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Competition with trees does not influence root characteristics of perennial grasses in semi-arid and arid savannas in South Africa

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ABSTRACT

Savannas support mixed tree-grass communities and interactions between these are typically viewed as being competitive based on studies that focused on grass aboveground production. However, an important plant response to competition and resource limitation is an increase in root reserves. We investigated root characteristics of perennial grasses in the presence and absence of trees as a proxy of competition in South African savannas in three sites that differed in rainfall. We based our study on the hypothesis that competition from trees and water limitation will result in increased storage in roots of grasses under trees. Results indicate no significant effect of variation in rainfall of the different study locations on root characteristics of grasses. Furthermore, trees did not significantly influence most grass root characteristics that we measured. The only exception was nitrogen-content that showed an increase with rainfall and tree presence through potentially higher mineralization rates and nitrogen availability in the under-tree canopy environment. As the study sites are in the drier rainfall range in South Africa, it is likely that trees and grasses in these dry savannas may have a positive relationship conforming to the stress-gradient hypothesis. Alternatively, grasses and trees may be using complementary water and nutritional resources.

1. Introduction

Mixed tree-grass communities characterize savannas and tree-grass interactions in savannas are typically viewed as being competitive (Ludwig et al., 2004b; Sankaran et al., 2004; Scholes and Archer, 1997). Trees in savannas (beyond the seedling, sapling and juvenile stages) are regarded to have a higher nutrient capture capability due to their extensive spread of roots than grasses, consequently reducing grass aboveground production (Belsky, 1994; Ludwig et al., 2004b; Scholes and Archer, 1997; Sternberg et al., 2004). However, this is not a general rule and the absence of competition also has been shown under varying climatic conditions (Belsky, 1994; Simmons et al., 2008). Data on grass and tree root distributions show that there is no spatial segregation of tree and grass roots as proposed by the Walter's two layer hypothesis (February and Higgins, 2010; Hipondoka et al., 2003) indicating the dependence on the same pool of soil resources by both the plant functional types. Furthermore, meta-analysis and landscape level studies based on grass aboveground production suggest that the relationship between trees and grasses varies from competitive to facilitative with increasing aridity conforming to the stress-gradient-hypothesis (Dohn et al., 2013; Moustakas et al., 2013). Most studies addressing tree-grass interactions have focused on the effects of trees on aboveground grass production (Belsky, 1994; Dohn et al., 2013; Ludwig et al., 2004a, 2004b, 2001; Moustakas et al., 2013; Simmons et al., 2008). However, aboveground responses of plants to competition cannot be extrapolated

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belowground since plant allocation of resources to roots is neither predictable from the aboveground parts nor proportionate to it (Casper and Jackson, 1997; Zobel and Zobel, 2002). The roots of grasses are the principal belowground organs that not only capture nutrients but are also the primary storage organs. In this study, we examined the influence of trees and increasing aridity on the roots of perennial grasses in South Africa.

Resource limitation is reported to influence interplant interactions (Chapin et al., 1990). Studies suggest that plants respond to resource limitation by increasing allocation of resources to storage organs (Bloom et al., 1985; Busso et al., 1990; Chapin et al., 1990; Craine, 2006; Oosthuizen and Snyman, 2003; Snyman, 2009). For example, a water stress experiment done with the perennial grass *Themeda triandra* (Forssk.), a dominant grass species in arid and semi-arid regions of southern Africa, found that both biomass and starch content of roots in non-defoliated plants increased by about 20% with 25% increase in water stress (Oosthuizen and Snyman, 2003). Most arid and semi-arid savannas in southern Africa are dominated by perennial grasses (O'Connor, 1991) and the consequences of resource limitation or competition on the roots of these grass types remain poorly understood. Adequate reserve storage in roots, particularly for perennial grasses, is not only critical for growth and reproduction but also as a buffer against effects of aboveground herbivory and fire (Danckwerts, 1993; Fargione and Tilman, 2002; Thornton et al., 2000).

In this exploratory study, we examined whether competition with trees influences root characteristics (as proxies of storage) of under-tree canopy perennial grasses compared with root characteristics of perennial grasses in gaps between trees (outside-tree canopy) and are outside the influence of tree roots. We did this in different sites in South Africa that varied in rainfall reflecting differences in water availability since water limitation intensifies competition among plants (Chapin et al., 1987; Craine, 2006; Gersani et al., 2001). The underlying hypothesis is that competition with woody species and water limitation results in higher allocation of resources to roots of grasses. Specifically we investigated the following:

1. Does variation in rainfall at the different study sites affect root characteristics of perennial under-tree canopy grasses?
2. Are the root characteristics of under-tree canopy perennial grasses affected by the presence of trees in these different study sites?
3. Does the presence of trees and the variation in rainfall at the different study sites influence the root characteristics of these perennial under-tree canopy grasses?

