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Tree species from different functional groups respond differently to environmental changes during establishment

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Abstract Savanna plant communities change considerably across time and space. The processes driving savanna plant species diversity, coexistence and turnover along environmental gradients are still unclear. Understanding how species respond differently to varying environmental conditions during the seedling stage, a critical stage for plant population dynamics, is needed to explain the current composition of plant communities and to enable us to predict their responses to future environmental changes. Here we investigate whether seedling response to changes in resource availability, and to competition with grass, varied between two functional groups of African savanna trees: species with small leaves, spines and N-fixing associations (fine-leaved species), and species with broad leaves, no spines, and lacking N-fixing associations (broad-leaved species). We show that while tree species were strongly suppressed by grass, the effect of resource availability on seedling performance varied considerably between the two functional groups. Nutrient inputs increased stem length only of broad-leaved species and only under an even watering treatment. Low light conditions benefited mostly broad-leaved species' growth. Savannas are susceptible to ongoing global environment changes. Our results suggest that an increase in woody cover is only likely to occur in savannas if grass cover is strongly suppressed (e.g. by fire or overgrazing). However, if woody cover does increase, broad-leaved species will benefit most from the resulting shaded environments, potentially leading to an expansion of the distribution of these species. Eutrophication and changes in rainfall patterns may also affect the balance between fine- and broad-leaved species.

Keywords Soil nutrients · Rainfall · Light · Trees-grasses interactions

Introduction

Savannas are plant communities dominated by trees and grasses, which account for approximately one-third of the

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land cover (Cole 1986; Sala 2001). These ecosystems can have high plant species diversity (Cole 1986) and are found in environments characterised by spatial and temporal variability in water resources (Kanegae et al. 2000; Kottek et al. 2006) and nutrient resources (Venter et al. 2003; Schwinning and Sala 2004). In addition, frequent disturbances by fire (Barbosa et al. 1999; Russell-Smith et al. 2003) and herbivory (Staver et al. 2009) often characterize these environments. To date, a wealth of information has been collected on the life histories and environmental responses of individual species within savannas (see reviews by Van Auken 2000; Bond 2008), yet few studies have compared the growth performance of multiple savanna species (Bond 2008). Consequently, our understanding of the processes influencing plant species diversity, coexistence and turnover along environmental gradients in savannas is poor, partly because we lack the baseline data to parameterise models that can predict changes in the species composition of savannas under different environmental conditions (Van Langevelde et al. 2011). Given that savannas are considered to be one of the most susceptible habitats to climate change (IPCC 2007), this limitation is an important reason for concern.

Understanding how plant communities change with ongoing environmental changes (e.g. climate, land use) is a central issue in ecology (e.g. Sala et al. 2000; Lambin et al. 2001; Smith 2012). As seedling and juvenile growth are critical stages in the regeneration of trees and overall plant population dynamics (Higgins et al. 2000; Radford et al. 2001; Wiegand et al. 2006), a better understanding of how seedlings of different species in a community perform under different environmental conditions relative to one another will help to explain the composition of plant communities and how they develop under changed environmental conditions.

Differences in functional traits can mechanistically explain why species differ in their performance across resource and disturbance gradients (Chapin et al. 1993; Violle et al. 2007). Qualitative trait differences between species which are associated with nutrient and water gradients have been recognised (Cole 1986; Scholes 1997; Pennington et al. 2000). Notably, within African savannas, dystrophic or humid savannas are dominated by non-spinescent, broad-leaved, non-N-fixing species, while eutrophic or arid savannas are dominated by fine-leaved species which may additionally be spinescent or N-fixing (Scholes 1997; Venter et al. 2003; Mucina and Rutherford 2006; Kottek et al. 2006). These two groups can also be distinguished on the basis of their leaf chemistry, physiology and morphology (Table 1). Therefore, there is reason to believe that seedlings of species representing these functional groups respond differently to changes in supply rates of resources, and that these differences may in part explain why they dominate in different environments.

Here we use a multi-species experiment in an African semi-arid savanna to investigate whether juveniles of four locally abundant fine-leaved tree species and four common broad-leaved tree species (Table 1) differ in their responses to variation in water, nutrient and light supply during their first growing season, and whether they differ in their response to competition from a C_4 grass species (*Digitaria eriantha*, Steud.) for these resources. To test whether and how the seasonal variation in the resource distribution affected survival and growth of tree seedlings

Table 1 Functional trait data for the tree species used in the experiment

Species	Family	Sub-family	N_2-fixing[a]	Leaf type[b]	Leaf size[c] (cm^2)	Spinescence
Fine-leaved species						
Acacia nigrescens Oliv.	Fabaceae	Mimosoideae	Yes	Bipinnate	16.0 (±3.61)	Yes
Acacia nilotica Willd.	Fabaceae	Mimosoideae	Yes	Bipinnate	12.0 (±2.1)	Yes
Acacia tortilis Hayne	Fabaceae	Mimosoideae	Yes	Bipinnate	12.5 (±7.0)	Yes
Dichrostachys cinerea Wight and Arn	Fabaceae	Mimosoideae	Yes	Bipinnate	31.7 (±28.44)	Yes
Broad-leaved species						
Colophospermum mopane J. Léonard	Fabaceae	Caesalpinioideae	No	Bifoliate	47.2 (±21.69)	No
Combretum apiculatum Sond.	Combretaceae	–	No	Simple	25.3 (±5.35)	No
Schotia brachypetala Sond.	Fabaceae	Caesalpinioideae	No	Pinnate	42.6 (±17.64)	No
Peltophorum africanum Sond.	Fabaceae	Caesalpinioideae	No	Bipinnate	99.5 (±81.81)	No

For continuous variables, the values are means (±SD)

[a] Treydte et al. (2007); Cramer et al. (2010)

[b] Coates (2002)

