

DISSERTATION

TREE AND GRASS INTERACTIONS GOVERNING THE PRODUCTION AND
DISTRIBUTION OF SAVANNAS: LINKING META-SCALE PATTERNS TO
UNDERLYING MECHANISMS

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Justin Dohn

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Doctoral Committee:

Advisor: Alan K. Knapp

Co-Advisor: Niall P. Hanan

David J. Augustine

Jessica G. Davis

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ABSTRACT

TREE AND GRASS INTERACTIONS GOVERNING THE PRODUCTION AND DISTRIBUTION OF SAVANNAS: LINKING META-SCALE PATTERNS TO UNDERLYING MECHANISMS

Savannas, characterized by the co-dominance of herbaceous and woody vegetation, support an estimated 20% of the global human population and account for ~30% of terrestrial net primary productivity. Interactions among savanna trees and grasses determine important ecosystem functions such as hydrological and biogeochemical cycles and production and transpiration rates, and impact the availability of resources (fuel-wood, grass for livestock) fundamental for human wellbeing. Additionally, interactions among trees may be an important driver of savanna vegetation structure, though few existing studies empirically estimate the intensity and importance of savanna tree-tree interactions. A clear understanding of the mechanisms that govern the coexistence of trees and grasses and their interactions in savanna landscapes is crucial to our ability to predict their responses to changing climatic and anthropogenic disturbance regimes.

I present research aimed at advancing our understanding of emergent trends in savanna plant interactions and the underlying mechanisms responsible for observed patterns. First, I present the results of a meta-analysis of empirical studies that quantify the net effect of savanna trees on grass production under tree canopies relative to production away from trees. We found that the effect of trees on subcanopy herbaceous production varies predictably with climate, such

that trees in arid savannas generally promote grass growth and trees in mesic regions suppress growth. This finding is consistent with a general theoretical model predicting the relative importance of facilitative processes for species coexistence. Termed the stress gradient hypothesis (SGH), the theory predicts an increasing importance of facilitation with increasing environmental stress, such as high water-stress typical of arid savannas. I then present results from two empirical studies designed to experimentally test the predictions of the SGH and infer mechanistic drivers by relating abiotic covariates to plant growth in the presence and absence of neighbors. In the shortgrass steppe (SGS) in northeastern Colorado, we found a net-neutral effect of shrubs and grasses on the other life form, contrary to expected facilitation. We suggest shrub morphology and interactive effects of topography and soil texture are primarily responsible for observed patterns of growth. At five savanna field sites situated along a rainfall gradient (i.e. water-stress gradient) in Mali, West Africa, we found the net effect of trees on grass growth to be consistent with SGH predictions. Light availability and distance to tree boles best explained shifts in herbaceous production along the rainfall gradient. Lastly, I present results from a longitudinal study in an East African savanna estimating tree growth as a function of the size and distance of neighboring woody competitors. In so doing, we quantified the magnitude of inter-tree competition and inferred its impact on stand spatial structure through spatial point pattern analysis.

Overall, this research increases our understanding of biotic interactions among savanna plants. The effects of savanna trees on subcanopy grass production generally conform to the predictions of the SGH, and appear to be mediated by microclimate modification by tree canopies related to light availability and water balance. The effects of grasses on trees along environmental gradients are less clear, though we found net neutral effects on woody growth

over one growing season in tropical and temperate shrub-grass systems, suggesting that active competitive and facilitative mechanisms largely offset, or that the effects of grasses on plant-available resources for woody species are negligible. Finally, we found that shrubs aggregate at local scales, despite significant neighbor competition. We suggest competition among woody plants influences production and relative species abundance, but dispersal and establishment bottlenecks are likely more important for landscape-scale spatial structure. These results have important implications for our theoretical understanding of coexistence between woody and herbaceous vegetation. Furthermore, we provide empirical data that can be used to refine and parameterize vegetation models predicting savanna ecosystem processes and the global distribution of mixed tree-grass systems.

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DEDICATION

For Warren M. Dohn

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Chapter 1: Introduction

The coexistence of trees and grasses characterizes the savanna biome, though their relative abundance and distribution vary considerably across climatic and environmental gradients at regional to global scales. A great deal of research has fittingly sought to determine the factors that maintain tree-grass coexistence within a landscape and identify drivers of historical and ongoing shifts in the global distribution of savannas. High structural and functional diversity and highly variable land use characteristic of global savannas necessitate careful consideration of environmental properties specific to particular ecosystems in order to understand local vegetation dynamics. Nevertheless, it is evident that general theory on the primary mechanisms sustaining herbaceous-woody assemblages is attainable, and emergent trends in the response of savannas to disturbance and interactions among savanna vegetation and the abiotic environment have greatly increased our understanding of the mechanistic processes regulating vegetation structure.

In general, savanna structure and distribution is a function of four main variables: fire, herbivory, water availability and nutrient availability (Frost et al. 1986). The former two factors represent disturbance pressures integral to the persistence of grasses or trees in regions climatically suitable for closed-canopy forests or tree-less grasslands (Sankaran et al. 2005; Scheiter and Higgins 2007; Bond 2008; Murphy and Bowman 2012; Tredennick et al. *In press*). The latter two factors regulate the interplay of biotic interactions among savanna vegetation and the abiotic template, and are closely linked with important ecosystem functions such as hydrological and biogeochemical cycles and the production and relative distribution of trees and grasses in the landscape (Scholes and Archer 1997; House et al. 2003; Sankaran et al. 2004; Ratnam et al. 2008). It follows that our ability to predict the response of savannas to changing

climatic and disturbance regimes depends on our understanding of the underlying mechanisms of tree and grass interactions.

Initially, tree-grass coexistence was thought to be sustained primarily through niche partitioning of resource capture associated with differences in the primary rooting depths of trees and grasses (Walter 1971; Walker et al. 1981; Walker and Noy-Meir 1982), but empirical evidence contradicting root partitioning as a ubiquitous mechanism of coexistence encouraged alternate explanations (e.g. February and Higgins 2010; February et al. 2012; Ward et al. 2013). In particular, the integration of both positive and negative interactions among neighbors in plant coexistence theory has advanced our understanding of drivers of plant community assembly (Bruno et al. 2003; Callaway 2007; Brooker et al. 2008). Trees and grasses compete directly for belowground resources, but may also promote growth of neighboring plants through beneficial modification of the abiotic environment. For example, trees may increase subcanopy nutrient availability through litterfall (Belsky et al. 1989; Dijkstra et al. 2006), or improve water balance in subcanopy regions by reducing incoming solar irradiance (Breshears et al. 1997; Caylor et al. 2005). Woody or herbaceous plants may also trap runoff from adjacent bare or sparsely-vegetated patches, promoting establishment and growth in close proximity to existing vegetation (Franz et al. 2011). *In situ* studies within savanna systems suggest these facilitative and competitive interactions are prevalent in savannas, particularly for the effects of trees on grass growth. However, there is no consensus on their relative importance in determining the outcome of plant neighborhood interactions across the wide climatic and environmental gradients of global savannas. Furthermore, very few studies have examined impacts of grasses on woody growth, or explicitly considered the importance of inter-tree interactions for community structure.

My dissertation focuses broadly on advancing our understanding of savanna tree and grass interactions by investigating the impact of neighbors on plant growth and analyzing observed trends with respect to local abiotic factors. Specifically, I address the following questions:

1. How does the net effect of trees on subcanopy grass production change with climate across global savannas?
2. Do grasses affect woody growth in savannas, and do these effects change with climate?
3. What are the underlying mechanisms driving observed patterns of tree-grass interactions in arid and mesic savannas?
4. What is the degree and spatial extent of inter-tree competition in savannas?

In the following chapters, I address these questions by analyzing existing empirical studies and implementing observational and experimental field studies. In Chapter 2, I present the results of a meta-analysis on the effects of trees on subcanopy grass production in tropical and temperate savannas. Chapters 3 and 4 employ neighbor removal experiments in the shortgrass steppe of northeastern Colorado and across a rainfall gradient in a West African savanna, respectively, to investigate underlying mechanisms driving patterns of tree-grass interactions. Lastly, Chapter 5 quantifies the degree and spatial extent of inter-tree competition from an East African savanna and discusses the role of tree-tree interactions for landscape-scale woody spatial structure.

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Chapter 2: Tree effects on grass growth in savannas: Competition, facilitation and the stress-gradient hypothesis¹

Summary

The stress-gradient hypothesis (SGH) predicts an increasing importance of facilitative mechanisms relative to competition along gradients of increasing environmental stress. Though 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 in order to explore emergent patterns of tree-grass relationships in global savannas in the context of the SGH. We quantified the net effect of trees on understory 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 analyzed soil and plant nutrient concentrations in sub-canopy and open-grassland areas to investigate the potential role of nutrients in determining grass production in the presence and absence of trees. Our meta-analysis revealed a shift from net competitive to net facilitative effects of trees on sub-canopy 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. Nutrient analyses indicate no change in nutrient ratios along the rainfall gradient, but consistent nutrient enrichment under tree canopies. Our results help to resolve questions about the stress gradient hypothesis 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

¹ This chapter is an edited version of Dohn, J., Dembele, F., Karembe, M., Moustakas, A., Amevor, K.A. & Hanan, N.P. 2013. *Journal of Ecology*, 101: 202-209.

bioclimates, respectively. The results of this meta-analysis advance our understanding of tree-grass interactions in savannas and contribute a valuable dataset to the developing theory behind the SGH.

