 2.65 g cm^{-3} for the density, ρ_s, of the grains of quartz sand (Brady and Weil, 1999).

Soil pH values were measured using a portable pH meter (Hanna Instruments-HI 9023, Woonsocket, RI, USA) on 5-g samples of composite soil mixed with DI water. The mixing consisted of 1 h of shaking, followed by a half-hour-long settling before making measurements (Thomas, 1996). To quantify the soil surface CO_2 along the transect, soil respiration was measured in 24 random locations using EGM-4 CO_2 analyzer at each site in January 2006. To examine the effect of precipitation on the soil surface CO_2 flux, 600 ml water was poured into a soil collar (40 cm × 20 cm) before measurement, and CO_2 fluxes were measured immediately after the water had infiltrated.

The water retention curves for composite soil samples from both intercanopy and subcanopy soils were determined at each site by measuring the water potential values—using a water activity meter, DECAGON AquaLab Series 3T (DECAGON Devices, Pullman, WA, USA) and gravimetric moisture content. Water activity readings,

Table 2
Soil physical and hydraulic properties of Kalahari sands

		Tshane	Ghanzi	Okwa	Pandamatenga	Mongu
Porosity	n	0.47^a, 0.45^b	0.49^a, 0.47^b		0.45^a, 0.43^b	0.44^a, 0.43^b
Sat. hydr. conductivity	K_s (m day^{-1})	6.39^{aA}, 3.73^{bB}	5.02^{aA}, 5.01^{bA}		13.23^{aA}, 15.54^{bB}	20.09^{aA}, 12.72^{bB}
Bulk density	(g cm^{-3})	1.41^a, 1.47^b	1.34^a, 1.42^b		1.46^a, 1.51^b	1.47^a, 1.50^b
Soil texure[3]		98.0–0.0–2.0[1]	96–1–3[2]	95.9–2.4–1.6[1]	96.8–2.1–1.1[1]	97.5–1.9–0.6[1]
pH		5.2[1], 6.36^a, 6.10^b	6.12^a, 6.16^b	5.6[1]	6.62^a, 6.10^b	5.02^a, 5.11^b

[1]Aranibar et al. (2004), Global Change Biology 10, 359–373.
[2]Ravi et al. (2006), Sedimentology 53, 597–609.
[3]Sand–silt–clay ratio.
Different capital letters in K_s indicate different means between under canopy and intercanopy at 0.05 significance level.
[a]Under canopy.
[b]Inter-canopy.

$\alpha_w = \mathrm{RH}/100$, (with RH being the relative humidity), were converted into matric potential values as $\Psi_m = (RT/M_w)*\ln(\mathrm{RH}/100)$ (Edlefson and Anderson, 1943), where R is the universal gas constant ($8.314472\,\mathrm{J\,K^{-1}\,mol^{-1}}$), T the absolute temperature (K) and M_w is the molecular mass of water. The water potentials in the wetter range (>-0.5 MPa) were measured using a WP4-T Dewpoint Potential Meter (DECAGON Devices, Pullman, WA, USA).

2.3. Geochemical analyses

Soil samples for isotopic and elemental analysis were oven dried (at 60 °C) in the laboratory, sieved and homogenized using mortar and pestle. Each of the five replicates of samples collected from soils beneath tree canopies and open areas was analyzed for soil organic C, total nitrogen (N), δ^{13}C and δ^{15}N. Total C and N content were measured using an Elemental Analyzer (EA, Carlo Erba, NA1500, Italy). Stable C/N isotopic analysis was performed using a Micromass Optima Isotope Ratio Mass Spectrometer (IRMS) connected to the EA (GV/Micromass, Manchester, UK). Stable isotopic compositions are reported in the conventional form

$$\delta^x E(‰) = [(^xE/^yE)_{\mathrm{sample}}/(^xE/^yE)_{\mathrm{standard}} - 1] \times 1000,$$

where E is the element being measured, x the heavier isotope and y the lighter isotope. So that $(^xE/^yE)_{\mathrm{sample}}$ and $(^xE/^yE)_{\mathrm{standard}}$ are the isotopic ratios of the sample and standard, respectively. The stable isotopic composition of C and N will be denoted as δ^{13}C (‰) and δ^{15}N (‰), respectively. The standards for C and N stable isotopes are Pee Dee Belemnite (PDB) and atmospheric molecular N (N_2), respectively. Reproducibility of these measurements is typically better than 0.2‰. One-way ANOVA was used to test the significance of differences (0.05 significance level) found in each parameter between intercanopy and subcanopy soils at each site.

3. Physical properties of Kalahari sands

3.1. Soil texture

With the exception of the fine-textured soils found in pan and fluvial deposits, the Kalahari is dominated by sandy soils, including mostly white, pink, and red in color (Leistner, 1967). The Kalahari sands are chiefly quartz, with small contributions of zircon, garnet, felspar, ilmenite and tourmaline. Compared to other sand deposits in Africa (e.g., the Namib or the Sahara) the sand grains in the Kalahari are less well-rounded (Leistner, 1967) likely the results of weathering (Ringrose et al., 2006). The porosity of the Kalahari sands ranges between 0.43 and 0.49 for the four locations considered in this study (Table 2), whereas the bulk density is between 1.34 and $1.51\,\mathrm{g\,m^{-3}}$ (Table 2). Both the porosities and the bulk densities of the Kalahari sands have limited variation between the canopy and intercanopy (Table 2).

The soil texture is dominated by sand (>95%) at all sites (Table 2). Soils are acidic (pH < 7.0) along the entire transect. Soils at Ghanzi and Pandamatenga have a slightly higher pH than the other sites, possibly resulting from a proximity of near surface bedrock in these areas (Table 2). In the case of Ghanzi, the higher pH is probably due to the calcareous substrate while the higher pH value in Pandamatenga is likely influenced by agriculture practices taking place in the commercial farms surrounding this site (e.g. fertilizer use, tillage). There are also only limited differences in soil pH between areas located under tree canopy and in open canopy at all sites (Table 2). At the dry end of the Kalahari transect the carbonate rich layer is deeper under the canopy than in open canopy areas, while these differences are much smaller at the wet end (D'Odorico et al., in review). In addition, the depth of the carbonate rich layer increases with the mean annual precipitation along the rainfall gradient, with a mean depth (between canopy and intercanopy sites) of 40 cm at Tshane, 65 cm at Pandamatenga and 72 cm at Mongu (D'Odorico et al., in review). The variations in the depth of the carbonate rich layer between the soils under the canopy and in open canopy areas are indicative of differences in long-term soil moisture dynamics, with deeper moisture percolation in the soils under tree canopies. This fact has implications for the nutrient distribution reported in Section 4.

