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INSIGHTS

Competitive response of savanna tree seedlings to C_4 grasses is negatively related to photosynthesis rate

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ABSTRACT

Savanna tree species vary in the magnitude of their response to grass competition, but the functional traits that explain this variation remain largely unknown. To address this gap, we grew seedlings of 10 savanna tree species with and without grasses in a controlled greenhouse experiment. We found strong interspecific differences in tree competitive response, which was positively related to photosynthesis rates, suggesting a trade-off between the ability to grow well under conditions of low and high grass biomass across tree species. We also found no competitive effect of tree seedlings on grass, suggesting strong tree-grass competitive asymmetry. Our results identify a potentially important trade-off that enhances our ability to predict how savanna tree communities might respond to variation in grass competition.

Key words: African savannas; photosynthesis rates; stomatal conductance; tree growth; tree-grass competition; tropical savanna.

TREE-GRASS COMPETITION IS A FUNDAMENTAL DRIVER OF VEGETATION DYNAMICS IN SAVANNAS AND OTHER GRASSY ECOSYSTEMS (Scholes & Walker 1993, Bond 2008). Grasses have been shown to compete strongly with trees at multiple demographic stages (Riginos 2009), but their effects are most dominant and consequential at the seedling stage, where grasses can strongly limit the ability of trees to recruit into larger, established size classes (Davis *et al.* 1999, Higgins *et al.* 2000). Despite the fact that competitive effects of grasses on trees (and *vice versa*) have been shown to be pervasive (Riginos 2009, Cramer *et al.* 2010, February *et al.* 2013, Werner & Prior 2013), much of the research in tree-grass interaction studies has tended to group grasses and trees into monolithic groups, despite increasing evidence that trees species vary in their response to grass competition (Cramer *et al.* 2010, 2012, Holdo & Brocato 2015). As a result, we lack a mechanistic basis for understanding interspecific variation in tree responses to grass competition. To address this gap, we conducted an experiment to (i) quantify tree seedling competitive responses and effects when grown with and without grass competitors, and (ii) explore how the competitive response is related to key tree functional traits. Specifically, we tested the hypothesis that tree species with low intrinsic growth (R_{max}) and photosynthetic rates are better competitors against grasses than fast growing species, based on prior work in tallgrass prairie ecosystems (Goldberg & Landa 1991).

We obtained seeds of ten savanna tree species from a commercial seed supplier in South Africa (Silverhill Seeds, www.silverhillseeds.co.za/). We scarified seeds of hard-coated species to promote germination, and soaked all seeds in water for 24 h. In mid-Dec 2015, we planted seeds in seed trays containing Pro-Mix (a peat-based, soil-less mix) in the Botany Greenhouse at the University of Missouri, and watered them daily. Simultaneously, we planted small (5–10 cm tall) cuttings of the perennial grass *Panicum maximum* (obtained from a supply of greenhouse-grown individuals) into seed trays. In early Jan 2016, we set up rows of pots (45 cm tall × 15 cm diam.) containing Pro-Mix in the greenhouse, randomly assigned half of the pots to a grass (G+) treatment and half to a no grass (G−) treatment ($N = 60$, plus five additional pots containing grass only for assessment of grass growth in the absence of a tree competitor), and then transplanted *Panicum* seedlings into the G+ pots. We watered pots daily to field capacity. In late Jan 2016, we randomly transplanted six seedlings per species (*Acacia burkei*, *Acacia xanthophloea*, *Combretum apiculatum*, *Combretum collinum*, *Combretum imberbe*, *Colophospermum mopane*, *Kigelia africana*, *Philenoptera violacea*, *Schotia brachypetala,* and *Terminalia prunioides*) into the pots (three each into G+ and G- treatments, one species per pot). For the remainder of the experiment, we provided fixed amounts (250 ml) of water to each pot three times/week, with total watering amounts designed to simulate an annual rainfall regime of 650 mm spread over a 7-month growing season (~ 23 mm/week). This value falls within the range of mean annual rainfall encountered by most of these species in their native range (Holdo & Brocato 2015). We provided double the usual amount of water on one occasion (April 8), having noticed that many of the plants appeared to be suffering from a degree of moisture stress.

To account for possible variation in light availability across the experimental layout, we quantified photosynthetically active radiation (PAR) over the course of the experiment, which extended over 8 wk. We used an Apogee Quantum Flux (Apogee Instruments, Logan, UT) sensor mounted on a tripod at canopy

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height to record light readings at every corner of the experimental layout between 1000 and 1400 h two to three times a week. At the end of the experiment, we harvested all tree and grass shoot biomass, and all tree root biomass (due to the difficulty of separating grass roots from the Pro-Mix mixture, we did not attempt to collect grass roots). We oven-dried all biomass at 60°C for 48 h prior to measuring dry biomass.