[c] Tomlinson et al. (2012, 2013); species grown under common greenhouse conditions. Leaf size (and leaf N content) measured on 20-week-old plants

of different species, we measured aboveground growth parameters (total shoot biomass, leaf to stem ratio (LSR) and stem length) as proxies for seedling performance under the different treatment conditions. As several studies suggest that water stress (Midgley and Bond 2001; Sankaran et al. 2005; Kraaij and Ward 2006; Meyer et al. 2007), nutrient shortage (Bardgett and Wardle 2003; Van der Waal et al. 2009), and shade (Gerhardt 1996; Loth 1999) may limit seedling survival and establishment in dry systems, we expected all species to respond positively to regular water availability, increased nutrient supply and full light, and negatively when competing with grass for water and nutrients (hypothesis 1). Secondly, because fine-leaved species have greater leaf nutrient concentrations and photosynthetic rates (Kgope 2004) than broad-leaved species (Table 1), we expected fine-leaved species to respond more positively to added nutrients than broad-leaved species (hypothesis 2). Thirdly, fine-leaved species are dominant tree species in nutrient-rich savannas, and experience higher browsing pressure (Mucina and Rutherford 2006; Kottek et al. 2006). To protect young leaves from herbivores, these species have high lateral branch growth (cage-like structural form) (Archibald and Bond 2003); hence, we expected seedlings of fine-leaved species to have lower stem length than broad-leaved species (hypothesis 3). As broad-leaved species are suggested to be more tolerant to shade than fine-leaved species (Smith and Goodman 1986, 1987), we expected broad-leaved species seedlings to have a better growth performance in shaded environments, showing more efficient adaptations (LSR) to growth under shaded environments (hypothesis 4).

Materials and methods

Study area

This study was conducted in a savanna region, at Timbavati Private Game Reserve, Limpopo Province, South Africa (24°15′20.23″S, 31°23′23.63″E) during the wet season of 2009–2010 (November–May), in a fenced area that excluded large herbivores. The growing season mean rainfall (from October till April) of the previous 10 years (2000–2010) was ca. 456 mm (Satara Camp, Kruger Park ca. 40 km northeast of the research site). The mean maximum temperature during January (hottest month) is 33.7 °C and the mean minimum temperature for June (coolest month) is 9.4 °C (Venter et al. 2003). The vegetation is described as Granite Lowveld (Mucina and Rutherford 2006), and the area is classified as semi-arid under the Köppen-Geiger System (see Kottek et al. 2006). Soils in the experimental site are shallow (ca. 1.5 m depth) and mainly derived from granite (Venter et al. 2003) with occasional gabbro extrusions. Soils derived from granite tend to be coarse-textured and nutrient poor (i.e. low availability of N and P) on crests and mid-slopes (Treydte et al. 2007), but nutrient availability may be elevated in bottom positions in the landscape, and very locally such as on termitaria or underneath large *Acacia* trees (Grant and Scholes 2006; Treydte et al. 2007).

Species

To test whether various savanna tree species differed in their response to environmental conditions, we selected eight locally abundant tree species that make up a large proportion of vegetation cover in the Lowveld savanna region in South Africa. In African semi-arid savannas, broad-leaved and medium-leaved species are found on dystrophic soils, characterised by high fire frequency (annual to triennial) and mean annual precipitation (MAP) from 600 to 1,500 mm (Kraaij and Ward 2006). The study species were separated into two different functional groups: four with characteristic small leaves, spines, and N-fixing associations (hereafter termed ‘fine-leaved species’), and four with characteristic broad leaves, no spines, and lacking N-fixing associations (hereafter termed ‘broad-leaved species’) (see Table 1). Since these species are abundant in the savannas of southern Africa, changes in their populations due to varying environmental conditions will likely have substantial effects on the local vegetation structure. Most species found on eutrophic soils or skeletal soils with low fire frequency (quinquennial or longer) and MAPs of 300–800 mm (Cole 1986) are fine-leaved species (largely Mimosoideae). The unusual exception to this is the broad-leaved *Colophospermum mopane*, which also occurs on heavy eutrophic soils in warmer parts of south-central Africa (Mucina and Rutherford 2006). Other broad-leaved species are most common in soils with low nutrient levels.

Experimental design

The study site was ploughed (about 20 cm deep) to homogenize the soil and to give all treatments similar starting conditions. Five blocks were laid out within an area of 90 × 90 m. Inside each block, different treatment combinations involving manipulation of grass competition [with grass (G1), or without grass (G0)], water [regular water supply (W1), or natural rainfall (W0)], light [with light (L1), or without light (L0)] and nutrients [with N (N1), or without N (N0)], which were applied in 2 × 2-m plots separated by 2-m gaps. As shade cloth could intercept natural rainfall, thereby causing differences in water supply between shaded and unshaded treatments with natural rainfall, we used an incomplete treatment design where light and water were not fully crossed (all combinations of

W0 × L0 were absent). To examine whether and how seasonal variation in the distribution of rainfall affected survival and growth of tree seedlings of different species, we set up two water treatments that differed in the regularity with which they supplied water to plants. For the regular watering treatment (W1), natural rainfall was excluded from the treatments by rain-out shelters and we supplied a fixed amount of 46.3 mm (185 L per 2 × 2-m plots) of water to the seedlings every 2 weeks for the 6 months of the experiment (November 2009–May 2010), yielding a total of 556 mm water over the experiment. This amount of water in W1 was based on the water deficit rules as defined in the Köppen-Geiger system climate classification (550 mm per season), based on a recent update of these regional classifications (Kottek et al. 2006). The irregular, natural rainfall treatment (W0) received 623 mm during the period of the experiment, which was higher than the long-term mean for the area (438 mm/season). The 2009–2010 wet season rainfall distribution had two major rain peaks in November–December 2009 (320 mm) and April–May 2010 (202 mm), with an intervening 3-month dry period (January–March) (Fig. 1).