2.1 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 *et al.* 2003; Brooker *et al.* 2008; Bullock 2009; Freckleton *et al.* 2009). Positive interactions between neighboring organisms are now considered fundamental ecosystem processes, and these processes interact dynamically with the abiotic environment to determine community structure (Bruno *et al.* 2003). Indeed, ecological theory predicts an increasing importance of facilitation relative to competition along gradients of increasing abiotic stress (Bertness and Callaway 1994; Brooker and Callaghan 1998; Pugnaire and Luque 2001; Callaway *et al.* 2002; Maestre *et al.* 2009). Termed the stress-gradient hypothesis (SGH), the theory postulates that beneficial environmental modification by neighboring organisms outweighs competition for resources under conditions of high environmental stress, such as high disturbance frequency or low resource availability (Bertness and Callaway 1994; Brooker and Callaghan 1998). As the local stressor decreases along a gradient, the relative strengths of the positive and negative interactions between neighboring 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.* 2006). While competitive and facilitative processes occur simultaneously along the entirety of environmental gradients (Brooker and Callaghan 1998; Callaway 2007; Smit *et al.* 2009; Malkinson and Tielborger 2010), the degree to which certain mechanisms impact the growth and fitness of neighboring organisms may change significantly along these gradients. Two neighboring 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 and Callaghan 1998). Amelioration of the extreme conditions of a high-stress environment by neighboring 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 and Novoplansky 1997; He *et al.* 2013; Lortie and 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 *et al.* 2001) and the type of stress gradient (Kawai and Tokeshi 2007; Maestre *et al.* 2006). 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 and McGeoch 2010). Goldberg and 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 and 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 sub-canopy 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 sub-canopy grasses, thus attracting grazers (Treydte 2007, 2008; Ludwig 2008). Increased animal deposits in sub-canopy 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 sub-canopy herbaceous production.

Though small-scale experiments in savannas have demonstrated a strong effect of water availability on herbaceous productivity (e.g. Baruch and 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 and 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 and Bartolome 1989; K.A. Amévor *et al.* unpublished data; A. Moustakas *et al.* unpublished data).

This paper 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 and 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 analyze soil and plant nutrient concentrations in sub-canopy and open-grassland areas in order to assess tree effects on understory nutrient availability and diagnose the potential role of nutrients in grass responses to tree canopies.

2.1.1 Hypothesized impacts of trees on grasses in savannas

Our hypotheses for how trees impact grasses across typical savanna rainfall gradients are shown in Fig. 2.1, separating effects mediated by soil moisture (Fig 2.1a), light and energy balance (Fig 2.1b), and nutrient availability (Fig 2.1c). Figure 2.1a 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 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 2.1b illustrates how decreased light availability due to shade may shift from net facilitative to net competitive effects by affecting the energy balance of sub-canopy grasses. In dry, water-limited regions, shade reduces evapotranspiration rates for sub-canopy 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 sub-canopy 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 sub-canopy 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 2.1c illustrates the potential effects of nutrient availability on sub-canopy 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 sub-canopy 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. 2.1 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 favor 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.

2.2 Materials and methods

2.2.1 Data collection

We reviewed published data reporting direct measurements of herbaceous production or peak biomass in both sub-canopy areas and open-grassland (see Table A2.1 in Appendix A2). We reduced methodological variability among the data included in the meta-analysis using the following selection criteria: i) sub-canopy 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. Since 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 we included in the meta-analysis. These data were then translated into normalized tree-effect ratios (y) of sub-canopy (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 (sub-canopy 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; Zomer *et al.* 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 S2.1) generally reflect the number of trees sampled rather than the total number of quadrats. Our selection criteria excludes a substantial body of research quantifying sub-canopy herbaceous productivity in savannas but were chosen in order 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 in order to allow for meaningful comparisons across diverse systems.

We also recorded sub-canopy/open-grassland herbaceous leaf and soil nutrient ratios if these data were available in the source literature reporting biomass (see Table A2.2 in Appendix A2). While soil and leaf concentrations differ substantially in magnitude, we normalized them using the same ratio of sub canopy 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 dataset.

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 – 26.3 degrees 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 and Chaieb 2009), the temperate dataset in this meta-analysis was thus limited exclusively to the savannas of the Western United States, while the tropical dataset 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.

2.2.2 Data analysis

Regression analyses were used to identify correlations between annual rainfall and the normalized ratio of sub-canopy to open-grassland biomass and nutrient contents. An analysis of covariance (ANCOVA) was used to test the effects of climate (i.e. tropical versus temperate),

soil texture (i.e. coarse versus 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 and Fabricius 2000) and hierarchical variance partitioning (Mac Nally 1996, 2002) were also investigated as supplements to linear regression analyses in order to more fully explore the influence of the categorical variables (i.e. soil texture, bioclimatic zone, and tree size) and test for potential non-linear patterns in the tree-effect ratio. Student's *t* tests were used to test if 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).

2.3 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. 2.2). 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. 2.2; $F=24.46$ on 91 degrees of freedom (df), adjusted $r^2=0.428$, $p<0.0001$). 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. 2.2, we also used hierarchical variance partitioning and regression tree analyses to further explore the dataset in case interaction effects not considered in the regression analysis, or non-linear 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, since our focus in this paper 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: Percent evapotranspiration represents a measure of the ability of the atmosphere to remove water via evapotranspiration under optimal growing conditions (Zomer *et al.* 2007;

Zomer *et al.* 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 datasets 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. Since the PPT/PET index did not provide any advantage over rainfall alone, only the model with annual rainfall is presented in Fig. 2.2 (see Appendix A2.3 for PPT/PET results).

Regression analyses revealed no significant correlations between the normalized ratio of sub-canopy to open-grassland nutrients and annual rainfall for nitrogen in grass leaves (df=19, p=0.590) or soil (df=20, p=0.421), nor for phosphorous in grass leaves (df=12, p=0.131) or soil (df=16, p=0.351) (Fig. 2.3). However, Student's *t* tests indicated that the mean nutrient ratios for leaf and soil nitrogen contents as well as phosphorous 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. 2.3 inset). The mean nutrient ratio for leaf phosphorous 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.

2.4 Discussion

The results of our meta-analysis suggest that the impact of trees on grass production in both tropical and temperate savannas shift from facilitative to competitive interactions as annual rainfall increases, consistent with the stress-gradient hypothesis. 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 on coarse soils, 943 +/- 204 on fine soils) and in temperate North America (479 +/- 177 mm/annum; Fig. 2.2). 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. 2.1). 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. 2.1 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 *et al.* 1999; Sage and Kubien 2003). The increased size and canopy cover of savanna trees in wetter regions, combined with the shade intolerance of sub-canopy C₄ grasses, potentially translates into a strongly light-limited understory 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 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. 2.1) 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 favor 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 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. 2.2) indicates an increase in competition between trees and sub-canopy 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 and Beare 1997; Hassink 1997). The island of fertility effect (Kellman 1979; Belsky *et al.* 1989) in sub-canopy 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 sub-canopy to open-grassland ratios and rainfall were found for nitrogen or phosphorous concentrations in either tropical or temperate sites. Mean ratios for both nutrients were consistently greater than 0 (though marginally non-significant for phosphorous leaf content), suggesting nutrient enrichment in sub-canopy 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 and Goldberg 1999; Maestre *et al.* 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 and McDougald 1989; Callaway 2007), rainfall seasonality (Kikvidze *et al.* 2006), and tree size and life history stage (Stuart-Hill and Tainton 1989; Callaway *et al.* 1991; Callaway 2007). While such processes likely 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 sub-canopy 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.

Unraveling the complex of mechanisms behind trees-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 and 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 Houerou 1989). The results of this study, coupled with further investigation into mechanistic drivers of herbaceous production, can help inform the management of savanna systems in order to optimize the yield and sustainability of ecosystem goods and services critical to the livelihoods of local managers and communities.

2.4.1 Supporting Information

Table A2.1 Data sources for sub-canopy to open-grassland herbaceous biomass ratios

Table A2.2 Data sources for sub-canopy to open grassland soil and leaf matter nutrient ratios

Appendix A2.3 Results of precipitation over percent evapotranspiration (PPT/PET) analysis.

2.5 Figures

Hypothesized tree effects on grass

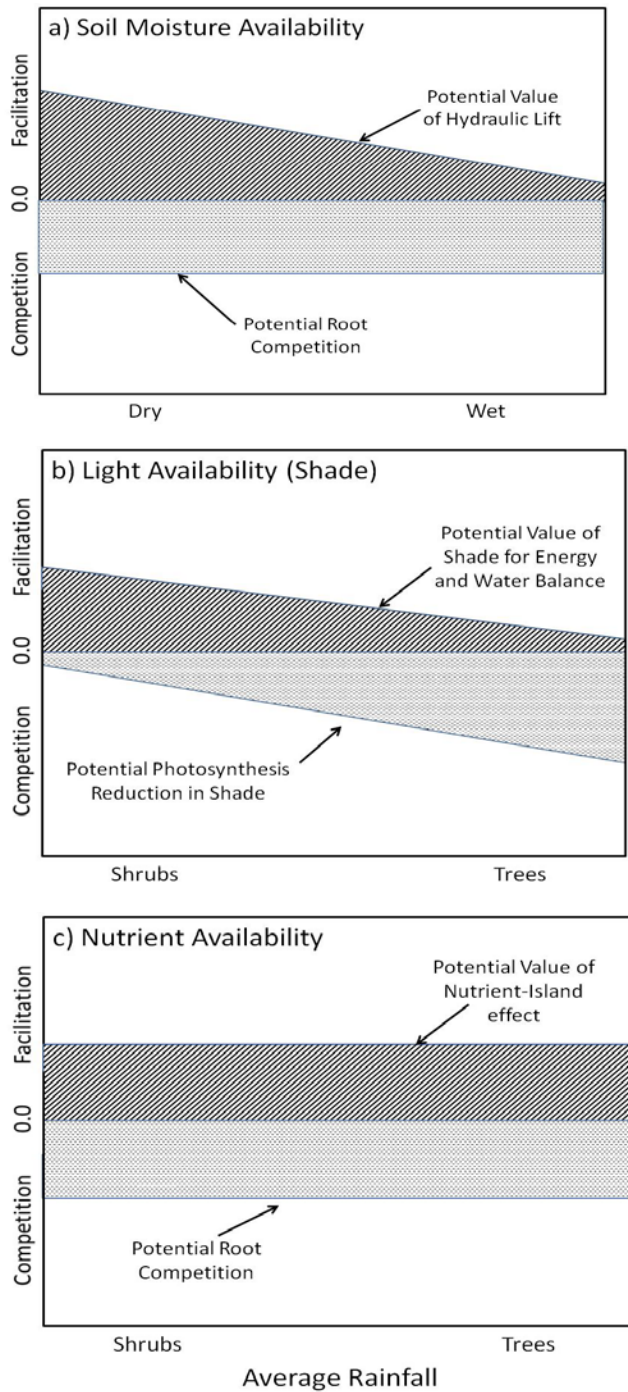


Fig. 2.1. Hypothesized impacts of trees on grasses in savannas, as mediated by a) soil moisture, b) light and energy balance, and c) nutrient availability. Shading indicates postulated range of likely facilitative (dark grey) and competitive (light grey) impacts, with the crossover point between the two net effects represented by a normalized ratio of 0.0.

