Another look at the savannah conundrum: evidence of niche segregation and competition avoidance with grasses in establishing trees

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Abstract

The savannah vegetation, although iconic, is a curiosity due to the coexistence of the two dominant, but remarkably different life-forms: trees and grasses. However, despite an apparent competitive advantage grasses do not dominate over trees in these systems and this presents a conundrum: how are savannah trees are able to establish in the face of such strong competition from grasses? As this is when trees are most susceptible to competition from grasses. This makes the knowledge of establishment phase critical for understanding the tree-grass co-existence. Despite this, there is a paucity of knowledge of this phase and the long-term aspects of the competitive interactions between trees and grasses, where the focus should be on seedling establishment and survival rather than biomass accumulation This study investigated the natural levels of tree establishment amongst differing amounts of grass as we sought to identify the limitation, both aboveground for light and belowground for resources, imposed by grasses on tree establishment. To uncover this limitation we searched for naturally established *Acacia nigrescens* (the dominant savannah tree species in our research area) seedlings at 12 sites in the Limpopo Province, South Africa. We also collected data on seedling health to determine the effect of proximate grass canopy on their performance. Finally, we compared the root lengths of established seedlings and co-occurring grasses to determine if seedlings were rooted in the same soil horizons as grasses. We hypothesised that tree establishment would be facilitated by low levels of grass biomass, as the lower the grass biomass, the more gaps would be present in the grass layer for seedlings to establish. We found that establishing seedlings were more resilient to grass competition than had previously been appreciated, as we found established seedlings (at a density of 9 seedlings per 100m^2) with a grass canopy cover of 65%. We also found no correlation between our measure of grass competition and seedling performance. Finally, we found that even very young tree seedlings consistently root deeper than co-occurring grasses, despite establishing on different geologies, soils and across a rainfall gradient ($p < 0.0001$) - demonstrating that this resilience to grass competition is due to a specialised rooting strategy present in seedlings that allows them avoid belowground competition with grasses. In light of this, we propose a dynamic two-niche hypothesis of savannah tree-grass co-existence.

Introduction

Savannahs are geographically extensive, biologically productive, and socioeconomically important biomes that occupy 54% of southern Africa (Rutherford, 1997; Scholes & Archer, 1997), and 12% of global land area (Scholes & Hall, 1996). They occur where the mean annual precipitation is between 300mm to 1600mm (Frost *et al.,* 1986). Rainfall is strongly seasonal, primarily occurring in one “wet season” (Frost *et al.,* 1986). The “dry season” is associated with a shortage of plant available water in the upper (1m-2m) soil layers (Frost *et al.,* 1986). This water shortage can last as long as 9 months in xeric savannahs and as short as 3 months in mesic savannahs (Frost *et al.,* 1986). The soils are often sandy and nutrient poor – especially in arid regions (Frost *et al.,* 1986; Feral *et al.,* 2003).

The savannah vegetation, although iconic, is a curiosity due to the coexistence of the two dominant, but remarkably different, life-forms: trees and grasses. This co-existence is seen in the landscape as a discontinuous tree layer superimposed on a continuous grass layer (Frost *et al.*, 1986). These different life-forms are, rather unsurprisingly, different in their competitive ability, demographic structure, nutrient and water requirements, and their resilience to disturbance caused by fire and herbivory. Grasses are formidable competitors for nutrients and water as they possess extensive root systems which can have as much as nine times more fine-root biomass compared with their aboveground biomass (Pärtel & Wilson, 2002; Riginos, 2009; February *et al.,* 2013). Grasses also have rapid growth due to their high water use efficiencies and lack of woody tissue (Beale *et al.,* 1999), allowing them to be more responsive than trees to resource pulses (Bond, 2008). Despite this apparent competitive advantage grasses do not dominate over trees in these systems, but why? This question is often referred to as the “savannah question” and its answer has remained, for the most part, elusive to ecologists.

It is reasonably well understood that nutrients, water, fire and herbivory influence the competitive equilibrium between trees and grasses and in so doing alter the structure and function of savannahs (Frost *et al.,* 1986). However, there is little consensus on the relative contribution of each factor to the competitive equilibrium (Bond, 2008). With no apparently simple answer, hypotheses about the tree-grass co-existence are numerous and are often markedly different, but these hypotheses can be largely grouped into two fundamental classes: disturbance-based hypotheses (fire and herbivory) and resource-based hypotheses (nutrients and water) (Sankaran, 2004).

Disturbance-based hypotheses argue that the critical challenges facing trees in savannahs are demographic in nature: seedlings seldom establish because of frequent droughts and competition with grasses (Higgins et al. 2000) and even when they do successfully establish, juvenile trees are prevented from reaching reproductive size classes by frequent fires and herbivory (Bond and van Wilgen 1996, Higgins et al. 2000).

Resource-based hypotheses on the other hand, argue that competition for water and nutrients is the primary driver of savannah structure. The first resourced based hypothesis was proposed by Walter in 1971 and developed into an analytical model by Walker and Noy Meier in 1982. Walter’s hypothesis, or the two-layer hypothesis, proposed that trees and grasses access resources in two distinct soil horizons, with trees avoiding competition from the shallow-rooted grasses by rooting below them and exclusively accessing resources in deeper soil horizons, and that this allows both life-forms to co-exist in the savannah (Walter, 1971). Although intuitive and simple, this hypothesis has lost favour in recent years, as both trees and grasses have been shown to exploit the upper soil layers (February & Higgins, 2010; Kulmatiski *et al.,* 2010; February *et al.,* 2013a).

Recent research also suggests that competition is not only for water but that it is in fact predominantly for nutrients - especially nitrogen (February & Higgins, 2010; Cramer *et al*., 2007, 2010, 2012). This is because water is not limiting during the growing season (wet season) and a strong correlation has been found between root biomass (both trees and grasses) and the nitrogen concentration of the soil (February & Higgins, 2010; February *et al.,* 2013a). These studies demonstrate that the highest concentration of nitrogen is in the top 5cm of soil and that this concentration rapidly diminishes down the soil profile (February & Higgins, 2010; February *et al.,* 2013a). It has also been demonstrated that large juvenile trees (3-4m) rely heavily on their shallow lateral roots for nutrients and water, as severing these roots causes severe water stress and negatively affects plant performance (Verweij *et al.,* 2011). This suggests that trees in older demographic stages rely on lateral roots in the top horizons of the soil for most of their nutrient demands. These studies therefore demonstrate that both trees and grasses actively exploit the upper, relatively nutrient-rich, layers of the soil for nitrogen in this nutrient-limited system (Craine *et al.,* 2005, 2008).

