

Tree effects on grass growth in savannas: competition, facilitation and the stress-gradient hypothesis

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Summary

1. The stress-gradient hypothesis (SGH) predicts an increasing importance of facilitative mechanisms relative to competition along gradients of increasing environmental stress. Although developed across a variety of ecosystems, the SGH's relevance to the dynamic tree–grass systems of global savannas remains unclear. Here, we present a meta-analysis of empirical studies to explore emergent patterns of tree–grass relationships in global savannas in the context of the SGH.

2. We quantified the net effect of trees on understorey grass production relative to production away from tree canopies along a rainfall gradient in tropical and temperate savannas and compared these findings to the predictions of the SGH. We also analysed soil and plant nutrient concentrations in subcanopy and open-grassland areas to investigate the potential role of nutrients in determining grass production in the presence and absence of trees.

3. Our meta-analysis revealed a shift from net competitive to net facilitative effects of trees on subcanopy grass production with decreasing annual precipitation, consistent with the SGH. We also found a significant difference between sites from Africa and North America, suggesting differences in tree–grass interactions in the savannas of tropical and temperate regions.

4. Nutrient analyses indicate no change in nutrient ratios along the rainfall gradient, but consistent nutrient enrichment under tree canopies.

5. *Synthesis.* Our results help to resolve questions about the SGH in semi-arid systems, demonstrating that in mixed tree–grass systems, trees facilitate grass growth in drier regions and suppress grass growth in wetter regions. Relationships differ, however, between African and North American sites representing tropical and temperate bioclimates, respectively. The results of this meta-analysis advance our understanding of tree–grass interactions in savannas and contribute a valuable data set to the developing theory behind the SGH.

Key-words: Africa, competition, facilitation, North America, plant–plant interactions, rainfall gradient, savanna, stress-gradient hypothesis, tree–grass interactions, hypothesis

Introduction

Competitive interactions between coexisting plants have traditionally been believed to shape community structure (Grime 1977; Connell 1983), but recent research indicates the importance of both competitive and facilitative mechanisms (Bruno, Stachowicz & Bertness 2003; Brooker *et al.* 2008; Bullock 2009; Freckleton, Watkinson & Rees 2009). Positive

interactions between neighbouring organisms are now considered fundamental ecosystem processes, and these processes interact dynamically with the abiotic environment to determine community structure (Bruno, Stachowicz & Bertness 2003). Indeed, ecological theory predicts an increasing importance of facilitation relative to competition along gradients of increasing abiotic stress (Bertness & Callaway 1994; Brooker & Callaghan 1998; Pugnaire & Luque 2001; Callaway *et al.* 2002; Maestre *et al.* 2009). Termed the stress-gradient hypothesis (SGH), the theory postulates that beneficial

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environmental modification by neighbouring organisms outweighs competition for resources under conditions of high environmental stress, such as high disturbance frequency or low resource availability (Bertness & Callaway 1994; Brooker & Callaghan 1998). As the local stressor decreases along a gradient, the relative strengths of the positive and negative interactions between neighbouring organisms change, and competitive mechanisms begin to outweigh facilitative mechanisms. Furthermore, the SGH predicts that the change in a response variable (e.g. biomass, population growth) from net negative (i.e. competition) to net positive (i.e. facilitation) with increasing abiotic stress may occur due to a change in the *intensity* of competitive or facilitative interactions, and/or in the *importance* of these interactions relative to the impact of the abiotic environment (Brooker *et al.* 2005). While competitive and facilitative processes occur simultaneously along the entirety of environmental gradients (Brooker & Callaghan 1998; Callaway 2007; Smit, Rietkerk & Wassen 2009; Malkinson & Tielborger 2010), the degree to which certain mechanisms impact the growth and fitness of neighbouring organisms may change significantly along these gradients. Two neighbouring species may compete similarly for a limiting resource in both high- and low-stress environments, but their productivity and fitness in high-stress conditions may be determined to a greater degree by their ability to cope with their environment, whereas in low-stress conditions, competition for the resource may be the most limiting factor (Brooker & Callaghan 1998). Amelioration of the extreme conditions of a high-stress environment by neighbouring plants may therefore have greater influence on the growth and fitness of plants than direct competition for resources.