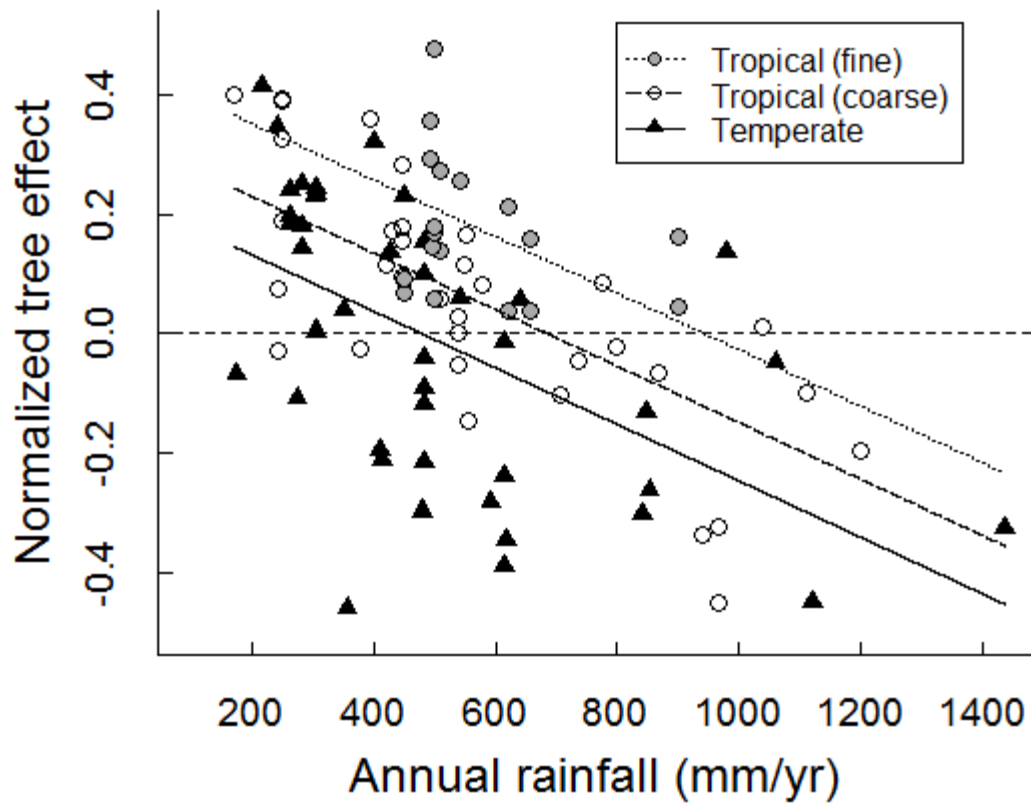


Fig. 2.2. Normalized ratio of sub-canopy to open-grassland herbaceous biomass along a gradient of annual rainfall for temperate North American savannas and tropical African savannas on coarse and fine soils. Regression lines represent the final simplified model with equal slopes but statistically distinct intercepts among datasets (adjusted $r^2=0.428$, $p<0.0001$).

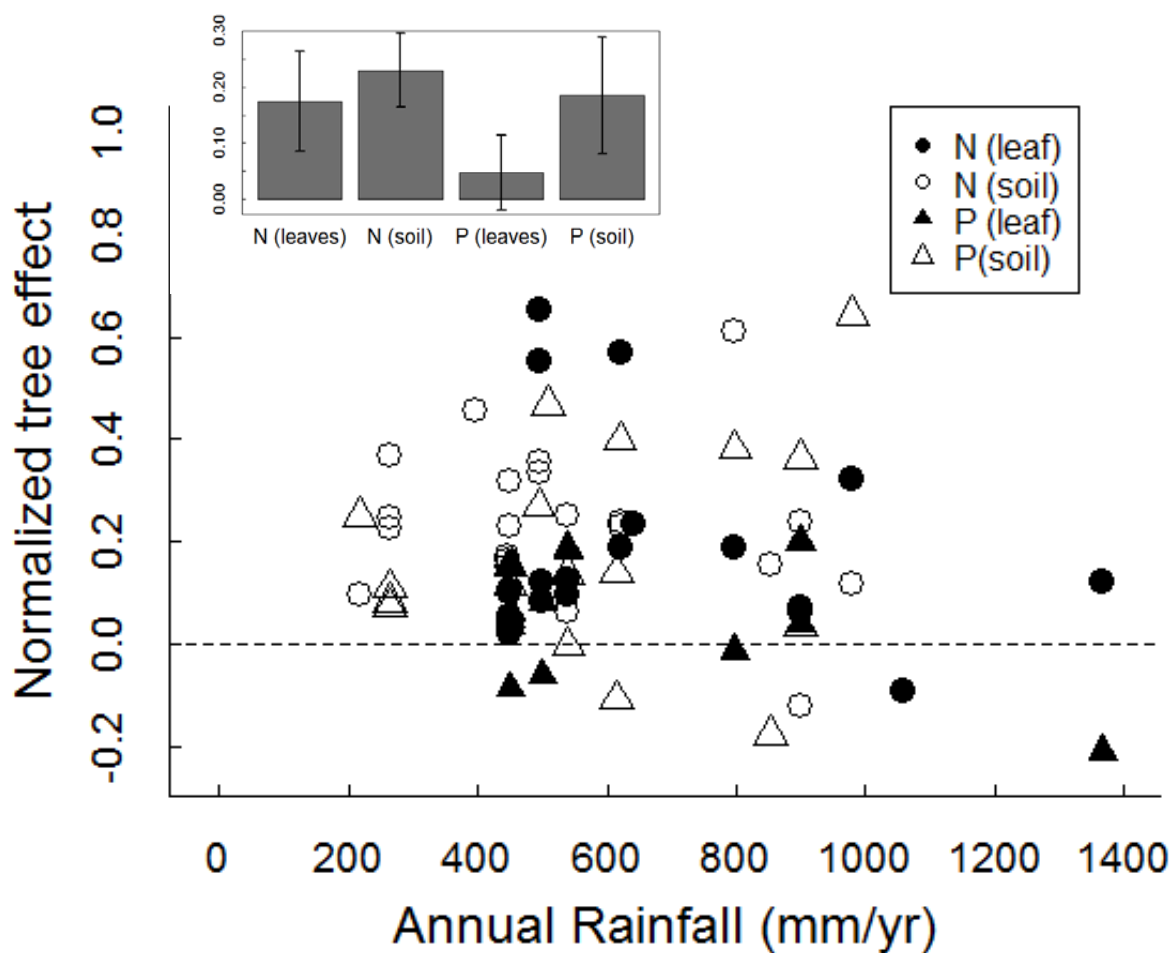


Fig. 2.3. Ratio of sub-canopy to open-grassland nutrient contents along a rainfall gradient. Nitrogen concentrations in soil ($p=0.590$) and leaf matter ($p=0.421$), as well as phosphorous concentrations in soil ($p=0.131$) and leaf matter ($p=0.351$) showed no correlation with annual precipitation. Inset figure shows nutrient ratio means and 95% confidence limits.

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Chapter 3: Shrub-grass interactions, inverse texture and stress gradient hypotheses: insights from the Colorado shortgrass steppe

Summary

Woody and herbaceous vegetation in shrub-grass systems may simultaneously compete for resources while improving microclimate conditions; the net outcome of these competitive and facilitative mechanisms varies predictably across environmental gradients but is likely sensitive to local conditions. We investigate whether shrubs and herbaceous communities in the shortgrass steppe (SGS) suppress or promote the growth of the other and evaluate the influence of soil texture and topographic position on these neighborhood interactions. We analyzed trends in aboveground net primary productivity, grass production as a function of distance from shrubs, and shrub allocation to woody biomass in the presence and absence of neighbors. We discuss our findings in the context of two prominent ecological theories, the stress gradient hypothesis (SGH) and the inverse texture hypothesis (ITH). We found relatively small competitive effects of shrubs on grasses and vice versa, suggesting that facilitative and competitive mechanisms largely offset in the SGS. Total shrub and grass ANPP was highest on fine-textured soils, contrary to the predictions of the ITH. While meta-scale patterns in plant production and competition embodied in the SGH and ITH may hold at regional scales, their validity at local scales is contingent on properties such as plant morphology and landscape-scale hydrology.

3.1 Introduction

The coexistence of shrubs and grasses characterizes many arid and semiarid regions, yet the mechanisms that enable this coexistence across broad climatic gradients are not fully understood (House et al. 2003; Sankaran et al. 2004; Cipriotti and Aguiar 2010). For years the

niche separation model proposed by Walter (1971) persisted as the primary conceptual model dictating our understanding of shrub-grass coexistence. Walter's hypothesis assumes a competitive advantage for grasses in shallow rooting layers and posits that coexistence is maintained by deep-rooted shrubs accessing soil water resources at depths unattainable by grasses. Several studies have supported Walter's hypothesis, showing that shrubs and grasses do indeed utilize resources from different rooting depths (Sala et al. 1989; Weltzin and McPherson 1997; Dodd et al. 1998; Kambatuku et al. 2012). Other studies, however, describe rooting profiles inconsistent with Walter's model (Mordelet et al. 1997; Hipondoka et al. 2003; February and Higgins 2010; February et al. 2012) or suggest that root partitioning alone may be insufficient to allow for prolonged shrub-grass coexistence (Jeltsch et al. 1996; Scholes and Archer 1997; Scheiter and Higgins 2007; Ward et al. 2013). More recent empirical work has therefore focused on elucidating the influence of disturbances (i.e. herbivory, fire, and drought; Roques et al. 2001; Carrick 2003; Staver et al. 2009) as well as interactions with biotic and demographic mechanisms (Riginos 2009; Cipriotti and Aguiar 2010) as integral components enabling shrub-grass coexistence (for reviews see Scholes and Archer 1997; House et al. 2003; Sankaran et al. 2004). Mounting evidence in this regard suggests that the density and net primary productivity of shrubs and grasses across climatic gradients in savannas is subject to a complex of interactions between disturbance, biotic and edaphic factors. To improve our understanding of shrub-grass coexistence, a clearer understanding is needed of how the abiotic template of a particular system influences the biotic interactions between these two life forms.