The extensive utilisation of these shallow soil horizons by both older trees and the hypercompetitive grasses presents a problem for establishing savannah trees, as their roots are initially forced to occupy this zone of intense competition and they are thus susceptible to competitive exclusion (Hardin, 1960). Grass competition has been demonstrated to have a severe impact on juvenile tree and seedling performance (Cramer *et al*., 2007, 2010, 2012; Higgins *et al.,* 2007; Riginos, 2009; February, 2013b) and this makes an understanding of grass competition essential to understanding the limitation this competition imposes on tree establishment. However, competition with grasses in the past has typically been inferred from indirect measurements of competition such as aboveground, belowground and net productivity. While it is true that grass competition has been shown to supress the growth of trees, preventing them from reaching maturity (Cramer *et al*., 2007, 2010, 2012; Higgins *et al.,* 2007; Riginos, 2009; February, 2013b), grass competition has not been demonstrated to cause the mortality of juvenile trees or even seedlings. Such studies therefore neglect the long-term aspects of the competitive interactions between trees and grasses where the focus should be on seedling establishment and survival rather than biomass accumulation (Brown *et al.,* 1998). This illuminates a fundamental gap in our understanding of the establishment phase of savannah trees, as no studies have demonstrated the impact of grass competition on seedling establishment or seedling survival.

Despite the establishment phase being heralded as “the critical demographic bottleneck in arid savannahs” (Bond, 2008), knowledge of this “critical” phase is severely lacking. This phase is particularly important, because once established, juvenile trees may persist in the landscape for decades without reaching maturity (Bond and van Wilgen 1998; Higgins *et al.,* 2007). However, no studies have looked at the natural levels of tree establishment in the savannah in response to grass biomass. Knowledge of this will shed light on the crucial question: how is it that savannah trees are able to establish in the face of such strong competition from grasses at the seedling stage?

This study investigated the natural levels of tree establishment amongst differing amounts of grass as we sought to identify the limitation, both aboveground for light and belowground for resources, imposed by grasses on tree establishment in the savannah. To determine this limitation we investigated a previously overlooked size class of seedling. This size class includes seedlings that are less than one year old and have naturally established amongst grasses in just one growing season. Knowledge of this demographic stage is essential, because trees in this size-class are predicted to be the most vulnerable to disturbance and competition, however, if they survive, they immediately enter the next demographic stage. This is because seedlings even as young as one year old have been demonstrated to resprout and persist in the landscape (Hoffmann, 1999). This demographic stage therefore represents the critical phase in seedling establishment when grass competition is most likely to limit such establishment. To address our hypothesis we determined the effect of grass canopy cover (an indirect measure of limitation by light) and grass sward successional state (an indirect measure of resource limitation) on the natural establishment levels of *Acacia nigrescens* (the dominant savannah tree species in our research area). We also determined the effect of grass cover in close proximity to seedlings (an indirect measurement of grass biomass) on their performance. Finally, we compared the root lengths of established seedlings and co-occurring grasses to determine if seedlings were rooted in the same soil horizons as grasses at this stage (an indication of the strength of belowground competition with grasses). We hypothesised that tree establishment would be facilitated by low levels of grass biomass, as the lower the grass biomass, the more gaps would be present in the grass layer for seedlings to establish.

Methods

This study was comprised of two parts, the first was conducted in the field to locate and excavate naturally established seedlings. The second part was a seedling-growth experiment in the University of Cape Town’s glasshouse for age calibration of the seedlings found in the field. Field data were collected from 12 study sites in the Limpopo Province, South Africa between 12 May and 1 June, 2014 (middle of the dry season) The glasshouse experiment was conducted between 21 July and 9 October, 2014 – approximately 2 months growing time.

Field Research

Research area

This part of our study was conducted at four locations in the Limpopo Province of South Africa: Grietjie Private Nature Reserve, Balule West Private Nature Reserve, the town of Phalaborwa and at Satara camp in the Kruger National Park.

Grietjie Private Nature Reserve (24°06'S, 31°00'E) is a 2,800 hectare reserve in the Greater Kruger National Park on the Olifants River broken up into several 10-25 hectare plots. This reserve is situated within the Lowveld Rugged Mopaneveld bioregion (Mucina & Rutherford, 2006). The underlying geology for this bioregion is Goudplaats Gneiss and Makhutswi Gneiss (Mucina & Rutherford, 2006) and the soils are red-yellow apedal, freely drained and shallow (Mucina and Rutherford). This bioregion receives summer rainfall of approximately 400-600mm a year and has very dry winters (Mucina & Rutherford, 2006). The dominant tall tree species are *Acacia nigrescens* and *Sclerocarya birea* subs. *caffra*, and the dominant grass species are *Aristida congesta*, *Enneapogon cenchroides* and *Sporobolus panicoides* (Mucina & Rutherford, 2006).

Balule West Private Nature Reserve (24°09'S, 30°59'E) is a privately owned 40,000 hectare reserve in the Greater Kruger National Park situated on the Olifants River to the south of Grietjie Private Nature Reserve. This reserve is situated within the Granite Lowveld bioregion (Mucina & Rutherford, 2006) where the underlying geology is mostly Archaean gneiss and granite. These rocks weather into the clayey soils found in the region (Mucina & Rutherford, 2006). This bioregion has a mean annual precipitation of around 500mm (Mucina & Rutherford, 2006). The dominant tall tree species are *Acacia nigrescens* and *Sclerocarya birea* subs. *caffra*, and the dominant grass species are *Brachiaria nigropedata*, *Digitaria eriantha* subsp. *eriantha* and *Eragrostis rigidior* (Mucina & Rutherford, 2006).

The town of Phalaborwa (23°56'S, 31°07'E) is situated in the Mopani District Municipality, Limpopo province, South Africa and is located near the confluence of the Ga-Selati River and the Olifants River, halfway up along the eastern border of the Kruger National Park. This town is also situated in the Lowveld Rugged Mopaneveld bioregion (Mucina & Rutherford, 2006), and so has similar underlying geology, soils, and rainfall as Grietjie Private Nature Reserve.

Satara camp (24°23'S, 31°46'E) is the Kruger National Park's third biggest rest camp and is situated in the central and southern section of the park. The camp is situated in the Tshokwane-Hlane Basalt Lowveld bioregion (Mucina & Rutherford, 2006). Its underlying geology is mostly Letaba Formation basalts of the Karoo Supergroup (Mucina & Rutherford, 2006). These rocks give rise to dark clayey soils that are usually less than 1m deep (Mucina & Rutherford, 2006). This bioregion receives between 400-80mm of rain a year and has dry winters. The dominant tall tree species are *Acacia nigrescens* and *Sclerocarya birea* subs. *caffra*, and the dominant grass species are *Bothriochloa radicans, Digitaria eriantha* subsp. *eriantha* and *Panicum coloratum* (Mucina & Rutherford, 2006).