Empirical studies confirm the predictions of the SGH (see Goldberg & Novoplansky 1997; Lortie & Callaway 2006; Callaway 2007; Maestre *et al.* 2009 for reviews), but other studies indicate that the balance of competition and facilitation can vary with species composition (Choler, Michalet & Callaway 2001) and the type of stress gradient (Maestre, Valladares & Reynolds 2006; Kawai & Tokeshi 2007). Such variables can drastically alter the responses of competitive and facilitative mechanisms along an abiotic gradient, thus potentially changing the shape of the curve describing these relationships (Maestre *et al.* 2009; le Roux & McGeoch 2010). Goldberg & Novoplansky (1997) suggest that the shift from facilitative to competitive interactions with decreasing stress may be most prevalent in gradients driven by water. The SGH may therefore be particularly relevant along rainfall gradients in drought-seasonal savanna regions.

In savannas, trees may suppress grass growth through direct competition for water, light and nutrients resulting from overlapping root profiles and canopy shading (Scholes & Archer 1997; Ludwig *et al.* 2004b). Conversely, trees may facilitate grass growth by improving the biophysical or biogeochemical conditions for herbaceous growth. Such facilitation may occur through improved soil water availability related to hydraulic lift (the movement of water from wet to dry soil layers through tree roots), or through a reduction in incoming solar irradiation, thus decreasing subcanopy

evapotranspiration and soil temperatures and reducing water stress for the herbaceous community (Ludwig *et al.* 2004a,b). Facilitation might also result from improvements in nutrient availability related to litter inputs from trees. Elevated nutrient availability can improve forage quality of subcanopy grasses, thus attracting grazers (Treydte *et al.* 2007, 2008; Ludwig, Kroon & Prins 2008). Increased animal deposits in subcanopy areas may further increase nutrient availability, contributing to an 'island of fertility' effect (Belsky *et al.* 1989; Belsky 1994; Dijkstra *et al.* 2006). The interactions of these controls with climatic, edaphic and biotic variables result in a net positive, negative or neutral effect of trees on subcanopy herbaceous production.

Although small-scale experiments in savannas have demonstrated a strong effect of water availability on herbaceous productivity (e.g. Baruch & Fernandez 1993), an earlier meta-analysis found no significant effect of precipitation on the direction (positive or negative) of tree impacts on grass production, contrary to the predictions of the SGH (Mordelet & Menaut 1995). More recent savanna studies, however, provide support for the SGH, with suggestions that there may be a transition from net facilitation of grasses by trees in drier savannas to net competitive interactions in more mesic regions (Belsky *et al.* 1993; McClaran & Bartolome 1989; Moustakas *et al.*, in press; K. A. Amévor, unpubl. data).

This study is a synthesis of a multitude of empirical studies in an attempt to identify emergent trends in savanna tree–grass interactions, particularly with respect to annual precipitation. In so doing, this synthesis expands on the analysis of Mordelet & Menaut (1995) to include more recent field data reporting herbaceous production in the presence and absence of competitors (i.e. trees) and examines how the ratio of herbaceous production (or production estimated based on peak standing crop) under tree canopies relative to the same measure in locations remote from the woody canopy changes with rainfall. Additionally, we analyse soil and plant nutrient concentrations in subcanopy and open-grassland areas to assess tree effects on understory nutrient availability and diagnose the potential role of nutrients in grass responses to tree canopies.