Shrubs and grasses compete directly for resources but may also facilitate growth of the other, primarily through microclimate amelioration resulting in improved water balance and soil fertility (Callaway 1995). The interaction between competitive and facilitative mechanisms

produces a net effect on growth of neighboring plants, which varies with environmental and climatic variables (Dohn et al. 2013). Prevailing theory predicts an inverse relationship between competitive relative to facilitative mechanisms and abiotic stress (Bertness and Callaway 1994). Termed the stress gradient hypothesis (SGH), these predictions have been supported in a variety of ecosystems and among many plant functional types (Callaway 2007; Maestre et al. 2009; He et al. 2013), including shrubs and grasses (Pugnaire and Luque 2001; Maestre et al. 2003; Holzappel et al. 2006; Silva et al. 2010; Madrigal-González et al. 2012). Other studies, however, indicate that the response of plants to their neighbors may depend on a number of ecosystem-specific factors, particularly in arid regions (Tielborger and Kadmon 2000; Maestre and Cortina 2004; Maestre et al. 2005; Maestre et al. 2009). As such, further empirical investigations are needed to determine the conditions in which shrubs facilitate sub-canopy herbaceous growth and likewise the conditions in which grasses promote or suppress shrub growth.

This study quantifies the effect of shrubs on grass growth in a shortgrass steppe (SGS) ecosystem, and the corresponding effects of grasses on shrub growth. We also examine the relative contributions of woody, leaf, and flower biomass to the overall growth of shrubs to test if shrubs alter their allocation strategies in the presence or absence of neighbor interactions or in response to environmental factors (i.e. site location, corresponding to differences in soil texture and topography). A previous study on grass production in the SGS found no differences in overall herbaceous growth with respect to distance from shrubs (Hart et al. 1997). This net neutral effect observed in the SGS seemingly contrasts with facilitative trends documented in other semi-arid, water-limited systems, thus offering an intriguing opportunity to explore potential underlying mechanisms responsible for driving shrub-grass interactions away from the predicted response. The effects of grasses on adult shrub growth have rarely been quantified (but

see Sala et al. 1989; Köchy and Wilson 2000; Peltzer and Köchy 2001; Riginos 2009) and it is unclear whether these biotic interactions parallel competition-facilitation trends across environmental gradients observed for the effects of woody species on grasses.

Here we describe a shrub and grass removal experiment replicated across a soil texture gradient to evaluate the impact of edaphic factors on production in the presence and absence of neighbor interactions. Specifically, we assess whether the net outcome of shrub-grass interactions in the SGS is primarily facilitative, as predicted by the SGH in highly water-limited systems, and we examine the interactive effects of a soil texture gradient on these neighborhood interactions. The inverse texture hypothesis (ITH) predicts an increase in ANPP on coarse- relative to fine-textured soils in arid regions such as the SGS (Noy-Meir 1973; Sala et al. 1988). High sand contents in arid soils increase percolation to deeper levels, thus reducing bare soil evapotranspiration and increasing water availability for vegetation. In mesic regions, this advantage is conferred to fine-textured soils, as the high water holding capacity of soils with high clay contents reduces drainage losses to soil layers below the rooting zones of plants. Furthermore, in dry conditions, plants growing on fine-textured soils reach a wilting point threshold at higher levels of soil volumetric water content than those growing on sandy soils (Fernandez-Illescas et al. 2001; Caylor et al. 2009). Thus, plants on coarse-textured soils in arid regions remain above critical levels of stress at lower levels of plant available water, further promoting the inverse texture effect.

Based on SGS and ITH theory, we predict (i) shrub and grass removal will result in decreased primary production of the corresponding life form due to degraded microclimatic conditions related to soil water availability (*sensu* SGH), (ii) primary production will be highest on coarse-textured sites due to decreased evaporation rates and reduced water stress (*sensu* ITH),

and (iii) neighbor facilitation will be highest on fine-textured sites, where increased abiotic stress due to decreased soil water availability increases the importance of facilitative mechanisms (SGH-ITH interaction).

3.2 Methods

3.2.1 Study Site

The study was conducted on the Shortgrass Steppe Long Term Ecological Research (SGS-LTER) site on the Central Plains Experimental Range (CPER) in northeastern Colorado (40°49' N, 104°43' W). The SGS is characterized by a sparse canopy of C₄ grasses and shrubs with low leaf area index and low aboveground net primary productivity (ANPP; Lauenroth et al. 2008). Mean annual precipitation at the nearest weather station is 356 mm yr⁻¹ since 1960, with a cumulative average of 282 mm for the months of April through August (the duration of this study). Precipitation in the experimental year totaled 361 mm, with a growing season rainfall of 285 mm, representing only a 0.90% deviation from the historical mean. All shrubs within the plots were *Atriplex canescens* and the dominant grasses were C₄ perennials *Bouteloua gracilis* and *Bouteloua dactyloides*. We chose three sites with varying soil properties and topographic location in order to test for potential differences in vegetation responses related to differences in soil texture and rainfall infiltration and plant community composition (Table 3.1). Site 1 was located on level ground on high clay-content soil and low forb density. Site 2, located approximately 1.2 km northeast of site 1, was on moderately (< 2%) sloping ground mid-way up the toposequence with comparatively higher sand content, and with more forbs and cacti (*Opuntia polyacantha* Haw.) intermittent throughout the plots (average aboveground cactus dry biomass within one meter radius of experimental shrubs = 14.5g). Site 3, located approximately 3.1 km east of site 2, was situated on level ground on the crest of the toposequence with sandy

soil and greater densities of forbs (most notably *Artemisia frigida*) and *O. polyacantha* interspersed among the shrubs (average cactus biomass within 1 m radius of experimental shrubs = 18.7g). The three sites are hereafter referred to as swale, midslope, and upland, respectively. We performed a particle size analysis using the hydrometer method (Gee and Bauder 1979) on five samples taken from the top 20 cm in each site (Table 3.1).

3.2.2 Biomass removal treatments

At each site, we removed all aboveground shrub biomass from 20 x 20 m plots in April, 2010. In adjacent plots of the same size we cut all herbaceous growth, forbs and cacti at ground level within a minimum of one meter radius from 15 randomly selected shrubs. A previous study on similar soils in the SGS revealed a lateral root length of approximately 30 cm for a small number of excavated *A. canescens* shrubs (Lee and Lauenroth 1994). For the purpose of this study, this rooting zone was extended to one meter to account for variation in shrub size and root morphology. A third plot was left untouched as a control, and all plots were surrounded by cattle fences to exclude grazing. In each treatment plot, re-growth of shrubs and grasses, respectively, was removed at weekly intervals throughout the growing season to minimize the possibility of competition. At the end of the growing season (September 2010), all aboveground biomass from all treatment shrubs in the grass-removal plots and 15 randomly selected shrubs from the control plots was harvested and subsequently sorted into old woody growth, new woody growth (i.e. woody biomass accumulation from the experimental year's growing season only), leaves, and flowers. Separation of woody components into current and past years' growth was accomplished by separating the dark brown wood distinctive of wood that has survived a winter season from the light tan wood of the current season's growth. Grasses and forbs from 15 randomly selected

0.25 m² plots were cut at ground level from shrub-removal plots and control plots. We recorded the distance from the nearest two shrubs (or shrub stumps where shrubs had been removed in the treatment plots) to each harvested grass quadrat and estimated shrub volume of all experimental shrubs prior to removal by recording height, length, and width of the shrub canopy. All biomass was dried and weighed. Hectare-scale estimates of woody ANPP were calculated based on shrub counts from 400 m² plots at each site (Table 3.1). Total hectare-scale ANPP was calculated by estimating surface area occupied by shrubs at each site based on measurements of shrub volume and shrub density counts while assuming all area not occupied by shrubs was occupied by site-specific average herbaceous ANPP (Table 3.1).

3.2.3 Data analysis

We analyzed the effects of treatment (i.e. presence or absence of competitor) and site (i.e. variable soil properties, community composition) on the growth of shrubs and grasses using analysis of variance (ANOVA). Tukey's HSD post-hoc tests were used to evaluate pairwise differences. Shrub growth was evaluated using relative growth rate (RGR; y) calculated as a function of biomass at the beginning (mass W_1 at time t_1) and end (mass W_2 at time t_2) of the growing season, where $y = (\ln W_2 - \ln W_1) / (t_2 - t_1)$. We also tested the effects of treatment and site on shrub growth using an analysis of covariance (ANCOVA) with new biomass (the sum of new woody growth, flowers, and leaves) as the response variable and shrub size as a continuous explanatory variable. Shrub volume and old woody biomass were tested separately as proxies for shrub size in this model. Replication at site-scale for the response of shrubs to grass presence was N=15 (i.e. in each soil type we measured growth parameters for 15 shrubs with herbaceous competitors and 15 shrubs without herbaceous competitors, for a total sample of 90 shrubs across the three sites/soil types). Similarly for the response of herbaceous communities to shrub

presence we harvested 15 quadrats in undisturbed vegetation and 15 quadrats in areas where all above ground shrub biomass was removed. Regression analyses were used to determine the relationship between grass production and distance from the nearest shrub and/or the mean distance from the nearest two shrubs. Regression analyses were also used to examine the influence of soil clay contents (i.e. site) on shrub and grass ANPP. All analyses were conducted in R 2.14.1 (R Development Core Team 2013, Vienna, Austria).