Study sites

Sites 1-5 were situated at Grietjie Private Nature Reserve in varying levels of woody cover and grass biomass. Sites 6-9 were situated on the outskirts of the town of Phalabrowa. These were all full-grass (grass dominated) sites either on the eastern or western edge that formed a buffer between the town and the surrounding bush. These buffers were created by the municipality by removing all the small trees and shurbs, and leaving only the larger *Acacia nigrescens* adults. These buffers were being maintained by the exclusion of fire. Sites 10 and 11 were situated within Balule West Private Nature Reserve in varying levels of woody cover and grass biomass. Site 12 was situated inside a fenced-off portion of a buffalo enclosure just outside Satara camp. This was another full-grass site where fire and herbivory had been excluded for 13 years.

Field sampling and analysis

We searched large areas of Grietjie Private Nature reserve on foot for small *Acacia nigrescens* seedlings (<30 cm in height). When seedlings were located the area was deemed a "site". This process was repeated for the searches in Balule West Private Nature Reserve, the town of Phalaborwa and in a buffalo enclosure outside Satara camp. At each site grass canopy cover, specific grass cover, specific forb cover, seedling density, seedling aboveground height, seedling rooting depth, seedling stem diameter, grass aboveground height and grass rooting depth was determined. Notable exceptions are the full-grass sites where no seedlings were ever located and so only grass data were collected. Finally, grass species presence at each site was noted.

Grass canopy cover of a site was determined through an average of estimated grass percentage-cover in ten randomly placed $1m^2$ quadrats. We also estimated specific grass and forb cover in a circle of area $0.13m^2$ centred on a seedling. Seedling aboveground height, rooting length and stem diameter measurements were taken using a 30cm steel ruler after the seedling had been carefully excavated. A maximum of ten seedlings were excavated from a site and special care was taken to remove seedlings without breaking their roots. Seedling density was the number of seedlings of the correct size-class (<20 cm in height) in a $1m^2$ quadrat centred on the first seedling found at a site and grass height and rooting length came from the average of 10 carefully excavated randomly-selected grasses (the closest grass to the centre of each grass canopy cover quadrat) at each site. Grass species were identified using *Guide to Grasses of southern Africa* (van Oudtsoorn, 2012). This guide was later used to determine a grass species' "successional niche" (climax, sub-climax or pioneer), which represent a continuum of the following traits: fecundity, dispersal, growth rate and tolerance to resource limitation. Early successional species (pioneer species) have high fecundity, large dispersal and rapid growth when resources are abundant, thus making them well-adapted for colonising recently disturbed sites (Grime, 1979). Whereas, late successional species (climax species) have relatively low fecundity, short dispersal, slow growth and an ability to survive under resource-poor conditions which are present in areas that have been free from disturbance (Grime, 1979). The number of climax species present in a grass sward was then used as an indication of its successional state (either early- or late-successional) which reflects the time since it was last disturbed.

Seedling-growth experiment

For this experiment we used a common savannah tree species and the dominant tree species at our field sites, *Acacia nigrescens*. Seeds were soaked overnight in warm water and then placed between layers of moist absorbent-paper on a plastic tray. This germination tray was then put on a sunny windowsill and the layers of paper kept moist by periodic soaking. After three days (21 July 2014) germinated seeds were planted in pots (9 cm X 8 cm) filled with washed river sand containing no organic matter. The pots were then placed inside the University of Cape Town's southern glasshouse. All seeds that germinated were planted. Seedlings were then left to grow in the seedling pots for 5 weeks and were supplied only with water during this time.

On the 25 August 2014 all surviving seedlings (some died due to dessication) were transferred to larger, tall and narrow (50 cm X 10 cm), pots also filled with thoroughly washed river sand containing no organic matter. At the time of this transfer, seedling height above ground (cm), root length (cm) and stem diameter (mm) at the widest point (almost always at the level of the soil surface) were determined.

The seedlings were left to grow for a further seven weeks (a total of 60 days overall). During this time they were watered three times a week and twice-weekly 300ml of fertilizer was applied [$MgSO_4 .7H_2O$ (0.15M), K_2SO_4 (0.2M), $CaCl_2 .2H_2O$ (0.4M), $NaH_2PO_4 .2H_2O$ (0.067M), $Na_2HPO_4.12H_2O$ (0.15M), H_3BO_3 (0.23M), $MnSO_4 .4H_2O$ (0.04M), $ZnSO_4 .7H_2O$ (0.005M), $CuSO_4 .5H_2O$ (0.007M), $Na_2MoO_4 .2H_2O$ (0.0005M), Fe EDTA and 4mM $NaNO_3$].

On 08 October 2014 all seedlings were removed from their pots, had their roots washed, and seedling height above ground (cm), root length (cm) and stem diameter (mm) we determined as before.

Statistical analyses

We analysed data from each site using simple regression. Where root-length means were tested for significant difference we first tested data for normality using a Shapiro-Wilk normality test. Data were non-normal and so a non-parametric Wicoxon rank sum test was employed to test the means for significant difference. For age calibration all seedlings found in the field had their stem diameter and root length used to estimate their age by substituting the value into a linear model (with y-intercept = 0) created from glasshouse seedling data and solving for time (the x axis). The estimated ages of all seedlings were then used to calculate the average age of the seedlings based on stem diameter or root length found in the field. All regressions, correlations and statistical tests were performed using R statistical software (Austria, 2013).

Results

Our results show that seeding establishment is limited by the grass canopy cover of a site regardless of geology, rainfall, or herbivory (R^2 = 0.66; Fig. 1). Once grass canopy cover is above 80% seedlings are unable to establish. An increase in grass canopy cover is also strongly correlated with an increase in grass sward average height (R^2 = 0.92; Fig. 2). Furthermore, our data reveal that grass sward successional state is a major determinant of grass canopy cover at a site (R^2 = 0.83; Fig. 2) and this successional state also limits the number of seedlings able to establish in an area (R^2 = 0.64; Fig. 2). These results show that grass sward canopy cover, height, and successional state are all tightly correlated (Fig. 1 & 2) and that grass species composition changed with successional state.