To test whether species differed in their ability to tolerate shade and whether shade affected the competitive effects of grass on seedlings, we included a low-light treatment (L0) that mimicked the level of shading (around 20 % natural light) that is found under closed tree canopies of savanna tree species (Kanegae et al. 2000; Bauhus et al. 2004). To create this level of shading a 2-m-high shade net was placed above the seedlings, consisting of one layer of polyurethane shade cloth that blocked 80 % of incident solar radiation. In the high-light treatment (L1) plants were grown in full sunshine.

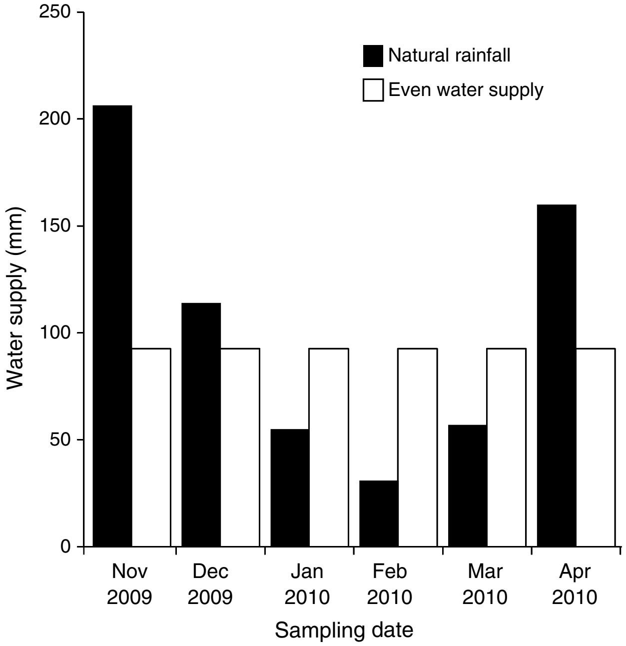

Fig. 1 Water supply during the experiment. *Closed bars* show monthly rainfall in the area during the wet season of 2009–2010 (natural rainfall treatment). *Open bars* show the water supplied monthly in the even watering treatment. Rainfall data were obtained from the weather station in Satara Camp, Kruger Park, 40 km northeast of the research site

To test whether seedlings of different species differed in their growth response to increased soil nutrient supply and whether this affected the competitive effect of grasses on tree seedling growth, we included two nutrient treatments: no nutrients added (N0) and nutrients added (N1). Granular slow-release 3:1:2 NPK inorganic fertilizer (Osmocote Exact Standard 15:9:11; Scotts International, the Netherlands) was added to the N1 treatment plots once at the start of the experiment at a rate of 4 g N m^{-2} per plot (Kraaij and Ward 2006). A normal annual amount of N mineralized in the study region was estimated at 5.8 g N m^{-2} (Scholes et al. 2003), so the N1 treatment increased the local soil N availability ca. 1.7 times.

To test whether grass competition for resources affected tree seedlings, we included plots with grass (G1) and plots without grass (G1). For the plots with grass a single local common grass species, *Digitaria eriantha,* was seeded and established in the plots a year before transplanting the seedlings, leading to a well-established grass sward in all plots. The grass biomass in the plots ranged from 3,141.6 (shaded plots) up to 5,725.8 kg dry matter (DM) ha^{-1} (natural rainfall and full light) (Supplementary information, Table S1). These values on non-shaded plots were very close to the values naturally occurring in the study region [Kruger National Park, range 5,905.2–6,633.1 kg DM ha^{-1} (Zambatis et al. 2006)]. Although a total absence of grass is not common, it can occur after a drastic disturbance event (e.g. heavy herbivory levels, intensive fires or severe drought) and for a short period (personal observation), potentially increasing tree establishment and growth (van Langevelde et al. 2003).

Four weeks before the experiment began, seeds of all tree species were sown in nursery bags filled with soil of the experimental area. At the start of the experiment four seedlings of each species were randomly transplanted for each treatment combinations. Thus a total of 240 seedlings were planted per species across the 12 treatment combinations in five blocks. The seedling density in the plots was 20 seedlings m^{-2}, which was lower than the natural early seedling density in savannas [more than 50 seedlings m^{-2} in the seed/seedling bank (Tefera 2011)].

Measurements

Each seedling was monitored for 6 months from November 2009 to May 2010. At the end of the experiment, the number of surviving seedlings per species per treatment combination was recorded. The longest stem length (from ground level to tip) was measured on each individual seedling. After that, the shoot of each seedling was harvested, separated into leaf and stem, dried at 70 °C for at least 48 h and the leaf biomass (g) and stem biomass (g) were weighed separately. Total shoot biomass was calculated as the sum of leaf and stem biomass. The LSR was calculated using the measurements of leaf and stem biomass.

Data analysis

To establish whether the established functional groups (fine-leaved versus broad-leaved species) were significantly different from one another in terms of their summed response to all treatments, we performed multivariate analyses on the data for shoot mass, stem length and LSR, respectively, using the R vegan package (http://cran.r-project.org/web/packages/vegan/vegan.pdf). Firstly, the data for each variable were log transformed (log natural) to normalise residuals. Subsequently, we calculated average values per species per treatment combination per block, yielding five values per species per treatment. Finally to ensure even weighting between the treatments, we standardised the treatment values; the sample mean and the sample SD are computed and then used to standardize the value. We performed principle components analysis (PCA) on the three data sets (shoot mass, stem length and LSR) and plotted the species' scores and treatment scores along the first two axes.

After visual interpretation, we identified groups discriminated in two-dimensional space. We started by looking for the two posited groups, fine-leaved versus broad-leaved species, but allowed for the possibility of finding additional groups. Following this analysis, we then regrouped the species and formally tested differences between groups using permuational ANOVA (Anderson 2001), implemented in the adonis command in vegan.