3.3 Results

3.1.1 Grass effects on shrub growth

We found no significant differences in shrub relative growth rate (RGR) among sites ($P = 0.076$), or in the effect of the presence or absence of grasses on shrub RGR ($P = 0.720$; Fig. 3.1). Using total new biomass as the response variable (i.e. not accounting for original shrub size inherent in RGR), ANOVAs similarly revealed no treatment effect ($P = 0.361$) but significant differences in shrub growth between sites ($P = 0.010$), with greater growth ($\mu = 250 \text{ g shrub}^{-1}$) in the upland site relative to both the swale ($\mu = 105 \text{ g shrub}^{-1}$, $P = 0.013$) and midslope ($\mu = 129 \text{ g shrub}^{-1}$, $P = 0.046$) sites. An ANCOVA with new biomass as the response variable and shrub volume as a continuous explanatory variable adjusting for original shrub size showed no significant departures from the results of the RGR analysis and thus only the RGR results are presented here. The mean size of shrubs in the upland site ($\mu = 796 \text{ g shrub}^{-1}$) was significantly greater than both the swale ($\mu = 334 \text{ g shrub}^{-1}$, $P < 0.0001$) and midslope ($\mu = 371 \text{ g shrub}^{-1}$, $P = 0.0002$). However, aboveground woody biomass (i.e. standing wood at the beginning of the growing season) was highest in the swale site (1080 kg ha^{-1}) and lowest in the midslope site (756 kg ha^{-1}) due to higher shrub density in the swale site (Table 3.1). There were no differences in shrub size between grass removal plots and control plots in any of the sites.

ANOVAs examining the percent of new biomass allocated to the woody component versus flower and leaf biomass revealed significant differences in allocation patterns between treatments ($P = 0.042$) and between sites ($P < 0.0001$), but no interaction between treatment and site ($P = 0.143$). These results demonstrate a general decrease in the proportion of total growth allocated to woody biomass in the presence of grass competition (Fig. 3.2). Allocation to woody biomass was highest in the midslope site and lowest in the swale site (Fig. 3.2), suggesting an increase in allocation to woody growth with increasingly sandy soils. Analysis of new wood, leaf and flower production, normalized by mean shrub size, showed no significant differences among sites and treatments (data not shown).

3.3.2 *Shrub effects on grass growth*

An ANOVA found no significant effect of treatment (i.e. presence or absence of shrubs) on grass production ($P = 0.831$; Fig. 3.3), but did detect significant differences in production between sites ($P < 0.0001$), perhaps demonstrating the influence of soil properties on herbaceous growth. Grass production increased with soil clay content (Fig. 3.3), with the swale site producing the most grass biomass ($\mu = 232 \text{ g m}^{-2}$), followed by the upland site ($\mu = 158 \text{ g m}^{-2}$) and the midslope site ($\mu = 110 \text{ g m}^{-2}$).

An ANCOVA revealed no overall effect of the presence or absence of shrubs on the relationship between grass production and shrub proximity ($P = 0.828$; Fig. 3.4). Interestingly, when shrub presence/absence is ignored, the ANCOVA ($P < 0.0001$) found no consistent effect of shrub (or shrub stump) proximity on grass production, but significant differences emerged between sites ($P < 0.0001$) and in the interaction between site and shrub proximity ($P = 0.030$). Subsequent post-hoc analysis at the site level suggested a slight decrease in herbaceous production with increasing distance from the nearest shrub in the midslope site ($P = 0.059$),

implying a neutral or facilitative effect of shrub presence. The upland site, on the other hand, revealed a significant increase in grass biomass with increasing distance from the shrub ($P = 0.007$; adjusted $R^2 = 0.205$), suggesting a competitive effect of shrub proximity.

3.4 Discussion

Our analyses revealed no significant changes in the RGR of entire shrubs (wood, leaves, and flowers) in the presence or absence of grass and likewise no strong effect of shrub removal on grass growth, suggesting that the balance between the competitive and facilitative mechanisms in the shortgrass steppe (SGS) results in net-neutral effects. Previous analyses of woody-herbaceous interactions along environmental gradients suggest a facilitative effect of shrubs on grass production in arid, temperate regions such as the SGS. Following the regressions calculated in a meta-analysis by Dohn et al. (2013) on global mixed woody-grass systems, one would expect a facilitative effect of ~16% increase in herbaceous production in close proximity to shrubs relative to production in open grasslands. The net-neutral effect detected in this study and previously by Hart et al. (1997) may indicate that the biotic and edaphic properties characteristic of the SGS drive the observed response away from trends documented in climatically similar regions. In particular, recent studies show that canopy height can alter competition-facilitation relationships predicted by the SGH (Moustakas et al. 2013), whereby increased competition for light beneath low-canopy woody plants limits the effectiveness of facilitative mechanisms such that competitive interactions predominate (Blaser et al. 2013). Intense shading in sub-canopy areas due to the short stature and dense morphology of *A. canescens* may thus override any beneficial effects of microclimate amelioration related to improved water balance. Competitive effects on neighboring plant growth may also be marginal

in this system due to root niche partitioning between woody and herbaceous life forms. In a previous study conducted in the SGS, shrubs and grasses largely accessed distinct water sources, with *A. canescens* primarily utilizing groundwater and subsoil sources and *B. gracilis* exclusively utilizing water extracted from shallow soil layers (Dodd et al. 1998). Thus, the net neutral effects of shrub and grasses on neighbor growth may be attributed largely to low interaction intensity rather than offsetting competitive and facilitative mechanisms.

We found contrasting effects when we analyzed the growth response of grasses as a function of distance from shrubs, with a slight (non-significant) decline in grass production with distance from the nearest shrub in the midslope and swale sites, and a significant increase in production with distance from shrubs, suggesting a net competitive effect of shrubs on grass growth, in the upland site. This shift from a neutral or marginally facilitative effect to a competitive effect is not clearly related to the soil texture gradient. Given the predictions of the SGH, increased water availability on coarse soils should increase the importance of competitive interactions. Though we did detect a significant suppressive effect on the relatively coarse soils of the upland site, the opposite trend found on coarser soils in the midslope site and no discernible effect in the fine-textured swale site suggests that soil texture alone does not account for the observed patterns.

Alternatively, shrub size differences among sites may affect shrub-grass competitive outcomes. Individual shrubs in the upland site were on average more than twice as large as those in the other two sites (Table 1). Conceivably shrubs might thus reach a certain size threshold after which effects on adjacent herbaceous communities switch from net neutral or slightly facilitative to net competition, likely due to increased competition intensity resulting from higher resource demands and dense root systems characteristic of larger shrubs. However, grass

production did not respond to the removal of nearby shrubs, perhaps reflecting legacy effects related to differences in species composition and plant density in close proximity to large shrubs in the upland site.

Grass production and shrub growth varied substantially between sites within the SGS, perhaps attributable to differences in water availability related to soil permeability and topographic effects on landscape-scale hydrology. Grass and woody ANPP declined with increasing soil sand content, contrary to the predictions of the ITH. These results seemingly contrast field experiments within the SGS (Dodd and Lauenroth 1997; Lane et al. 1998) and syntheses along broad climatic and textural gradients across the Central Grassland region of the United States (Sala et al. 1988; Lauenroth et al. 2008; but see Lane et al. 1998), wherein authors report general support for the ITH. However, examination of results from such studies suggests that environmental variables other than soil texture may play a larger role in determining ANPP, most notably functional group composition. For example, Liang et al. (1989), Dodd and Lauenroth (1997), and Lane et al. (1998) compare ANPP on coarse- and relatively fine-textured sites in the SGS that markedly differ in their community compositions, with a significant and characteristic drop in woody abundance with increasingly clayey soils such that in all cases the finest-textured sites represent total or near exclusion of woody biomass by graminoid species. In this study, we aimed principally to evaluate the competitive interactions between shrubs and grasses, and thus purposefully selected sites along a soil texture gradient while controlling for significant shifts in vegetative composition. While high woody biomass on fine-textured soils contributed to the increase in ANPP observed in the swale site (Table 1), high grass ANPP in this site relative to the coarse-textured sites suggests other factors are more closely linked with observed differences in biomass production across the soil texture gradient, perhaps most notably

differences in soil water availability driven by landscape-scale topography. Previous studies in the SGS indicate that landscape position can significantly alter community composition and ANPP, with particularly high variability in swale areas, attributable to occasional downhill water and nutrient flows (Burke et al. 1999; Lauenroth et al. 2008). In addition to affecting total ANPP, such effects may interact with site properties such as soil texture to drive the community away from the net outcomes of biotic interactions predicted by the SGH. For example, in the swale site, fine-textured soils decrease soil water availability (ITH), thus increasing the importance of facilitative mechanisms (SGH). However, when rare large rain events produce downhill runoff or sub-surface lateral flow, this may supplement soil water in the swale site and offset these soil texture effects, producing the observed neutral relationship between distance from shrubs and grass production (i.e. balanced facilitative and competitive effects).

While we observed no effects of grass presence on shrub production, shrubs did adjust relative allocation to woody biomass in the absence of grasses and across the soil texture gradient. In the absence of grass competition, we saw an increase in the fraction of total production allocated to wood growth, particularly in the midslope site (i.e. coarsest soil), and a general increase in wood growth allocation with increasing sand content in the soil. Theory suggests that soil resource depletion due to high plant density may lead to increased allocation to root growth (Poorter et al. 2012). Thus, the observed increase in allocation to woody growth in the absence of grasses may reflect a release from belowground competition, enabling the shrubs to allocate more resources to aboveground growth. Under this framework, observed shifts in allocation following the removal of grass competition may be attributable to differential allocation in favor of wood biomass relative to leaves and flowers as a response to increased nutrient and/or water availability. We are unable to fully quantify this response, however, as we

lack root biomass and root growth data. Similarly, the observed increase in relative allocation to woody stems in coarse-textured soils may actually be indicative of an increase in allocation to root biomass at the expense of leaves and flowers. Previous studies suggest that plants grown in sandy soils may adjust biomass allocation away from leaves and invest in root growth (Weigelt et al. 2005), while leaving stem allocation relatively constant (Xie et al. 2012).

The results of this study contribute a valuable dataset to a growing body of literature aimed at unraveling the mechanisms governing global shrub-grass coexistence. Previous analyses in mixed woody-herbaceous systems have often focused on interactions with larger trees and shrubs (e.g. Dohn et al. 2013 and references therein), while analyses of biotic outcomes between short-statured shrubs and grasses are comparatively scarce or represent limited environmental gradients. It is plausible that the morphological characteristics of short shrubs and the corresponding effects on sub-canopy microclimates alter the response of vegetative communities to varying levels of environmental stress. It is unclear whether observed deviations from the facilitative effect predicted by the SGH in semi-arid regions such as the SGS reflect natural variation due to site-specific environmental variables or are indicative of a deviation from the overall trend seen in global savannas. Further empirical studies in shrub-grass systems around the world are needed before a synthesis can reliably evaluate large-scale trends.

