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Soil microbial biomass and functional diversity in shrub-encroached grasslands along a precipitation gradient

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ABSTRACT

The use of soil microbial and biochemical parameters could play an important role in monitoring effects of shrub encroachment in grasslands due to their rapid reaction to environmental fluctuations. We compared total organic carbon (C_{org}), soil total nitrogen (TON), microbial biomass, basal respiration, soil microbial quotient (C_{mic}/C_{org}) species and functional diversity between pairs of neighbouring, leguminous shrub-encroached and open grassland plots along a rainfall gradient (300 mm to 1500 mm mean annual precipitation (MAP)) in South Africa. "In semi-arid regions, soil Corg was higher in shrub-encroached grasslands than in open grasslands while the reverse was true in humid regions (1500 mm MAP)". Soil total nitrogen was generally higher in the shrub-encroached grasslands compared to open grasslands. Soil microbial biomass and basal respiration was higher in shrub-encroached grassland across the precipitation gradient. There was also a difference in microbial functional diversity between the encroached and adjacent open grasslands, which was most evident in the semi-arid regions. Our results suggest that land-cover change might influence microbial properties along the rainfall gradient.

1. Introduction

Grasslands and savanna ecosystems are experiencing intensive land-cover change due to woody-plant encroachment (Archer et al., 1995; Mureva and Ward, 2016). Such land-cover changes are of concern because of the strong influence of different land usages on soil quality, natural resource supply and carbon sequestration (Zeng et al., 2009; Barger et al., 2011). Change in land cover can affect the amount of carbon stored in the soil. Land cover has a marked effect on soil carbon as a result of the interactions between organic inputs and subsequent input transformation by soil microbes. Soils are a major terrestrial carbon sink, containing approximately three times more carbon (1 555 Pg C) than in vegetation (650 Pg C) and twice as much that in the atmosphere (750 Pg C) (Batjes and Sombroek, 1997; Jobbágy and Jackson, 2000; Cook et al., 2014).

Most studies on shrub encroachment have focused on soil chemical properties while less attention has been paid to microbial activities (Ross et al., 1999; Chen et al., 2000; Zeng et al., 2009). The use of soil microbial parameters could play an important role in monitoring effects of woody plant encroachment in grasslands relative to soil physical and chemical properties due to the rapid reactions of the former to any environmental fluctuations (Gryta et al., 2014). Some microbial parameters that have been used to assess soil quality include soil microbial biomass (Araújo et al., 2008; Truu et al., 2008; Zeng et al., 2009), soil respiration (Zeng et al., 2014) and functional diversity of soil microbial community (Zak et al., 1994; Gryta et al., 2014). Soil microbial biomass, the living part of organic matter, comprises 1% to 3% of the total organic C in the soil (Truu et al., 2008), and is both a source of labile nutrients and an agent for the transformation of soil nutrients (Alvarez et al., 1998; Araújo et al., 2008). The dynamics of soil microbial biomass can be used to predict long-term trends of soil organic matter (Truu et al., 2008). Soil respiration is a measure of carbon dioxide (CO_2) released from the soil from decomposition of soil organic matter (SOM) by soil microbes and respiration from plant roots and soil fauna. Soil respiration is an important indicator of soil health because it indicates the level of microbial activity, SOM content and its decomposition. Changes in C_{mic}/C_{org} (the ratio of microbial biomass carbon (SMB-C) to total soil organic carbon (SOC)) and the metabolic quotient (ratio between basal respiration (CO_2–C and microbial biomass)) have been used to reflect changes in organic matter input to soils, microbial efficiency in converting available C to SMB-C, C losses from soil, and the stabilization of organic C by soil mineral fractions (Liao and Boutton,

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2008)

Functional diversity of microbes can be examined from a variety of perspectives, paralleling concepts analogous to those of taxonomic diversity. The simplest aspect is substrate richness, i.e. the number of different carbon substrates that are used by a microbial community (Zak et al., 1994). Ros et al. (2008) reported that, by determining the diversity of microbial heterotrophic functions related to C utilization, more relevant information on the roles of microorganisms in the ecosystem can be obtained. This method has proved useful as a highly reproducible means of studying soil microbial functional diversity (Ros et al., 2008) and of differentiating between microbial communities in natural soils, such as those under different land uses (Ros et al., 2008).

