



Savanna tree–grass competition is modified by substrate type and herbivory

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Keywords

Acacia mellifera; Biomass; Bush encroachment; Interspecific competition; Nutrient status; Semi-arid savanna; Substrate.

Nomenclature

Gibbs Russell et al. (1991), Van Oudtshoorn (1999), Coates Palgrave (2005)

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Abstract

Question: Woody plant and grass interactions in savannas have frequently been studied from the perspective of the response of one growth form on the other but seldom evaluated as two-way interactions. What causes woody plant encroachment in semi-arid savannas and what are the competitive responses of tree seedlings and grasses on rocky and sandy substrates?

Methods: In this greenhouse study, we investigated the influence of substrate and grazing on responses to interspecific competition by tree seedlings and grasses. We measured competitive/facilitative responses on biomass and nutrient status of tree seedlings and grasses grown together.

Results: Interspecific competition suppressed growth of trees and grasses. Tree seedlings and uncut grass accumulated double the biomass when grown without competition relative to when they competed. Competitive responses varied on different substrates. Grass biomass on rocky substrate showed no response to tree competition, but appeared to be facilitated by trees on sandy substrate. Grass clipping resulted in higher tree seedling biomass on rocky substrate, but not on sandy substrate. There was a positive response of grass nutrient status to competition from tree seedlings.

Conclusion: Selective grass herbivory in the absence of browsing or suppression of shade-intolerant grasses by trees are commonly cited reasons behind bush encroachment in savannas. We show that grazing may confer a competitive advantage to tree seedlings and promote bush encroachment more readily on rocky substrates. This may be due to the imposed sharing of the soil depth niche on rocky substrates, whereas possible niche separation on sandy substrates minimizes the advantage conferred by reduced competition.

Introduction

The co-occurrence of trees and grasses in savannas is associated with reciprocal competitive interactions between these two growth forms (Walker & Noy-Meir 1982; Tainton & Walker 1992; Scholes & Archer 1997). Tree–grass interactive dynamics are primarily driven by the availability of soil moisture and nutrients (Frost et al. 1986; Wiegand et al. 2006; van der Waal et al. 2009). Reported interspecific competitive responses and effects of co-existing savanna trees and grasses on either growth form vary from positive to neutral to negative interactions that sometimes change over time (Belsky 1992; Scholes & Archer 1997). For example, grass production is either

enhanced (Belsky et al. 1989) or hindered (Mordelet & Menaut 1995; van der Waal et al. 2009) by the presence of trees. Suppression of tree seedling growth, survival and establishment by grass competition has also been shown (Cramer et al. 2007; Riginos & Young 2007), although grasses may facilitate the germination of trees by moderating microclimatic conditions (Aide & Cavelier 1994).

Through directly competing with grasses for light, mineral nutrients and soil moisture, trees cause a reduction in the growth of grasses (Scholes & Archer 1997; House et al. 2003; Ludwig et al. 2004b; van der Waal et al. 2009). Trees may also reduce soil moisture availability through the interception of precipitation by the canopy. Beneficial effects of trees on grasses include the use of

water in the surface soil hydraulically lifted by deeper roots of trees (Caldwell et al. 1981; Ludwig et al. 2004b), cooler temperatures with accompanying minimized evapotranspiration under the shade of trees (Scholes & Archer 1997; Ludwig et al. 2004a) and enhanced nutrient availability due to leaf litter and possible N_2 fixation (Scholes & Archer 1997), which increase the nutrient content of grasses (Treydte et al. 2007; Ludwig et al. 2008). For example, augmented grass production below tree canopies has been attributed to increased soil fertility (Callaway et al. 1991; Anderson et al. 2001), although this does not always lead to higher grass biomass.

For woody plants, competition with grasses may impede seedling and sapling survival and establishment (Weltzin & McPherson 1997; Jurena & Archer 2003; Riginos & Young 2007). Shade intolerance has been reported for many savanna woody plants, especially leguminous trees (Smith & Shackleton 1988; Belsky 1994). Thus, a high standing grass biomass may suppress the growth of woody seedlings (Brown & Booysen 1967; Walker et al. 1981; Knoop & Walker 1985; Harrington 1991). High grass biomass may also suppress woody plant growth for reasons other than shading (Brown & Booysen 1967; Walker et al. 1981; Harrington 1991). For example, Riginos (2009) recently showed that the suppressive effect of grasses on savanna trees affects all demographic stages of woody plants in a wet and nutrient-rich savanna, although the applicability of this finding to nutrient-poor low-rainfall savannas (e.g. Knoop & Walker 1985) is unclear. While instances of facilitation of tree seedling establishment by standing grass biomass have been reported (e.g. Holmgren et al. 1997; Davis et al. 1998), there is strong evidence that competition with grasses in arid ecosystems, together with the increased fire risk, limits the invasion of grasslands by *Acacia* trees, irrespective of soil type (Nano & Clarke 2010). High grass productivity that results in high biomass accumulation, together with slow decomposition rates and dry season senescence of grasses (Ehleringer & Monson 1993), combine to accumulate combustible fuel (Knapp & Seastedt 1986). This results in fires that are detrimental to tree seedlings and saplings (Higgins et al. 2000; Bond 2008). Fires are harmful to trees but not to the herbaceous/grass layers, which regrow readily (Wolfson 1999; Riginos 2009).