Increases in the abundance of woody plants in systems with co-dominant woody and herbaceous life forms have been documented in many global systems (Eldridge et al. 2011) and efforts by land managers to preserve biodiversity and ecosystem services in the face of changing climatic and disturbance regimes may depend on our understanding of the responses of shrubs and grasses to changes in abiotic, biotic, and edaphic factors. Our results contribute to this

understanding and will hopefully encourage further empirical investigations into the mechanisms that promote shrub-grass coexistence.

3.5 Tables

Table 3.1. Site characteristics for three experimental sites in the shortgrass steppe. Production estimates are for full growing season and represent averages across treatments (N=30); values in parentheses represent standard errors of the mean.

Location	Soil texture			Shrubs					Grasses		Total
	Sand	Silt	Clay	Density (shrubs ha ⁻¹)	Size (woody g shrub ⁻¹)	Growth (g shrub ⁻¹)	AGB* [^] (kg ha ⁻¹)	ANPP* [^] (kg ha ⁻¹)	Growth (g m ⁻²)	ANPP [^] (kg ha ⁻¹)	ANPP [^] (kg ha ⁻¹)
Midslope	76% (2)	15% (2)	10% (0)	2038	371 (50)	129 (13)	756 (101)	262 (27)	110 (4)	860 (34)	1122 (61)
Upland	70% (1)	14% (1)	16% (1)	1163	796 (108)	251 (59)	925 (126)	291 (69)	158 (8)	1315 (64)	1606 (133)
Swale	7% (3)	46% (1)	47% (4)	3238	334 (42)	105 (11)	1080 (137)	339 (34)	232 (12)	1544 (77)	1882 (111)

*Aboveground biomass (standing dead wood only); +Aboveground net primary productivity; ^Error terms extrapolated from production error terms

3.6 Figures

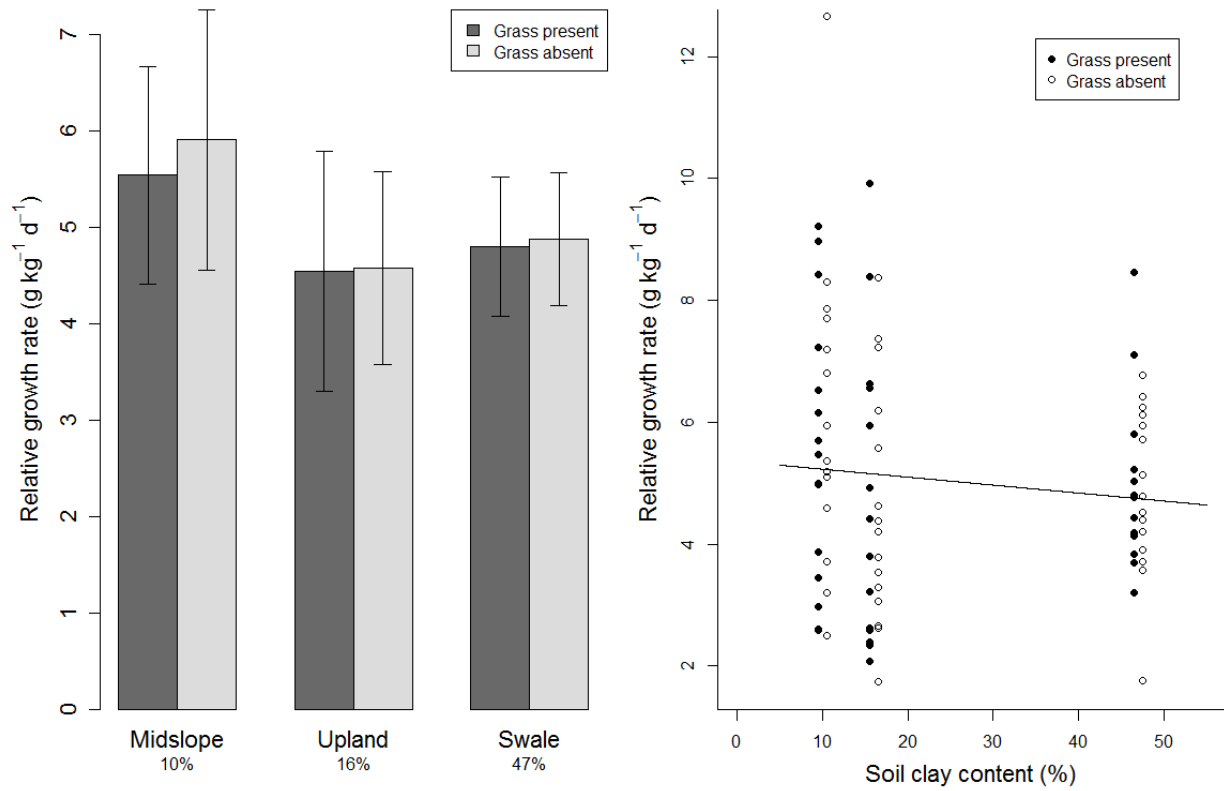


Figure 3.1. Relative growth rate (RGR) of shrubs in the presence and absence of grass on three soil types. Bar graph (left panel) represents site means with 95% confidence limits; there are no significant differences among sites or treatments in these data ($P = 0.379$). Shrub RGR did not vary significantly with respect to soil texture (clay content) (right panel; $P = 0.337$). Site labels indicate topographic location and soil clay contents. Soil clay contents in grass absent and grass present plots within each site are identical but are offset here to improve visibility.

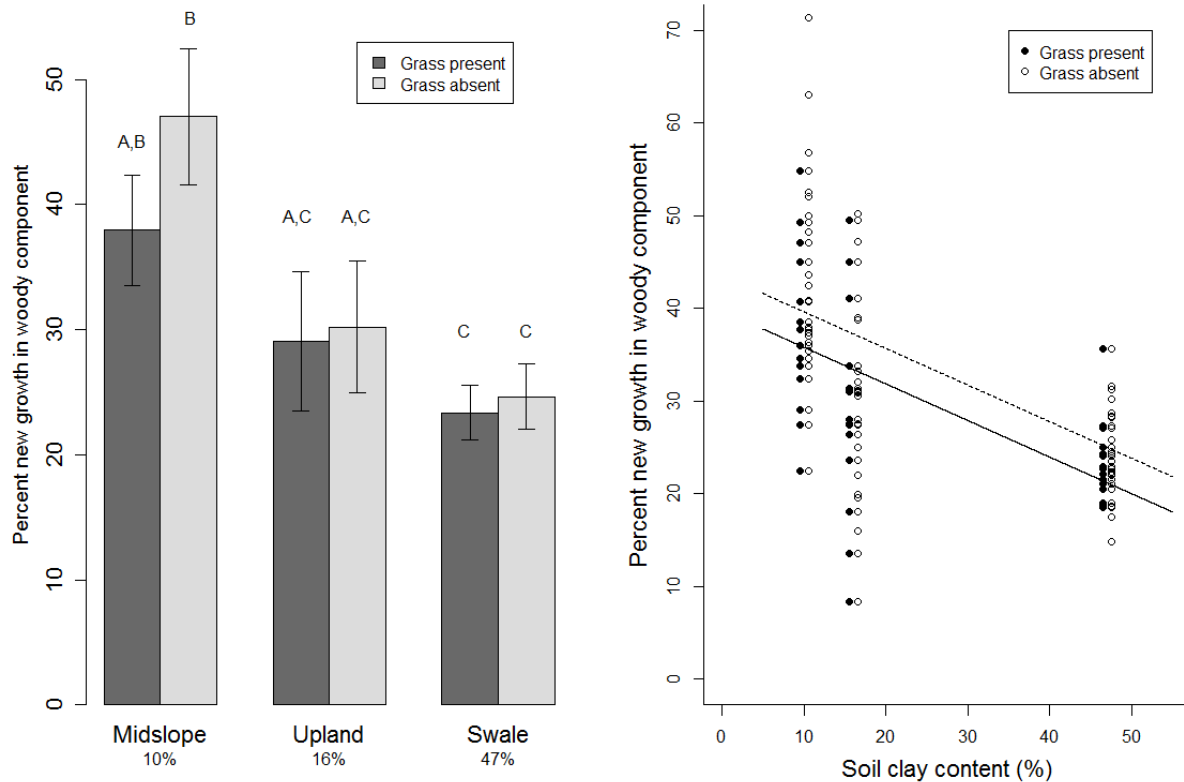


Figure 3.2. Percentage of total new growth of shrubs allocated to the woody component in the presence and absence of grasses on three soil types. Bar graph (left panel) represents site means with 95% confidence limits; bars that do not share the same letter are significantly different ($P < 0.05$, Tukey HSD post-hoc tests). Analysis of variance (ANOVA) indicates that woody growth allocation varies among sites ($P < 0.0001$) and in the absence of grasses ($P = 0.045$). Allocation to woody biomass decreased with increasing soil clay content (right panel; $P < 0.0001$; adjusted $R^2 = 0.29$) and an analysis of covariance indicates that grass competition (solid line) tends to reduce allocation of growth to wood production relative to growth without grass competitors (dashed line; $P = 0.0695$ across all sites, where treatments are separated because of significance of grass competition in the ANOVA). Site labels indicate topographic location and soil clay contents. Soil clay contents in grass absent and grass present plots within each site are identical but are offset here to improve visibility.