Based on particle size distributions, the sands from Ghanzi are the finest among the four sites with mean particle size of 2.15ϕ under the canopies (0–192 cm) and 2.56ϕ for intercanopy samples (0–190 cm). No significant change in grain size is observed until the lower calcrete layer is reached, where the grain size increases to $1–1.8\phi$. Sand particle sizes from Tshane are the second finest with a mean particle size of 2.23ϕ under the canopy and 2.11ϕ for intercanopy (20–200 cm), and the particle size did not change along depth (20–500 cm) in both cases. Mean particle size in Pandamatenga is 1.84ϕ under canopy (0–200 cm) and 1.79ϕ for intercanopy (0–200 cm) with limited variation with depth in both cases. Mean particle size in Mongu is similar to Pandamatenga with particle size of 1.72ϕ under the canopy (10–300 cm) and 1.71ϕ (10–300 cm) for intercanopy with limited variation with depth in both cases (Table 3). These results suggest that the soil profiles are relatively uniform and that at the wet end of the transect (Mongu and Pandamatenga) there are no significant differences in grain size between canopy and intercanopy soils, while the drier (Tshane and Ghanzi) sites have finer soils under the canopy. Moreover, at the drier sites soils are slightly finer than at the wetter sites.

For the surface soil (0–20 cm), there is no noticeable particle size difference between inter-canopy sands and those from under the canopy from Mongu. In Tshane, however, there is an obvious difference in particle size distribution between intercanopy and under canopy. In fact, the fine particle size fraction (i.e., with size <0.063 mm) was 1.44% and 0.34% in the soils located under and between the tree canopies, respectively (Table 4).

The portion of the sample finer than 0.063 mm was comprised of sub-rounded to sub-angular quartz particles, with evidence of a secondary Si coating for under canopy soils in Mongu (Fig. 2A). Coatings do not occur extensively around the grains although there is localized evidence of greater Si accumulation with subsequent coating disintegration in the form of pock-marking. There is no evidence of chemical etching on the grain surfaces with some of the surfaces being angular and depicting the original crystal structure. The under canopy sample from Mongu is chiefly quartz with less than 5% non-quartz. The non-quartz particles, which are mainly feldspars and micas, show more weathering effects (and are therefore more disintegrated) than the quartz. Fungal hyphae and organic remnants were also evident (Fig. 2A).

Similar patterns are evident in the intercanopy samples in Mongu. In the sample fraction finer than 0.063 mm, cleaner sub-rounded but mainly sub-angular quartz particles were evident with less evidence of a secondary Si coating (Fig. 2B). Again, the sample consists mainly of quartz particles with less than 5% non-quartz, comprising feldspars and micas

Table 3
Soil color and particle distribution with depth for under canopy and intercanopy soil samples for the four Kalahari-transect sites

Soil name	Mean (phi units)	Munsell color
Mongu pit1-10 cm[a]	1.70	5YR 6/4 light reddish brown
Mongu pit1-50 cm[a]	1.70	5YR 6/6 reddish yellow
Mongu pit1-100 cm[a]	1.75	5YR 6/6 reddish yellow
Mongu pit1-150 cm[a]	1.65	7.5YR 6/8 reddish yellow
Mongu pit1-200 cm[a]	1.72	5YR 6/6 Reddish yellow
Mongu pit1-300 cm[a]	1.75	5YR 6/6 reddish yellow
Mongu pit2-10 cm[b]	1.62	5YR 6/2 pinkish gray
Mongu pit2-50 cm[b]	1.70	5YR 6/6 reddish yellow
Mongu pit2-100 cm[b]	1.75	5YR 6/6 reddish yellow
Mongu pit2-150 cm[b]	1.72	5YR 6/6 reddish yellow
Mongu pit2-200 cm[b]	1.73	7.5YR 7/6 reddish yellow
Mongu pit2-300 cm[b]	1.78	7.5YR 7/8 reddish yellow
Mongu pit3-150 cm[b]	1.77	5YR 6/6 reddish yellow
Mongu pit3-200 cm[b]	1.78	5YR 7/8 reddish yellow
Mongu pit3-300 cm[b]	1.80	5YR 7/8 reddish yellow
Pandamatenga 0 cm[b]	1.77	10YR 4/2 dark grayish brown
Pandamatenga 50 cm[b]	1.81	10YR 6/4 light yellowish brown
Pandamatenga 100 cm[b]	1.76	7.5YR 6/6 reddish brown
Pandamatenga 150 cm[b]	1.79	7.5YR 6/6 reddish yellow
Pandamatenga 200 cm[b]	1.81	10YR 6/6 brownish yellow
Pandamatenga 0 cm[a]	1.67	10YR 4/2 Dark grayish brown
Pandamatenga 50 cm[a]	2.13	10YR 6/4 Light yellowish brown
Pandamatenga 100 cm[a]	1.80	7.5YR 6/6 reddish yellow
Pandamatenga 150 cm[a]	1.75	10YR 6/8 brownish yellow
Pandamatenga 200 cm[a]	1.85	7.5YR 6/6 reddish brown
Ghanzi 0 cm[a]	2.50	5YR 4/6 yellowish red
Ghanzi 50 cm[a]	2.40	2.5YR 4/6 Red
Ghanzi 100 cm[a]	2.45	2.5YR 4/6 Red
Ghanzi 150 cm[a]	2.45	5YR 5/8 yellowish red
Ghanzi 192 cm[a] (reaching calcrete layer)	0.97	10YR 6/4 Light yellowish red
Ghanzi 0 cm[a]	2.55	5YR 5/6 yellowish red
Ghanzi 50 cm[a]	2.52	5YR 5/6 yellowish red
Ghanzi 100 cm[a]	2.50	5YR 5/8 yellowish red
Ghanzi 0 cm[b]	2.50	5YR 4/4 reddish brown
Ghanzi 50 cm[b]	2.90	2.5YR 4/6 red
Ghanzi 100 cm[b]	2.37	2.5YR 4/6 red
Ghanzi 150 cm[b] (reaching calcrete layer)	1.53	2.5YR 6/4 light reddish brown
Ghanzi 190 cm[b] (reaching calcrete layer)	1.83	2.5YR 6/4 light reddish brown
Tshane 20 cm[a]	2.32	5YR 5/6 yellowish red
Tshane 50 cm[a]	2.20	5YR 5/6 yellowish red
Tshane 100 cm[a]	2.27	5YR 6/8 yellowish red
Tshane 150 cm[a]	2.30	5YR 6/6 yellowish red
Tshane 200 cm[a]	2.10	5YR 6/8 yellowish red
Tshane 500 cm[a]	2.18	5YR 6/8 yellowish red
Tshane 20 cm[b]	1.92	5YR 5/6 yellowish red
Tshane 50 cm[b]	2.18	5YR 5/6 yellowish red
Tshane 100 cm[b]	2.15	5YR 5/6 yellowish red
Tshane 150 cm[b]	2.02	5YR 5/8 yellowish red
Tshane 200 cm[b]	2.30	5YR 5/8 yellowish red