Hypothesized impacts of trees on grasses in savannas

Our hypotheses for how trees impact grasses across typical savanna rainfall gradients are shown in Fig. 1, separating effects mediated by soil moisture (Fig. 1a), light and energy balance (Fig. 1b), and nutrient availability (Fig. 1c). Figure 1a illustrates how hydraulic redistribution might be more important to grass growth in drier regions (where water is more limiting) than in wetter regions (where rainfall is more plentiful). On the other hand, tree roots may compete strongly for limiting soil moisture in dry savannas. As rainfall increases along the gradient, increased moisture availability may be offset by an increased demand by the larger trees and more expansive root systems characteristic of mesic savannas, thus potentially balancing total root competition along the

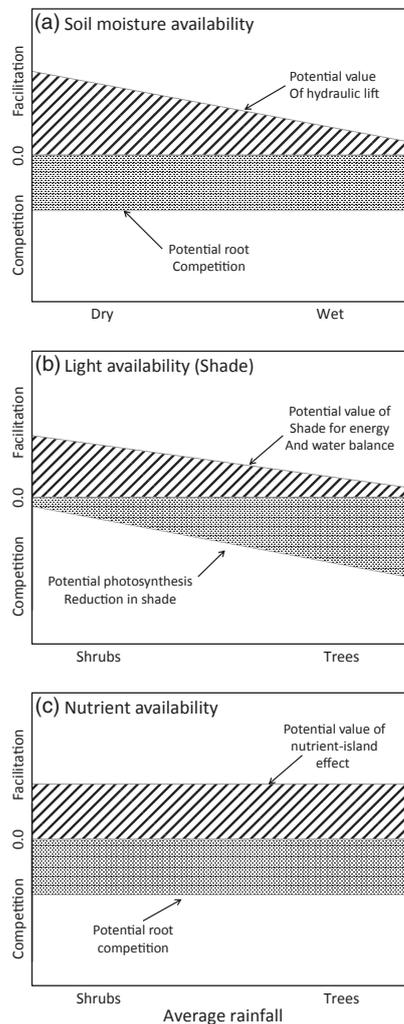


Fig. 1. Hypothesized impacts of trees on grasses in savannas, as mediated by (a) soil moisture, (b) light and energy balance and (c) nutrient availability. Shading indicates postulated range of likely facilitative (dark grey) and competitive (light grey) impacts, with the crossover point between the two net effects represented by a normalized ratio of 0.0.

rainfall gradient. While the intensity of competition for moisture may therefore remain relatively constant along the rainfall gradient, the importance of facilitative hydraulic lift may increase in highly water-limited arid savannas, consistent with the predictions of the SGH.

Figure 1b illustrates how decreased light availability due to shade may shift from net facilitative to net competitive effects by affecting the energy balance of subcanopy grasses. In dry, water-limited regions, shade reduces evapotranspiration rates for subcanopy grasses. As water availability increases with increased rainfall, light may begin to replace water as the limiting factor in C4 grass photosynthetic reactions, thus shading by trees may begin to inhibit subcanopy primary production in wetter systems. The hypothesized interactions governing light availability and energy balance therefore parallel the predictions of the SGH: the value to grasses of facilitation (i.e. reduced subcanopy evapotranspiration rates due to shading) decreases as water availability increases, while the intensity

of competition for light may be increasingly limiting to grasses in communities with large trees and high water availability.

Figure 1c illustrates the potential effects of nutrient availability on subcanopy grass growth. Small trees and shrubs characteristic of dry savannas trap wind and water-borne sediments, contributing to an island of fertility effect (Kellman 1979; Bernhard-Reversat 1982; Belsky *et al.* 1989). As the size of trees increases along the rainfall gradient, litterfall and deposits from animals seeking shade may increase subcanopy nutrient levels, while the impact of wind-trapped sediments decreases. The potential value of nutrient island effects, therefore, remains relatively constant along the gradient. Similarly, trees and shrubs directly compete with grasses for nutrients in arid regions. While nutrient availability may increase from large litter inputs in wet regions, the larger trees and more expansive root systems of mesic savannas might increase total tree nutrient capture, thus potentially balancing the intensity of competition for nutrients along the rainfall gradient.

While several of the processes depicted in Fig. 1 are considered to be constant in their effect across rainfall gradients, those that are likely to change with rainfall (hydraulic lift, shade impact on energy and water balance, and shade suppression of grass photosynthesis) seem likely to suppress grass in mesic savannas and favour grass growth in dry savannas: we therefore predict that the net effect of trees on grasses shifts from competition to facilitation with decreasing annual rainfall, consistent with the SGH.

