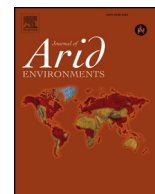




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# Above- and below-ground allocation and functional trait response to soil water inputs and drying rates of two common savanna grasses

Ciro Cabal\*, Daniel I. Rubenstein

Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ, 08544, USA

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## ABSTRACT

The study of functional trait plasticity and optimal allocation strategies in a water competition context may help to explain the mechanisms relating plant competition to ecological semi-arid patterns. We measured four functional plant traits –root to shoot ratio, superficial to deep roots ratio, root diameter, and root estimated surface area to shoot ratio– in wild populations of two C4 grasses in a Kenyan savanna to assess their responses to different water inputs (changing with latitude) and soil drying rates (driven by canopy cover). Root:shoot allocation was different between the two species. We show that to account for root architecture helps understanding root allocation strategies, especially in species with high plasticity in root geometry. Concretely, in our case, a higher root allocation in wetter conditions was driven by water storage and not water foraging in the species with high root diameter variability. Superficial root allocation responded to changes associated with drying rates but not to water input, and shallower root systems developed under higher water stress conditions, supporting rainfall intermittency models of savanna tree-grass competition. We also suggest self-shading as a facilitation mechanism that may affect spatial patterns according to the scale-dependent feedback hypothesis.

## 1. Introduction

Semiarid biomes are characterized by complex vegetation patterns that regionally generate a mosaic landscape of grassland, shrubland and woodland patches (Whittaker, 1975). Particularly, extensive C4 permanent grasslands in semiarid systems have attracted the attention of ecologists (Bond, 2008). Complex grass-tree patterns in savanna systems are a problem that has been addressed from bottom-up processes, particularly at broad scales like the biomes (Breckle, 1999; Woodward et al., 2004). However, at regional to local scales most work focus on top-down approaches to explain the permanence of grassland patches, focusing on the effects of disturbances (Bucini and Hanan, 2007), namely fire (see Louppe et al., 1995; Keeley and Rundel, 2005; Sankaran et al., 2005; Staver et al., 2011; Schertzer et al., 2015), herbivory (see Owen-Smith, 1987; Van de Koppel and Prins, 1998; Kartzinel et al., 2014) and human activity (see Young et al., 1995; Bugalho et al., 2011; Boughton et al., 2013). Some theoretical work has connected semi-arid plant community spatial patterns to plant-plant water competition (see for instance Pärtel and Wilson, 2002; Rietkerk et al., 2004; Martínez-García et al., 2013) but we need more empirical work devoted to disentangling belowground water competition between C4 grasses and trees, especially when the latter are at the seedling stage and the competition for water may asymmetrically favor

grasses (Campbell and Holdo, 2017).

The study of plant functional traits is a growing branch of functional ecology, and belowground traits, despite being more cryptic and poorly understood, may contribute valuable information about plant resource foraging (Zemunik et al., 2015). Disentangling the patterns of variation of plants' belowground responses to different soil resource availability can contribute to our understanding of resource acquisition strategies and may forecast species survival (Li et al., 2017). The examination of both belowground and aboveground plant functional traits may not only help understand species coexistence (Mueller et al., 2013; Zuppinger-Dingley et al., 2014; Ravenek et al., 2014), but can also provide useful information for explaining complex patterns of vegetation physiognomy driven by competitive exclusion of completely different functional groups, such as tree thickets and C4 grasses in savannas. In this study, assessing the architectural response of roots, we examine variation in four belowground functional traits in response to different water availability conditions: Root to shoot biomass ratio (R:S), superficial (< 6 cm) to deep root biomass ratio (S:D), root diameter ( $\emptyset$ ), and root estimated surface area to shoot biomass (Rs:S). By assessing these four key functional traits, we explore strategies that grasses may use to compete with neighbors for water, may these neighbors be other grasses, forbs, or woody plant seedlings and saplings.

\* Corresponding author.