Munsell color system has three components: hue (a specific color), value (lightness and darkness), and chroma (color intensity). Soil color is noted as hue value/chroma and actual color.

[a]Under canopy.

[b]Inter-canopy.

Table 4
Surface soil (0–20 cm) particle distribution for under canopy and inter-canopy sands at the Mongu and Tshane locations

	Depth (cm)	%Coarse sand (ϕ−1 to 1 or 2–0.5 mm)	%Medium sand (ϕ1–2 or 0.5–0.25 mm)	%Fine sands (ϕ2–4 or 0.25–0.063 mm)	%Silt and Clay (ϕ>4 or >0.063 mm)
Mongu					
Under canopy	10	1.96	72.39	25.01	0.43
Inter-canopy	10	0.88	77.83	20.89	0.40
Tshane					
Under canopy	20	0.45	37.27	60.84	1.44
Inter-canopy	20	7.44	73.15	19.07	0.34

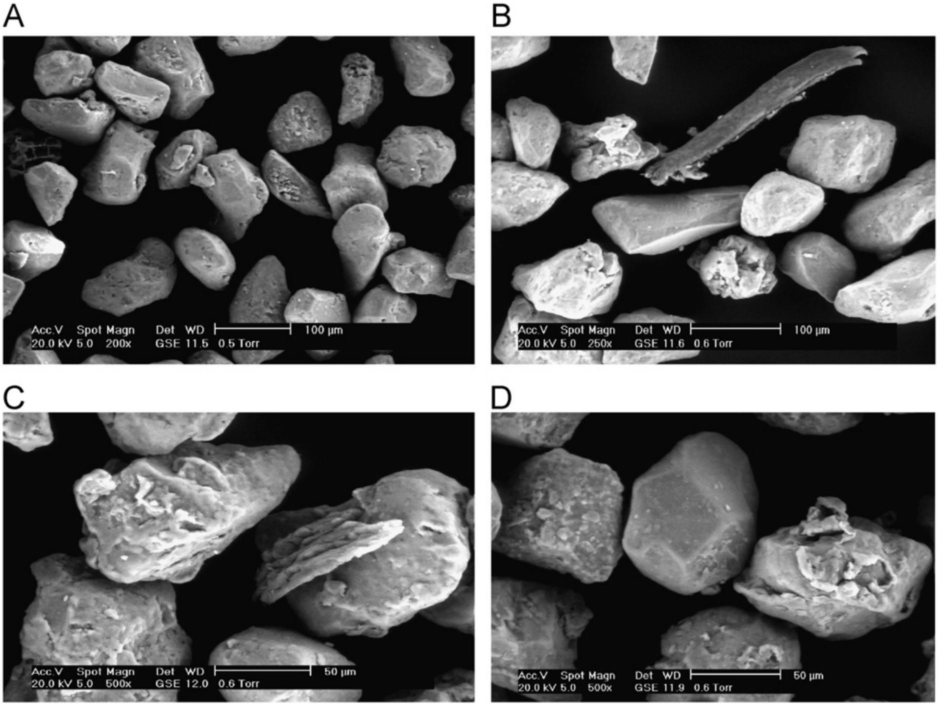

Fig. 2. Scanning electron microscope analysis of soil particles under canopy (A), inter-canopy (B) in Mongu and under canopy (C), inter-canopy (D) in Tshane.

which show more disintegrated weathering effects than the quartz. Fungal hyphae were also evident (Fig. 2B).

More equi-granular quartz grains were found in the under canopy in Tshane which also exhibited relatively abundant fungal hyphae. The sample consisted of mixed coated and angular (faces showing) fragments but at this location the secondary silica-rich SiO_2

coating was more apparent and much of the coating was pitted and disintegrated. The disintegration was flaking off the coating, adding fine particles which may be mixed with possible clay flakes and organic fragments (Fig. 2C).

The intercanopy sample in Tshane also consisted of equi-granular grains, which are coated and weathered with evidence of coating disintegration. There was a higher proportion of quartz grains in the Tshane samples with non-quartz grains approximating 2%. There is more evidence of particle fracturing/fragmentation and coating induced angularity, i.e. when coating peels off, angular particles remain beneath, as the coating itself induces a form of weathering preferentially along the crystal faces as seen in Okavango delta samples. Organic fragments and fungal hyphae were also evident (Fig. 2D).

3.2. Soil hydraulic properties

The saturated hydraulic conductivity (K_s) was found to increase, from south to north along the rainfall gradient (Table 2), presumably due to a higher soil organic matter existing at the more humid sites. At Tshane and Mongu (the two extreme ends of the transect), K_s was significantly higher under canopy than in open areas, while no difference existed at Ghanzi.