Materials and methods

DATA COLLECTION

We reviewed published data reporting direct measurements of herbaceous production or peak biomass in both subcanopy areas and open grassland (see Table S1 in Supporting Information). We reduced methodological variability among the data included in the meta-analysis using the following selection criteria: (i) subcanopy measurements of herbaceous production were included only if collected directly underneath a tree canopy and (ii) open-grassland production measurements were included only if collected at a distance $> 0.5 \times$ canopy radius beyond the edge of the canopies of adjacent trees. The potential database of studies also included areas with variable levels of grazing intensity. As grazing intensity was often evaluated qualitatively, we eliminated all studies ranked with 'heavy' (or equivalent terminology) levels of grazing and included only studies in savannas with 'medium' or 'light' grazing intensities. With these selection criteria, 24 independent studies and 95 grass production measurements were included in the meta-analysis. These data were then translated into normalized tree-effect ratios (y) of subcanopy (s) to open-grassland (g) herbaceous production, where $y = (s - g)/(s + g)$. We chose the normalized ratio because it responds linearly to proportional changes in the two components, and in initial examinations, we found improved correlation and linearity relative to the use of the simple ratio (s/g). Ratios also have the beneficial effect of reducing the impact of different sampling methodologies among studies. A tree-effect ratio > 0 indicates facilitative effects (subcanopy biomass exceeds open-grassland biomass), and a ratio of < 0 indicates net competitive effects. In cases where year-specific rainfall was not

reported, a long-term MAP for the site location was substituted, as reported by the authors of the study. For each site, we also calculated precipitation over potential evapotranspiration (PPT/PET, an index often used to describe water availability in relation to temperature regimes), using PET values obtained from gridded data from the CGIAR-CSI Global-Aridity and Global-PET Database (Zomer *et al.* 2007, 2008).

All points included in the meta-analysis are averages of several replicates. Data reported at the same site but for different tree species were included as separate data points. Sample sizes (reported in Table S1) generally reflect the number of trees sampled rather than the total number of quadrats. Our selection criteria exclude a substantial body of research quantifying subcanopy herbaceous productivity in savannas but were chosen to minimize the effects of variables that would mask emergent trends in tree–grass relationships at a continental scale and to standardize the response variable to allow for meaningful comparisons across diverse systems.

We also recorded subcanopy/open-grassland herbaceous leaf and soil nutrient ratios if these data were available in the source literature reporting biomass (see Table S2). While soil and leaf concentrations differ substantially in magnitude, we normalized them using the same ratio of subcanopy to open-grassland concentrations [$y = (s - g)/(s + g)$] and assessed both together as indices of nutrient enrichment (or depletion) associated with trees and shrubs. For studies reporting nutrient concentrations at multiple depths, only data from near-surface soil layers were incorporated into the data set.

For analysis purposes, sites were also classified as either ‘tropical’ ($N = 52$ for biomass data; $N = 58$ for nutrient data) or ‘temperate’ ($N = 43$ for biomass data; $N = 17$ for nutrient data) as determined using a bioclimatic approach (i.e. not strictly by latitude) that classified locations with hot season rainfall and no winter freezing as tropical (in practice, this transferred 14 sites at latitudes between 23.8 and 26.3° south in South Africa into the ‘tropical’ class). However, few data were found in the literature outside of Africa or the United States. With the exception of a few data points from North Africa (Abdallah *et al.* 2008; Jeddi & Chaieb 2009), the temperate data set in this meta-analysis was thus limited exclusively to the savannas of the Western United States, while the tropical data set was comprised solely of African sites. This geographic restriction, while perhaps presenting an incomplete picture of global trends in tropical and temperate savannas, provides an opportunity to contrast the savannas of temperate and tropical regions on two separate continents. All data points were additionally organized into two soil texture classifications (coarse and fine soils) using information on soil texture or soil type reported in the literature to allow us to explore soil texture effects. Finally, canopy diameter (or canopy area) measurements were recorded when available as these data represented the most commonly reported proxy for tree size effects.