We measured photosynthesis (A) and stomatal conductance (g_s) rates on 40 tree seedlings (N ranged between 1 and 6 per species) from the G- treatment prior to the final harvest with a LI-6400 XT Portable Photosynthesis System (LI-COR Biosciences, Lincoln, NE). We were able to increase our sample size for photosynthesis measurements in some species by using plants from a second cohort of late-germinating individuals subjected to the same growing conditions that prevailed in the experiment. We found that including these individuals in our analyses did not affect our conclusions. Prior to conducting the measurements, we watered the pots to field capacity to ensure uniform (unstressed) conditions of soil moisture availability. To minimize unwanted variation in environmental conditions, we took measurements between 10:00 and 14:00. We placed one fully expanded leaf in the LI-6400 leaf chamber and exposed it to a constant light regime of 1000 μmol/m^2/s^{1}and CO$_2$ concentration of 400 ppm. For leaves that did not take up the entire area of the analysis chamber, we normalized readings to a per-area basis by using digital photographs of the portion of the leaf that had been inserted into the chamber, taken through a 3 × 2 cm cardboard cut-out designed to match the chamber dimensions. We subsequently analyzed each photograph using ImageJ to obtain the leaf fractional area present in the chamber, and adjusted all photosynthesis and conductance measurements to a unit area basis using these corrections (where necessary).

We used the *lme* function from the *nlme* package (Pinheiro & Bates 2000) in R v.3.0.2 (R Development Core Team 2011) to test whether tree seedlings were affected by grass competition, treating tree species as a random effect. We used log-transformed values of total seedling dry mass (M), seedling dry shoot mass (S), and root mass ratio (RMR) as dependent variables, and compared differences in these variables between the G+ and G- treatments. Having found clear treatment effects on M and S, we calculated mean values of M and S per species per treatment (G+ or G-), and then used the ratios M_{G+}/M_{G-} and S_{G+}/S_{G-} as indices of tree seedling competitive response to grass. Ratios of 0 and 1 indicate complete suppression of tree growth and no effect of grass competition, respectively. We then used regressions to examine the relationship between these competitive responses and mean values of: (i) A, (ii) g_s, and (iii) intrinsic growth rate as captured by M_{G-} and S_{G-} (final size in the absence of grass competition) across species. We used differences in grass shoot mass between pots containing only grass and pots with tree-grass mixtures as indices of the tree competitive effect.

Prior to analyzing the results of the competition experiment, we tested for heterogeneity in the light environment across our experimental layout, using PAR measured at each of four locations as our response variable and measurement day as a random effect. We found no systematic effect of position on PAR ($P = 0.15$). We found highly significant tree competitive responses to grass in terms of final total M ($P < 0.0001$) and shoot S ($P < 0.0001$) seedling dry mass across the ten species (Fig. 1A), but no effect of RMR. Conversely, there was no clear competitive effect of tree seedlings on final grass biomass (compared to grass-only pots, Fig. 1B). We found that the relative effect of grass competition across species was negatively correlated with species-specific A (M_{G+}/M_{G-}: $P < 0.05$; S_{G+}/S_{G-}: $P < 0.001$; Fig. 2), but not with g_s or final seedling size in the absence of grass (a proxy for maximum relative growth rate or RGR_{max}).

Our experiment found clear support for a relationship between competitive response to grasses and seedling