We studied the effects of recent woody plant encroachment along a precipitation gradient in South African grasslands by comparing pairs of encroached and unencroached grasslands from 300 mm MAP to 1500 mm MAP. We predicted that:

(1) Soil organic carbon (SOC) and soil total nitrogen would increase under woody plant stands relative to grassland (Archer et al., 2004; Blaser et al., 2014);
(2) This increase in C and N content should result in an increase in soil microbial biomass and respiration (Liao and Boutton, 2008);
(3) The C_{mic}/C_{org} ratio would decrease with woody plant encroachment due to the more recalcitrant nature of lignified woody litter compared to herbaceous litter (Liao and Boutton, 2008); and
(4) The qCO_2 would be higher in encroached grasslands suggesting lower microbial efficiency and/or that the woodland C is of poorer quality as also reflected by a lower C_{mic}/C_{org} ratio and
(5) There should be low similarity in bacterial functional diversity between encroached and open grasslands because of the difference in the carbon compounds produced by woody plants and herbaceous plants (Parfitt et al., 2003; Liao and Boutton, 2008; Zeng et al., 2009).

2. Methods

2.1. Study sites

The study was carried out at six sites across a rainfall gradient in South Africa. The sites were: KwaMbonambi (1500 mm MAP), Stanger (900 mm MAP), Bergville (800 mm MAP), Bloemfontein (500 mm MAP), Pniel (350 mm MAP) and Middelburg (300 mm MAP). In three of our sites (Middelburg, Pniel and Bergville) there is documented evidence (Britz and Ward, 2007; Grellier et al., 2012; Ward et al., 2014; Mureva and Ward, 2016), while for the other three sites we have strong oral evidence suggesting that our sites were once open grasslands 20–50 years ago. Further details of the sites are listed in Table 1. There were also differences in soil type, herbivory, fire frequency and species composition among the study sites. In this study, we could not control for these other variables. However, we believe that the study can still make a significant contribution to the understanding of effects of encroachment in savanna grasslands.

2.2. Soil sampling

At each site, 12 10 m × 10 m plots (six in grass-dominated and six in shrub-encroached plots) were selected. The plots at each site had the same soil type and were on a level topography. In each plot, after removing the plant litter, five soil samples were randomly collected from 5 to 15 cm depth. The soil samples in each plot were then bulked and divided into three subsamples. The first subsample was used to quantify bulk density (BD) using the core method (Burt, 2004; Liu et al., 2013). The second subsample was air dried at 40 °C, passed through a 2 mm sieve and analysed for total organic carbon and total nitrogen. The third soil subsample was sieved through a 2 mm sieve and used for the determination of soil respiration, microbial biomass and bacterial

Table 1
Study site descriptions.

Site	GPS coordinates	Annual Rainfall (mm)	Temperature (°C)		Biome	Soil characteristics	Major plant species
			Min	Max			
KwaMbonambi	28° 49′ 60.61″S 32° 16′ 96.92″E	1500	3.5	35	Maputaland wooded grasslands	Quaternary redistributed sands supporting yellowish redistributed sands of the Berea formation	*Sporobolus fimbriatus, Digitaria natalensis* (grass species); *Diospyros lycioides* (shrub); *Terminalia sericea* (tree),
Stanger	29° 18′ 59.05″ S 31° 22′ 13.24″E	900	5.8	32.6	KwaZulu-Natal Coastal Belt	Ordovician Natal group sandstone	*Themeda triandra, Aristida junciformis* (grass); *A. karroo* (tree)
Bergville	28° 79′ 06.30′S 29° 38′ 98.40″E	750	5.8	32.6	KwaZulu-Natal moist grasslands	Ordovician Natal group sandstone	*Themeda triandra, Hyparrhenia hirta* (grasses); *Acacia karroo, A sieberiana* (trees)
Bloemfontein	28° 59′ 16.77″S 26° 16′ 54.24E	450	0	32	Bloemfontein dry grasslands	Sedimentary mudstones and layers of sandstone	*Aristida congesta, A. diffusa, Cynodon dactylon* (grass); *Acacia karroo* (tree)
Pniel	28° 34′ 50.00″S 24° 30′ 30.70″E	350	−4.1	37.5	Kimberley thornveld	Sandy to loam soils of the Hutton soil form	*Eragrotis curvula, Schmidtia pappophoroides* (grass); *Acacia erioloba, A tortilis, A. karroo, A. mellifera, Tarchonanthus camphoratus* (trees)
Middelburg	31° 25′ 98.83″S 24° 58′ 82.10″E	300	−7.2	36.1	Eastern Upper Karoo	Sandy to loam soils of the Hutton soil form	*Aristida* and *Eragrostis* (grass); *Searsia erosa, S. burchellii, Diospyros lycioides* and *Eriocephalus ericoides* (shrubs)