The main drivers of grass production, in addition to water and light, are soil physical properties and nutrient availability (Scholes & Walker 1993). For example, augmenting the availability of nutrients through addition of nitrogen (N) and phosphorus (P) resulted in increased grass production outside and beneath tree canopies, respectively (Ludwig et al. 2001). Natural increase in grass N concentration beneath the canopies of savanna trees

relative to grasses in open areas often exceeds the magnitude of increase in P, especially under *Acacia* species (Callaway et al. 1991). Increased grass nutrient content (Belsky 1992) and high protein concentration (Laclau et al. 2008; Treydte et al. 2008) underneath *Acacia* trees have been reported. These trends could be attributed to higher concentrations of nutrients under woody plant canopies due to animal activities (Belsky 1994; Scholes & Archer 1997), or grasses benefitting from N_2 fixed by leguminous *Acacia* trees (Bernhard-Reversat 1982; Tolsma et al. 1987). However, competition for soil moisture and shading by trees may also lead to reduced grass biomass (Ludwig et al. 2008), resulting in higher concentrations of nutrients per unit grass biomass (Laclau et al. 2008).

Tree–grass interactions in savannas have mainly been considered as competition for soil moisture and nutrients or avoidance thereof (e.g. Walter 1971; Walker et al. 1981; Walker & Noy-Meir 1982; Knoop & Walker 1985). This is based on Walter's (1939) two-layer hypothesis of vertical niche separation in rooting depth and thus differentiation of soil resource use between the herbaceous layer and the woody component. Grasses, with their fibrous root systems, are more effective at exploiting soil resources in the upper layer than trees, which they tend to outcompete, while trees dominate resource capture from deeper soils (Pärtel & Wilson 2002). Defoliation of grasses by grazers is thought to diminish their competitiveness against tree seedlings by limiting grass carbon assimilation and root production (Chapin & Slack 1979). The outcome is reduced density of above- and below-ground grass biomass (Pandey & Singh 1992), which reduced the competitive effect of grasses on trees (Walker & Noy-Meir 1982; Skarpe 1991; Jeltsch et al. 1997) and increased the availability of soil moisture for woody plants (O'Connor 1995; Weltzin & McPherson 1997). Consequently, reduced grass competition and low magnitudes of fires due to a diminished fuel load may lead to bush encroachment (van Langevelde et al. 2003; Graz 2008). Low frequencies of fires have been associated with shrub encroachment by enabling the establishment of tree seedlings (Van Auken 2000). Woody plant encroachment in arid environments is thought to be principally driven by grazing pressure, above average precipitation events and anthropogenic alteration of fire regimes (Kraaij & Ward 2006; Nano & Clarke 2010). Browsers play a role in keeping bush encroachment in check by browsing on young tree seedlings, minimizing their establishment and curtailing regeneration of woody plants (Prins & Van der Jeugd 1993; Ripple & Beschta 2007, 2008). Displacement of browser populations from savanna ecosystems by grazers (predominantly cattle) has reduced herbivory on woody plants, altered the timing and intensity of grass defoliation, as well as its recovery periods, often

contributing to bush encroachment (Van Vegten 1983; Jeltsch et al. 1997; Graz 2008).

Both bottom-up resource limitations and top-down disturbance regimes (herbivory, fire) are important in suppressing woody plant recruitment, but their relative significance varies across environmental gradients and regions (Bond 2008; Nano & Clarke 2010). Bush encroachment has been observed to be most prevalent on rocky outcrops and/or areas with shallow soil horizons (Ward 2005; Wiegand et al. 2005; Kraaij & Ward 2006; Britz & Ward 2007). Britz & Ward (2007) showed a relatively constant (but high) tree density on rocky areas that has changed little over many years, whereas they found that there has been a recent increase in bush encroachment on sandy substrates.

Grass defoliation may promote the growth of already established seedlings as opposed to seedlings in the initial stages of establishment (O'Connor 1995). We used a manipulative greenhouse experiment to test the effects of grass defoliation and soil substrate type (rocky versus sandy) on *Acacia mellifera* tree seedling biomass and nutrient concentration. *A. mellifera* (Vahl) Benth is a drought-adapted woody shrub commonly occurring in arid to semi-arid environments, where it is often among the most frequent encroacher species (Skarpe 1991; Kraaij & Ward 2006; Wiegand et al. 2006; Joubert et al. 2008). It commonly grows as a multi-stemmed shrub up to 3 m in height, but may reach up to 7 m (Smit 1999). We predicted that tree seedling sizes and nutrient status would respond negatively to grass competition and that frequent clipping of the grass to simulate herbivory would negatively affect the suppressive competitive influence of grass. Rocky substrates are likely to impede and restrict tree seedling rooting depth (Savory 1963; Rutherford 1983), thus limiting the scope for niche separation. We predicted that the advantages conferred by grass defoliation to tree seedlings would be greater on rocky substrates than on sandy soils due to a greater overlap in rooting zones of tree seedlings and grasses, resulting in a greater influence of competition. We also tested the responses of grass biomass and nutrient status to competition with tree seedlings. We predicted that grass grown with tree seedlings would have higher forage quality (i.e. higher nutrient concentration) due to N derived from tree seedling N₂ fixation.

Methods

Plants were grown in the greenhouse in 90 bins (95 L), which were 0.45 m in diameter and 0.60 m in height, in a completely randomized experimental design. Bins were filled with an alluvial sandy-gravel aggregate. This aggregate is 17% gravel (≥ 2 mm) and 83% soil (≤ 2 mm), of

which 1.7% was clay and 4% silt, with 53% of the sand portion being coarse (0.5–1 mm), 25% medium (0.25–0.5 mm), 14% fine (125–250 μ m) and 3% very fine (62.5–125 μ m) particles with a low nutrient content. This sand aggregate mix was mixed with cobbles ($\geq 64 \leq 256$ mm) and boulders (≥ 256 mm) in 45 of the bins. All bins were filled with sand up to 0.05 m below the rim, resulting in a sand column of ca. 55 cm in depth in the bins.

