

Woody overstorey effects on soil carbon and nitrogen pools in South African savanna

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Abstract Woody plant encroachment in savannas may alter carbon (C) and nitrogen (N) pools over the long-term, which could have regional or global biogeochemical implications given the widespread encroachment observed in the vast savanna biome. Soil and litter %C and %N were surveyed across four soil types in two encroached, semi-arid savanna landscapes in northern South Africa. Litter at sampling points with a woody component had a higher %N and lower C : N ratio than litter at solely herbaceous points. Severely encroached areas had lower C : N ratios throughout the soil profile than less encroached areas. Soil %C and %N were highly influenced by soil texture but were also influenced by the presence of a woody overstorey, which increased surface soil %C on three soil types but decreased it on the most heavily encroached soil type. Soil C sequestration may initially increase with bush encroachment but then decline if bush densities become so high as to inhibit understorey grass growth.

Key words: bush encroachment, carbon sequestration, fire suppression, Ganyesa, grazing, litter inputs, Madikwe, overgrazing, semi-arid savanna, soil texture

INTRODUCTION

The global soil carbon (C) pool is twice that in the atmosphere and three times that in above-ground biomass (Eswaran *et al.* 1993). Post *et al.* (1982) estimated the size of the global soil C pool and calculated that tropical and subtropical woodlands and savannas, with an area of 24×10^8 ha, contain 129 Tg of soil C. This represents the third largest soil C pool of any Holdridge life-zone, despite having the third lowest soil C density, simply because tropical and subtropical woodlands and savannas comprise the largest terrestrial biome. Estimates of soil C density in global savannas vary widely, for example, 3700 g C m^{-2} (Schlesinger 1977) and 5400 g C m^{-2} (Post *et al.* 1982), due at least in part to the large uncertainties associated with extrapolating field soil C data to larger scales.

Given the vast extent of tropical savannas, increased C fluxes from these systems could greatly influence the global C cycle feedback to predicted global warming (Townsend *et al.* 1992). Over decadal time scales, land use change probably has more influence on regional C balance than climate change (Burke *et al.* 1991). Many studies have predicted potential effects of land use change on soil organic carbon (SOC) storage (Balesdent *et al.* 1988; Harrison *et al.* 1993; Solomon *et al.* 1993; Woerner 1993; Fisher *et al.* 1994). Nevertheless,

controls on C sequestration in savannas are complex (Scholes & Archer 1997) and poorly understood (Seastedt 2000). Accelerating land use change has great potential to affect C balance in the tropics, but rates and extent of change are poorly quantified (Crutzen & Andreae 1990; Schimel 1995a; Tiessen *et al.* 1998).

Bush encroachment is the gradual proliferation of trees and shrubs in grasslands and savannas. Continuous or heavy grazing thins the grass understorey that would normally fuel fires during the dry season; fire suppression over many years promotes woody plant proliferation (Huntley 1982; Trollope 1984; Trollope & Tainton 1986; Graetz 1994). Bush encroachment has been widely documented in global rangelands during the past century (Archer 1995) and has been most definitively linked to historic grazing practices rather than climate or enhanced carbon dioxide (Grover & Musick 1990; Archer *et al.* 1995).

Altered C sequestration is one of many potential biogeochemical consequences of bush encroachment (Archer *et al.* 2001). Soil C levels are linked to rates of decomposition, plant production and plant litter inputs into the soil system (Ojima *et al.* 1993). The distribution of soil organic matter (SOM) globally suggests moisture and temperature are the major environmental constraints controlling the balance between primary production and decomposition. Given that bush encroachment induces obvious changes in savanna vegetation structure, litter inputs into the soil system have also changed. This could alter SOC storage when integrated over the decadal time scales of bush encroachment.