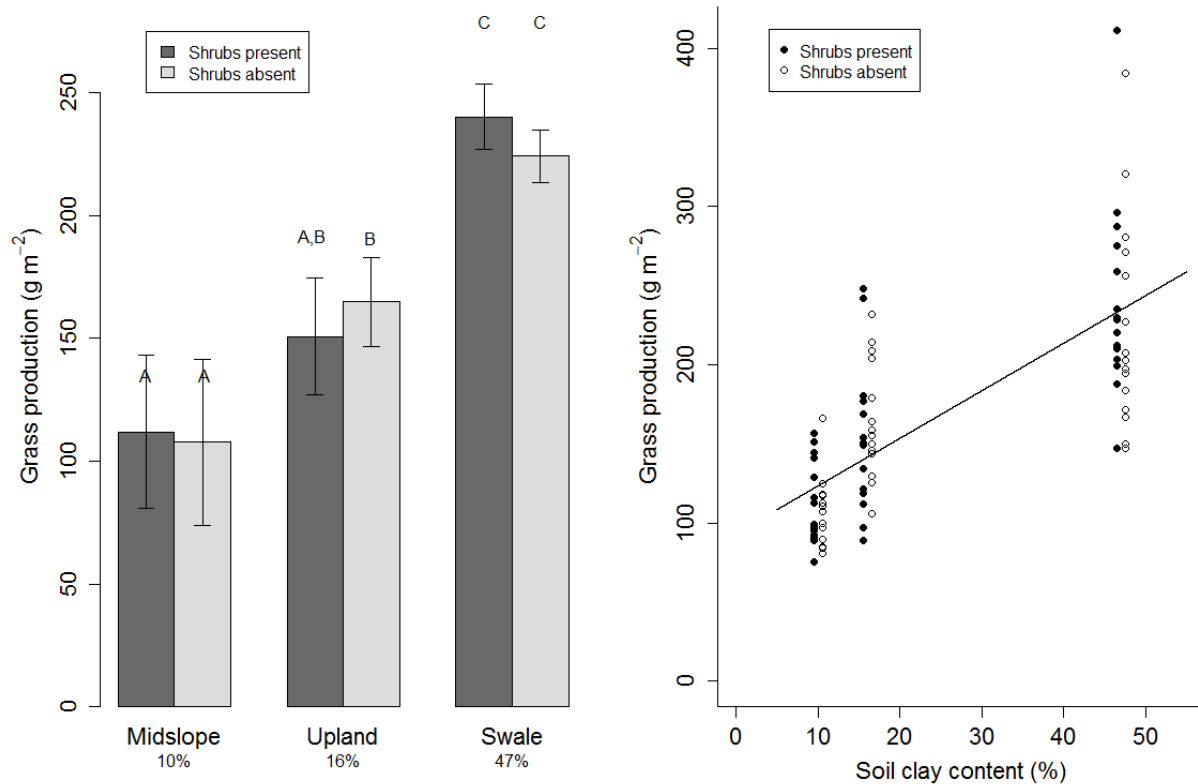


Figure 3.3. Grass production in the presence and absence of shrubs on three soil types. Bar graph (left panel) represents site means with 95% confidence limits; bars that do not share the same letter are significantly different ($P < 0.05$, Tukey HSD post-hoc tests). Grass production significantly increased with increasing soil clay content (right panel; $p < 0.0001$, adjusted $r^2 = 0.514$) with no significant effect of shrub presence ($P = 0.831$). Site labels indicate topographic location and soil clay contents. Soil clay contents in shrubs absent and shrubs present plots within each site are identical but are offset here to improve visibility.

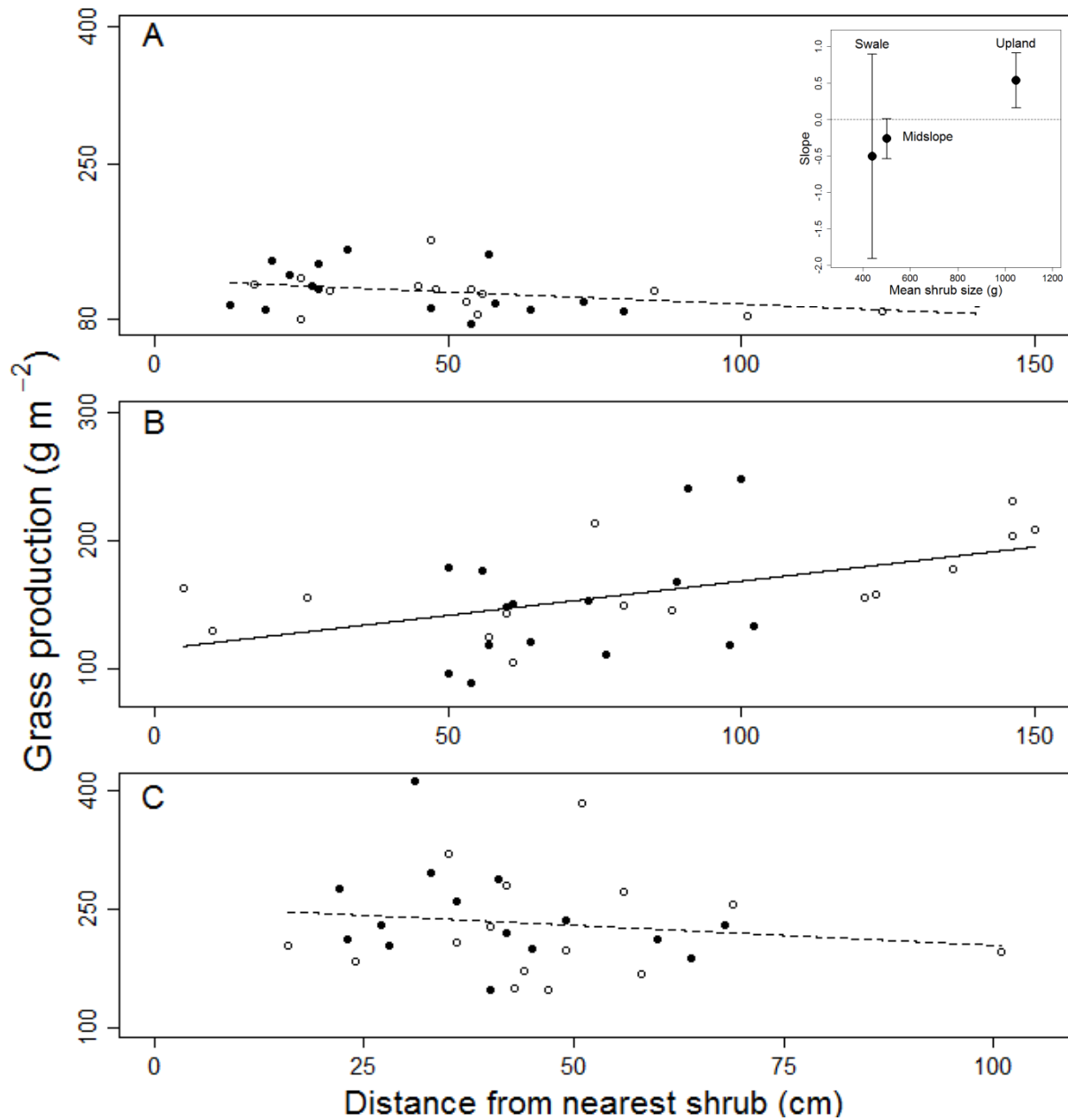


Figure 3.4. Grass production as a function of distance from the nearest shrub or shrub stump in the presence (solid circles) and absence (open circles) of shrub competition. The presence or absence of shrubs had no effect on the relationship between grass production and shrub proximity ($P = 0.828$), thus only the site-level regressions are reported here. Regression analyses revealed no significant relationship between distance and herbaceous production in the midslope (A; $P = 0.059$; 10% clay) or swale (C; $P = 0.466$; 47% clay) sites, but a significant positive correlation in the upland site (B; $P=0.007$; adjusted $R^2 = 0.205$; 16% clay). Inset shows slope of the grass production to distance from shrub relationship (A-C) as a function of mean shrub size within each site. The suppressive effect of shrubs on nearby grasses detected in the upland site (B) may be attributable to increased shrub size (i.e. increased competition for resources) in this site.

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Chapter 4: Investigating mechanisms of tree-grass interactions in West African savannas

Summary

The stress gradient hypothesis (SGH) predicts an increasing importance of facilitative interactions among neighboring plants with increasing levels of environmental stress. Trends at continental to global scales suggest that interactions among woody and herbaceous species in savannas generally conform to the predictions of the SGH, but little is known on the mechanisms driving observed patterns. Here we report results from a neighbor removal experiment at five sites situated along a rainfall gradient in Mali, West Africa. At each site, we measured aboveground production and soil moisture, nutrient and light availability in the presence and absence of neighbors, allowing inferences into the relative importance of abiotic factors in determining net outcomes of tree-grass interactions. We found evidence that the net effect of trees on subcanopy grasses shifts from positive to negative with increasing mean annual rainfall (i.e. decreasing water stress), consistent with the predictions of the SGH. Linear mixed effects models revealed that the amount of light reaching the herbaceous layer and the distance to the nearest tree bole best explained site-level subcanopy grass production. Grass presence did not affect woody growth over the course of one growing season in any of the sites. Our results suggest that regional climate and light availability strongly influence the net outcomes of plant interactions in savannas, with important implications for the management of ecosystem services critical for local communities. Further work is needed to improve our understanding of the complex interactions among plants and the abiotic environment along stress gradients in savannas, particularly with regards to the influence of soil moisture on observed patterns of production in the landscape.

4.1 Introduction

The integration of both positive and negative interactions among neighbors into plant coexistence theory has advanced our understanding of plant community assembly (Bruno et al. 2003; Lortie et al. 2004; Callaway 2007; Brooker et al. 2008). Once thought to be of minimal importance, positive interactions among life forms are now recognized as pervasive components of ecological systems. A surge of empirical investigations over the last two decades has identified facilitative processes in plant communities and enabled the development of theory that predicts the intensity and relative importance of positive interactions based on ecosystem properties. In particular, the stress gradient hypothesis (SGH) predicts an increasing importance of facilitation along gradients of increasing stress (Bertness and Callaway 1994). Species compete for limiting resources at all points along an environmental gradient, but alleviation from stressful abiotic conditions may be more important for plant survival than resource acquisition under conditions of high stress. Accordingly, the SGH predicts that resource competition dominates plant interactions in benign ecosystems, whereas beneficial modification of the abiotic environment by neighboring plants is more important for plant fitness when stress is high.

Recent reviews of empirical studies demonstrate broad support for SGH predictions across ecosystems and types of stress gradients (Lortie and Callaway 2006; He et al. 2013), including tree effects on grasses along a mean annual precipitation gradient in savannas (Dohn et al. 2013). However, some recent work also questions the generality of the SGH (Maestre et al. 2009, Holmgren and Scheffer 2010, Michalet et al. 2014), prompting a call for studies that experimentally quantify plant responses in the presence and absence of competitors at multiple levels along a stress gradient (He and Bertness 2014). Field experiments that rigorously test the predictions of the SGH will contribute to refining general predictions of plant responses given

distinct ecosystem properties, and will also enable the identification of ecosystem- and stressor-specific mechanisms driving outcomes of plant interactions along stress gradients. The latter consideration is crucial for the precision and efficacy of models built on SGH principles.