Moisture retention curves obtained for a range of soil water potentials vary between 0 and -7 MPa (Fig. 3). These curves were used to calculate the moisture content at the wilting point separately for areas located beneath the canopy and in the intercanopy

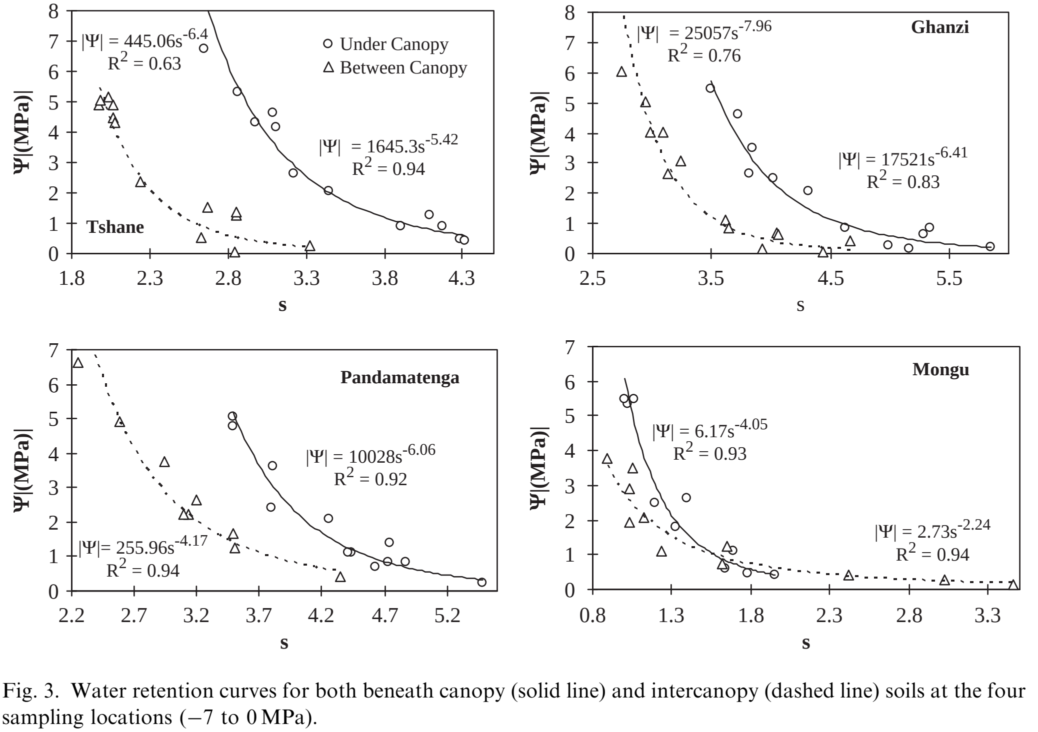

Fig. 3. Water retention curves for both beneath canopy (solid line) and intercanopy (dashed line) soils at the four sampling locations (-7 to 0 MPa).

Table 5
Relative soil moisture at wilting point between inter-canopy and under canopy soils of the four locations along the Kalahari transect

Species	Ψ_w (MPa)	Tshane (%)		Ghanzi (%)		Pandamatenga (%)		Mongu (%)	
		Between canopy	Under canopy	Between canopy	Under canopy	Between canopy	Under canopy	Between canopy	Under canopy
Typical value for crops	−1.5	2.41	3.63	3.43	4.34	3.41	4.28	1.10	1.35
Burkea africana (Woody)	−3.1[a]								0.69
Ochna pulchra (Woody)	−3.2[a]								0.66
Terminalia sericea (Woody)	−1.9[a]		3.48		4.21				
Digitaria eriantha (Grass)	−2.9[a]	2.26	3.23	3.22	3.98	2.94	3.88	0.25	0.76
Eragrostis pallens (Grass)	−3.9[a]	2.10	3.07	3.13	3.83	2.75	3.71	0.13	0.47
Elionurus muticus (Grass)	−2.9[a]	2.26	3.23	3.22	3.98	2.94	3.88		

[a]The values are from Scholes and Walker (1993).

(Table 5). The soil water potential at the wilting point, Ψ_w, for crops is typically assumed to be at −1.5 MPa; however, dryland vegetation is generally well adapted to more arid conditions and can tolerate dryer soil moistures. Thus, the values of Ψ_w for southern African vegetation have been observed to be significantly lower (Scholes and Walker, 1993). Values from the literature have been compiled for species observed at the different sites along the KT (Table 5). The moisture retention curves were used to calculate the corresponding relative soil water contents (fraction of pore space filled by water) at the wilting point. Because grasses have been observed to grow also beneath tree canopies, soil moisture values at the wilting point were calculated both for between canopy and under canopy soils. Moisture contents at the wilting point were found to be consistently higher under the canopy than in the interspace areas, suggesting the existence of slight differences in soil texture, i.e., the existence of higher clay fractions under the canopy (see Fig. 3), consistent with the differences in fine fractions found at the drier sites. Whether this difference implies higher likelihoods of water stress in vegetation growing under the canopy cannot be assessed on the basis of these data. In fact, differences in soil texture are also associated with different moisture contents which, in turn, could offset the effect of the higher wilting points on water stress conditions in vegetation (e.g., D'Odorico and Porporato, 2006; Noy-Meir, 1973).

4. Biogeochemical properties of Kalahari sands

4.1. Vertical profiles of soil C, N and their isotopic composition

The vertical profile of soil organic carbon (SOC) exhibits higher concentrations in the top 10–20 cm at all sites along the KT for both the open areas and the areas under the