The set-up consisted of 45 bins with sandy and 45 with rocky substrate. Each of the two groups of 45 bins was made up of nine bins with trees only, 18 bins with grass only and 18 tree+grass combination bins. A total of 24 *A. mellifera* seeds were planted per bin on 10 December 2006 in the tree only and tree+grass bins and germinated within 4 days. Seeds of *Eragrostis curvula* grass were introduced into bins 1 month after the germination of tree seedlings on 19 January 2007, and allowed to grow until the end of winter (end of July 2007). Soil nutrient content was low, being 0.02% (w/w) N, 0.01% (w/w) P and 0.74% (w/w) organic matter. No fertiliser was added in the experiment and plots were watered on a weekly basis using an automated sprinkler system.

At the onset of the second growing season (beginning of August 2007), grasses from half the bins (i.e. grass-only as well as tree+grass treatments) were harvested by cutting the above-ground material at 2 cm above the ground. Harvesting of grass above-ground material from treatment bins was repeated every 2 months until the end of the experiment in July 2008. This clipping of above-ground grass material to simulate grazing was performed on 18 of the bins exclusively planted with grass, and 18 of the bins with mixed tree+grass plants, nine having sand–rocky combinations and the other nine containing pure sand. Although grass clipping is not an accurate representation of herbivory by diverse animals (Irving et al. 1995; Tripathi & Shukla 2007) and may preclude mutualistic animal–plant interactions, trampling or selective herbivory (Walker et al. 1989), it does have the benefit of uniformity and repeatability. We also note that *E. curvula* is a highly palatable grass species that is preferred by domestic livestock (Van Oudtshoorn 1999).

Clipped grass from each bin was collected in paper bags, weighed, dried at 65 °C for 48 h and re-weighed. Grass biomass from each sequentially harvested bin over the course of the season was added progressively to estimate biomass accumulation. At the end of the experiment in July 2008, after 1.5 years (two growing seasons) all tree seedlings were harvested (including roots). Final stem heights/root lengths, number and lengths of branches and the basal diameters of stems/roots were documented. Grass not harvested during the course of the experiment served as controls for simulated herbivory and was

collected at the end of the experiment. All uncut grass (herbivory controls) was carefully removed (including roots) from bins. The roots of regularly clipped grass were also harvested at the end of the experiment. Excess soil was washed from the roots with water. Final harvested above-ground biomass of grass from bins not subjected to grass clipping was compared to the cumulative biomass of grass from bins subjected to regular harvesting.

Harvested plant material was separated into above- and below-ground components and oven dried at 65 °C for 48 h. While above- and below-ground components of tree seedlings were dried individually, all grasses from a particular bin were combined. In the case of regularly harvested grass, only the below-ground parts were collected for drying. All oven-dried plant components were weighed. Tree leaves from individual seedlings were separated from twigs and bulked into a single composite sample per bin.

Plant material was milled to a fine powder with a Culatti Type MFC micro-fine pulverizing electrical grinder (Janke and Kunkel GmbH, Staufen, Germany) to pass through a 1-mm pore size sieve. Ground plant samples were analysed for total N and total P. Samples were digested with sulphuric acid, hydrogen peroxide and a selenium catalyst using a block digester at 360 °C. Total N in dry plant samples was determined with a LECO FP2000 Nitrogen Auto Analyser (Leco Corporation, St. Joseph, MI, USA) using the micro-Dumas combustion method (AOAC International 2000). Phosphorus was determined using continuous flow analysis with a Technicon Auto-analyser II colorimeter (SEAL Analytical, Hampshire, UK), which measures the absorbance of the phosphomolybdo vanate complex at a wavelength of 420 nm.

Statistical analysis

We measured the competitive responses of trees and grasses to interspecific competition. We did not measure competitive effects *sensu* Goldberg & Fleetwood (1987) and Miller & Werner (1987), which would have required altering the densities of tree seedlings (Goldberg 1996). We did, however, measure the effects of grass competition on tree seedlings through our clipping treatment (plus control). Final harvest plant biomass, tree seedling stem/root diameters for plots subjected to grass clipping, were compared to the plant biomass and tree seedling stem/root sizes from plots not subjected to clipping by means of two-way analysis of variance (ANOVA), as were the comparisons of similar plant combinations on different soil types (rocky versus sandy). Resultant values were used to evaluate plant performances under interspecific competition, biomass accumulation by plants on sandy/rocky substrate, as well as a comparative study of tree/grass biomass accumulation under conditions of regular

grass clipping and when left to grow undisturbed on either soil type. Repeated measures of grass biomass and nutrient concentration were compared in a general linear repeated measures ANOVA model using tree competition as a between-subject factor and substrate type as a co-variate. Means and pair-wise multiple comparisons were tested with Bonferroni *post hoc* tests, with adjusted confidence intervals set at $\alpha=0.05$ significance level.

Results

Responses of tree seedling biomass to grass competition

Competition from uncut grass had a significant negative effect on above- ($F=6.89$, error $df=17$, $P=0.018$) and below-ground ($F=11.54$, error $df=17$, $P=0.010$) biomass accumulation by tree seedlings on both rocky and sandy substrates (Fig. 1). We found no significant difference between tree-only and frequently cut grass bins in either above-ground ($F=1.17$, error $df=17$, $P=0.284$) or below-ground ($F=1.14$, error $df=17$, $P=0.290$) biomass of trees, indicating that grass clipping resulted in a situation similar to that of grass absence. Tree seedling overall shoot (10.4 ± 1.3 g) and root (7.9 ± 0.9 g) biomass was reduced by half to 5.9 ± 0.8 and 4.6 ± 0.7 g, respectively, in the presence of uncut grass. Uncut grass also had a significant negative effect on shoot and root diameters as well as the mean number of branches per seedling on both substrates (Table 1). While the root:shoot ratios of seedlings on sandy substrate were significantly reduced by uncut grass competition relative to seedlings without grass, this was not the case for root:shoot ratio on rocky substrates (Table 1).