DATA ANALYSIS

Regression analyses were used to identify correlations between annual rainfall and the normalized ratio of subcanopy to open-grassland biomass and nutrient contents. An analysis of covariance (ANCOVA) was used to test the effects of climate (i.e. tropical vs. temperate), soil texture (i.e. coarse vs. fine) and tree size (i.e. canopy diameter) on the relationship between annual rainfall and the tree-effect ratio, beginning with a complete model including climate, soil texture and tree size as random effects. Model selection was subsequently conducted using Akaike Information Criterion (AIC) via stepwise deletion until an optimally simplified model remained. This process, beginning with

a complete model of all effects, was repeated using PPT/PET in place of annual rainfall, and the two models were compared using AIC. Regression trees (De’ath & Fabricius 2000) and hierarchical variance partitioning (Mac Nally 1996, 2002) were also investigated as supplements to linear regression analyses to more fully explore the influence of the categorical variables (i.e. soil texture, bioclimatic zone and tree size) and test for potential nonlinear patterns in the tree-effect ratio. Student’s *t*-tests were used to test whether nutrient ratio means were greater than 0.0 (because in this case, we found no significant effect of the climate covariates), indicating consistent nutrient enrichment beneath tree canopies. All statistical analyses were conducted with the statistical package R 2.12.1 (R Development Core Team 2010).

Results

The results of our linear regression analyses indicate a shift from net facilitation in dry, water-limited savannas to net competition in mesic savannas, as predicted by the SGH (Fig. 2). Furthermore, we found a consistently larger tree-effect ratio along the rainfall gradient in tropical savannas, suggesting that higher mean annual temperatures (i.e. increased environmental stress) may increase the importance of facilitative mechanisms, also consistent with the SGH.

Model simplification based on AIC stepwise deletion statistics resulted in the removal of canopy size as an independent covariate as well as all potential interaction terms between rainfall, bioclimatic zone and soil texture. The simplified model included only the main effects of rainfall, with similar sensitivity to rainfall (i.e. slope) across all sites ($P = 0.479$), but distinctly different intercept values between tropical and temperate bioclimatic zones ($P < 0.0001$) and between the coarse and fine soil textures in tropical regions ($P = 0.013$, Fig. 2; $F = 24.46$ on 91 degrees of freedom (d.f.), adjusted

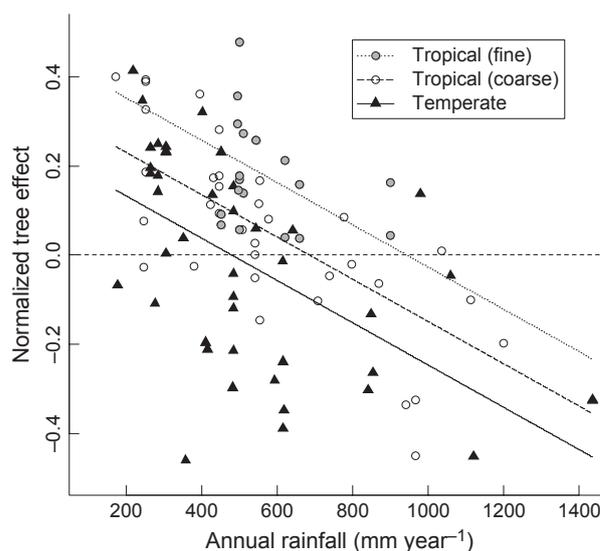


Fig. 2. Normalized ratio of subcanopy to open-grassland herbaceous biomass along a gradient of annual rainfall for temperate North American savannas and tropical African savannas on coarse and fine soils. Regression lines represent the final simplified model with equal slopes but statistically distinct intercepts among data sets (adjusted $r^2 = 0.428$, $P < 0.0001$).

$r^2 = 0.428$, $P < 0.0001$). Consequently, both regional climate and soil texture appear to significantly affect the observed decline in the importance of facilitative mechanisms with increasing annual rainfall.

In addition to the linear regression analyses of Fig. 2, we also used hierarchical variance partitioning and regression tree analyses to further explore the data set in case interaction effects were not considered in the regression analysis, or nonlinear patterns in the response variable might emerge. In the event, regression tree and hierarchical variance partitioning results were consistent with the linear regressions presented above, but provided no additional statistical strength or new insight into the observed patterns. Further, as our focus in this study is on the SGH, the strong relationships emerging with rainfall are more directly relevant to the hypotheses under scrutiny.