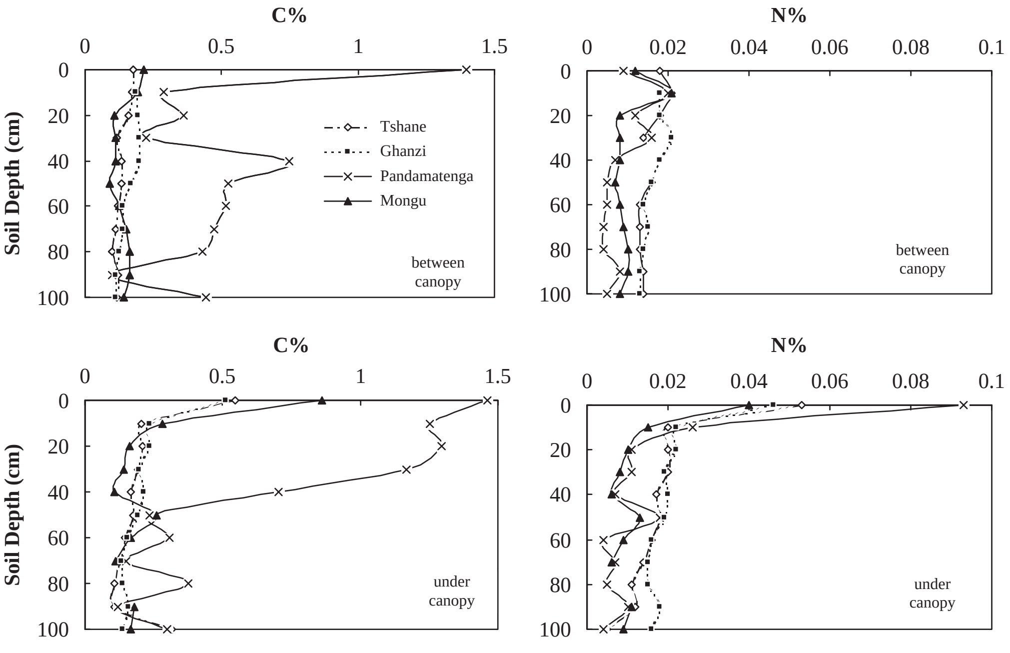

Fig. 4. Depth profiles of carbon (left) and nitrogen (right) content of soil samples collected along the Kalahari transect both from intercanopy and canopy areas.

canopy. The SOC is typically higher in the areas under canopy than in the intercanopy soil (Fig. 4). The soil total N content is also concentrated in the top 10 cm both in intercanopy and canopy areas with the total N content being higher under the canopy (Fig. 4). Furthermore, the variation in C and N content in the soil column is higher under the canopy than in the open area for all four sites. At depth, the soil N content is higher at the drier sites (e.g. Tshane and Ghanzi) than at the wetter end of the KT (e.g. Mongu and Pandamatenga) both in intercanopy and canopy areas (Fig. 4), possibly suggesting that N is more limiting at the wetter sites of this transect (Aranibar et al., 2004; Scanlon and Albertson, 2003).

The $\delta^{13}C$ values increase with depth under canopy whereas there is no clear pattern of $\delta^{13}C$ in the soil profiles in intercanopy areas (Fig. 5). The $\delta^{13}C$ values in Pandamatenga exhibit large variations both in open areas and under the canopy, although in a different way, in that the $\delta^{13}C$ values were more variable in the top 40 cm under canopy but less variable in open areas (Fig. 5). The anomalous and high variability in soil $\delta^{13}C$ along the soil column observed in Pandamatenga was likely influenced by the two major soil types existing in Pandamatenga, the vertisol and arenosols (Almendros et al., 2003; Pardo et al., 2003). The arenosols are light-textured soils like those found in most of the Kalahari region. The vertisols, however, are heavy, clayey, nutrient-rich soils used for dryland crop production in the Pandamatenga area (Pardo et al., 2003). Field sampling was carried out in the woodlands underlain by arenosols; however, the proximity to the vertisols existing on the surrounding commercial farms inevitably influenced the soil chemical and physical properties of soils at the woodland site in Pandametenga.

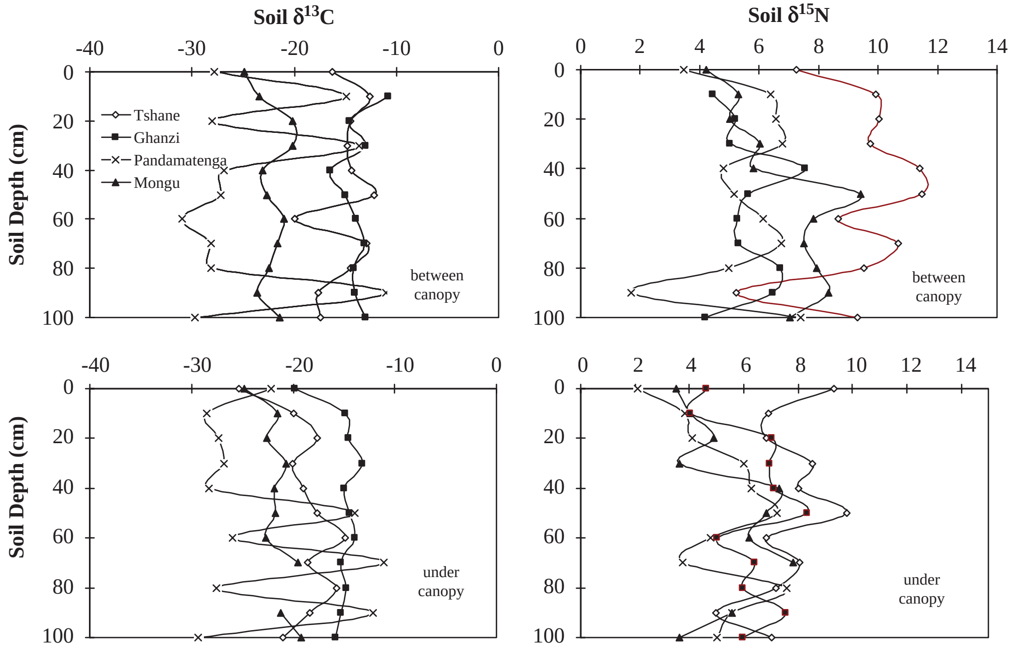

Fig. 5. Depth profiles of soil δ^{15}N (left) and soil δ^{13}C (right) both for canopy and intercanopy soils along the Kalahari transect.