Grass species composition differed on full-grass sites which had an average of 3.4 climax grass species present. These were *Panicum maximum* (Sites 5-9), *P. coloratum* (Site 12), *Cenchrus ciliarus* (Sites 5-9), *Eriochloa meyeriana* (Sites 5-9), *Themeda triandra* (Sites 7, 8 & 12) and *Setaria sphacelata* (Site 12), all these species were perennial tufted grass (grow for more than five seasons) . All other sites had only one climax grass species present (*Panicum maximum*) and these were often small individuals. These sites were not dominated by climax species but were rather dominated by the pioneer and sub-climax species, with the dominant species being: *Aristida congesta subsp. congesta* (an annual pioneer species), *Sporobolous panicoides* (an annual pioneer species), *Enneapogon cechroides* (a perennial pioneer species) and Tricolena *monachne* (a perennial sub-climax species).

Our results also show that establishing *Acacia nigrescens* seedlings, even on different geologies and along a rainfall gradient (470mm at Phalaborwa and 550mm at Satara), consistently root deeper than grasses (W = 438, n grass = 120, n seedling = 67, $p < 0.0001$; Fig. 3). Grasses root with a mean depth of 14.8 ± 4.18 cm, while tree seedlings root with a mean depth of 27.3 ± 6.92cm (Fig. 3). Our results also show that the grasses in the buffalo enclosure at Satara which had not burnt in 13 years had large individuals who also had particularly deep roots (mean root length = 21.7 ± 581 cm and mean height aboveground = 92.6 ± 20.64 cm; Fig. 3)

The results of our model based on stem diameter or root length from our growth experiment demonstrate that seedlings found in the field were on average around 83 days, or 41.5 days, depending on which seedling dimensional measurement (stem diameter or root length) is used to calibrate age (Fig. 4). However, it is apparent that even with the most conservative estimate all the seedlings are younger than 4 months old (Fig. 4). These results show that all of the seedlings found in the field were less than one year old.

Neither specific grass cover nor specific forb cover had any correlation with any of the seedling dimensional traits or root to shoot ratios. On average, seedlings (n = 77) had a root to shoot ratio of 3.1 ± 0.96**:** 1, while the root to shoot ratio of grasses (n = 120) was 0.3±0.18: 1.

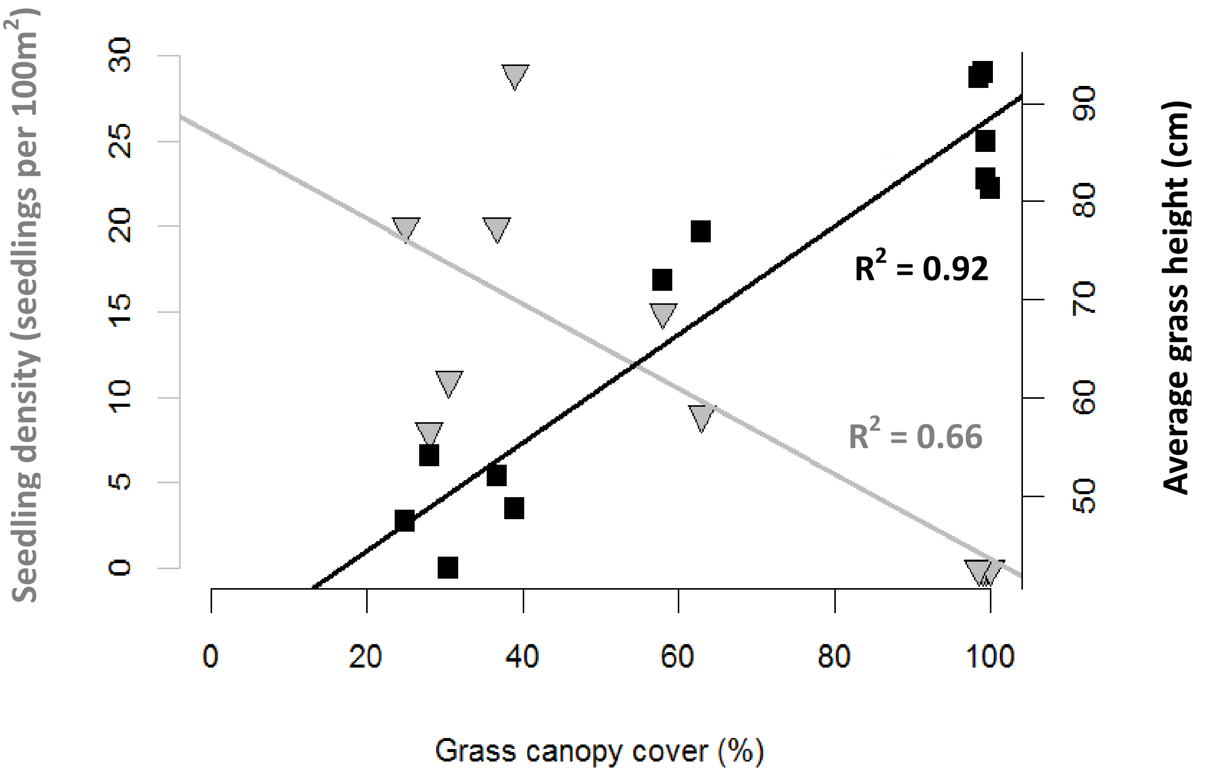

Fig. 1. Relation between grass canopy cover, seedling density (■) and average grass height (▽), for all sites (n = 12). The coefficient of determination (R^2) is displayed for the linear best-fit line: $y = 0.55x + 33.37$ (grass height) and $y = -0.2495x + 25.484$ (seedling density).