Responses of grass biomass to tree seedling competition

The presence of tree seedlings had no significant ($F=3.08$, error $df=17$, $P=0.100$) influence on the above-ground biomass of uncut grass on rocky substrates. In contrast, on sandy substrates, uncut grass growing together with tree seedlings yielded significantly ($F=7.20$, error $df=17$, $P=0.020$) higher above-ground biomass (172.2 ± 23 g), which was double the yield of grasses on their own (85.6 ± 10 g). Thus, in the absence of clipping, the presence of trees on sandy substrates increased grass productivity relative to the absence of tree seedlings (Fig. 2). The converse was observed when grass was subjected to repeated clipping, where tree seedling competition had a significant deleterious effect ($F=3.1806$, error $df=32$, $P=0.002$) on cumulative above-ground grass biomass (Fig. 3). Clipped grass in half of the tree+grass combination bins failed to regrow after the fourth harvest.

Significant differences were found between harvested biomass of grass at different harvest dates, with a

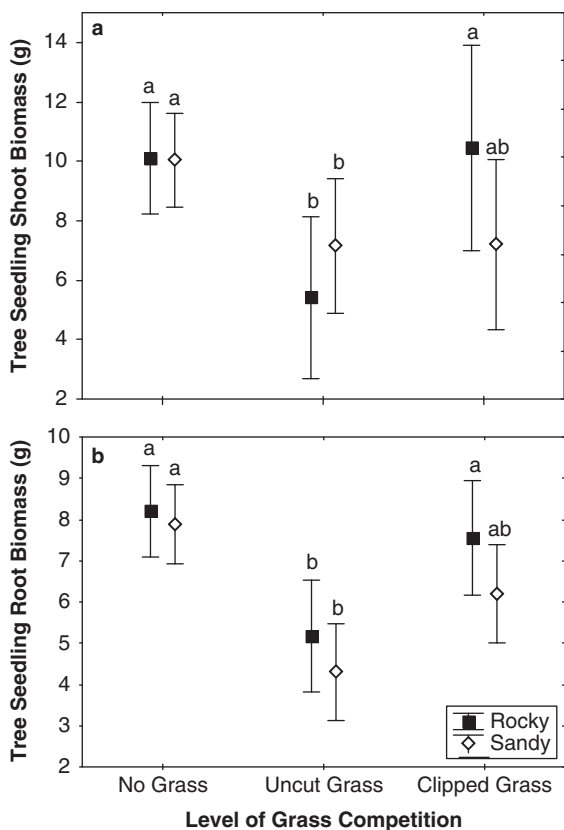


Fig. 1. Comparisons of (a) above- and (b) below-ground biomass of tree seedlings when grown with and without either uncut or cut grass and on either rocky or sandy substrate. Note that the suppressive effect of grass competition in the absence of clipping significantly suppressed shoot biomass on rocky substrate and root biomass on sandy substrate. Vertical error bars denote 95% confidence intervals.

significant harvest \times interspecific competition interaction (Table 2). Tree seedlings suppressed biomass accumulation in the repeatedly clipped grass treatment such that grasses competing with trees yielded lower biomass towards the later sampling dates than grass growing on its own on either substrate (Fig. 3). No significant differences were found between harvested grass biomasses for any treatments at first harvest ($F=0.63$, error $df=30$, $P=0.603$) or cumulative biomass at subsequent harvests until the last two harvests (Fig. 3). For the last two harvests in March 2008 ($F=13.94$, error $df=32$,

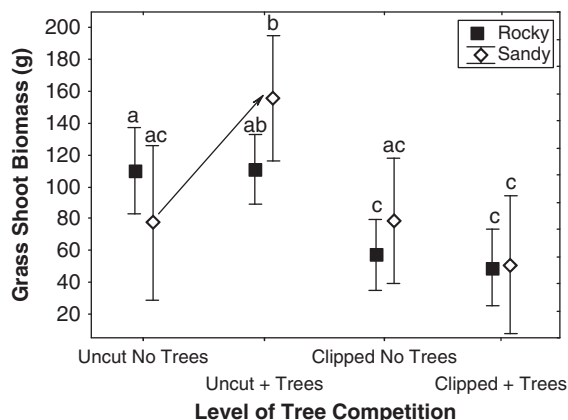


Fig. 2. Comparisons of cut and uncut grasses with and without tree seedling competition in terms of above-ground biomass on rocky and sandy substrates. Vertical error bars denote 95% confidence intervals. The arrow indicates the significant increase in uncut grass biomass on sandy substrate in the presence of tree seedlings relative to when grass was grown on its own.

Table 1. The influence of uncut (intact) grass competition on final shoot, root and branch lengths, diameters (mean \pm SE cm) and root:shoot ratios of tree seedlings grown on their own (Trees Only) and in competition with grass on rocky and sandy substrates. Error df in all cases was 17. Note that grass competition had a more severe effect on tree seedling diameter and branch length on sandy soil than on rocky soil.

Plant Measured	Substrate Type	Measurement		F	Significance (P)
		Tree+Grass	Trees Only		
Stem Length	Rocky	50 \pm 2.	53.20 \pm 2	1.41	0.236
	Sandy	48. \pm 2	56 \pm 2	8.093	0.005
Stem Diameter	Rocky	0.51 \pm 0.2	0.59 \pm 0.1	14.97	< 0.001
	Sandy	0.47 \pm 0.1	0.59 \pm 0.2	31.06	< 0.001
Root Diameter	Rocky	0.44 \pm 0.02	0.51 \pm 0.02	9.40	0.002
	Sandy	0.42 \pm 0.01	0.53 \pm 0.02	22.45	< 0.001
Number of Branches	Rocky	0.92 \pm 0.1	2.05 \pm 0.1	34.70	< 0.001
	Sandy	1.02 \pm 0.1	2.06 \pm 0.1	45.39	< 0.001
Mean Branch Length	Rocky	32 \pm 2	32 \pm 1	0.004	0.953
	Sandy	29 \pm 2	34 \pm 1	5.26	0.023
Root:Shoot Ratio	Rocky	0.90 \pm 0.03	0.89 \pm 0.03	0.07	0.796
	Sandy	0.91 \pm 0.03	0.84 \pm 0.02	5.23	0.023