To assess the effect of functional group (fine-leaved, broad-leaved), grass (presence, absence), water (regular, irregular), light (full sun, shade) and nutrients (natural, nutrients added) on tree seedling survival and growth performance (total shoot biomass, LSR and stem biomass), we used generalized linear mixed models (GLMMs) (Pinheiro and Bates 2000; Zuur et al. 2009). To account for inter-specific variability, species was treated as a random factor in the GLMMs (Species, eight levels), and plot nested within experimental block. As the inclusion of block and plot position did not significantly improve the model, these two random factors were dropped from the final model.

Seedling survival (counts of seedlings that survived) was analysed using a Poisson distribution, and the remaining variables were analysed using Gaussian distributions. Due the incomplete block design we ran two separate sets of analyses. Firstly, we used the data from the plots where light was always maximal (L1, full sun) and analysed the effect of functional group, water, grass and nutrients and their interactions on seedling survival and growth performance (total shoot biomass, LSR and stem length). Subsequently, we repeated the analyses using the data from plots where water was always regularly applied (W1) and tested the effects of functional group, light, grass and nutrients and their interactions on the same response variables.

The treatment W1L1G0N1 was chosen as the control due to the fact that it was common to both analyses, and also because it was the treatment where the best growth performance in all study species was expected (all tested resources were relatively abundant in space and time). While all individuals of all species were germinated under similar conditions, the size of seedlings at the beginning of the experiment differed among some species (see interspecific variation in the control values in Supplementary information, Table S2). As we sought to study the effect of the treatments independently of the species' intrinsic growth rate, for each tree species and growth parameter, we calculated the relative performance of each individual (i.e. the growth relative to control conditions) ($R_{i,j}$) by dividing the value for the individual ($T_{i,j}$) by the average value for the parameter of the species in the control treatment, $\overline{C_j}$ (W1L1G0N1)

$$R_{(i,j)} = \mathrm{Log}\left(\frac{T_{i,j}}{\overline{C_j}}\right) \tag{1}$$

This procedure was used for the two growth performance parameters, total shoot biomass and stem length. The procedure removes variation of the initial condition of the species while keeping intraspecific variation in relative growth. A log natural transformation of the raw data was necessary to normalise the residuals.

Mixed model analyses were conducted in R (R Development Core Team 2013) using the lmer function of the package lme4 (Pinheiro and Bates 2000). Output from lmer includes SE estimates for the random effects and regression model coefficients for the fixed effects. To test the significance of the terms in the statistical model we ran Monte Carlo Markov chain (MCMC) simulations (100,000 iterations) using the MCMCglmm package (http://cran.r-project.org/web/packages/MCMCglmm/MCMCglmm.pdf) to analyse seedling survival and the LanguageR package (http://cran.r-project.org/web/packages/languageR/languageR.pdf) to analyse seedling growth performance.

Results

Functional group (fine-leaved versus broad-leaved) differences

In contrast to our expectations, we did not found a sharp division between fine-leaved species (*A. nigrescens*, *A.*

nilotica, *A. tortilis*, *D. cinerea*) and broad-leaved species (*C. apiculatum*, *P. africanum*, *S. brachypetala* and *C. mopane).* This result is mainly due the odd combination of trait and responses showed by *C. mopane*, which in the PCA (Fig. S1) lies between fine-leaved species and other broad-leaved species. Based on these results, *C. mopane* was excluded from the broad-leaved group in subsequent analyses, and tested separately. These analyses show that shoot mass responses of *C. mopane* across treatments did not differ from those of fine-leaved species (PERMANOVA, $P = 0.21$), whereas the broad-leaved species group differed highly significantly from fine-leaved species ($P < 0.001$) and from *C. mopane* ($P < 0.001$). These differences appeared to be mainly associated with different responses to the shaded versus unshaded treatments (for more details see Fig. S1). Stem length responses to treatments differed between all three groups (fine-leaved versus *C. mopane*, $P = 0.02$; fine-leaved versus broad-leaved, $P < 0.001$; *C. mopane* versus broad-leaved, $P < 0.001$). This difference in performance between the groups appeared to be largely associated with a difference in stem growth in the sun-grown plots without grass competition, which was associated with the second axis of discrimination. Finally, with respect to LSR, fine-leaved species were significantly distinguished from broad-leaved species ($P < 0.001$), but *C. mopane* was not distinguished from fine-leaved species ($P = 0.25$) nor from the other broad-leaved species ($P = 0.76$). As for stem length, the difference in performance between the groups appeared to be largely associated with a difference in stem growth in the sun-grown plots with and without grass competition (see Fig. S1b).

Seedling survival and growth response

Seedling survival rate (overall percentage of seedlings that survived at the end of the experimental period) did not differ significantly between species groups (fine-leaved species versus broad-leaved species), nor was it significantly affected by the different treatments (Table 2). In all treatments, the seedling survival rate was high (>80 %) in all species.

Seedling growth parameters (total shoot biomass, LSR and stem length) were significantly affected by the different growth conditions (Table 3; Figs. 2, 3). Grass had a negative effect on seedling performance of all species (Table 3), reducing shoot biomass and stem length across all water, light and nutrient treatments (Figs. 2, 3). Seedling responses to grass competition differed across resource treatments (Table 3; Figs. 2, 3). The negative effect of grass on stem length of broad-leaved species was less severe under natural rainfall plots than under an even water supply (Fig. 2).

Nutrients addition only had a positive effect on the stem growth of broad-leaved species, but only under regular water supply, the effect being most accentuated in the presence of grass (Fig. 2; see significant four-way interaction functional group:water:grass:N result in Table 3).

Shade negatively affected total shoot biomass in both species groups (fine-leaved, broad-leaved species) as well as in *C. mopane* (Table 3), but the negative effect was relatively stronger for fine-leaved species and *C. mopane* than for broad-leaved species (Fig. 3). Moreover, the stem length of broad-leaved species was enhanced by shade (Fig. 3). Furthermore, all three species groups showed a tendency to increase LSR under low light and grass conditions (Table 3; Fig. 3).