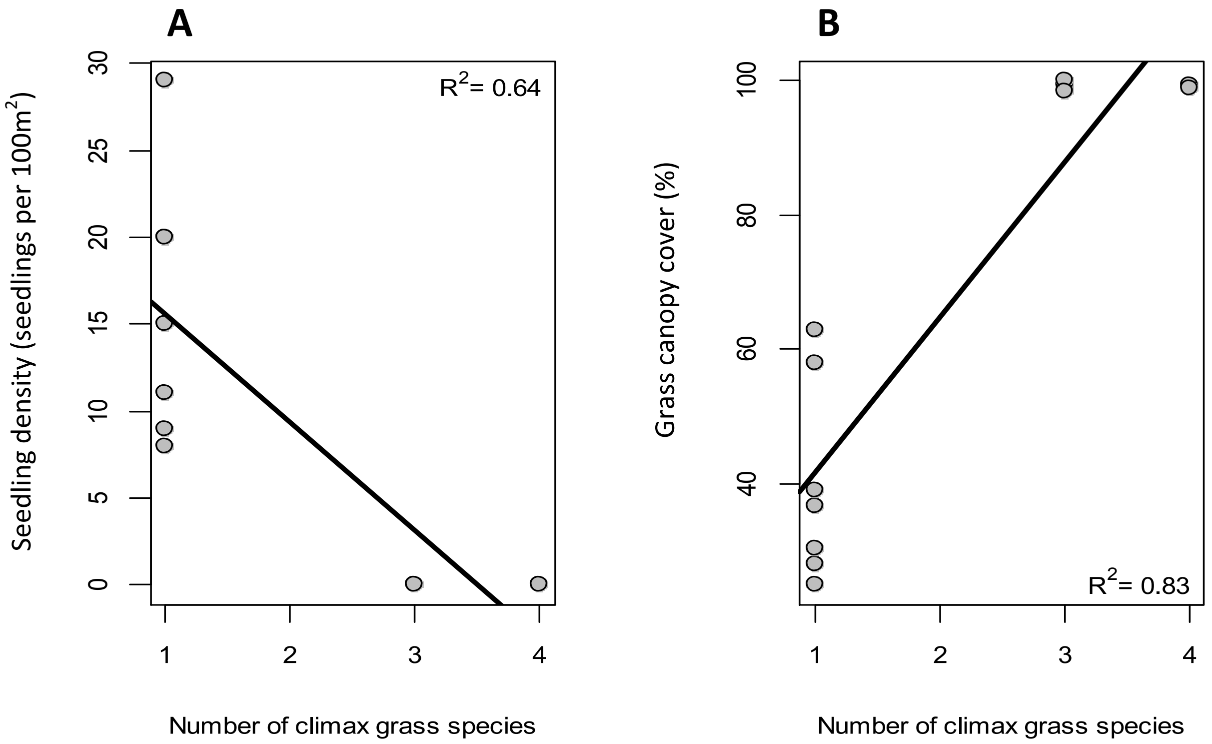

Fig. 2. The effect of grass successional state (number of climax species in a site) on the natural density of established *Acacia nigrescens* seedlings (less than one year old) [**A**], and the relation between grass successional state and grass canopy cover [**B**]. Average data used from all sites (n for both graphs = 12). The coefficient of determination (R^2) is displayed for the linear best-fit line ($y = mx + c$) to the data for each graph. Where [**A**]: $y = -6.2222x + 21.778$, [**B**]: $y = -2.9775x + 24.469$.

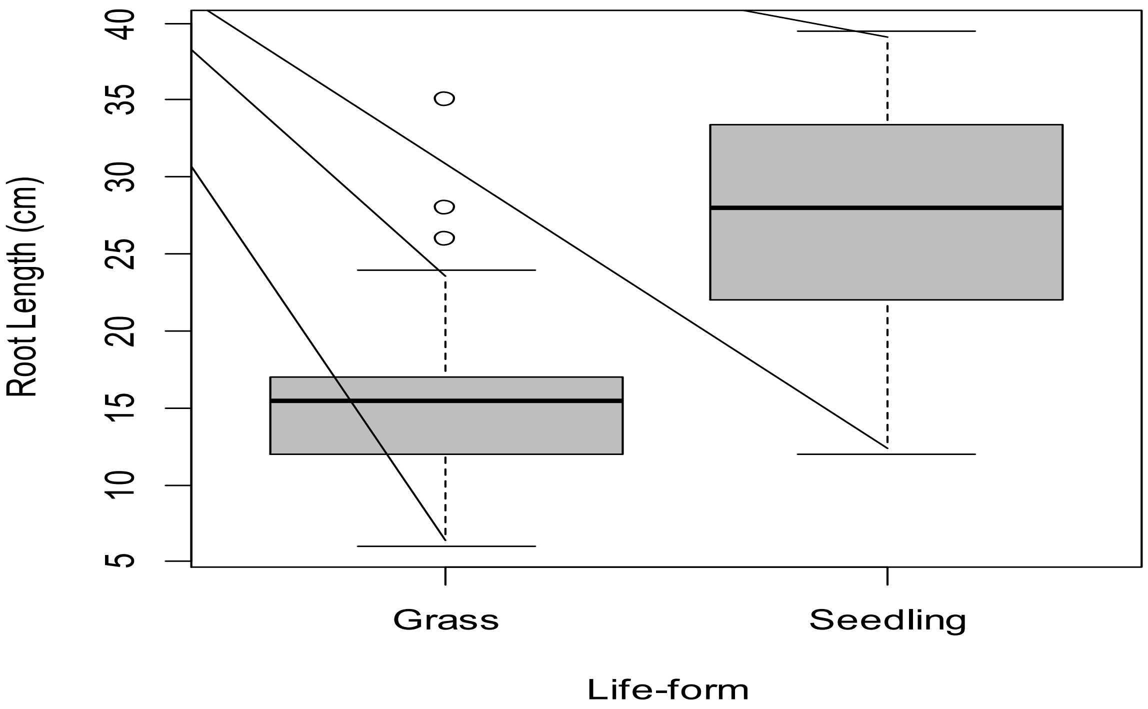

Fig. 3. Boxplot illustrating differences in rooting depth between established *Acacia nigrescens* seedlings (mean = 27.3 ± 6.92cm, n = 67) and randomly selected grasses (mean = 14.8 ± 4.18cm, n = 120) from all sites. A statistically significant difference is observed between the rooting depth of the two life-forms (W = 438, n grass = 120, n seedling = 67, $p < 0.0001$). Grass outliers are all individuals from Satara camp.

