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Large shrubs increase soil nutrients in a semi-arid savanna

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ABSTRACT

The soil under savanna woody species is often enriched in nutrients in what is termed an 'island of fertility'. We tested for positive feedbacks between encroaching woody plants and soil fertility in two co-occurring shrub species at three sites. One of these shrub species is nitrogen-fixing, *Acacia mellifera*, and the other is non-nitrogen-fixing, *Tarchonanthus camphoratus*; we compared these effects to the grasslands surrounding the shrub patches. We found that soil nutrient concentrations were usually related to shrub size rather than the species. Fertile patches developed underneath large shrubs as indicated by higher carbon and nitrogen concentrations, a higher CEC_{eff} (especially sodium, which is a limiting nutrient for grazing livestock) and a pH near 6. We found no difference in soil nitrogen between the N-fixing *A. mellifera* and *T. camphoratus*. Plant cover under large shrubs was less than in open grassland. There are 'islands of fertility' under large shrubs. However, the development of fertility islands did not facilitate understorey growth. Thus, increased soil fertility had no positive feedback on overall vegetation composition. Negative effects of the woody vegetation may override the positive effects of increased soil nutrient availability.

1. Introduction

The changes in vegetation composition involved in the encroachment of native woody species have been well described (e.g. Ward et al., 2013; Wiegand et al., 2006). Often these changes are ascribed to changes in the disturbance regime (Simberloff et al., 2012), such as changes in grazing, fire, physical disturbance, or global climatic change (Ward et al., 2014). Less attention has been paid to the consequences of the encroachment of native species on soil properties. One of the most interesting aspects to consider is whether there are positive effects of encroaching shrubs on soil fertility, that may lead to the formation of 'islands of fertility' (Charley and West, 1975; Ravi et al., 2010; Schlesinger et al., 1996). There may be positive effects of the presence of shrubs that lead to positive feedbacks by means of further deposition of nutrients in these shrub 'islands of fertility', leading to increased shrub growth and reproduction (Charley and West, 1975). Litter input can alter soil pH, which changes soil nutrient availability (Scheffer and Schachtschabel, 2010) and organic matter content, and consequently alters soil bulk density (Chapin et al., 2002). Enrichment of nutrients under arid tree and shrub canopies has repeatedly been reported (e.g. Abule et al., 2005; Hagos and Smit, 2005; Munzbergova and Ward, 2002).

An important factor for soil decomposers is the C:N ratio, which is commonly used as an index of decomposition, both in plant litter (Bell et al., 2014) and in soil (Manzoni et al., 2008). Decomposer organisms tend to grow following relatively constrained stoichiometric requirements (Cleveland and Liptzin, 2007), and are limited by both carbon (C) and nutrients, especially nitrogen (N). Soil organic matter and plant

Abbreviations: N, nitrogen; P, phosphorus; K^+, potassium; Ca^{2+}, calcium; CEC_{eff}, effective cation exchange capacity; Mg^{2+}, magnesium; Mn^{n+}, manganese; Fe^{n+}, iron; H^+, hydrogen; Na^+, sodium; Al^{3+}, aluminium; Zn, zinc; Cu, copper; Co, cobalt; MAP, mean annual precipitation

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litter with low C:N ratios tend to decompose faster than those with higher C:N ratios (Manzoni et al., 2008). With shrub encroachment of grasslands, there should be an increase in plant-bound C due to increasing woodiness of the vegetation (Weintraub and Schimel, 2005).

While a consensus exists about the creation of 'islands of fertility' (e.g. Eldridge and Wong, 2005; Ravi et al., 2010; Schlesinger et al., 1996), there are some uncertainties concerning the details of the soil-nutrient enrichment. For example, the distribution and re-allocation of certain cations and effective cation exchange capacity (CEC_{eff}) - a common measure of a soil's ability to provide cationic nutrients (Perkins et al., 2013) - varied considerably among studies (e.g. Hagos and Smit, 2005; Isichei and Muoghalu, 1992; Schlesinger et al., 1996). Furthermore, the mechanisms of 'islands of fertility' are not entirely explained (Johnson and Lehmann, 2006; Smit, 2004). It is known, though, that stemflow and throughfall (Johnson and Lehmann, 2006), increased input of litter and animal faeces (Belsky, 1994), and the fixation of N by leguminous woody species (Kambatuku et al., 2013a) contribute to different degrees to the phenomenon of 'fertility islands'. In this study, we consider two shrub species in three different places at the same time, so 'islands of fertility' explanations can be separated from possible alternative explanations, such as the effect of plant size (larger plants contribute more to the soil than smaller plants – Throop and Archer, 2008). Furthermore, we studied an N-fixing plant (*Acacia mellifera*) and a non-N-fixing plant (*Tarchonanthus camphoratus*), allowing us to determine whether it is nitrogen fixation or the size of the plant that is important.

The influence of woody vegetation on soil properties in arid and semi-arid savannas is a field of considerable interest (e.g. Cramer and Bond, 2013; Hagos and Smit, 2005; Ludwig et al., 2004). While water limitation is an obvious constraint in arid savannas, there is evidence for co-limitation by water and N (Austin and Sala, 2002; Kraaij and Ward, 2006). An additional issue of importance is the differential use of soil nutrients by woody and graminaceous plants in savannas (Chapin et al., 2002; Cramer et al., 2010). For example, higher N levels in the soil cause grasses and forbs to outcompete N-fixing woody species (Kraaij and Ward, 2006). However, N-fixing legumes typically have higher levels of N in their soils than non-N-fixing woody and grass species (Kambatuku et al., 2013a).