Discussion

Functional group (fine-leaved versus broad-leaved) differences

While *C. mopane* was not clearly associated with fine-leaved or broad-leaved species groups, after excluding this species the two functional groups were distinct. Although *C. mopane* has the characteristics of a broad-leaved species (large-leaved, non-spinescent and non-N-fixing), this species responded to treatments more similarly to the fine-leaved species than to the other broad-leaved species. Indeed, while most savanna broad-leaved species are found on dystrophic soils (Kraaij and Ward 2006), the distribution of *C. mopane* is heavily linked with eutrophic soils, where fine-leaved species are abundant (MacGregor and O'Connor 2002). Empirical evidence on seedling growth and establishment of this species is limited (but see Mushove et al. 1995; Veenendaal et al. 2008; Van der Waal et al. 2009), as well as on the mechanisms that allow this species to prevail in dystrophic soils (e.g. architecture of root system; production of compounds to suppress grass growth). As the aim of this study was to test general patterns of species groups that exist in several savannas, and not to focus on a given species, we will focus the discussion of our results on the dissimilarities between the responses of fine-leaved and broad-leaved species. It is, however, possible that other ecological traits, which we did not consider in this study, interact with this functional group division. Further studies focusing on broad-leaved species, which are common in dystrophic areas, could help unveil another important functional group of savanna trees.

Seedling survival and growth response

Although theoretical studies suggest diverse responses of plant species within a community to environmental

Table 2 Effect of even water supply [water–nutrients–grass (*WNG*) model], light [light–nutrients–grass (*LNG*) model], presence of grass and nutrient addition on the survival of seedlings from different savanna tree species

WNG	Estimate	MCMC mean	*p* MCMC	LNG	Estimate	MCMC mean	*p* MCMC
F	−0.07	12.4	0.51	F	0.05	41.9	0.72
W	0.09	5.1	0.63	L	0.06	40.1	0.52
G	0.06	22.3	0.32	G	0.01	45.0	0.89
N	−0.12	16.3	0.55	N	0.09	44.8	0.43
F × W	−0.03	4.54	0.69	F × S	−0.06	30.8	0.76
F × G	−0.02	9.78	0.89	F × G	−0.14	51.4	0.48
F × N	−0.12	8.12	0.59	F × N	−0.08	46.7	0.51
W × G	0.06	13.9	0.58	L × G	−0.15	27.6	0.47
W × N	−0.01	11.5	0.74	L × N	−0.25	35.2	0.25
G × N	−0.03	16.9	0.85	G × N	−0.20	29.8	0.36
F × W × G	−0.08	14.4	0.96	F × L × G	0.10	38.2	0.73
F × W × N	0.10	6.74	0.75	F × L × N	0.35	14.1	0.32
F × G × N	0.05	15.2	0.96	F × G × N	0.33	30.3	0.29
W × G × N	0.19	12.6	0.47	L × G × N	0.35	24.4	0.27
F × W × G × N	−0.16	13.2	0.49	F × L × G × N	−0.58	15.2	0.31

Test and significance values are based on general linear mixed models (GLMMs) (Poisson distribution), with species as a random factor, calculated using the R Monte Carlo Markov Chain (*MCMC*) glmm package (100,000 MCMC iterations). Explanatory variables are: functional group (*F*), water (*W*), grass (*G*), nutrients (*N*) and light (*L*)

variations (Grubb 1977), the majority of the current models on savanna vegetation dynamics assume similar responses of species to increased water availability and decreased grass competition (e.g. Higgins et al. 2000; Wiegand et al. 2006). Despite the variation caused by differences among the tree species, here we have shown that savanna tree species belonging to different functional groups perform differently under different light and soil nutrient availabilities. This suggests that distinguishing functional groups in these models might provide a richer and more realistic interpretation of the population dynamics in savannas.

Effect of environmental on tree seedling survival rate

Our study shows that the different environmental conditions simulated by the treatments did not substantially change the survival rate of savanna species. This result contradicts our initial expectations of lower seedling survival in less favourable conditions [grass presence, full sun and natural (seasonal) rainfall plots]. We thus partly reject hypothesis 1. Several studies suggest that water stress and grass competition are important factors causing savanna tree seedlings' failure to survive (e.g. Midgley and Bond 2001; Van der Waal et al. 2009; Ward and Esler 2011). However, our study focuses on water variation during a rainy season, whereas most of the other studies compare low and high water supply. Although, our study site is characterized by water scarcity (456 mm per season) and unbalanced rainfall distribution during the raining season (mostly in the beginning of the wet season, November–January), the 2009–2010 wet season rainfall distribution had two major rain peaks in November–December 2009 (320 mm) and April–May 2010 (202 mm), with an intermittent 3-month dry period (January–March). This particular rainfall distribution created a more balanced water distribution during the wet season, reducing the effect of wet season droughts on seedling survival. Moreover, it is also possible that the effect of water limitation takes place only at an earlier stage of recruitment (e.g. germination) or during the subsequent dry season, neither of which was tested.

Effect of environmental changes on tree seedling performance

Although grass competition did not affect seedling survival during the wet season, it negatively affected seedling growth (stem growth and aboveground biomass) for all species under all resource treatments (Figs. 2, 3). This result is in agreement with our expectations (hypothesis 1), suggesting that belowground competition for resources plays an important role in seedling establishment (see also Kambatuku et al. 2011), possibly reducing the period of suitable growing conditions for tree seedlings. However, as absence of grasses (simulated by our treatment G0) is only likely to occur for a short time period (a few months) as a consequence of a heavy herbivory event, intensive fires or droughts, the expected effects of this in natural

Table 3 Effect of water supply (WNG model), light (LNG model), presence of grass and nutrient addition on the performance of seedlings from different savanna tree species