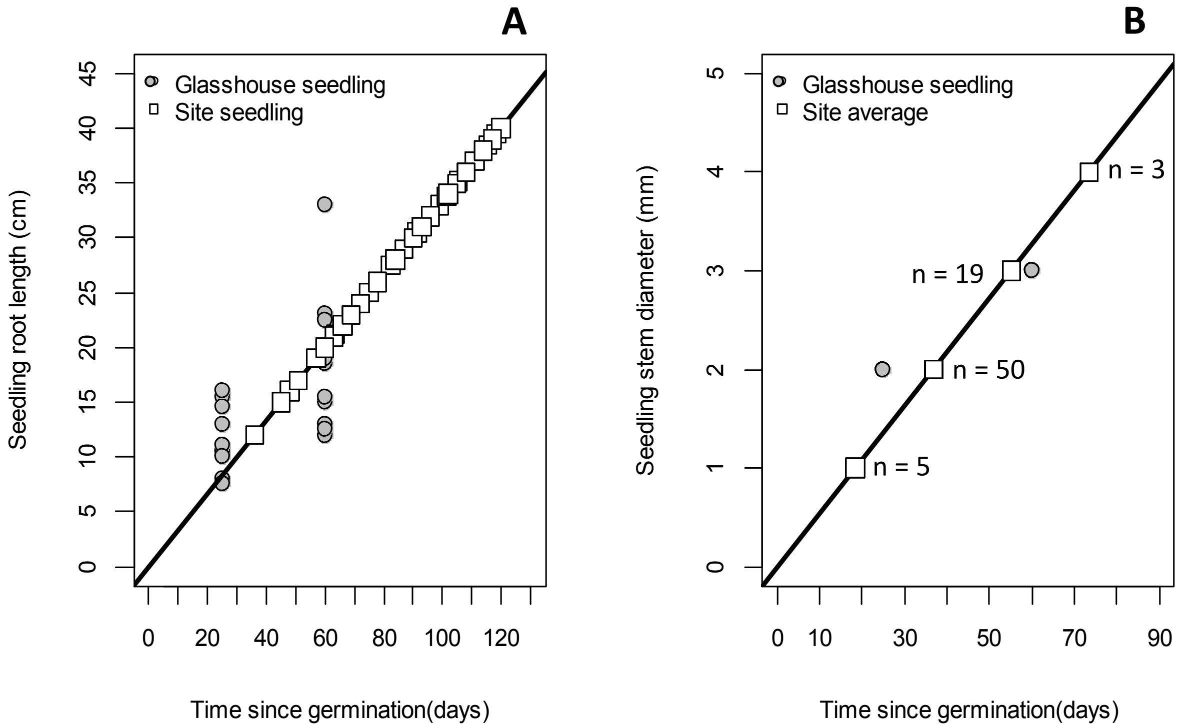

Fig. 4. All seedlings found in the field (n = 77) are forced onto the linear best-fit line forced through the origin (*y = mx*) of the associated dimensional measurement of glasshouse seedlings grown for two months (n = 26) to produce an estimated age. Where [**A**]: *y = 0.3336x* and [**B**]: *y = 0.0544x.* Average estimated seedling age: [**A**] = 83.0 ± 22.01 days since germination, and [**B**] = 41.5 ± 11.70 days since germination. The number of seedlings found in the field with a particular stem diameter (from different sites) is presented.

Discussion

Surprising results and identification of an evasive rooting strategy in seedlings

In trying to understand the limitation that grasses pose to seedling establishment and the long-term interactions of tree-grass competition we identified the natural establishment levels of trees with varying amounts of grass biomass (Fig. 1). Our results indicate that savannah trees are unable to establish amongst grasses that have reached a late successional state and have developed into a dense grass sward with a canopy cover above 80% (Fig. 1 & 2).

Our results also demonstrate that such grass swards can only develop when they reach a late successional state (Fig. 2). This indicates that such a transition is in response to a lack of disturbance from fire and herbivory, resulting in a change in grass species composition where more climax species are present. Furthermore, our results show that the progression of a grass sward to a late-successional state is strongly correlated with an increase in grass canopy cover (R = 0.83; Fig. 2) and grass height

(R = 0.92; Fig. 1) which is due to the perennial habit of climax grass species (van Oudtshoorn, 2012). This allows climax species to increase in both above- and belowground biomass in the absence of disturbance (in the form of fire and herbivory) relative to pioneer species which tend to be annuals with relatively lower below- and aboveground biomass regardless of disturbance (van Oudtshoorn, 2012). Our results demonstrate that at a threshold level of grass canopy cover (which can only be surpassed by a late-successional grass sward) light becomes a limiting factor for seedling establishment - not belowground competition - as our results show that tree seedlings root significantly deeper than grasses (Fig. 3). These sites also had grass canopy cover close to 100% indicating a deficit of light on the soil surface (Fig 1). Studies have also shown savannah tree seedlings are sensitive to competition for light (Smith & Shackleton, 1988) while cropped grass suppresses seedling growth but does not cause mortality (Cramer *et al.,* 2010). However an exception may be at the Satara site where grasses were found to have particularly long roots, however, these individuals were also tall and so the exclusion of fire and herbivory for 13 years has allowed these climax species (mostly *Panicum coloratum*) to become very large.

Our results therefore show that disturbance will not only cause a reduction of grass biomass, but that it will in fact result in a species compositional change. This compositional change favours seedling establishment as pioneer species, which come in after disturbance, are seen to be shallower-rooted and having lower above- and belowground biomass relative to the climax species. Grass swards such as the one at our Satara site therefore represent a situation where tree seedlings are unable root below these deep-rooted, late-successional, species and are therefore overwhelmed by superior competition for both light and resources. However, with the high levels of fire and herbivory disturbance inherent in the savannah, it is unlikely that such late-successional grass swards could develop without anthropogenic influence.

Apart from full-grass sites we found ubiquitous seedling presence at all sites (Fig. 1). This suggests that if grass canopy cover is maintained below 80% by fire and herbivory, grass does not represent a significant problem for tree establishment. This is supported by our observation that seedling density was as high as 9 seedlings per 100m^2 even at 63% grass canopy cover - the highest recorded grass canopy cover outside of the full-grass sites (Fig. 1).

Our results therefore show that tree establishment is resilient to grass competition where fire and herbivory is present in the system. This is further substantiated by our finding that grass biomass in close proximity to seedlings had no effect on seedling performance. This unexpected result raises an important question: how are tree seedlings so resilient to competition from the hyper-competitive grasses which we had hypothesised would severely limit their establishment?

Our data show that young *Acacia nigrescens* seedlings are capable of avoiding belowground competition with co-occurring grasses. This can be seen in the highly significant difference in rooting length between trees and grasses over a range of environmental, geological and climatic variables ($p < 0.0001$; Fig. 3). Our results also demonstrate that young tree seedlings have roots three times longer than their shoots whereas grasses have shoots three time longer than their roots. This indicates that young tree seedlings are investing resources to belowground biomass rather than aboveground biomass. The observation that this belowground biomass was primarily in the form of a long tap root suggests that these young seedlings are using stored resources in their cotyledons to drive their roots below the grasses. This is supported by the observation of vigorous germination from the relatively large seeds of savannah tree species (Brown *et al.*, 1998). Such a rooting strategy is therefore likely to be a strategy for competition avoidance with grasses, as this strategy provides a means of avoiding the overwhelming competition present in the shallow, relatively nutrient-rich, soil horizons. This evasive rooting strategy does, however, make use of the deeper, nutrient-deficient, soil horizons and so whilst competition has been avoided, the seedlings are still nutrient limited - especially for nitrogen (February & Higgins; February *et al.,* 2013a). However, the dominant tree species in the savannah are in the family *Fabaceae,* many of whose species are known to nodulate (DeFaria *et al.,* 1989; Midgley & Bond, 2001). This ability to fix atmospheric nitrogen through symbiosis with nitrogen fixing bacteria in the soil provides legume seedlings with the nitrogen they need to initially expand their root system in these deeper nitrogen-deficient soil horizons. This is supported by the work of Cramer and colleagues (2007, 2010 & 2012) who demonstrate the importance of nitrogen fixation in *Acacia* seedlings at this stage.