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Given its widespread occurrence, bush encroachment could explain a portion of the 'missing' terrestrial C sink often cited in studies of the global C cycle (Broecker *et al.* 1979; Tans *et al.* 1990; Hudson *et al.* 1994; Schimel 1995b; IPCC 1996; Pacala *et al.* 2001). In North American savannas, bush encroachment may be accumulating over 1 Mg of C ha⁻¹ year⁻¹ (Pacala *et al.* 2001), and significantly more soil C can be found beneath woody plants than beneath grasses (Gill & Burke 1999; Hibbard *et al.* 2001). Similarly, we hypothesized that bush encroachment over the past century in South African savannas has increased soil C sequestration. We surveyed %C and %N of soil and litter on four soil types across two encroached study landscapes in northern South Africa. Our objective was to assess bush encroachment effects on soil C and nitrogen (N) pools both between and within these soil types, which are representative of this semi-arid savanna region.

METHODS

Study areas

The Ganyesa and Madikwe study areas are approximately 300 km apart in the North West Province of the Republic of South Africa, in a semi-arid savanna region used almost exclusively for grazing cattle (Fig. 1). The study areas together represent the major regional soil types and vegetation communities, which exhibit

varying degrees of bush encroachment. Because of generally infertile soils and unreliable rainfall, croplands comprise less than 5% of the total area. Mean annual rainfall increases from west to east, from about 350 mm at Ganyesa (26.5°S, 24.0°E) to about 520 mm at Madikwe (24.8°S, 26.3°E), and is distinctly seasonal, occurring largely during the summer (November–March). In both study areas, the mean minimum temperature of the coldest month is 14°C, while the mean maximum temperature of the hottest month is 28°C.

Soils at Ganyesa are unusually homogeneous as they consist of aeolian sands up to 150 m deep, almost exclusively derived from Kalahari sand. Soil pH varies between 5 and 6, and some exposures of calcrete occur (Agricor 1985). Soils at Madikwe are much more heterogeneous. According to a detailed soil and vegetation survey (Loxton *et al.* 1996), 69% of this landscape is composed of three soil types: black clay, red clay loam and rocky loam. The remaining 31% consists of a variety of predominantly loam soils. The black clay soils occur across a gently sloping, colluvial pediplain derived from a base rich gabbro or diabase provenance; they are mainly non-calcareous, but local areas of calcrete exist. These self-mulching clays expand and become sticky upon wetting, then shrink as they dry to form hummocky microrelief, called gilgai. The red clay loam soils are also colluvial but are well drained and not sticky when wet. They are derived from granite and overlie saprolite or ferricrete at a depth of approximately 1000 mm. The rocky loam soils occur across a gently sloping plain derived from banded ironstone; they are brown and shallow with frequent shaly dolomite and chert outcrops.

At the Ganyesa landscape, the principal encroaching species (all native) are *Acacia mellifera* and *Grewia flava*. At the Madikwe landscape, the red clay loam soils were broadly observed to be those most heavily encroached, with woody cover fractions approximately double those of the other soil types. The principal encroaching species (also native) are *Dichrostachys cinerea* ssp. *africana*, *Acacia tortilis*, *Acacia erubescens* and *A. mellifera* (Hudak 1999a).

Field sampling

Our initial intent was to compare C and N pools on farms with contrasting grazing and fire histories, but our knowledge about the land use history of most farms was limited to largely anecdotal information gathered through interviews (Hudak 1999b). However, bush density served as a useful indicator of former fencelines and other historic land use features, and we were successful in classifying historic bush densities across the landscape from historical aerial photography (Hudak & Wessman 1998). Similar to the stratification