2. Methods

2.1. Study sites

The study was carried out in three study sites – Tswalu Nature Reserve (200 mm – Dry site), Venetia-Limpopo Nature Reserve (400 mm – Intermediate site) and Andover Game Reserve (600 mm – Wet site) in South Africa that vary in the mean annual rainfall (Fig. 1). In all sites most of the rain occurs between October and March. All three sites were chosen such that the soils were sandy and nutritionally poor with prominently a granitic bedrock. However, there were differences in vegetation composition largely due to the differences in the annual precipitation. The location, type of bedrock, mean annual precipitation and the common trees and grasses found in the three study sites are given in Table 1. Fire is not common in Tswalu and Venetia-Limpopo Nature Reserves. However, in the latter fire management is practiced on a multi-year rotational basis that is decided by the reserve managers. In Andover GR, the Park management practices fire management with rotational block burning every 5 years. The study sites hereafter will be referred to as Dry, Intermediate and Wet sites.

2.2. Study design and vegetation sampling

We used a split-plot sampling design. Within each study site we sampled 12 main plots. From each main plot two ungrazed subplots, one under the tree canopy and the other outside the tree canopy were sampled. The ungrazed subplots were not situated inside exclosures in any of the three study sites. Grazing was not prevalent in these sites as the animal densities were very low. We were careful that there was no grazing on these subplots as there could be grazing related compensatory growth by the grasses due to defoliation. We wanted to avoid this and solely focus on the effects of trees. A tuft of grass was selected for sampling from each subplot. We took care that all the grass tufts were similar in size in all the study sites in terms of grass height (range 55–60 cm) and grass tuft diameter (range 8–10 cm).

We selected commonly occurring acacia tree species in all three sites for sampling under-tree canopy areas. The tree species were *Vachellia nilotica* (Linn.) in the wet site, *Vachellia tortilis* (Forssk.) in the intermediate site and *Vachellia erioloba* (E. Meyer.) in the dry site. The grass species sampled under- and outside-tree canopy were all perennial tuft grasses: *Panicum maximum* (Jacq.) in the wet site, and *Aristida stipitata* Hack *var stipitata* in the intermediate and dry sites. These were the dominant under-tree canopy grasses in the three sites but were also found in a high abundance outside the tree canopy. Grass tufts were sampled around the base of the tree (under-tree canopy site) within a radius of 1 m around the tree trunk and in the paired adjacent area at a 30 m distance away from the tree canopy in the open grassland (outside-tree canopy site). We maintained a distance of approximately 30 m which is considered well outside the rooting zone of any of the trees (Ludwig et al., 2003; Sternberg et al., 2004).

2.3. Sampling and analysis of roots

All sites were sampled for grass roots during the peak dry season (August 2010) when grass root reserves are expected to be at their maximum and the root turnover dynamics would be minimal (Coyne and Cook, 1970; Danckwerts and Gordon, 1990; McNaughton et al., 1998; White, 1973). The aboveground grass leaf and stem material was removed. We collected the base of the grass tuft with the stolon, rhizomes, and the roots with root crowns of the grass tuft where the maximum storage in tropical grasses is reported (Coyne and Cook, 1970; Danckwerts and Gordon, 1990). Using an auger with a diameter of 10 cm, the grass tuft was cored at the centre of the tuft until a depth of 120 cm in 20 cm increments. For analysis, the biomass of only the first 20 cm was used as both the number of roots and associated biomass became almost negligible below this depth.

Root samples along with the soil were collected and sieved with 2 mm sieves using fine water jets for separating root material. Dead root material was determined visually (whenever needed, a handheld lens was used for confirmation) and was removed. Root biomass is essentially the dry weight of the roots per unit volume of soil. The roots were air dried in an oven at 50 °C (to avoid loss of organic compounds such as sugars and starch as well as to prevent volatilization of N from the plant tissues) to constant weight. The samples were finely ground in a grinding mill (2 mm mesh size) for further analysis. Root biomass was measured for all 12 main plots (24 grass tufts per site) whereas root characteristics (Section 2.4) were measured in the laboratory for only 5 main plots (10 grass