The evasive rooting strategy identified in our study, coupled with an almost unique ability to fix nitrogen, may provide legume species with advantage in savannahs where both trees and the hyper-competitive grasses root in shallow, relatively nutrient-rich, soil horizons (February & Higgins, 2010; Kulmatiski *et al.,* 2010, 2013; Verweij *et al.,* 2011; February *et al.,* 2013a) and may provide an explanation for why *Fabaceae* species, particularly species in the genus *Acacia,* are taxanomically overrepresented in the savannah – an overrepresentation that is well stablished (Midgley & Bond, 2001).

Following the initial expansion of their root systems using nitrogen fixation, we postulate that the now juvenile trees begin to explore the shallower relatively nutrient-rich soil horizons, as sufficient nutrients to escape the fire and herbivory trap can only be found in these horizons (February & Higgins; February *et al.,* 2013a). However, these top soil horizons can only be exploited for resources at a time when the grasses are still dormant. Trees achieve this by flushing their leaves just before the first summer rains (Scholes & Archer, 1997). This allows them to rapidly utilize mineralised nitrogen that becomes available as soon as the first rains fall (Scholes & Archer, 1997). This is a time when grasses are still dormant and thus allows trees to access nutrients in the shallow soil horizons for a short period of time before they are susceptible to being outcompeted for these nutrients by grasses (Scholes & Archer, 1997). Following the first rains, trees stop exploiting these shallow soil layers as the now active grasses begin to out-compete them for the remaining nutrients in these horizons (Scholes & Archer, 1997). This strategy allows trees to gain enough resources to escape the fire and herbivory trap and recruit in older demographic stages and following this, reproductive adults are able to persist in the landscape for decades, continuously setting seed and experiencing a freedom from disturbance, particularly fire (Higgins *et al.,* 2007).

A dynamic two-niche hypothesis

The presence of an evasive rooting strategy at the establishment phase to avoid competition with grasses has been identified in our study as well in several other studies (Archer & Brown, 1990; Bragg *et al.,* 1993; Weltzin & McPherson, 1997; Wilson & Witkowski, 1998; Kambatuku *et al.,* 2012) and the temporal separation of nutrient acquisition with grasses in older trees (Scholes & Archer, 1997), suggests that there is strong intraspecific competition between trees. This is supported by the demonstration of strong intraspecific competition at the seedling stage (Pillay & Ward, 2014) and evidence of strong intraspecific competition in the older demographic stages of trees as well (Meyer *et al.,* 2008; Kambatuku *et al.,* 2010). In fact, intraspecific competition becomes so strong in these older demographic stages that it results in the regular spacing of adult trees in the savannah (Meyer *et al.,* 2008; Kambatuku *et al.,* 2010). Some authors have even suggested that interspecific competition between trees and grasses is negligible in the savannah (Weltzin & McPherson, 1997; Brown & Archer, 1989; Brown *et al.,* 1998).

The presence of strong intraspecific competition in all the demographic stages of trees and competition avoidance with grasses from early on suggests that trees and grasses may not be engaged in a competitive struggle with each other, as previously thought, but may in fact occupy two different niches present in the savannah system. The presence of strong intraspecific competition and competition avoidance was predicted by Walter’s hypothesis, however, it must be viewed in the light of the recent literature which challenges some of its aspects, such as strong competition for nutrients (Cramer *et al*., 2007, 2010, 2012; February *et al.,* 2013a, 2013b) and the exploitation of the shallow soil horizons by both tree and grass roots (February & Higgins, 2010; Kulmatiski *et al.,* 2010, 2013; Verweij *et al.,* 2011; February *et al.,* 2013a).

In light of this and our demonstration of seedling resilience to grass competition we propose a dynamic two-niche hypothesis of savannah tree-grass co-existence, where trees and grasses occupy two distinct niches that arise due to the disturbance inherent in the savannah system. The herbaceous (gramminoid) niche selects for short life histories and ecological responsiveness to favourable smallscale heterogeneities which persist in the landscape for several years – essentially a short-lived hyper-competitive life history - whereas the woody (phanerophytic) niche selects for longer life histories and disturbance tolerance to persist and maximise favourable heterogeneities that may persist in the landscape for decades. This stark contrast in life histories and strategies for coping with disturbance allows for the presence of two primary niches in the savannah within which intraspecific competition is stronger than interspecific competition, even if only slightly. However, due the hyper-competitive nature of the gramminoid species the woody niche can only exist if its species are capable of avoiding competition, for the most part, with these species – especially at the establishment phase. Such competition avoidance creates a highly dynamic give-and-take situation between tree and grass roots in the top layers of the soil, resulting in a four-dimensional (vertical, latitudinal, longitudinal and temporal) dynamism in these layers that is influenced by substrate, nutrients, rainfall and disturbance.

Conclusion

We conclude that establishing savannah tree seedlings are more resilient to grass competition than previously thought and that savannah trees are likely to experience relatively stable recruitment rates with the incorporation of individuals already in the storage phase. This is not to say that the interspecific effect of grass competition was not present (fewer seedlings in areas with higher grass canopy cover), but in addressing the long term aspects of tree-grass interactions and avoiding the caveats of traditional methods for testing grass competition (focussing on biomass accumulation rather than establishment and survival), we demonstrate that tee establishment is ubiquitous and present even at the highest recorded level of grass canopy cover outside of anthropogenically modified sites. Furthermore, we demonstrate that the competitive resilience of tree seedlings to grass competition is due to a specialised rooting strategy allowing them to avoid belowground competition. We show that such competition avoidance is achieved by seedlings using stored resources to drive their roots below the shallow, nutrient-rich, soil horizons where they would normally experience overwhelming competition from both trees and grasses. We propose that *Acacia* and other legume species, which are able to nodulate, are particularly well adapted to utilise such a rooting strategy, as their roots are initially forced to occupy the deeper nitrogen-deficient soil horizons and we postulate that this may account for the over representation of this family in the savannah. Finally, we propose that trees and grasses occupy two distinct niches in the savannah that arise due to the disturbance inherent in this system. We conclude that these niches experience dynamic root overlap in the shallow, relatively nutrient-rich, soil horizons, but little interspecific competition due to a temporal separation of nutrient acquisition and competition avoidance at the establishment phase. This results in varying facilitation throughout the landscape due to substrate effects, nutrients, rainfall and disturbance (where fire, herbivory and floods cause favourable grass species successional-transitions) - resulting in sporadic recruitment and a rich mosaic of tree-grass coexistence in savannah, that is dynamic in both space and time.