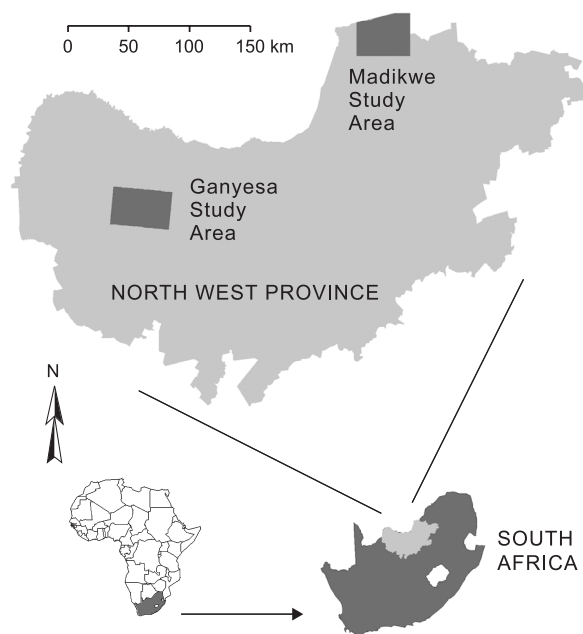


Fig. 1. Location of the Ganyesa and Madikwe study areas within the semi-arid savanna region of South Africa.

approach of Ruggiero *et al.* (2002), we conducted a preliminary geographic information system (GIS) and image analysis of our study areas, stratifying by soil type and bush density. We then surveyed soil and litter C and N along sixteen 240-m transects on four soil types (Kalahari sand, 4; black clay, 4; red clay loam, 5; rocky loam, 3) across the full range of observed bush densities.

The Kalahari sand soils of Ganyesa and red clay loam soils of Madikwe were of particular interest for this analysis due to their comparatively heavy encroachment. On each of these two soil types, three of these transects just described were placed on farms where we had some knowledge of the land use histories, and which exhibited varying degrees of encroachment. On the Kalahari sand soils, one transect (Kgamadintsi) consisted almost entirely of young trees and shrubs coppicing since a 1987 fire, while another transect (Woodlands) exhibited a broader range in tree sizes since a 1986 fire of likely lower severity. The third transect (Maroba) was the most heavily encroached and had not burned. On the red clay loam soils, two transects were located 170 m apart in a field cleared for cultivation between 1955 and 1970. Half of this field has since been kept clear of woody vegetation (Weltevreden-C), while the other half was abandoned between 1970 and 1984, and severe bush invasion ensued (Weltevreden-B). The third transect was situated on a heavily encroached farm (Middelpoort) grazed continuously since 1936 at near-carrying capacity.

Basal areas at ankle height were measured for all woody stems within a 5-m radius of each sample point, separated by 15-m intervals. Above-ground woody biomass was estimated using allometric equations formulated by Tietema (1993) for the major local woody species, summed for each of the 17 sample points, and finally totalled for each transect. Percent woody canopy cover was measured at the ends and centre of each transect using the plotless Bitterlich technique (Mueller-Dombois & Ellenberg 1974; Friedel & Chewings 1988); three measurements per transect were sufficient because we were careful to locate each transect within landscape units of homogeneous bush density rather than along bush density gradients.

Soil samples were obtained at eight points separated by 30-m intervals along each transect. Soil samples were extracted with a 5.7-cm diameter, stainless steel soil auger. At each sample point, four holes were augered at a distance of 1 m from the centre point in the four cardinal directions; soils at each sampling depth were then mixed in a brass bottom pan to compensate for microsite heterogeneity. Kalahari sand and red clay loam soils were sampled to depths of 5, 15, 30, 55 and 90 cm. Black clay and rocky loam soils were only sampled to 5 and 15 cm depths,

because of difficulty augering. Soils were then passed through a 2-mm mesh sieve; the few fine roots and rocks >2 mm in size were discarded before air drying.

Litter samples were collected at the same points as soil samples. As with the soils, four collections were made in the four cardinal directions and combined. To allow more thorough data analysis later, litter and soil samples were divided into one of two categories: samples collected at points having only herbaceous vegetation or samples collected at points with a woody canopy component. A sample was judged as having a woody component if it occurred within the dripline of a tree or shrub. Soil and litter samples were allowed to air dry on storage shelves for several weeks to eliminate any residual moisture before sealing them in zip-lock bags to await later analyses. All field data were gathered in 1996 late in the dry season (August–October), when soil moisture is minimal.