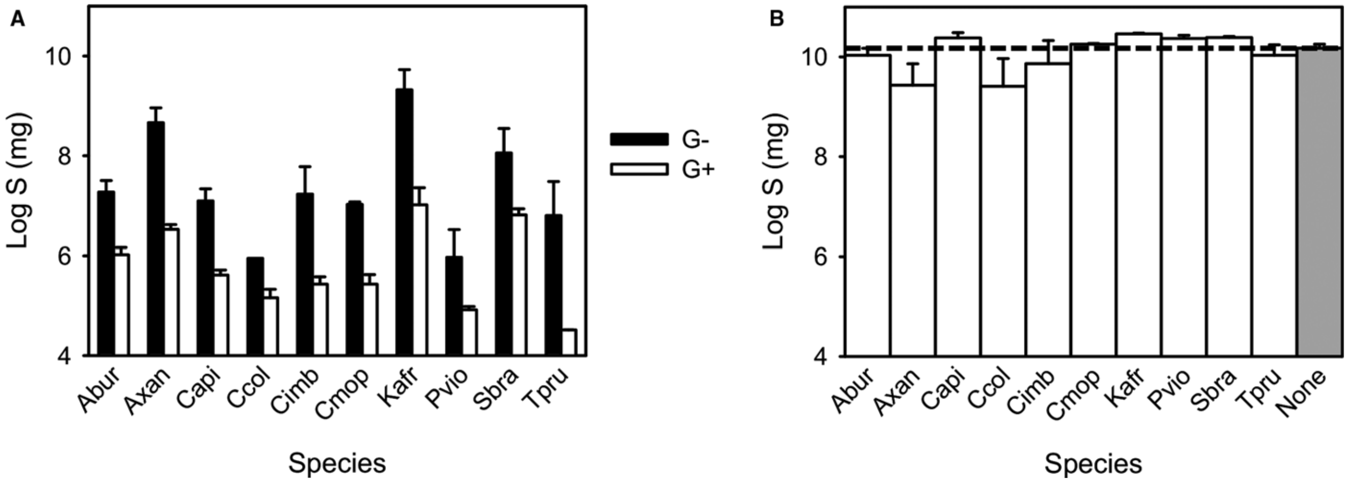

FIGURE 1. Tree competitive responses and effects (mean and SE) to grass competition across ten tree savanna species. (A) Variation in tree final shoot dry mass S as a function of grass competition (G+ = grass present, G- = grass absent), a proxy for tree competitive response. (B) Variation in final grass shoot dry mass S across tree species. Values for grass grown without tree competitors are shown for reference in gray, and the differences between white bars and the gray bar represent the tree competitive effect.

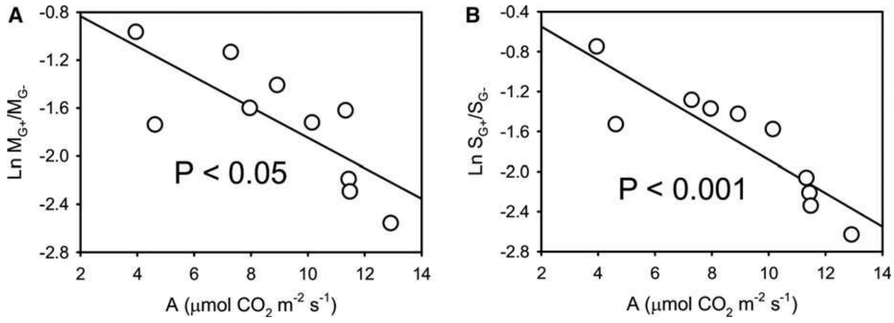

FIGURE 2. Effects of photosynthesis on the relative response of trees to competition from grasses across tree species. (A) Ratio of total dry mass for trees grown with grasses (M_{G+}) to total dry mass for trees grown without grasses (M_{G-}) as a function of A; (B) ratio of shoot dry mass for trees grown with grasses (S_{G+}) to shoot dry shoot mass for trees grown without grasses (M_{G-}) as a function of A.

photosynthetic rates (Fig. 2), suggesting that tree functional traits provide a platform for predicting interspecific variation in seedling responses to grass competition. The relationship with photosynthetic rates suggests a trade-off between the ability of tree seedlings to tolerate high grass biomass (*i.e.*, conditions of resource limitation) and their ability to perform under high-resource conditions. Previously, Pillay and Ward (2014) had found a positive relationship between SLA and tree competitive response across four savanna species (which would be broadly consistent with our hypothesis), but this response was in competition with other tree species rather than with grasses. This suggests that a trade-off exists between the inherent ability to acquire resources by savanna trees and their ability to tolerate grass competition. In this respect, our results are somewhat consistent with the finding that species with low inherent growth rates, while having small competitive effects against neighbors, have a higher ability to tolerate competition (Goldberg & Landa 1991). Although the relationship between competitive response and our RGR_{max} analog was not significant, the trend of the relationship was consistent with that for photosynthesis rates. Also in agreement with previous studies (Goldberg & Landa 1991, Wang *et al.* 2010), we found that there was no clear relationship between competitive effect and response for savanna seedlings competing with grasses. Moreover, there was little evidence of any competitive effect on grasses at all (Fig. 1B), suggesting a strong asymmetry in tree-grass competitive effects, as suggested by prior work (February *et al.* 2013).

Our experimental results suggest that competition between African savanna tree seedlings and C_4 grasses is highly asymmetric in favor of grasses, which cause strong reductions in tree growth rates. There is also a large amount of interspecific variation in tree response to grass competition. Previous work suggested that this variation may be due to interspecific variation in the extent of rooting depth differences between grasses and tree seedlings (Holdo & Brocato 2015), but other results from our group (Ketter & Holdo, in review) suggest that this is not the case, and that there is little evidence for rooting separation between grasses and tree seedlings growing under our experimental conditions. Our results suggest rather that interspecific variation in tree response to grass competition is negatively related to C assimilation capacity across tree species. This provides a novel framework for understanding interspecific variation in tree responses to grass effects in savannas, and suggests that there is a trade-off between the ability to grow with and without grass competition across tree species, with potentially important implications for our understanding of tree community assembly processes in savanna ecosystems.

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DATA AVAILABILITY

Data available from the Dryad Repository: https://doi.org/10.5061/dryad.57080 (Campbell & Holdo 2017).

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