Comparisons between the complete and simplified models using PPT/PET in place of annual rainfall revealed no difference in which factors constitute the optimally simplified model, but slightly lower AIC scores and a better overall model fit for the model using annual rainfall. The PPT/PET analysis also revealed no convergence among intercepts of the tropical and temperate climate groups. This is contrary to what would be expected if climatic factors related to temperature strongly influenced the observed difference between tropical and temperate interactions: Per cent evapotranspiration represents a measure of the ability of the atmosphere to remove water via evapotranspiration under optimal growing conditions (Zomer *et al.* 2007, 2008). Dividing annual precipitation by PET adjusts mean annual rainfall relative to the regional atmospheric water demand, thus effectively normalizing broad climatic differences and allowing for meaningful comparisons between diverse biomes. We expected the PPT/PET analysis to result in convergence between the tropical and temperate data sets as the stark differences in mean annual temperatures between these bioclimatic zones were offset by the relative atmospheric water demands of the region, but no such convergence was observed. As the PPT/PET index did not provide any advantage over rainfall alone, only the model with annual rainfall is presented in Fig. 2 (see Appendix S1 for PPT/PET results).

Regression analyses revealed no significant correlations between the normalized ratio of subcanopy to open-grassland nutrients and annual rainfall for nitrogen in grass leaves (d.f. = 19, $P = 0.590$) or soil (d.f. = 20, $P = 0.421$), nor for phosphorus in grass leaves (d.f. = 12, $P = 0.131$) or soil (d.f. = 16, $P = 0.351$, Fig. 3). However, Student's *t*-tests indicated that the mean nutrient ratios for leaf and soil nitrogen contents as well as phosphorus soil content were significantly greater than 0.0 ($\mu = 0.174$, $P = 0.0006$; $\mu = 0.230$, $P < 0.0001$; $\mu = 0.185$, $P = 0.002$ respectively), indicating consistent nutrient enrichment in both leaf matter and soil in the presence of tree canopies (Fig. 3 inset). The mean nutrient ratio for leaf phosphorus content was marginally non-significant ($\mu = 0.048$, $P = 0.148$). There was no significant difference in leaf and soil N and P enrichment between tropical African and temperate North American sites.

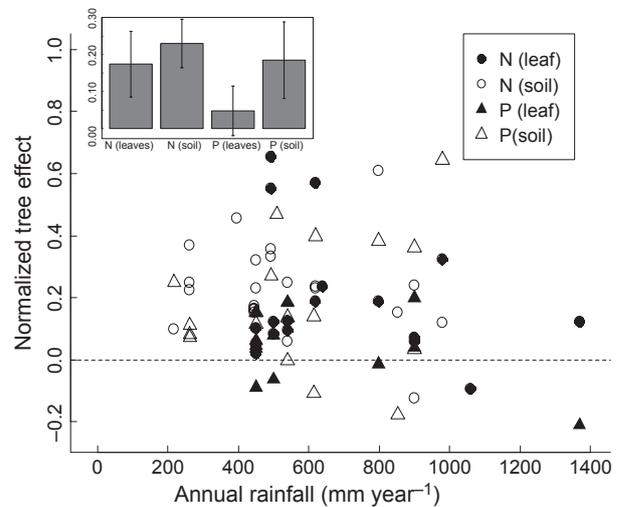


Fig. 3. Ratio of subcanopy to open-grassland nutrient contents along a rainfall gradient. Nitrogen concentrations in soil ($P = 0.590$) and leaf matter ($P = 0.421$), as well as phosphorus concentrations in soil ($P = 0.131$) and leaf matter ($P = 0.351$), showed no correlation with annual precipitation. Inset figure shows nutrient ratio means and 95% confidence limits.