Carbon and nitrogen analysis

Litter samples were separated into fine (ground duff) and coarse (standing dead grass and woody twigs) fractions. Coarse fractions were first shredded in a Wiley mill (Arther H. Thomas) and then ground in a Cyclotec-1093 sample mill (Tecator) along with the fine fractions. Samples composed of pure grass or pure woody litter were marked so that %C and %N of the major plant functional types could be determined.

Soil samples (~5 mL) were loaded into 25-mL plastic vials (2.5 cm diameter), each containing a pair of stainless steel pins. Up to 20 vials were loaded into a large plastic jar, which was then rolled for several hours (US Stoneware). The tumbling and pulverizing action ground most of the soil into a powder capable of passing through a 250- μ m mesh sieve (Fisher Scientific). Any remaining sand grains were ground by hand with a mortar and pestle and passed again through the mesh sieve in an iterative procedure until the entire sample was ground thoroughly.

Calcareous soils occur intermittently throughout the region, so soils were diagnosed for carbonates according to Allison (1965). One transect from the Ganyesa landscape showed evidence of carbonate content, so soil samples from this transect were simply excluded from C and N analysis.

Both litter and soil samples were shaken to ensure complete homogenization prior to C and N analysis. Subsamples for C and N analysis (14 ± 2 mg for soil; 5 ± 1 mg for litter) were weighed (0.001 mg precision; Sartorius Micro M2P Analytical Balance) and then combusted in a Carlo-Erba CHN Analyser (Fisons EA-1108). Approximately 10% of the subsamples were run as duplicates; absolute differences between the

means of the originals and duplicates were 3.3% for %C and 0.5% for %N.

Other soil analyses

Surface soil (0–5 cm) bulk density samples were extracted in the field by first pouring water on to the soil to ease extraction of the samples, then using a steel can with a volume of 134 cm³. Samples were stored in sealed, zip-lock bags until they could be processed at the Council for Geoscience (Mmabatho, South Africa), where they were oven dried at 110°C for 64 h, then weighed. Surface soil texture was measured with particle-size fractionations performed at the Institute for Soil, Climate and Water (Pretoria, South Africa) using the hydrometer method (Day 1965). Soil texture of the Kalahari sand and red clay loam soils was also determined at 50 cm depth.

Statistical analyses

Spreadsheet operations, summary statistics, simple linear regressions and student *t*-tests were carried out in Microsoft Excel 2000. Geostatistical tests were carried out in GSLIB (Statios) using diagnostic

semivariograms and in S-PLUS (Insightful) using Moran's *I*-test for spatial autocorrelation (Cliff & Ord 1981).

RESULTS

Geostatistical tests revealed no significant spatial autocorrelation in either the above-ground woody biomass data sampled at 15-m intervals or the soil or litter data sampled at 30-m intervals; hence, all sample points were considered spatially independent. Valid comparisons could thus be made between or within soil types by pooling the data accordingly. Furthermore, the data could be justifiably partitioned between sample points having a woody canopy cover component and sample points having solely herbaceous cover.

Comparisons between soil types

Surface soil texture differed greatly between the clay, loam and sand soil types (Table 1). There was no evidence of illuviation in the aeolian sand soils at Ganyesa, as particle fractions between 5 and 50 cm soils did not differ. However, the clay fraction in the red clay loam soils at 50 cm depth (24.2%) was signifi-

Table 1. Mean $\pm$ SE for particle-size fractions of surface soils (0–5 cm) from the four soil types surveyed

	Kalahari sand (<i>n</i> = 8)	Black clay (<i>n</i> = 8)	Red clay loam (<i>n</i> = 10)	Rocky loam (<i>n</i> = 6)
% Clay	6.5 $\pm$ 0.5	46.0 $\pm$ 1.7	16.4 $\pm$ 1.1	12.0 $\pm$ 0.9
% Silt	0.7 $\pm$ 0.2	23.2 $\pm$ 1.1	13.2 $\pm$ 1.7	15.1 $\pm$ 1.3
% Sand	92.8 $\pm$ 0.5	30.8 $\pm$ 2.6	70.4 $\pm$ 2.4	72.9 $\pm$ 1.7

Sample sizes indicated are twice the number of transects for each soil type, that is, two samples were collected per transect.