Depending on climate conditions, the vertical profile of soil δ^{15}N can either exhibit little variation like in montane elevation gradients, random distributions like in gravelly desert soil or, most commonly, a consistent (exponential) increase with depth like in grasslands (Amundson et al., 2003). Multiple factors contribute the soil δ^{15}N variation along depth (Amundson et al., 2003) including N transport processes, depth-dependent plant N inputs as dead roots, and multiple N pools other than those from plant tissues (e.g., microbial biomass). Despite the presence of greater fluctuations in the vertical profile of soil δ^{15}N, similar to those observed in gravelly desert soils (Brenner, 1999) (Fig. 5), the δ^{15}N in the Kalahari increases with depth through the "bulk" of the root zone (top 50 cm, see Section 5) to a maximum value and then decreases at greater depths; this pattern can be observed both in open areas and under canopy (Fig. 5). The variation of soil δ^{15}N content with depth is an important contributing factor to the plant δ^{15}N signature (e.g. plants taking up N from deeper soil layers should have higher values of δ^{15}N). The fact that grass roots dominate the surface soil (see Section 5), and the tendency of surface soils to have lower δ^{15}N values, explains the lower foliar δ^{15}N values found in grasses than tree tissues across southern Africa (Swap et al., 2004) as well as in semiarid and mesic sites of Australia (Cook, 2001). Although early hypotheses that trees and grasses utilize water from different layers (Walter, 1971) have been recently challenged both by field observations (Hipondoka et al., 2003; Scholes and Walker, 1993; Williams and Albertson, 2004), and theoretical models (Rodriguez-Iturbe et al., 1999), the fact that different plant functional types take N from different layers, at different times (e.g. grasses take up the recently mineralized N and trees take up the remaining N) or utilize different forms of N, could be one of the mechanisms contributing to tree–grass co-dominance in savannas.

4.2. Soil surface C, N and their isotopic composition changes along the transect

Both soil $\delta^{15}N$ and soil $\delta^{13}C$ content increase with elevated levels of aridity (Table 6), consistent with a number of other studies (Aranibar et al., 2004; Bird et al., 2004; Swap et al., 2004). The higher soil $\delta^{13}C$ with decreasing values of MAP was related to the changes in vegetation composition along the KT (i.e. C_4 vegetation has higher $\delta^{13}C$ values and higher proportions of C_4 plants exist at the dry end of the KT). The increase in soil $\delta^{15}N$ with decreasing values of MAP has been interpreted as the effect of higher N losses at the dry end of the transect owing to ammonia volatilization (Aranibar et al., 2004; Swap et al., 2004). In Pandamatenga, the soil $\delta^{15}N$ is anomalously lower than the values predicted by the empirical relation (between soil $\delta^{15}N$ and MAP) deduced by Swap et al. (2004) for the KT, presumably due to the existence of major commercial farms adjacent to the field sites (two 10,000 ha agricultural fields on both sides) and likely the use of inorganic fertilizers (application rates around 50–100 kg ha^{-1}, personal communication from local farmers) in these cropland fields. Because the $\delta^{15}N$ in inorganic N fertilizer is approximately 0‰, the deposition of wind-blown farm soils at the research site likely decreases the soil $\delta^{15}N$.

The C and N content at the soil surface increases along the rainfall gradient reaching a maximum value at Ghanzi, while it decreases at the more humid sites. The soil C/N ratio of the soil organic matter from the top 5 cm of soil, however, consistently increases with the MAP (Table 6), suggesting the existence of greater N limitation at the wet end of this transect. The differences in SOC, soil total N, and C/N ratios between under canopy and open canopy soils are significant only at Tshane (Table 6). At all four sites soil $\delta^{15}N$ values are not significantly different between subcanopy soils and intercanopy areas, while differences in soil $\delta^{13}C$ values between subcanopy and intercanopy areas are significant at all four sites except Pandamatenga (Table 6). These results suggest that the overall nutrient levels were similar beneath tree canopies and in intercanopy areas for these African savannas, except at the extreme dry end of the transect.

Soil nitrate concentrations are relatively constant along the transect (around 1–2 μg g^{-1}), whereas ammonium concentrations are much higher at the wet end of transect than at the drier sites (24 vs. 11 μg g^{-1}) (Table 7). Aranibar et al. (2003) estimated gross mineralization rates using $^{15}N\text{-}NH_4^+$ and $^{15}N\text{-}NO_3^-$ pool dilution techniques and found

Table 6
Soil surface (0–5 cm) C, N and changes in their isotopic composition (mean ± stderr, $n = 5$) along the transect measured for dry season (August) 2004

		%C	%N	C/N	$\delta^{13}C$	$\delta^{15}N$
Tshane	Under canopy	0.35 ± 0.05^A	0.04 ± 0.00^A	9.90 ± 0.21^A	-18.5 ± 1.1^A	7.3 ± 0.6^A
	Inter-canopy	0.18 ± 0.01^B	0.02 ± 0.00^B	9.11 ± 0.19^B	-12.8 ± 0.6^B	7.8 ± 0.9^A
Ghanzi	Under canopy	0.61 ± 0.05^A	0.05 ± 0.01^A	11.35 ± 0.97^A	-16.5 ± 1.0^A	7.5 ± 1.9^A
	Inter-canopy	0.42 ± 0.07^A	0.03 ± 0.00^A	12.09 ± 0.49^A	-13.4 ± 1.2^B	6.9 ± 0.3^A
Pandamatenga	Under canopy	0.63 ± 0.09^A	0.04 ± 0.00^A	15.15 ± 0.40^A	-22.4 ± 0.5^A	0.6 ± 0.2^A
	Inter-canopy	0.58 ± 0.12^A	0.04 ± 0.01^A	14.85 ± 0.35^A	-21.1 ± 0.6^A	1.2 ± 0.6^A
Mongu	Under canopy	0.38 ± 0.07^A	0.02 ± 0.00^A	20.52 ± 1.40^A	-25.4 ± 2.6^A	1.7 ± 0.5^A
	Inter-canopy	0.27 ± 0.01^A	0.01 ± 0.01^A	19.21 ± 0.55^A	-18.2 ± 0.9^B	2.9 ± 0.9^A

Different capital letters indicate different mean values between under canopy and intercanopy at 0.05 significance level for each measured parameter.