Discussion

The results of our meta-analysis suggest that the impact of trees on grass production in both tropical and temperate savannas shifts from facilitative to competitive interactions as annual rainfall increases, consistent with the SGH. We anticipated that the PPT/PET index (in place of PPT alone) would normalize some of the broad climatic differences between the tropical and temperate sites such that the relationships would converge. However, this proved not to be the case, suggesting either that more complex expressions of climate conditions and water relations are necessary (derived, for example, from a process-based model of water balance across all sites) or that other edaphic and biotic differences between Africa and North America create the observed bioclimatic differences.

While there is much variability among individual savanna sites, in broad terms, the shift from net facilitative to net competitive effects of trees on herbaceous productivity occurs in the transition between arid and mesic savannas in tropical Africa (685 ± 161 mm annum⁻¹ on coarse soils, 943 ± 204 on fine soils) and in temperate North America (479 ± 177 mm annum⁻¹; Fig. 2). Net facilitation in drier savannas suggests that improved water relations from some combination of reduced evapotranspiration in the shade of trees and hydraulic lift outweigh the effects of direct competition for water and nutrients (Fig. 1). The transition to net suppression in mesic savannas suggests that competition for water and nutrients and reduced light availability may be stronger than the facilitative effects of hydraulic lift, improved energy balance and nutrient islands in these regions. These results are generally consistent with the hypotheses embodied in Fig. 1 and, in particular, may indicate that both positive and negative shade effects are important contingent on rainfall. C₄ grasses do poorly in deep shade conditions (< 15% sunlight intensity) and are highly

dependent on warm temperatures in intermediate light (25–50% sunlight intensity; Sage, Wedin & Li 1999; Sage & Kubien 2003). The increased size and canopy cover of savanna trees in wetter regions, combined with the shade intolerance of subcanopy C₄ grasses, potentially translates into a strongly light-limited understorey microhabitat. Similarly, observed patterns of tree effects on grass production suggest that controlling factors may change between improved water relations in drier systems (related either to hydraulic lift or to improved energy and water balance) to competition for light in wetter systems. However, our data are not able to quantify the extent to which the multiple potential factors (Fig. 1) contribute to the emergent patterns across savanna rainfall gradients. Experiments isolating casual factors are needed to assess the relative strength of these drivers.

The correlations observed in tropical and temperate locations conform to the SGH hypotheses for plant interactions along stress gradients, but it is not immediately evident why the nature of these regressions depends on regional climatic conditions. The decrease in the tree-effect ratio in temperate savannas relative to tropical savannas suggests a more strongly competitive tree component. It is possible that distinct phylogenetic histories, and associated traits, could favour the tree component in temperate, North American, tree–grass systems. However, lower annual temperatures and reduced evapotranspiration rates in temperate regions may translate into a less resource-limited environment. In this respect, the observed increase in competition in these regions is consistent with the predictions of the SGH: tree–grass interactions in temperate savannas with higher resource availability demonstrate an increase in the importance and intensity of competitive mechanisms relative to facilitative mechanisms. That our PPT/PET analysis did not provide any convergence between tropical and temperate relationships does not necessarily mean that temperature-related factors are not important in the distinction between the two climate groups. Rather, the lack of convergence may reflect the need for more nuanced measures of regional climate indicators than the PPT/PET analysis utilized here.

When comparing tropical and temperate locations, the predictions of the SGH may be further complicated by competitive and facilitative mechanisms unique to tree–grass systems. The seasonality of rainfall, for example, may have profound effects on the water relations of trees and grasses. While the growing season of tropical locations coincides with the ‘wet’ season because temperature is rarely limiting, temperate locations receive a significant proportion of the annual rainfall during the winter season, when temperatures are generally too low for growth. Winter rainfall in temperate savannas will likely have time during the winter and early spring months to percolate to deeper soil layers than by rainfall during peak growing season, when herbaceous plants are physiologically active. Deep-rooted trees in temperate savannas may therefore benefit from sole access to winter rainfall that has percolated below the herbaceous root zone. This temporal and spatial asymmetry of resource availability in temperate and tropical savannas complicates the predictions of the SGH when applied to global tree–grass systems.