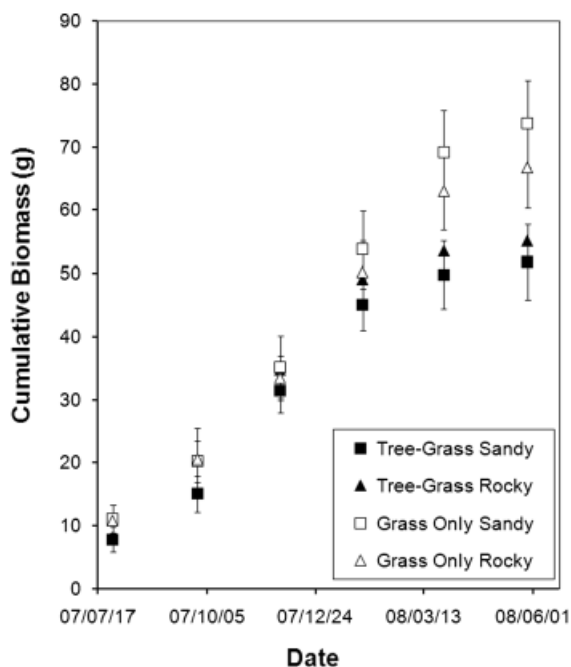


Fig. 3. Plots of above-ground accumulative biomass (mean ± SE) of frequently harvested grass on sandy and rocky substrate at different harvest dates as recorded at bimonthly intervals, starting with July 2007 (first harvest) and ending in May 2008.

$P \leq 0.001$) and May 2008 ($F = 3.62$, error $df = 32$, $P = 0.023$), grass grown without tree seedlings had higher biomass than grass competing with trees, but the cumulative biomass of the grasses was not significantly different ($F = 2.17$, error $df = 32$, $P = 0.111$) (Fig. 3). Significant differences ($F = 26.29$, error $df = 17$, $P \leq 0.001$) were found in below-ground biomass between regularly harvested grass growing on its own (which had higher root biomass) and grass growing with tree seedlings, while no significant differences ($F = 0.17$, error $df = 17$, $P = 0.686$) were evident for uncut grass (Fig. 2).

Substrate influence on tree and grass growth

There was no significant influence of substrate type (rocky or sandy) on individual tree seedling mean stem ($P = 0.988$) or root ($P = 0.426$) diameter, number of branches ($P = 0.981$), above- ($P = 0.803$) or below-ground ($P = 0.895$) biomass. Substrate type had no significant effect on uncut grass biomass grown without trees, either above- ($F = 0.085$, error $df = 17$, $P = 0.775$) or below-ground ($F = 0.014$, error $df = 17$, $P = 0.591$). Similarly, there was no significant effect on N ($F = 0.255$, error $df = 17$, $P = 0.621$) or P ($F = 0.236$, error $df = 17$, $P = 0.634$) concentrations. The most notable substrate-related difference was the effect of grass competition on tree seedling biomass, in which grasses significantly suppressed tree

Table 2. Results of repeated measures ANOVA general linear model (GLM) for regularly clipped grass. Differences in error df result from failure of harvested grass to regrow at subsequent harvest, as well as some grass samples being too small for nutrient analyses on certain harvest dates.

Source of Variation	Wilks' λ	F	Error df	Significance (P)
Biomass at Harvest				
Harvest Date	0.084	58.58	27	< 0.001
Harvest Date × Tree	0.178	24.96	27	< 0.001
Competition				
Harvest Date × Substrate Type	0.913	0.52	27	0.762
Cumulative Biomass				
Harvest Date	0.064	79.43	27	< 0.001
Harvest Date × Tree	0.205	20.94	27	< 0.001
Competition				
Harvest Date × Substrate Type	0.936	0.37	27	0.864
Nitrogen Concentration				
Harvest Date	0.032	125.06	21	< 0.001
Harvest Date × Competition	0.129	28.48	21	< 0.001
Harvest Date × Substrate Type	0.926	0.34	21	0.884
Phosphorus Concentration				
Harvest Date	0.024	129.00	16	< 0.001
Harvest Date × Tree	0.221	11.26	16	< 0.001
Competition				
Harvest Date × Substrate Type	0.842	0.59	16	0.701

shoot biomass ($F = 6.89$, error $df = 17$, $P = 0.018$) on rocky substrate and suppressed root biomass ($F = 11.54$, error $df = 17$, $P = 0.003$) on sandy substrate (Fig. 1). While grass competition significantly suppressed tree seedlings in all size aspects on sandy substrate, it had no significant effect on stem or branch length and root:shoot ratios on rocky substrate (Table 1). Substrate type had no significant influence on the biomass and nutrient content of regularly clipped grass (Table 2).

Nutrient concentrations

Competition with grass had no significant effect on tree seedling nutrient concentration (Tables 3 and 4). Tree seedlings on rocky substrate without grass competition did not have significantly different N ($F = 1.17$, error $df = 17$, $P \leq 0.293$) and P ($F = 0.77$, error $df = 17$, $P \leq 0.393$) concentrations compared to tree seedlings without grass competition on sandy substrate. Substrate had no significant effect on tree seedling nutrient concentration in all other treatment combinations.

The presence of tree seedlings had significant (range in $F = 8.37$ – 45.75 , range in error $df = 24$ – 32 , $P \leq 0.001$) positive effects on the N concentration of regularly harvested grass at all harvest dates. However, no significant differences were found between uncut grasses grown with and without tree competition (Table 3).