Table 7
Soil ammonium and nitrate concentration and their isotopic compositions along the Kalahari transect

	NH_4^{+}[1] ($\mu g\, g^{-1}$)	NO_3^{-}[1] ($\mu g\, g^{-1}$)	$\delta^{15}NH_4^+$ (‰)[2]	$\delta^{15}NO_3^-$ (‰)[2]	Gross mineralization rates (mg NH_4-N m^{-2} day^{-1})[1]	Gross nitrification rates (mg NO_3-N m^{-2} day^{-1})[1]
Tshane	11.15 ± 2.17	1.37 ± 0.26	12.3	5.2	50[a], 16[b]	135[a], 35[b]
Okwa	8.66 ± 3.34	1.64 ± 0.18	−0.3	−3.4	51[a], 20[b]	105[a], 48[b]
Maun	12.29 ± 1.36	1.91 ± 0.53	5.5	4.3	60[a], 25[b]	100[a], 65[b]
Mongu	24.00 ± 3.71	1.04 ± 0.41	5.8	1.4	38[a]	10[a]

[1]Feral et al. (2003), Journal of Arid Environments 54, 327–343.
[2]Aranibar (2003), Ph.D. Thesis, pp. 93–131.
[a]Under canopy.
[b]Inter-canopy.

higher mineralization rates in soils under the canopy than in open areas. These rates were dramatically lower at Mongu. A similar pattern (Table 7) was found in the gross nitrification rates. Nitrification rates were much higher than mineralization rates at all locations except Mongu. The higher mineralization rates and nitrification rates under the canopies indicates that conditions favorable to the formation of "fertility islands" (Schlesinger et al., 1990) also exist in these African savannas even when the overall N level and soil C/N are similar beneath tree canopies and in intercanopy areas. In particular, at research sites in Maun the NH_4^+ and NO_3^- contents were found (Feral et al., 2003) to be higher under the canopy (14.53–22.59 μg NH_4^+ g^{-1} and 4.50–13.11 μg $NO_3\, g^{-1}$) than in inter-canopy areas (9.96 μg $NH_4\, g^{-1}$ and 2.29 μg NO_3^- g^{-1}), consistent with differences detected in the mineralization and nitrification rates at the four sites considered in this review (Table 7). Nitrification rates were generally higher than mineralization rates, suggesting that ammonification is the limiting step in mineral N formation in these systems.

The isotopic analysis of ammonium and nitrate isolated from Transect soils (Aranibar, 2003) revealed that the NH_4^+ is more enriched in ^{15}N than the NO_3^-, likely a result of preferential use of ^{14}N during the oxidation of ammonium during nitrification. The magnitude of the difference between the $\delta^{15}N$ values of NH_4^+ and NO_3^- is greater at the drier end of Transect. Such a change in the absolute difference could be an indication of the reaction proceeding closer to completion, or of increased volatilization of residual ammonia, or a contribution of an additional source of N.

4.3. Soil respiration before and after wetting

Before wetting, soil surface CO_2 fluxes at the four locations ranged between 0.23 and 0.74 g $CO_2\, m^2\, h^{-1}$ along the transect. These fluxes increased with higher MAP and leveled off near Pandamatenga. Soil wetting significantly increased the soil surface CO_2 flux for all four locations. After wetting, the rate of soil respiration increased by a factor of 10 at Tshane, Ghanzi and Pandamatenga, while at Mongu, the wettest site along the transect, it increased 5-fold (Fig. 6).

5. Root distribution in the Kalahari

Despite the existence of specific studies on root function in the Kalahari, including for example, mycorrhizal nutrient uptake (Bohrer et al., 2001, 2003) and root inverse water

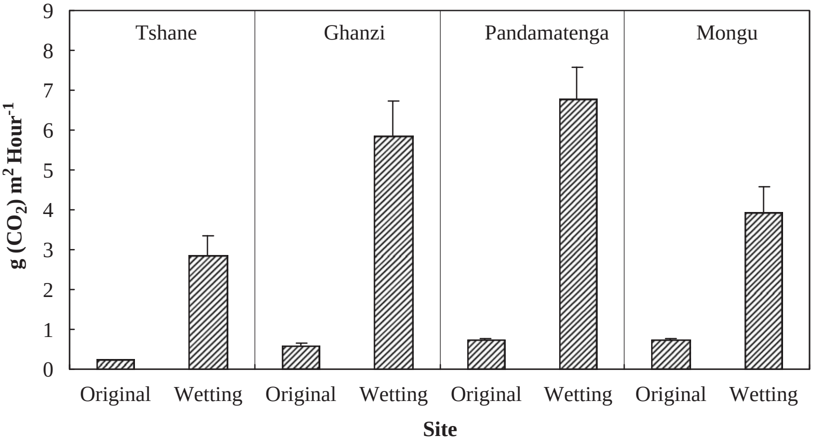

Fig. 6. Soil surface CO_2 flux before and after the soil wetting in four locations along Kalahari transect.

transport phenomena (Schulze et al., 1998), a comprehensive study of root distribution for the different tree, shrub and grass species existing in the region is still unreported. In an early exploration of the southern Kalahari soils, Leistner (1967) noticed that, although the depth of root systems varies considerably depending on local conditions and plant species, the rooting depths generally range from 20 cm to more than 300 cm, with the highest root concentration being between 8 and 50 cm. Leistner (1967) also found a number of morphological and anatomical features such as sand coats, spongy cortex, and succulent roots, which seems to play an important role for plant adaptation to the semi-desert habitats of the southern Kalahari. Laterally, most shrubs and trees in the Kalahari possess root systems that extend horizontally beyond the footprint of their canopies. For example, the horizontal roots of *Acacia Erioloba* (formerly *Acacia giraffae*) and *Albizia anthelmintica* can be longer than 20 m, whereas those of *Albizia mellifera* can extend laterally for more than 10 m (Leistner, 1967). More recently, Hipondoka et al. (2003) explored the vertical root distribution of the two main life forms (i.e. trees and grasses) existing in the savannas at Tshane and Ghanzi. These authors used the profile count technique (Böhm, 1979) to determine the vertical root distribution and composition both at sites located beneath tree canopies and in open areas. Both plant functional types were found to develop most of their roots at the surface. Grass roots were found to be more abundant and dominant close to the surface (i.e., in the top 30 cm of the soil column) even in the soil pits located under the tree canopies. Moreover, the distribution of tree roots did not exhibit a clear dominance over grasses at deeper soil layers as suggested by previous studies (e.g., Walter, 1971; Knoop and Walker, 1984). The vertical profile of root distribution measured by Hipondoka et al. (2003) exhibits a well-defined decrease in grass root density with depth, whereas smaller variations can be noticed in the tree root profile, with a peak in tree root density at 20–50 cm depth (Fig. 7A and B). A similar pattern of root profile (Fig. 7C) was found at the same site (Ghanzi) by Williams and Albertson (2004), though the actual values of root density differed by almost an order of magnitude, possibly owing to the different root sampling techniques used by those authors.