Table 2. Mean $\pm$ SE for stem density, basal area, biomass and qualitative description of woody overstorey on farms with strongly contrasting degrees of bush encroachment on the two heavily encroached soil types surveyed

Farm name	Stem density (stems ha ⁻¹)	Basal area (cm ² ha ⁻¹)	Above-ground woody biomass (kg ha ⁻¹)	Relative state of encroachment	Description of woody overstorey
Kalahari sand					
Kgamadintsi	18 531 $\pm$ 1767	28 359 $\pm$ 5213	9862 $\pm$ 1999	Early	Mostly small shrubs since 1987 fire
Woodlands	10 056 $\pm$ 1122	37 101 $\pm$ 8070	12 367 $\pm$ 2628	Intermediate	Size diversity since 1986 fire
Maroba	13 069 $\pm$ 2365	52 457 $\pm$ 10 681	23 976 $\pm$ 6131	Late	Mature trees and coppices, unburned
Red clay loam					
Weltevreden-C	112 $\pm$ 58	459 $\pm$ 374	175 $\pm$ 153	Negligible	Clearing maintained since 1970
Weltevreden-B	5133 $\pm$ 446	150 482 $\pm$ 15 930	93 927 $\pm$ 14 031	Severe	Reinvasion since 1970 abandonment
Middelpoort	7239 $\pm$ 533	119 412 $\pm$ 17 445	62 294 $\pm$ 17 483	Chronic	Overgrazed since 1936, self-thinning