	Total shoot biomass			Leaf-stem ratio			Stem length		
	Estimate	MCMC mean	*p* MCMC	Estimate	MCMC mean	*p* MCMC	Estimate	MCMC mean	*p* MCMC
WNG									
F	0.16	0.15	0.62	0.10	0.09	0.82	0.03	0.03	0.81
W	0.32	0.32	0.30	−0.18	−0.19	0.73	0.43	0.43	0.007
G	−2.29	−2.29	<0.0001	1.22	1.21	0.03	−0.40	−0.39	0.016
N	0.52	0.53	0.08	−0.61	−0.61	0.27	0.20	0.20	0.22
F × W	−0.26	−0.26	0.14	0.11	0.12	0.70	−0.26	−0.26	0.004
F × G	−0.09	−0.09	0.62	0.12	0.13	0.69	−0.27	−0.28	0.004
F × N	−0.49	−0.49	0.25	0.09	0.09	0.90	−0.31	−0.31	0.17
W × G	−0.22	−0.23	0.19	0.21	0.22	0.49	−0.09	−0.09	0.36
W × N	−0.48	−0.48	0.27	0.53	0.52	0.51	−0.41	−0.41	0.07
G × N	−0.49	−0.49	0.26	0.42	0.42	0.60	−0.45	−0.45	0.058
F × W × G	0.37	0.37	0.14	−0.42	−0.42	0.35	0.26	0.26	0.048
F × W × N	0.22	0.22	0.36	−0.26	−0.26	0.56	0.22	0.22	0.08
F × G × N	0.32	0.33	0.19	−0.34	−0.34	0.44	0.31	0.31	0.021
W × G × N	0.57	0.57	0.36	−1.87	−1.85	0.09	0.91	0.91	0.006
F × W × G × N	−0.38	−0.38	0.28	0.86	0.85	0.18	−0.52	−0.52	0.004
LNG									
F	−0.02	−0.02	0.94	0.30	0.30	0.49	−0.12	−0.10	0.49
L	−1.44	−1.43	<0.0001	0.87	0.87	0.14	−0.24	−0.24	0.057
G	−2.75	−2.75	<0.0001	1.37	1.37	0.022	−0.70	−0.70	<0.0001
N	0.12	0.12	0.67	−0.12	−0.12	0.84	−0.21	−0.21	0.21
F × L	0.35	0.35	0.032	−0.08	−0.08	0.81	0.10	0.10	0.28
F × G	0.26	0.26	0.10	−0.33	−0.33	0.33	−0.02	−0.02	0.81
F × N	1.16	1.16	0.005	−1.62	−1.62	0.056	0.05	0.05	0.82
L × G	−0.04	−0.04	0.78	−0.03	−0.03	0.92	0.13	0.13	0.18
L × N	0.02	0.01	0.98	0.54	0.54	0.52	0.42	0.41	0.08
G × N	0.02	0.02	0.96	−1.51	−1.50	0.07	0.45	0.44	0.07
F × L × G	−0.13	−0.13	0.57	0.71	0.70	0.14	0.06	0.06	0.64
F × L × N	−0.08	−0.08	0.73	−0.31	−0.32	0.50	−0.17	−0.17	0.21
F × G × N	−0.01	−0.01	0.95	0.54	0.54	0.26	−0.20	−0.20	0.15
L × G × N	−0.22	−0.22	0.70	1.81	1.81	0.13	−0.55	−0.55	0.11
F × L × G × N	0.21	0.21	0.51	−0.69	−0.69	0.31	0.31	0.31	0.11

Test and significance values are based on GLMMs (Gaussian distribution), with species as a random factor, calculated using the R language R package. Explanatory variables are: F, W, G, N and L; for abbreviations, see Table 2

conditions may be less accentuated than those reported in out experiment.

In contrast to previous studies which suggest that water stress limits seedling survival and establishment in dry ecosystems (Sankaran et al. 2005; Kraaij and Ward 2006), in our experiment seedling survival of most species was not affected by the differences in the water regime (Fig. 2). As mentioned before, rainfall during the 2009/2010 wet season was higher and more continuous than normal for the location, which may have brought about favourable conditions for seedlings under the natural rainfall treatment (556 mm evenly distributed in W1 versus 623 mm unevenly distributed in W0). However, there was still a drought period between the two major rain peaks in the 2009–2010 rainy season (Fig. 1). It is possible that the differences between these two water regimes were not large enough to have an effect on seedling survival and performance; it remains unclear if under more extreme droughts seedling establishment would be limited. Hence, the results from these treatments can not be used to infer much about severe drought years, but can still be used to infer conclusions under increased water availability. Furthermore, contrary to our expectations (part of hypothesis 1), nutrient addition did not enhance seedling biomass production per se,