By measuring the isotopic composition of both root C and soil organic matter C at different depths, Hipondoka et al. (2003) determined the proportion of soil C contributed

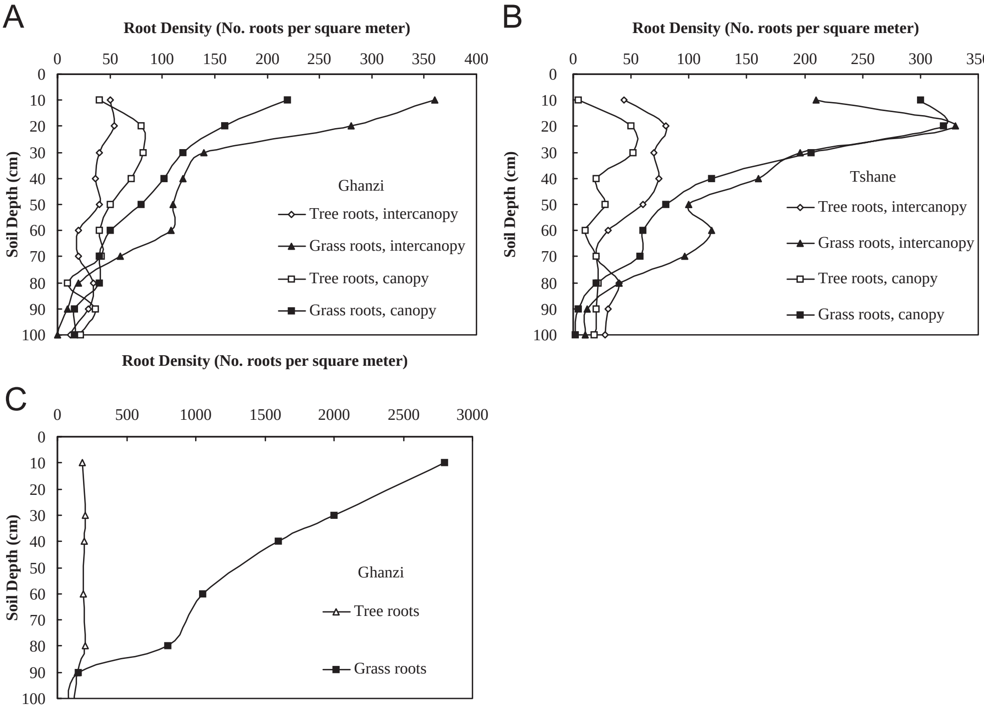

Fig. 7. Root density profiles for tree and grass functional types in different locations. A and B are from Hipondoka et al. (2003) and C is from Williams and Albertson (2004).

by each life form and found a dominance of grass root biomass at most depths, in agreement with their profiles of root density (Fig. 7A and B).

6. Soil crusts in Kalahari sand formations

Biological soil crusts (a complex soil surface community dominated by cyanobacteria, microfungi, mosses, and lichens) are a recurrent feature of arid and semi-arid ecosystems (Belnap and Lange, 2003). Numerous studies have documented the importance of these crusts to the stabilization of the soil surface (i.e., the increase in the resistance to wind and water erosion (Campbell et al., 1989), the enhancement of seedling establishment (St. Clair et al., 1984), and soil fertilization through biological N fixation (Skarpe and Henriksson, 1986; Zaady et al., 1998). In addition, soil crust communities are very sensitive to small pulsed water events (desert precipitation are usually less than 3 mm per event), a common feature in arid and semi-arid environment. For larger rainfall events, crusts may reduce the rate of soil drying, giving vascular plants more time to respond to increased water availability (Austin et al., 2004). However, the diverse functions of soil crusts in the Kalahari are still relatively understudied with only few reports available in the literature.

Aranibar et al. (2003) quantified the N-fixing activity of soil crusts in the Kalahari during the wet season using *in situ* acetylene reduction assays. The estimated annual rates of N fixation ranged from 8 to 44 g N ha^{-1} year^{-1} with higher N fixing activity at the dry end of the transect (Table 8). The N fixing activity of the soil crusts along the Kalahari

Table 8
Soil crusts N fixing activities along the Kalahari transect estimated by *in situ* acetylene reduction assays

	g N fixed ha^{-1} $year^{-1}$
Tshane	37
Okwa	44
Maun	14
Mongu (disturbed)	30
Mongu	8

Aranibar et al. (2003), Journal of Arid Environments 54, 345–358.

transect were several orders of magnitude lower than those estimated by other authors for the Kalahari desert (Skarpe and Henriksson, 1986), and for other regions like the Negev desert (Zaady et al., 1998), or Tucson desert (MacGregor and Johnson, 1971). Aranibar et al. (2003) argued that this was due to the anomalously wet conditions experienced during the year of their study (2000), which may have temporarily increased the availability of soil mineral N, thereby leading to a decrease in N fixation rates.

The spatial distribution of cyanobacterial soil crusts has been recently investigated (Berkeley et al., 2005) in the context of bush encroachment studies in the Kalahari at sites with two different dominant plant species (*A. mellifera* and *Grewia flava*) and different disturbance regimes. They found the highest degree of crust cover under the canopies of *A. mellifera*, interemediate levels of crust cover under *G. flava* and the lowest cover in the bare soil interspaces. This pattern was clearer in the presence of disturbances. Those results showed an enhanced cyanobacterial crust cover under *A. mellifera* canopies, where the crust cover was found to be resistant to even higher levels of disturbance. Conversely, disturbances were observed to limit the development of soil crust under the canopies of *G. flava* and in the bare soil interspaces. Thus, this canopy-crust association suggests that the encroachment of *A. mellifera* is intrinsically more resilient because of the ability of the crust to stabilize the soil surface and increase both nutrient retention and the soil nutrient content.

7. Summary

The data presented in this review show that the Kalahari soil is acidic, dominated by sand and nutrient poor. Soil nutrient dynamics in the Kalahari are significantly determined by the relatively strong rainfall gradient, whereas the soil physical properties remain overall the same along the transect. Differences in rainfall regime, vegetation composition and structure determine important changes in the soil organic matter, and vertical distribution of soil N content along the Kalahari Transect, as evidenced by the comparison of experimental results obtained at different sites, as well as at each site in canopy and inter-canopy areas.

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