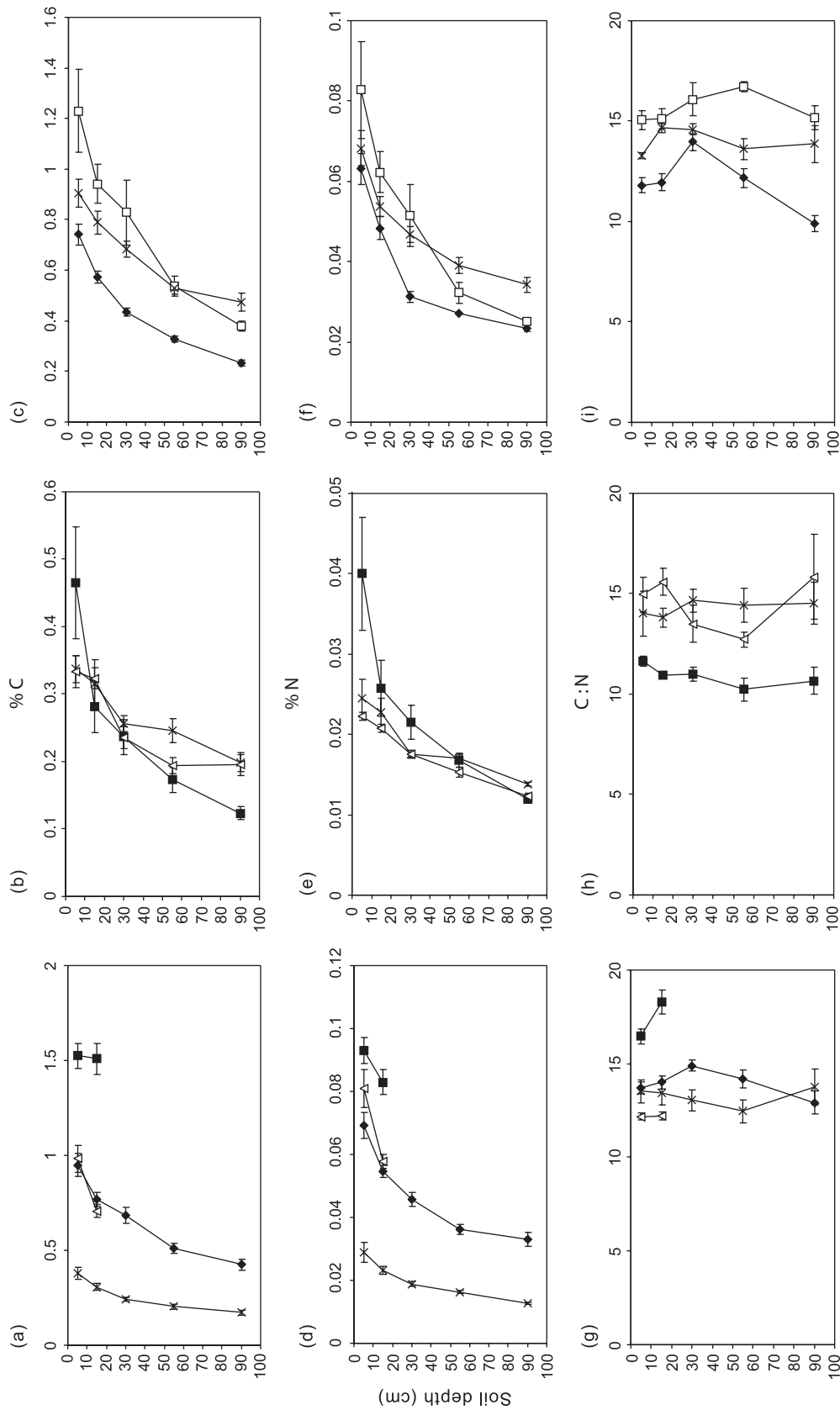


Fig. 2. Mean $\pm$ SE for soil (a–c) %C, (d–f) %N and (g–i) C:N for (a,d,g) the four soil types surveyed (no. transects pooled within each soil type: (X), Kalahari sand, 3; (■), black clay, 4; (◆), red clay loam, 5; (△), rocky loam, 3), (b,e,h) the three transects on Kalahari sand soils ((X), Kgamadintsi; (■), Maroba; (△), Woodlands) and (c,f,i) the three transects on red clay loam soils ((◆), Weldevreden-B; (□), Weldevreden-C; (X), Middelport). There are $n = 4$ samples at all depths for each transect, except the two Weldevreden transects, which have $n = 8$ samples at 5 and 15 cm depths. Table 2 provides details regarding the woody overstorey structure of transects in (b,e,h) and (c,f,i).

cantly higher than at 5 cm depth ($P = 0.0014$). Both %C and %N (but not C:N) differed markedly between clay, loam and sand soils, increasing with increasing clay fraction (Fig. 2a,d,g).

Comparisons within soil types

Allometric estimates of above-ground woody biomass differed dramatically among the three farms selected