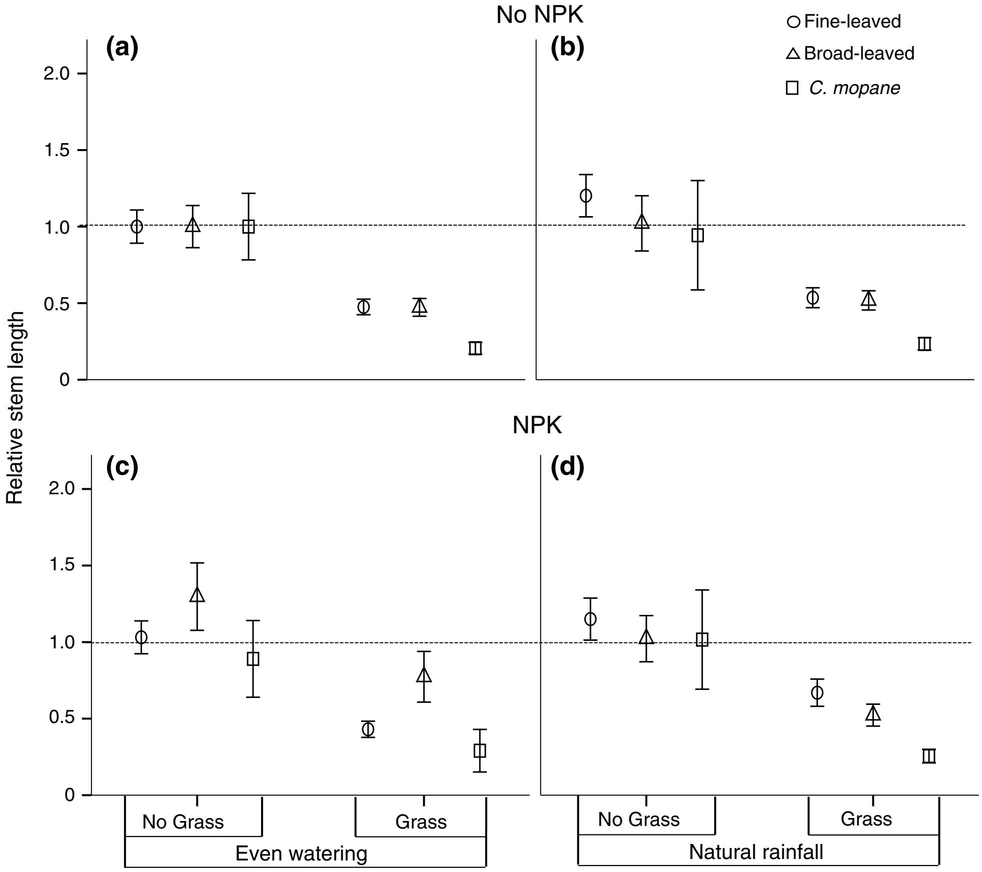

Fig. 2 Effect of experimental treatments of water supply, nutrient addition and grass presence on stem length of savanna tree seedlings of different functional groups relative to the control treatment (water–nutrients–grass model). Tree seedlings were subjected to different treatment combinations: **a** even water supply, no nutrient additions (*No NPK*), under grass competition or not; **b** natural rainfall, no NPK, under grass competition or not; **c** even water supply, nutrient addition (*NPK*), under grass competition or not; **d** natural rainfall, nutrient addition (*NPK*), under grass competition or not. The *x-axis* gives results for the different watering and grass treatments in the experiment for the nutrient treatments. The *dashed line* represents the control treatment (even watering treatment, no grass and nutrient addition). Values are means with 95 % confidence intervals

independently of functional groups (contradicting hypothesis 2; see Fig. 2). These results could be linked with the fact that some study species (e.g. *A. nilotica*, *C. mopane*, *D. cinerea* and *P. africanum*) are likely well adapted to variation in nutrient availability, which is observed over a wide range of habitats (Venter et al. 2003; Mucina and Rutherford 2006).

Contradicting our expectation, fine-leaved species did not show lower stem length than broad-leaved species (hypothesis 3), not even when growing under high nutrient conditions. Stem length growth only differed between the two functional groups when grass was present. Under even water supply the positive effect of fertilization was greater for broad-leaved species. We had expected fine-leaved species to perform better under nutrient-rich conditions, as they are more common on high-fertility soils than broad-leaved species, which are more common on low-fertility soils (Cole 1986; Frost 1992; Venter et al. 2003). However, the positive effect of fertilization was only significant for fine-leaved species under natural rainfall (W0G1N1). This is a surprising result. Two plausible explanations arise. Firstly, the nutrient additions may have been insufficient to cause a difference in growth potential between the fertilised and unfertilised plots. As pointed out in the "Material and methods", our additions may only have raised the available N in the soil by at most 70 %. This already assumes that all of the added N was made available, which is unlikely. A second explanation is that seedlings of the considered species are not limited by soil nutrient availability. If so, then the reason for the disparate distribution of fine-leaved and broad-leaved species across soil fertility gradients is not about their ability to utilise resources, but rather about some other characteristic associated with this environmental gradient. Certainly in other research we have shown that the relative growth rates of the considered species are rather comparable (Tomlinson et al. 2012). In this regard,