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References

Bond, W. J., van Wilgen, B. W. 1996. *Fire and Plants*. London: Chapman & Hall

Bond, W. J. 2008. What limits trees in C_4 grasslands and savannas? *Annual Review in Ecology and Evolutionary Systematics* **39:** 641–59

Bragg, W. K., Knapp, A. K., Briggs, J. M. 1993. Comparative water relations of seedling and adult *Quercus* species during gallery forest expansion in tallgrass prairie. *Forest Ecology and Management* **56:** 29-41

Brown, J.R. & Archer, S. 1989. Woody plant invasion of grasslands: establishment of honey mesquite (Prosopis glandulosa var. glandulosa) on sites differing in herba-ceous biomass and grazing history. *Oecologia* (Berl.) **80:** 19-26.

Brown, J. R. & Archer. 1990. Water Relations of a Perennial Grass and Seedling vs Adult Woody Plants in a Subtropical Savanna, Texas. *Oikos* **57:** 366-374

Brown, J. R., Scanlan, J. C., Mclvor, J. G. 1998. Competition by Herbs as a Limiting Factor in Shrub Invasion in Grassland: A Test withDifferent Growth Forms. *Journal of Vegetation Science* **6:** 829-836

Craine JM, Lee WG, Bond WJ, Williams RJ, Johnson LC. 2005. Environmental constraints on a global relationship among leaf and root traits. *Ecology* **86**: 12–19

Craine, J. M., C. Morrow, and W. D. Stock. 2008. Nutrient concentration ratios and co-limitation in South African grasslands. New Phytologist 179:829–836.

Cramer, M. D., Chimphango, S. B. M., van Cauter, A., Waldram, M. S., Bond, W. J. 2007. Grass competition induces N2 fixation in some species of African Acacias. *Journal of Ecology* **95:** 1123–1133

Cramer, M. D., van Cauter, A., Bond, W. J. 2010. Growth of N2-fixing African savanna Acacia species is constrained by below-ground competition with grass. *Journal of Ecology* **98:** 156–167

Cramer, M. D., Wakeling, J. L., Bond, W. J. 2012. Belowground competitive suppression of seedling growth by grass in an African savannah. *Plant Ecology* doi:10.1007/s11258-012-0120-7

DeFaria, S. M., Lewis, G. P., Sprent, J. I., & Sutherland, J. M. 1989. Occurrence of nodulation in the Leguminosae. *New Phytologist* **111:** 607–619.

February, E. C., & S. I. Higgins. 2010. The distribution of tree and grass roots in savannas in relation to soil nitrogen and water. *South African Journal of Botany* **76:** 517–523

February, E. C., G. D. Cook, & A. E. Richards. 2013a. Root dynamics influence tree–grass coexistence in an Australian savanna. *Austral Ecology* 38:66–75.

February, E. C., Higgins, S. I., Bond, W. J., Swemmer, L. 2013b. Influence of competition and rainfall manipulation on the growth responses of savanna trees and grasses. *Ecology* **94:** 1155-1164

Hardin, G. 1960. The competitive exclusion principle. *Science* **131:** 1292-1297

Higgins, S. I., Bond, W. J., Trollope, W. S. W. 2000. Fire, resprouting and variability: a recipe for grass–tree coexistence in savanna. *Journal of Ecology* **88:** 213–229

Higgins, S. I., Bond, W. J., February, E. C., Bronn, A., Euston-Brown, D. I. W., et al. 2007. Effects of four decades of fire manipulation on woody vegetation structure in savanna. *Ecology* **88:** 1119–1125

Hoffmann, W. A. 1999. Fire and population dynamics of woody plants in a neotropical savanna: matrix model projections. *Ecology* **80:** 1354–1369

Kambatuku JR, Cramer MD, Ward D (2010) Intraspecific competition between shrubs in a semi-arid savanna. *Plant Ecology* **212:** 701–713

Kambatuku JR, Cramer MD, Ward D (2012) Overlap in soil water sources of savanna woody seedlings and grasses. *Ecohydrology* **6:** 464-473

Kulmatiski, A., Beard, K. H., Verweij, R. J. T., February, E. C. 2010. A depth-controlled tracer technique measures vertical, horizontal and temporal patterns of water use by trees and grasses in a subtropical savannah. *New Phytologist* **188:** 199-209

Kulmatiski, A., Beard, K. H. 2013. Root niche partitioning among grasses, saplings, and trees measured using a tracer technique. *Oecologia* **171:** 25-37

Meyer, K. M., Ward, D., Wiegand, K., Moustakas, A. 2008. Multiproxy evidence for competition between savanna woody species. *Perspect Plant Ecology* **10:** 63–72

Midgley, J. J., Bond, W. J. 2001. A synthesis of the demography of African acacias. *Journal of Tropical Ecology* **17:** 871–86

Pärtel, M., Wilson, S. D. 2002. Root dynamics and spatial pattern in prairie and forest. *Ecology* **83:** 1199–203

R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. URL: http://www.R-project.org/.

Riginos, C. 2009. Grass competition suppresses savanna tree growth across multiple demographic stages. *Ecology* **90:** 335–340

Mucina, L. & Rutherford, M. C. 2006. Mucina, L. & Rutherford, M. C. (Eds.). The Vegetation of South Africa, Lesotho and Swaziland. South African National Biodiversity Institute, Pretoria.

Scholes, R.J. & Hall, D.O. 1996. The carbon budget of tropical savannas, woodlands and grasslands. *Modelling Terrestrial Ecosystems* (eds A. Breymeyer, D. Hall, J. Melillo & G. Agren), pp. 69–100. Wiley, Chichester.

Smith, T. M. & Shackleton, S. E. (1988). The effects of shading on the establishment and growth of *Acacia tortilis* seedlings. *South African Journal of Botany* **54:** 375- 379

Van Oudtshoorn, F. 2012. *Guide to Grasses of southern Africa.* Briza Publications, Pretoria. 287 pp.

Walker, B. H., and I. Noy-Meir. 1982. Aspects of the stability and resilience of savanna ecosystems. Pages 556–590 in B. J. Huntley, editor. Ecology of tropical savannas. Springer-Verlag, Berlin, Germany.

Weltzin, J. F., McPherson, G. R. 1997. Spatial and temporal soil moisture resource partitioning by trees and grasses in a temperate savanna, Arizona, USA. *Oecologia* **112:** 156-164

Wilson, T. B., Witkowski, E. T. F. 1997. Water requirements for germination and early seedling establishment in four African savanna woody plant species. *Journal of Arid Environments* **38:** 541-550