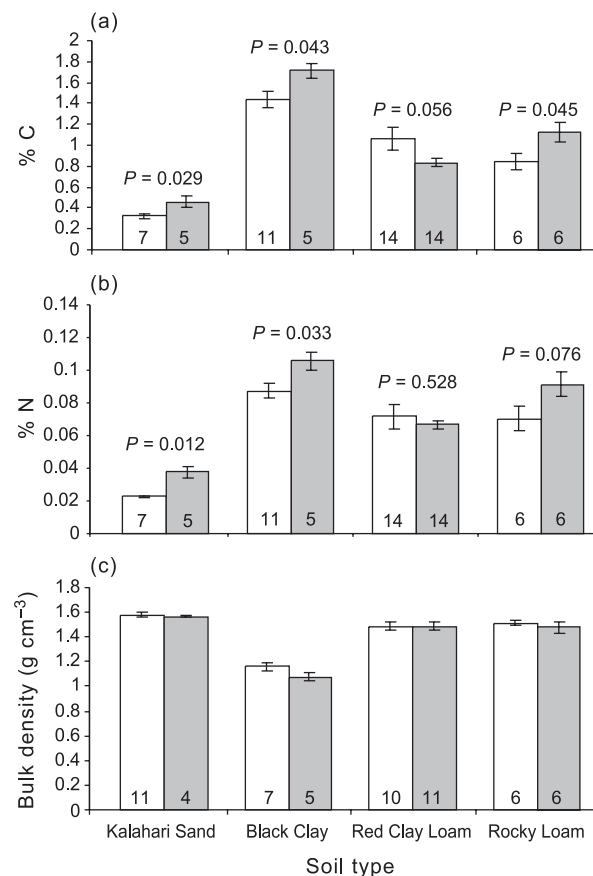


Fig. 3. Mean $\pm$ SE for surface soil (0–5 cm) (a) %C, (b) %N and (c) bulk density for the four soil types surveyed (no. transects pooled within each soil type: Kalahari sand, 3; black clay, 4; red clay loam, 5; rocky loam, 3). Data are partitioned into samples having (□) solely herbaceous vegetation versus (■) samples with an above-ground woody component. P -values from student t -tests of differences between means are given above columns. Numbers within columns indicate sample sizes.

Table 3. Mean $\pm$ SE for %C, %N and C:N of litter samples, partitioned according to whether or not the sample contained a woody component.

	Herbaceous only ($n = 38$)	Woody and herbaceous ($n = 26$)	t -test
%C	41.38 $\pm$ 0.62	40.90 $\pm$ 0.42	NS
%N	0.75 $\pm$ 0.04	1.17 $\pm$ 0.06	***
C:N	61.00 $\pm$ 3.29	36.80 $\pm$ 1.75	***

Student t -tests were used to test differences between means. *** $P < 0.0001$. NS, not significant ($P > 0.05$).

for comparisons within the Kalahari sand and red clay loam soil types (Table 2). A summary of the contrasting land use histories on these farms is also provided to aid interpretation (Table 2). On the Kalahari sand soils, Kgamadintsi and Woodlands did not differ significantly in %C, %N or C:N at any depth ($P > 0.05$), but Maroba had lower %C at 90 cm, higher %N at 5 cm and lower C:N at all depths compared to either of the other two transects (Fig. 2b,e,h). On the red clay loam soils, Weltevreden-B had significantly lower %C than either Weltevreden-C or Middelpoort at all soil depths ($P < 0.05$). Weltevreden-B also had lower %N than Weltevreden-C at 15 and 30 cm, lower %N than Middelpoort at 30, 55 and 90 cm, lower C:N than Weltevreden-C at all depths except 30 cm, and lower C:N than Middelpoort at all depths except 30 and 55 cm. Weltevreden-C did not differ from Middelpoort except for lower %N at 90 cm and higher C:N at 5 and 55 cm (Fig. 2c,f,i).

Litter %N and C:N differed significantly between solely herbaceous vegetation and vegetation having a woody component, while %C did not (Table 3). The surface soil %C and %N data, when partitioned into cover types, revealed significant differences for most soil types, while cover type did not significantly affect surface soil bulk density within any soil type (Fig. 3).

DISCUSSION

Comparisons between soil types

Just as soil texture strongly influences woody overstorey structure and pattern in these study landscapes (Hudak 1999a), soil texture also had a large effect on C storage in the soil. Differences in soil texture between clay, loam and sand soils were substantial (Table 1), and %C increased as a function of clay fraction (Fig. 2a). Others have found that soil texture greatly influences vegetation structure (Dodd *et al.* 2002; Ruggiero *et al.* 2002), SOM storage and turnover (Schimel *et al.* 1985; Burke *et al.* 1989b; Bonde *et al.* 1992; Schimel *et al.* 1994). However, soil texture alone cannot explain SOC storage patterns in savannas (Seastedt 2000). It is instructive to now consider the more subtle constraints on C and N storage within soil types.