E-mail address: [ccabal@princeton.edu](mailto:ccabal@princeton.edu) (C. Cabal).<https://doi.org/10.1016/j.jaridenv.2018.06.008>Received 8 January 2018; Received in revised form 9 June 2018; Accepted 20 June 2018  
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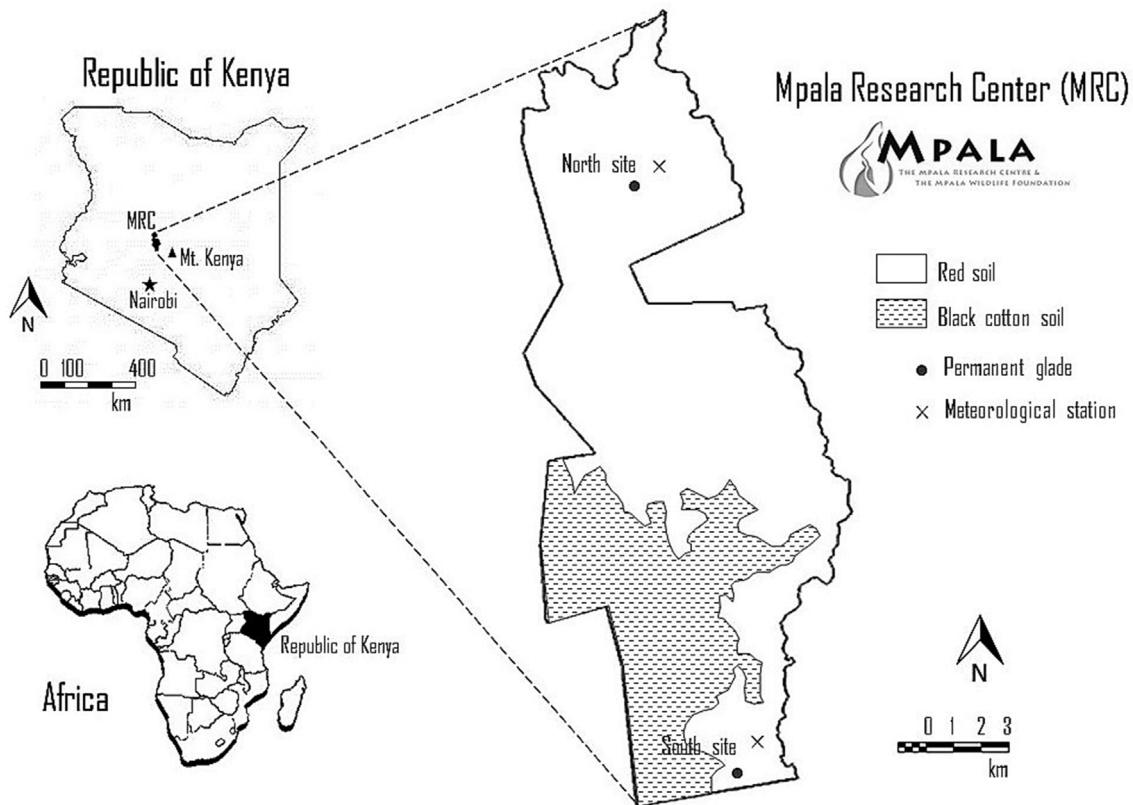


Fig. 1. Map of the study site.

Long-lasting glades are a characteristic vegetation feature in central Kenyan ecosystems, occurring alongside woodland communities. Medium sized (around 5 ha) glade patches are a common element in the vegetation mosaic dominated by savanna woodlands that have been associated with settlements of pastoralists abandoned decades ago (Young et al., 1995). As discussed above, the persistence of these patches could be facilitated by herbivory and fire, but few empirical studies have investigated whether competition between C4 grasses and tree seedlings could contribute to the permanence of these patches. We conducted a comparative study in the Mpala Research Center (MRC), in Laikipia County (Republic of Kenya). We assessed the phenotypical response of two species typically present at our study site, *Cynodon plectostachyus* (K.Schum.) Pilg., and *Pennisetum stramineum* Peter., that were commonly found on glades and in the neighboring grass-tree ecotones. Different water availability conditions were tested using a water input factor driven by average annual precipitations, and a soil drying rate factor driven by changes in insolation and soil temperature due to canopy cover. Our empirical work was focused on testing two main sets of hypotheses:

Firstly, we tested whether plants benefit from concentrating their roots in shallow soil depths under water stress (shallow roots hypothesis). This hypothesis is conceptually based on the “two-layer hypothesis” and the idea that differences in root vertical distributions may explain tree-grass codominance in dry savannas, each functional group being the superior competitor in its soil layer (Ward et al., 2013). A recently published model suggested that grasses may outcompete trees when rainfall is intermittent but frequent (D’Onofrio et al. 2015), predicated on the assumption that small burst of precipitation may evapotranspire faster than it infiltrates the soil, thus making water from such rain events rarely available in deeper soil layers. Alternative hypotheses state that grasses in drier environments should develop deeper root systems, but this would only be true when a large enough portion of rainfall is able to infiltrate before evaporating from the soil surface.

Secondly, we hypothesize that root diameter may interact with

root:shoot ratios, thus necessitating a different index that considers the overall geometry of roots in order to capture a deeper understanding on root to shoot variations (Root diameter hypothesis). Plants are generally assumed to follow optimization allocation strategies putting more resources into root growth (high R:S ratios) when growing under soil water limiting conditions, to increase their ability to uptake water or nutrients (Chapin et al., 1987; Crick and Grime, 1987; Gedroc et al., 1996; Schenk and Jackson, 2002). However, in species with high  $\emptyset$  variability, like *C. plectostachyus*, alternative indexes may provide supplementary information about plant biomass allocation strategies. Fundamental geometry demonstrates that a wider cylinder must have higher absolute surface area but less surface to volume ratio. For a given volume of root (root assumed cylindrical), increasing root diameter would result in less total surface. More allocation into roots may be driven by causes other than foraging nutrients: for instance as storage organs. Only by controlling for root geometry can we disentangle these causes. To control for  $\emptyset$  in our *C. plectostachyus* data, we created an alternative ratio Rs:S using an estimated root surface area Rs (as a function of R and  $\emptyset$ ) and the shoot biomass, and we tested its results and compared them with R:S ratios in different environments.

In addition to the shallow roots hypothesis and the root diameter hypothesis, we also evaluated two additional hypotheses. First, we hypothesized that plants investing in non-palatable aboveground organs may benefit from self-shading the soil, by means of reducing evaporation and facilitating the survival of rhizomes in high water stress conditions. This hypothesis is important to consider given the role that facilitation may play in self-organized spatial patterns in semi-arid grasslands according to the scale-dependent feedback hypothesis (Rietkerk et al., 2002). Second, we tested whether the net effect of thicket canopy on C4 grasses growth was negative (interference) or positive (facilitation). The net interaction between C4 grasses and savanna thickets results from complex interactions between antagonistic forces related to the effects of shade (Valladares et al., 2016). On the one hand, the presence of a canopy may reduce water stress (Brooker

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