Repeated measures ANOVA showed significant differences in N concentration at different harvest dates, with a significant harvest date \times tree competition interaction (Table 2). Regularly clipped grass growing with tree seedlings showed a consistent increase in N concentration in grass-only treatments, while grass grown with trees had declining N at the third and fifth harvests (data not shown).

As with N, the P concentration of frequently clipped grass was significantly (range in $F = 3.46\text{--}34.91$, range in error $df = 20\text{--}32$, $P = 0.029 - \leq 0.001$) enhanced by the presence of tree seedlings at all except the first harvest ($F = 0.44$, error $df = 29$, $P = 0.725$). There were significant differences in P concentration of grasses competing with tree seedlings (higher P than grass grown on its own), with a significant harvest date \times tree competition interaction (Tables 2 and 4). When considered separately for either soil type, the presence of trees had a significant influence on P concentration of grass on sandy substrates only (Table 4). Relatively higher initial mean N:P ratios of 7.1 and 6.9 at the first and second harvests, respectively, dropped significantly to 3.8–4.5 at the third and subsequent harvests ($F = 87.10$, error $df = 65$, $P \leq 0.001$) (data not shown).

Responses to simulated herbivory

Comparisons of tree seedlings competing with cut grass on sandy substrate to tree seedlings free of grass competition demonstrated that sustained clipping significantly influenced tree seedling size in terms of stem ($F = 9.01$, error $df = 17$, $P = 0.003$) and root diameters ($F = 5.93$, error $df = 17$, $P = 0.016$), mean branch number ($F = 5.81$, error $df = 17$, $P = 0.017$) as well as above-ground biomass ($F = 5.36$, error $df = 17$, $P = 0.021$). The mean number of branches per tree seedling was also significantly different ($F = 3.95$, error $df = 17$, $P = 0.048$) between those competing with harvested grass and those without grass competition. In all but the case of mean branch number, tree seedlings competing with uncut grass on either substrate had significantly smaller sizes than tree seedlings with clipped grass and, as indicated earlier, frequent cutting of grass reduced the negative effect of grass competition on tree seedling biomass on rocky substrate (Fig. 1). While mean branch length of tree seedlings competing with uncut grass was significantly longer ($F = 183.31$, error $df = 17$, $P \leq 0.001$) than tree seedlings growing with clipped grass on rocky substrate, there was no significant difference ($F = 0.84$, error $df = 17$, $P = 0.362$) on sandy substrate.

Table 3. Final shoot (grass) or leaf (trees) nitrogen (N) concentration (mean \pm SE mg g⁻¹ dw) in grass and tree seedlings grown on their own (= Grass/Trees Only) and in combination on rocky and sandy substrates.

Plant and Herbivory Treatment	Substrate Type	Plant Combination N		F	Error df	Significance (P)
		Tree+Grass	Grass/Trees Only			
Uncut Grass	Rocky	1.01 \pm 0.09	0.97 \pm 0.03	0.276	17	0.608
	Sandy	0.95 \pm 0.05	0.94 \pm 0.05	0.016	17	0.900
Cut Grass	Rocky	2.10 \pm 0.05	1.74 \pm 0.07	13.475	10	0.004
	Sandy	2.21 \pm 0.07	1.73 \pm 0.06	21.594	14	≤ 0.001
Trees (Uncut Grass)	Rocky	3.71 \pm 0.10	3.89 \pm 0.11	1.143	17	0.301
	Sandy	3.53 \pm 0.32	4.04 \pm 0.07	2.712	17	0.118
Trees (Cut Grass)	Rocky	3.88 \pm 0.07	3.89 \pm 0.11	0.002	17	0.968
	Sandy	3.92 \pm 0.08	3.99 \pm 0.06	0.507	17	0.489

Table 4. Final shoot/leaf phosphorus (P) concentration (mean \pm SE mg g⁻¹ dw) in grass and tree seedlings grown on their own (= Grass/Trees Only) and in combination on rocky and sandy substrates.

Plant and Herbivory Treatment	Substrate Type	Plant Combination P		F	Error df	Significance (P)
		Tree+Grass	Grass/Trees Only			
Uncut Grass	Rocky	0.081 \pm 0.008	0.069 \pm 0.006	1.168	17	0.299
	Sandy	0.092 \pm 0.007	0.074 \pm 0.009	2.524	17	0.138
Cut Grass	Rocky	0.385 \pm 0.041	0.312 \pm 0.028	2.173	8	0.179
	Sandy	0.469 \pm 0.045	0.313 \pm 0.023	17.341	12	0.001
Trees (Uncut Grass)	Rocky	0.175 \pm 0.036	0.194 \pm 0.031	0.161	17	0.694
	Sandy	0.157 \pm 0.018	0.263 \pm 0.076	1.680	17	0.212
Trees (Cut Grass)	Rocky	0.191 \pm 0.027	0.194 \pm 0.031	0.006	17	0.939
	Sandy	0.208 \pm 0.024	0.273 \pm 0.084	0.375	17	0.551

In comparison to seedlings grown in rocky substrate without grass competition, the seedlings growing with cut grass had a significantly smaller mean number of branches ($F = 3.953$, error $df = 17$, $P = 0.048$), which were significantly shorter ($F = 183.313$, error $df = 17$, $P \leq 0.001$). No significant differences were found for other parameters on rocky substrate. On the sandy substrate, similar significant differences were found between tree-only seedlings and those grown with clipped grass as occurred with the comparison of tree seedlings competing with clipped grass to tree seedlings competing with uncut grass (see preceding paragraph). Competition from grass subjected to clipping disadvantaged seedlings in all aspects relative to growing without grass on sandy soil. Thus, the frequent clipping of grass did not benefit tree seedlings on the sandy substrate, where grass had similar effects on tree seedlings regardless of clipping, but significantly benefited tree seedlings on rocky substrate. Grass clipping had no significant effect on tree seedling N ($F = 0.002$, error $df = 17$, $P = 0.968$; $F = 0.507$, error $df = 17$, $P = 0.489$) and P ($F = 0.006$, error $df = 17$, $P = 0.939$; $F = 0.002$, error $df = 17$, $P = 0.968$) concentrations on rocky and sandy soil types, respectively.