Comparisons within soil types

The effect of bush encroachment on soil C and N pools differed between the Kalahari sand and red clay loam soils sampled to 1-m depth. On the Kalahari sand soils, heavy encroachment at the Maroba farm changed the slope of the gradient in %C and %N relative to Kgamadintsi or Woodlands (Fig. 2b,e), while on the red clay loam soils, heavily encroached Weltevreden-B had less %C and %N at all depths compared to Weltevreden-C or Middelpoort (Fig. 2c,f). Herbaceous productivity data would help to quantify this discrepancy better, but an important qualitative difference was evident. Encroachment at the Maroba transect was severe enough to inhibit understorey grass growth but not exclude it. In contrast, very little herbaceous understorey existed beneath the thick woody overstorey at Middelpoort, and none beneath the even thicker woody overstorey at Weltevreden-B. The consistently lower soil C:N at the heavily encroached Maroba and Weltevreden-B transects, relative to the other transects for their respective soil types, might be due to higher-quality litter inputs (largely leguminous) at woody sites (Table 3). Gill and Burke (1999) found supporting evidence in North America.

Surface soil %C and %N of the coarse-textured sand soils at Ganyesa were very low, while at Madikwe they fell within the range of values reported from previous studies (Fig. 3a,b). Hibbard *et al.* (2001) cited nine studies (including their own) in semi-arid shrublands and savannas where surface soil %C and %N under woody canopies were higher or equal to surface soil %C and %N between woody canopies. Similarly in this study, soils beneath a woody overstorey exhibited higher %C than soils beneath a solely herbaceous canopy, except on red clay loam soils.

Less SOC beneath woody plants on red clay loam soils (Fig. 3a) may stem from the inability of grasses to compete with an especially dense woody overstorey. Schlesinger *et al.* (1990) similarly found that long-term grazing of semi-arid grasslands in southern New Mexico caused barren zones to develop between shrubs. Under woody thickets, herbaceous production declines due to competition between trees and grasses (Grunow *et al.* 1980; Stuart-Hill *et al.* 1987; Stuart-Hill & Tainton 1989; Mordelet & Menaut 1995). In more open savannas, herbaceous production is enhanced beneath tree canopies due to higher soil moisture, SOM and available nutrients (Belsky *et al.* 1989, 1993; Burke *et al.* 1989a; Isichei & Muoghalu 1992). Such facilitation of understorey grass production can be more pronounced if the woody overstorey species are leguminous (Belsky *et al.* 1993; Mordelet & Menaut 1995) as most were in this study.

Tree-grass interactions are complex (Scholes & Archer 1997) and can change significantly between wet and dry seasons (Ludwig *et al.* 2001). There may be an optimal woody plant age, size or density at which

herbaceous production is maximized. Beyond this point, the near-total sequestering of light, water and soil nutrients by competing trees in a thick woody overstorey (as on the red clay loam soils) hinders coexistence of grasses. We do not believe that woody plants are facilitating understorey grass production on the other soil types; late in the dry season, greater grass necromass was observed between trees and shrub clumps than beneath them. Cattle farmers are also decrying the decline in grazing capacity due to bush encroachment (Hudak 1999b). The increased soil %C and %N observed on the other three soil types are more likely due to higher total production from increased woody cover. Decomposition is probably not increasing to the same degree, leading to SOM accumulation. This argument is supported by earlier research suggesting that SOM accumulation may be more related to decomposition than to production in global terrestrial ecosystems (Cebrián & Duarte 1995). Because our data were only sampled at one point in time, they are insufficient to confirm this speculation. Soil monitoring is needed to determine if rates of soil C sequestration are in equilibrium with rates of bush encroachment, and to what extent the soil C sequestration rate may lag behind.

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