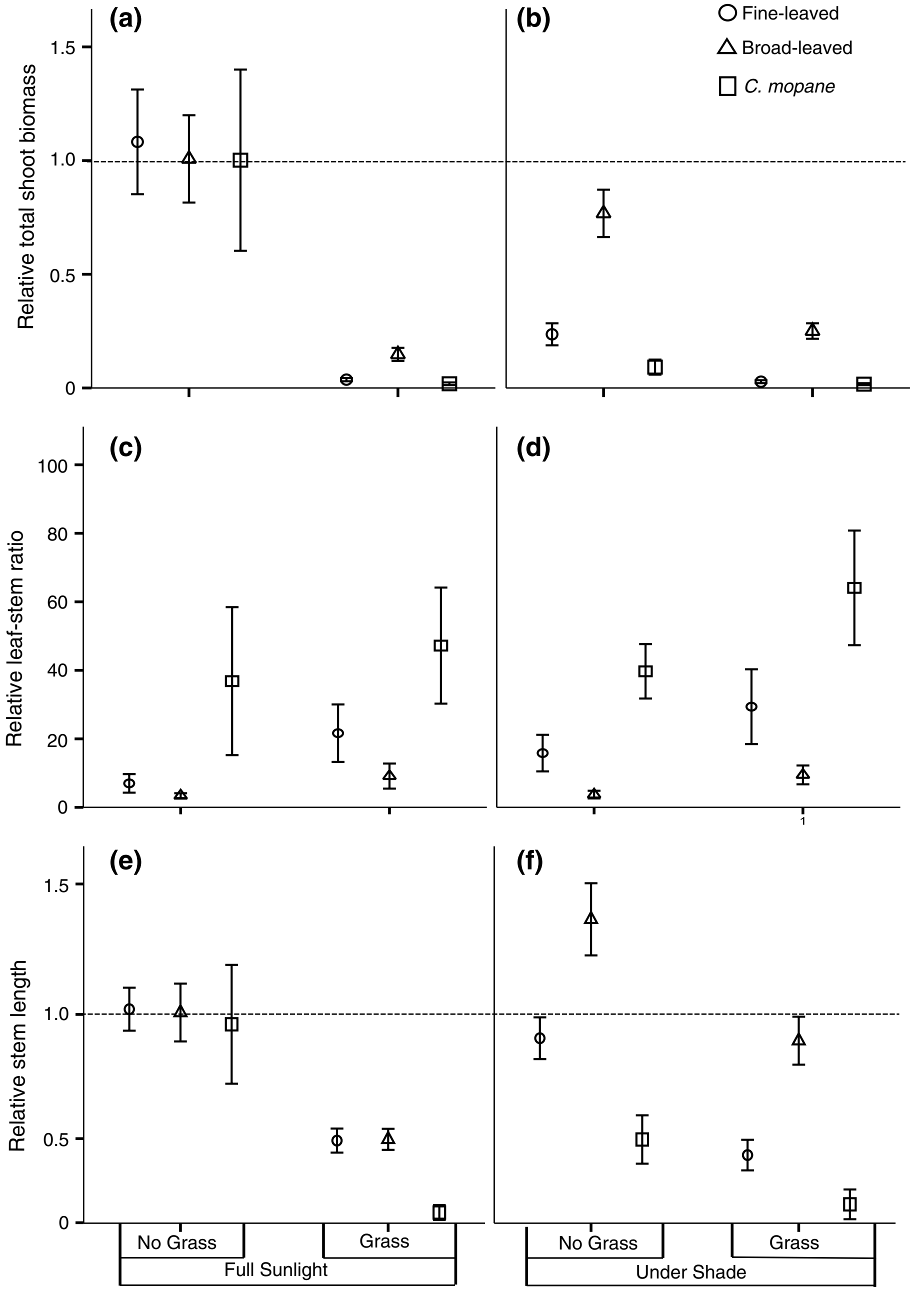

Fig. 3 Effect of shade, nutrient addition and grass presence on leaf biomass (**a**, **b**), stem biomass (**c**, **d**), and stem length (**e**, **f**) of savanna tree seedlings of different functional groups (light–nutrients–grass). Tree seedlings were subjected to different treatment combinations: **a**, **c**, **e** full sunlight, with or without grass competition; **b**, **d**, **f** shade, with or without grass competition. *x-axis* indicates the different treatments in the experiment: even water supply, natural rainfall, no grass, grass. The *dashed line* represents no effect relative to the control treatment (full sun, no grass and nutrient addition). Values are means with 95 % confidence intervals

a plausible explanation is that fertility affects the effective defences employed by plants against vertebrate herbivores. Evidence in favour of this can be provided by the fact that the fine-leaved species are all spinescent whereas the broad-leaved species are all non-spinescent.

Underneath trees, light availability is substantially diminished, and consequently savanna tree seedling growth can be considerably reduced (Loth 1999; Hoffmann et al. 2004). Indeed, our results show that most of the tree species were negatively affected by shade in terms of biomass (hypothesis 1). The lower light intensity found under parental trees might limit carbohydrate accumulation in seedlings (Wright and Van Schaik 1994; Mulkey et al. 1996), slowing their growth rates and prolonging their existence as juvenile plants. Here we show that this negative influence of shade is significantly more accentuated in the absence of grass. This result suggests that shade reduces the negative effects of grass on seedling growth. This positive effect of shade may be due to the suppression of grass growth under low light availability (personal observation; see also Siemann and Rogers 2003). However, this beneficial effect of grass was more accentuated for broad-leaved species (shoot biomass and stem length) than for fine-leaved species (Fig. 3; confirming hypothesis 4). The latter result may be because the light compensation point (the light intensity at which the rate of photosynthesis exactly matches the rate of respiration) is greater for fine-leaved species than broad-leaved species. Indeed our results give strength to the idea that fine-leaved species are less tolerant to low light conditions (shade) than the broad-leaved species (Smith and Goodman 1986, 1987). Furthermore, we expected a higher LSR among broad-leaved species than among fine-leaved species (hypothesis 4). However, seedlings of these two species groups growing under low light and grass competition showed a tendency to increase LSR, indicating a higher resource allocation to the leaves (Table 3; Fig. 3). Our results are in agreement with previous studies that suggested that trees growing in shade conditions adjust their leaf structure (e.g. increasing specific leaf area, leaf biomass, LSR) and photosynthesis characteristics (e.g. higher chlorophyll content) (Niinemets 2010; Perrin and Mitchell 2013). Despite the fact that light limitation is not severe enough to limit plant production in savannas (Belsky 1984; Ludwig et al. 2002), these results have important implications for savanna tree community dynamics, showing a certain degree of shade tolerance in African savanna trees.

Concluding remarks

There is growing concern about the consequences of environmental changes on savannas. Consequently several models have been developed to predict how climate change and land use changes will affect the co-existence of trees and grasses (e.g. Volder et al. 2013; Holdo 2013). These models are also used to predict how the balance among different vegetation states (forest, savannas and grasslands) may shift in relation to climate change (Warman and Moles 2009). Our study demonstrated that, across a large range of recruitment conditions, grass presence severely limits tree seedling growth, even under favourable recruitment conditions (e.g. high water and nutrient availability). These findings suggest that an abrupt transition from grassland to woodland savanna can only occur if grass abundance is severely reduced. Therefore, grass suppression caused by high levels of herbivory and/or changes in fire frequency (Jeltsch et al. 1998), or droughts (Higgins et al. 2000), could lead to abrupt vegetation-type transitions (Van Langevelde et al. 2003). Moreover, our study shows that species with different functional traits responded differently under high-stress conditions (grass competition or light shortage). Seedlings of broad-leaved species performed better in constantly watered, nutrient-rich and shaded environments. Given the high climatic variability, these differences in response to environmental conditions could allow species coexistence (Grubb 1977), and may help to explain the high diversity of plant species in savannas. As the functional groups considered here explained a large part of the variation in responses, information on species traits can be used to improve our ability to predict vegetation structure changes in savannas.

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