Uncut grass growing with trees accumulated significantly more biomass both above- and below-ground than grasses subjected to clipping, with the largest contrast being found for root biomass (Fig. 1). However, in terms of nutrient concentration, harvested grass growing with tree seedlings on both soil types had higher N and P concentrations than uncut grass (Tables 3 and 4).

Discussion

Grass competition exerted a significant inhibitory effect on the growth of tree seedlings in all size-related aspects (both above- and below-ground) on both soil types. This result is consistent with the widely reported capacity of grass competition to suppress woody plants at seedling and sapling life-history stages (Weltzin & McPherson 1997; Jurena & Archer 2003; Cramer et al. 2007; Riginos 2009). Reduction of tree seedling biomass by half due to grass competition could translate to reduced productivity, slow growth and delayed reproductive success of woody plants, creating a bottleneck for succession of trees in savannas (Higgins et al. 2000; Bond 2008).

Competition from uncut grass led to significantly higher tree seedling root mass on rocky substrate relative to tree seedlings on sandy substrate. Low water-holding capacity in rocky bins combined with grass competition would have necessitated enhanced below-ground root expansion by tree seedlings to increase resource capture. The physical obstruction presented by the rocks forced roots to grow around the rock barriers, resulting in a

larger root mass. Nobel et al. (1992) demonstrated that arid species growing among rocks and boulders had a higher number of lateral roots per length of main root, as well as higher total length of main roots, primary lateral roots and secondary lateral roots. The suppressive effect of grass competition on tree seedlings in rocky bins was eliminated when the competing grass was cut frequently, such that tree seedlings growing with harvested grass were not significantly different in biomass to tree seedlings growing on their own, but had higher biomass than those competing with uncut grass. It is probable that the architecture and overall morphology of grass roots render them prone to restriction by physical obstructions from rocks and other barriers, which in turn reduces grass competitiveness (see also Mbatha & Ward 2010 for differences in cover of grasses growing on rocky and sandy substrates at the Pniel study site, from where the *A. mellifera* trees were taken). When this was combined with simulated herbivory of aerial shoots, there was a two-fold suppression of grass vitality and its competitive effect (Fig. 2). Sparse grass cover on rocky substrates would mean low fuel load and thus less frequent fires of lower intensity, so that the combined effect of rocky substrate and release from competition through defoliation on trees would be accentuated with fire (Meyer et al. 2005; Bond 2008). However, on sandy substrate grass suppressed tree seedling size despite clipping, possibly because root growth was less impeded in sand and the grass could compete more vigorously.

Competition by herbaceous plants such as grasses for soil moisture, nutrients and light is thought to present a barrier to the establishment of woody seedlings (Scholes & Archer 1997; House et al. 2003), and weakening of grass competition by grazing may promote woody seedling growth leading to bush encroachment (van Vegten 1983; van Langevelde et al. 2003; Ward 2005). In our experiment, we allowed the tree seedlings to establish for a month before introducing grass competition, but grass nonetheless outgrew the tree seedlings after 2 months. While the tree seedlings emerged above the grass sward later, shading by uncut grass most likely led to light competition. Our results suggest that bush encroachment is likely to be enhanced by grass herbivory, especially on rocky substrates. A similar result was obtained by Ward & Esler (2010) in a field experiment at the Pniel study site.

Our results demonstrated the suppressive effect of uncut grasses on tree shoot biomass on rocky substrates, while its influence on sandy substrates was most significant on the root biomass of tree seedlings. This has major implications for the persistence of the deciduous encroaching *A. mellifera* in savannas with rocky soils. Rocks appear to either partially protect tree seedlings from below-ground competition for space and resources or to

require more root investment. The storage of carbon in plants is predominantly below-ground rather than above-ground (Schlesinger 1991; Schutz et al. 2009). Storage of assimilated resources in roots serves to increase plant survival and growth following adverse changes in environmental conditions (Iwasa & Kubo 1997; Wigley et al. 2008; Schutz et al. 2009). Thus, relatively larger root biomass production by *A. mellifera* in rocky areas may enable the trees to resprout, resume growth and reproduce after fire (Meyer et al. 2005; Wigley et al. 2008), herbivory or drought dormancy and to proliferate into dense thickets. Additionally, larger and deeper rooting in the presence of rocks may allow access to more soil moisture and nutrients.

The presence of tree seedlings significantly enhanced grass biomass accumulation above- and below-ground in the absence of clipping on sandy substrates, but tree seedlings had little effect on the grass on rocky substrates. Contrary to our hypothesis, tree seedling competition did not suppress grass biomass production, but rather seemed to facilitate grass biomass accumulation on sandy substrates when the grass was not subjected to frequent clipping. Low nutrient content in a sandy arid environment may necessitate greater below-ground investment by both grasses and trees. Grasses may be expected to establish higher rooting mass on sandy than on rocky areas due to the physical restriction presented by rocky barriers, and thus exert stronger competition for resources. While the roots of tree seedlings may be able to grow around and past such rocky barriers, the roots of grasses are restricted by the rocks. Our results showed that uncut grasses invested more in root production in competition with trees relative to when they grew without interspecific competition. This may, in turn, induce competing tree seedlings to fix atmospheric N₂ (Cramer et al. 2007) from which the grasses then benefit.