Another potential influence of woody vegetation on soils is the effect of plant size: a number of studies have shown that large shrubs and trees have much greater effects on the soils than small shrubs and trees due to their greater biomass that returns to the soil (De Soyza et al., 1996; Throop and Archer, 2008; Wiegand et al., 2005). Larger plants may also exude more root exudates than smaller plants (Zhao et al., 2009). Whether the effect of plant size outweighs that of functional traits such as N-fixing ability and plant type (e.g. grass vs. woody plants) has not been resolved.

1.1. Co-occurring encroachers

We investigated the effects of two co-occurring shrub species in a semi-arid savanna (Mean Annual Precipitation (MAP) = 350–400 mm) in the Northern Cape (South Africa) on soil fertility. In the northwestern parts of South Africa, and in large areas of Botswana and Namibia, *Acacia* (syn. *Senegalia*) *mellifera* (Fabaceae) and *Tarchonanthus camphoratus* (Asteraceae) frequently encroach in the same habitats (Schleicher et al., 2011; Ward et al., 2014). Both species are native-invasives *sensu* Simberloff et al. (2012). One of these species, *A. mellifera*, is a N-fixing legume (Kambatuku et al., 2013a), and the other, *T. camphoratus*, is a non-N-fixing shrub (Young and Francombe, 1991). We were particularly interested in the effects of these shrubs on the understorey and on relevant chemical properties of the soil in semi-arid savannas in an effort to establish whether changes in soil quality were associated with shrub encroachment.

We predicted the following:

(1) *A. mellifera* and *T. camphoratus* sampling points should contain higher levels of soil nutrients than adjacent grass-only sampling points; i.e. islands of fertility are present in this system.
(2) *A. mellifera* fixes N, while *T. camphoratus* does not. Thus, *A. mellifera* sampling points should have higher levels of soil N than either *T. camphoratus* or grass-only sampling points.
(3) The greater biomass of large shrubs eventually enters the soil during decomposition than biomass of small shrubs. Hence, large shrubs should contribute more to soil nutrient quantity than small shrubs, regardless of species (Mudrak et al., 2014).

2. Methods

2.1. Study species

Acacia mellifera (Fabaceae) is a drought-deciduous shrub or occasionally a small tree of up to 4–7 m tall that occurs in dry woodlands (Kraaij and Ward, 2006). *A. mellifera* is known to suppress the grass layer (Hagos and Smit, 2005), although Ward and Esler (2011) found that grasses usually outcompete young *A. mellifera* shrubs. *A. mellifera* can fix N (Kambatuku et al., 2013a).

Tarchonanthus camphoratus (Asteraceae) is a multi-stemmed and drought-deciduous shrub or small tree. Under semi-arid conditions, *T. camphoratus* remains a shrub about 2–3 m tall (Schleicher et al., 2011).

2.2. Study areas

Our three study areas are situated in semi-arid savannas at Pniel Estates (28.33 S, 24.30 E), Dronfield (28.36 S, 24.46 E) and Koopmansfontein (28.19 S, 24.08 E), ca. 10–100 km north of Kimberley, Northern Cape Province, South Africa (Fig. 1). Most of the research reported on here was done at Pniel Estates in 2009. All three study areas lie within the summer-rainfall area, with precipitation occurring mainly between November and April in the form of thunderstorms. MAP at Pniel Estates is 388 mm but is extremely variable (C.V. 39%). MAP of Dronfield and Koopmansfontein are ca. 400 mm at both sites. Temperatures at all three study areas can be as high as 44 °C during the summer months, while frosts can occur in winter (Britz and Ward, 2007). The soils at the Pniel and Dronfield study areas are nutrient-poor, moderately deep red-yellow sands of both aeolian and local origin (Kraaij and Ward, 2006) belonging to the Hutton soil form, while the Koopmansfontein soils are shallow of the Mispah form. The deep soils are apedal, freely drained and have a high base status (Smet and Ward, 2006).

The vegetation type is defined as Kimberley Thornveld (Mucina and Rutherford, 2006), with a tree-layer dominated by *Acacia erioloba*, *A. tortilis*, *A. karroo* and *Boscia albitrunca* and occasional dense shrub stands of *A. mellifera* and *T. camphoratus*. More specifically, at the Pniel and Dronfield study areas, the dominant trees/shrubs are *A. mellifera*

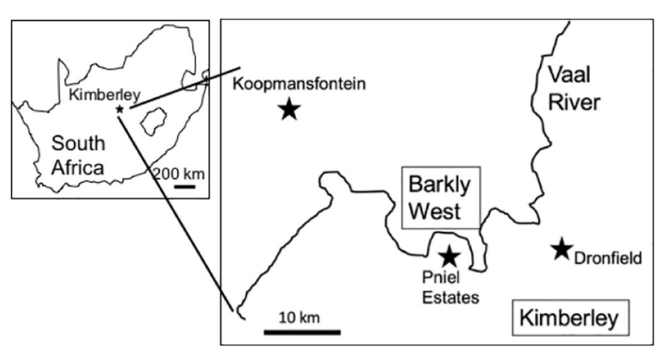

Fig. 1. The distribution of the study areas at Pniel Estates, Dronfield and Koopmansfontein (stars). The city of Kimberley, the town of Barkly West (in rectangles) and the Vaal river are also included. Inset = map of South Africa.