The observed effect of soil texture on the relationship between annual rainfall and the tree-effect ratio (Fig. 2) indicates an increase in competition between trees and subcanopy herbaceous growth on coarse soils relative to fine soils in tropical African savannas, perhaps due to the disparate nutrient retention capacity between the two broad soil types. Fine-textured soils with high clay and silt contents have an increased ability to adsorb soil organic matter, thus increasing pools of carbon, nitrogen and other nutrients available for plant uptake (Feller & Beare 1997; Hassink 1997). The island of fertility effect (Kellman 1979; Belsky *et al.* 1989) in subcanopy areas may therefore be enhanced in savannas with fine soils, and consequently, this elevated nutrient availability may help offset the negative effects of competition for light relative to savannas with coarse soils. The lack of impact of soil texture in temperate regions observed in this study is likely due to the low sample size ($n = 5$) of temperate sites with fine soils rather than indicative of actual differences in soil texture effects across climatic regions.

No correlations between subcanopy to open-grassland ratios and rainfall were found for nitrogen or phosphorus concentrations in either tropical or temperate sites. Mean ratios for both nutrients were consistently greater than 0 (although marginally non-significant for phosphorus leaf content), suggesting nutrient enrichment in subcanopy areas across the entirety of the rainfall gradient and in both tropical and temperate systems. Manipulative experiments are needed to reveal the degree to which this enrichment contributes to the production of herbaceous biomass and correspondingly to net competitive or facilitative interactions across the rainfall gradient.

The SGH has received widespread support from empirical studies within a number of ecosystems and types of stress gradient, but previous meta-analyses (e.g. Suding & Goldberg 1999; Maestre, Valladares & Reynolds 2005) have revealed inconsistent and occasionally contradictory results when these studies are combined (see Callaway 2007 for a comprehensive review). These discrepancies may be partially attributed to the effects of a range of environmental and biotic variables that can drastically alter the net outcome of competitive and facilitative interactions, including grazing intensity (Callaway *et al.* 2005), species-specific interactions (Frost & McDougald 1989; Callaway 2007), rainfall seasonality (Kikvidze *et al.* 2006) and tree size and life-history stage (Stuart-Hill & Tainton 1989; Callaway, Nadkarni & Mahall 1991; Callaway 2007). While such processes probably play a significant role in savannas, the expansive biogeographical scale incorporated in this meta-analysis effectively overrides community-scale variation, and the highly significant results observed in this study reflect large-scale trends in savanna tree–grass interactions with respect to local levels of environmental stress.

Empirical studies evaluating subcanopy production are absent from many worldwide savanna regions, and these sites may be vital to fully understanding competition–facilitation relationships. Data from tropical and temperate sites in the savannas of South America, Australia and India, to name a few, may contribute significantly to our understanding of the competitive and facilitative mechanisms of tree–grass systems

worldwide. In addition to geographic diversity, research is needed that specifically targets potential causal mechanisms determining herbaceous production. There exist very few, if any, studies that integrate light, water and nutrient controls on herbaceous production in the presence and absence of the putative competitor. Studies that isolate these mechanisms would provide valuable information on the relative strengths of direct and indirect environmental controls along the rainfall gradient.

Unravelling the complex of mechanisms behind tree–grass competition–facilitation represents a large step forward in savanna research. Understanding these interactions in varying environmental conditions will contribute to the creation of dynamic savanna vegetation models detailing the worldwide distribution of savannas (e.g. Scheiter & Higgins 2009). This will improve predictions of future savanna distributions and structure in the face of a changing climate and altered anthropological disturbance regimes.

The development of sustainable management practices for pastoral communities depends on a robust mechanistic understanding of tree–grass interactions and coexistence. Savanna trees and grasses are vital to surrounding communities as a source of fuelwood and grazing fodder (Le Houérou 1989). The results of this study, coupled with further investigation into mechanistic drivers of herbaceous production, can help inform the management of savanna systems to optimize the yield and sustainability of ecosystem goods and services critical to the livelihoods of local managers and communities.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Data sources for subcanopy to open-grassland herbaceous biomass ratios.

Table S2. Data sources for subcanopy to open grassland soil and leaf matter nutrient ratios.

Appendix S1. Results of precipitation over percent evapotranspiration (PPT/PET) analysis.

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