When subjected to repeated clipping, grass growing with tree seedlings had smaller above-ground and root biomass than grass growing free of tree competition. This result is consistent with findings that demonstrated a reduction in total grass biomass production as a result of intense defoliation (Pandey & Singh 1992). Tree seedlings thus had a positive influence on grass biomass output, but this benefit was reversed by the clipping perturbation (see also Ward & Esler 2010). The above-ground biomass showed tree seedlings significantly reduce above-ground biomass of grazed grass (Fig. 3). Grass clipping also suppressed below-ground biomass of grass, particularly when the grass was grown with tree competition on rocky soil. The uniform clipping achieved in the greenhouse may not be replicated by herbivores in nature because some animals remove all of the above-ground material while others may take the more palatable sections only

(Wolfson 1999). Tree–grass dynamics as well as plant–herbivore feedbacks in natural systems may create gradients in plant density and intensity of herbivory (Van Auken 2000).

Frequent defoliation of grasses meant that most resources were allocated to shoot reproduction and less to root growth, giving rise to shallower rooting depth of clipped grasses. Frequent clipping of grass may have depleted stored root resources and curtailed their photosynthetic replenishment, thus retarding grass vigour (Chapin & Slack 1979; McNaughton & Chapin 1985). Tolsma et al. (2010) showed that while plants show resilience to occasional clipping, more frequent defoliation led to significant depletion of carbohydrate reserves, accompanied by high mortality of tillers. The grass may have had to rely on translocation from an otherwise limited root biomass or photosynthate from shoot remnants to replace harvested parts above-ground and sustain growth. Studies from temperate regions have shown that N allocated to shoot growth by forage grasses/legumes during the first days following severe defoliation is primarily relocated from roots rather than taken from the soil (Ourry et al. 1989; Culvenor & Simpson 1991; Louahlia et al. 1999).

Unlike the responses in biomass, the influence of tree seedlings on grass nutrient concentration was only significant when the grass was frequently cropped. Frequent clipping initiated the replacement of old tissues with fresh growth high in nutrient content, whereas the bulk of uncut grass biomass had senesced at harvest at the end of the experiment. Relatively higher nutrient concentrations in grazed compared to ungrazed grass (McNaughton 1984, 1985; Frost & Robertson 1987; Mbatha & Ward 2010) may result from enhanced nutrient uptake by defoliated grass (Ruess 1984) and compensatory amplification of photosynthesis (Caldwell et al. 1981; Senock et al. 1991). Although care was taken to mill and analyse green foliage, the interference of a large amount of senescent leaf material in the uncut grass sample could not be entirely avoided. The possibility of nutrient dilution (Warren Wilson 1966; Shaver & Chapin 1980) as a contributing factor to the observed trends is unlikely as the nutrient concentration of grasses continued to increase when grass biomass output increased for the first harvest. The likely cause of elevated nutrient concentration in grass when grown with tree seedlings is that the grasses benefitted from fixed N₂ by the *Acacia* tree seedlings. Low relocation of N from leaves to shoots in *Acacia* tree species (Tolsma et al. 1987), coupled with comparatively higher N content in legumes relative to non-nodulated woody plants (Durr & Rangel 2000) resulted in relatively high N concentrations in the *Acacia* litter fall from which grasses profited (Tolsma et al. 1987). Nitrogen

in fallen tree leaves may have benefitted the grasses in our study, but high N concentrations of grasses grown with trees than in grass-only bins was found from the first harvest, at which stage no tree leaves had been abscised. Transfer of fixed N₂ from the woody seedlings to the grasses, probably via nodule and root turnover as well as root exudates (Sierra & Nygren 2006; Sierra et al. 2007), was therefore the most likely contributor to elevated grass N when grown with tree seedlings.

Sustained heavy defoliation of grasses delays and retards root activities for days (Wolfson 1999) and restricts root production to shallow soil depths (Schuster 1964). Repeated removal of above-ground biomass through herbivory might promote rooting niche separation by constraining below-ground biomass production and root depth penetration by grasses, but the resultant scant remnants of root mass (Hild et al. 2001) may not be sufficient to fully intercept and extract significant moisture. More water from precipitation is likely to infiltrate deeper and benefit the relatively deep-rooted trees when competing grass is continually removed by grazers. This is in agreement with the assertion that heavy grazing pressure that continually removes grass cover allows deeper percolation of soil moisture to subsoil layers exploited by woody plant species (Knoop & Walker 1985; McNaughton et al. 1988; Skarpe 1990), thereby encouraging shrub encroachment (Jeltsch et al. 1997; Graz 2008). When not subjected to regular harvesting, grasses were able to exploit a deeper and larger volume of soil for nutrients and moisture, utilizing a higher rooting mass, thus directly competing with the tree seedlings. Access to a larger volume of resource pool may have negated or balanced the reliance on fixed N₂ from tree seedlings, removing differences in nutrient concentration of uncut grass growing with and without tree seedling competition.

Conclusions

We found that competition with grass suppressed tree seedling growth and establishment. This is consistent with our prediction that encroachment by woody plants may result from heavy grazing pressure on the grass component of savanna ecosystems. The outcome of clipping and interspecific competition between trees and grasses combined to severely curtail grass performance. We found that this response was particularly acute on rocky substrates, which matches the empirical findings of Britz & Ward (2007) and Ward & Esler (2010). We suggest that encroachment resulting from heavy grazing occurs most frequently on rocky substrates because the trees and grasses are forced to share a depth niche for water and/or nutrient resources due to direct root competition.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Photo S1. Closed thicket formation by *Acacia mellifera* at Pniel.

Photo S2. Encroachment by *Acacia mellifera* on rocky substrate at Pniel in Northern Cape Province of South Africa.

Photo S3. Hilly rocky outcrop at Pniel with rain falling in background.

Photo S4. *Acacia mellifera* encroaching on rocky areas at Pniel.

Photo S5. Fresh pods and leaves on encroaching *Acacia mellifera* at Pniel in Northern Cape, South Africa.

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