In savannas, multiple beneficial processes proffered by trees offset competition for resources to varying degrees, resulting in a net effect of trees on subcanopy grass production that varies predictably with mean annual rainfall at regional to continental scales (Dohn et al. 2013). Trees increase soil nutrient concentrations through litterfall (Belsky et al. 1989; Dijkstra et al. 2006) and dung deposits from grazers seeking shade and high quality forage (Belsky 1992; Ludwig et al. 2008). Trees may also increase subcanopy soil moisture through reduced evapotranspiration rates (Frost and McDougald 1989; Breshears 1997; Breshears et al. 1998; Caylor et al. 2005) and hydraulic redistribution of water by tree roots from deep soil layers or inter-canopy patches to layers accessible by subcanopy grasses (Scholz et al. 2002; Ludwig et al. 2004; Scott et al. 2008). Empirical evidence from savanna systems suggests these processes are widespread, but their relative importance in determining the net effect of trees on grass production along water-stress gradients remains largely unknown.

It is plausible that reciprocal effects of grasses on tree growth are also important components of savanna ecosystems, insofar as grasses may modify the abiotic environment of trees through competition for belowground resources or hydrological effects on rates of infiltration and runoff. However, relative to studies examining the effects of trees on grasses, very little work has focused on the influence of herbaceous biomass on tree growth, particularly for mature trees that have progressed past the seedling stage. The few existing studies suggest that negative (Knoop and Walker 1985; Stuart-Hill and Tainton 1989; Riginos 2009; Volder et al. 2013), neutral (Knoop and Walker 1985; J. Dohn unpublished data) and positive (Maestre et

al. 2003; Riginos and Young 2007; Volder et al. 2013; Wan et al. 2014) effects of understory plants on the growth of overstory species are possible. To date, there is no consensus on the magnitude of grass effects on woody growth in general, much less an understanding of shifts in grass-on-tree effects along environmental gradients.

In this study, we investigated interactions between trees and grasses at five sites along a rainfall gradient in Mali, West Africa (Fig. 4.1). Mean annual rainfall at our sites ranges from 448 mm yr⁻¹ to 1132 mm yr⁻¹, representing a shift from highly water-stressed, semi-arid savannas to mesic environments. At each site, we experimentally removed trees and grasses from plots within herbivore exclosures to study growth in the absence and presence of the other life form. We also measured soil moisture, nutrient and light availability in ambient and neighbor-removal plots to study shifts in microclimate associated with neighbor presence, allowing inferences of driving mechanisms behind observed net outcomes of tree-grass interactions. Thus, our objectives were to 1) evaluate the effect of trees on growth of grasses along a water-stress gradient with respect to SGH predictions, 2) quantify effects of grasses on tree growth along the gradient, and 3) assess the relative importance of abiotic factors in determining observed trends in primary production.

4.2 Methods

4.2.1 Study area

The study was conducted at five long-term research sites located in Mali, West Africa established under a broad-scale ecological research project entitled the Sahelian Savanna Disturbance Experiment (SSDE; Table 1). The SSDE sites are situated along a north-south mean annual precipitation (MAP) gradient ranging from 448 mm yr⁻¹ in the northernmost site to 1132

mm yr⁻¹ in the south. For the purposes of this study, sites are labeled A through E corresponding with decreasing MAP (i.e. Site A is the southernmost, wettest site). Rainfall estimates were derived from bilinear interpolation of high-resolution gridded datasets assembled by the University of East Anglia's Climate Research Unit (Harris et al. 2014) and represent averages of annual rainfall amounts from 1980-2011. Efforts were made to minimize edaphic differences among sites by selecting for sandy-loam soils; however, due to unavoidable shifts in soil type associated with broad climatic differences between sites, sand contents differ among sites (Table 1). All data collection occurred within herbivore enclosure fences erected as part of the broader SSDE project design. Field work occurred during the growing season of 2011, with initial plot setup in June and final data collection in September, approximating the onset and conclusion of the rainy season in Mali.

4.2.2 *Experimental design & data collection*

To test for the effects of neighbors on plant growth, we performed tree and grass removal experiments at each site to measure growth of each life form in isolation compared to growth in ambient tree-grass mixtures. In two 625 m² (25 x 25 m) plots at opposite corners of 4 ha herbivore enclosures we removed all trees at ground level to simulate open grassland conditions. In plots adjacent to the tree removal plots we removed all herbaceous vegetation from 625 m² plots and selected twenty trees of the dominant species (see Table 4.1 for species chosen) to study tree growth and soil moisture dynamics in the absence of grasses. Hereafter we refer to these treatments as “tree removal” and “grass removal”, respectively. Twenty trees within each site were then selected from the remaining population of the dominant species growing with grasses within the enclosures to serve as controls. In the two arid, northern sites, low tree

abundance limited available sample sizes to 15 trees for control and experimental groups. In the northernmost Site E, two tree species of high relative abundance were required to reach the requisite 15 individuals within sub-plots due to very low woody cover (Table 4.1). Grass removal and tree removal treatments were maintained throughout the growing season by local site managers. Soil moisture and light availability sampling, described in detail below, occurred intermittently throughout the growing season. Grass biomass, soil and leaf nutrient concentrations and changes in tree circumference were measured at the end of the growing season. Since tree impacts on grass growth and resource availability likely vary with proximity to individual trees, we measured responses on transects away from selected trees. However, because transects away from individual stems in sites with higher tree density would generally approach another stem before being fully away from the focal stem, the tree removal plots provide the ‘no-tree-effect’ end-point for those transects. Measurement points along transects were a function of individual tree canopy size, taken at 25%, 75% and 125% canopy radius originating at tree bole. Samples taken in ‘tree removal’ plots were replicated randomly throughout each 625 m² sub-plot.

4.2.3 *Light: Plant canopy analyzer*

The amount of light reaching the herbaceous layer under tree canopies was estimated by measuring diffuse non-interceptance (DIFN), a measure of the fraction of visible sky, using a LAI 2000 Plant Canopy Analyzer (PCA; Li-Cor, Lincoln, NE, USA). Measurements were taken at each transect point away from experimental trees and in open-grassland areas (tree removal plots), providing measurements of light above and below canopies. Because tree leaf area index was assumed to be relatively constant throughout the growing season, light measurements taken throughout the growing season were treated as replicates and averaged to create one estimate of

light interceptance for each tree transect location. Replicates for each tree were taken at opposite cardinal directions from tree boles, generating a seasonal index for light availability to the herbaceous layer. DIFN values range from 0 (zero visible sky) to 1 (zero sky obstruction).

4.2.4 *Soil moisture: TDR moisture meter*

We estimated soil moisture availability by measuring soil volumetric water content (VWC) with a FieldScout TDR 300 Soil Moisture Meter (Spectrum Technologies, Aurora, IL, USA). Soil VWC measurements were taken three times over the course of the study, roughly corresponding with the beginning, middle and end of the growing season. During each sampling event, a minimum of two replicates at opposite cardinal directions from tree boles were taken at each point (25%, 75% and 125%) along transects for all study trees, including control (i.e. trees with herbaceous vegetation present) and grass removal plots. A minimum of 30 measurements were also taken in tree removal plots, replicated randomly throughout each sub-plot. Soil moisture was measured using 20 cm TDR probes, thus providing an average for the 0-20 cm soil layer, representing water availability in soil layers with high herbaceous root densities.

4.2.5 *Soil nitrogen: Ion exchange resin bags*

To estimate plant available nitrogen (N), we buried ion exchange resin bags at the beginning of the growing season. Bags were prepared using mixed-bed ion exchange resin beads encased in nylon stockings. Due to budgetary constraints, we sampled soil N on ten control tree transects (with herbaceous vegetation) and at 10 randomly selected locations in the tree removal plots in three of the five sites, representing the extremes and middle of the rainfall gradient (sites A, C and E). Resin bags were buried at a depth of 20 cm for consistency with maximum soil moisture

sampling depth. The bags were removed at the end of the growing season and the resin was extracted with 100 mL of 1M KCl. Samples were analyzed for ammonium and nitrate concentrations in an Autoanalyzer at the Natural Resource Ecology Laboratory at Colorado State University. All resin bag analysis procedures followed the laboratory protocol described by Binkley and Matson (1983).

4.2.6 Plant leaf nitrogen concentration

We collected grass samples at each point along the transects relative to 10 control trees and 10 samples from open grassland plots. Samples were dried and analyzed for nitrogen concentrations in the laboratory using a Carlo Ebra NA1500 elemental analyzer (C. E. Elantech, Milan, Italy).

4.2.7 Plant growth

We measured grass aboveground net primary productivity (ANPP) by cutting and weighing aboveground herbaceous biomass from 0.25 m² quadrats at the end of the growing season on two transects north and south from sample trees and at 40 locations in the tree removal plots. Fresh weights were measured in the field and samples specific to each sub-plot were returned to the laboratory for use in calculating dry weights.

To estimate tree growth in the presence and absence of grasses, we placed dendrometer bands on all study trees at the beginning of the growing season. Dendrometer bands are a frequently used tool to measure tree circumference growth and are valued for low maintenance and operating costs and utility for repeated measurements over long time periods (Keeland and Sharitz 1993). Custom bands were made using 1.25 cm stainless steel embossing

tape (DYMO Corporation, Stamford, CT, USA) and stainless steel extension springs (Lee Spring, Brooklyn, NY, USA) following protocol described by Keeland and Young (2014). Bands were placed at 1m height, or directly below occurrences of major stem branching. In instances where stem branching was unavoidable, bands were placed on all major stems at 1 m height. Stem circumference increments were recorded at the end of the growing season and used to represent tree growth in analyses below.

4.2.8 *Data analysis*

To quantify the effect of trees on grass growth at each site along the rainfall gradient, we calculated normalized tree effect ratios (y) comparing mean grass growth under tree canopies (s ; averages of measurements taken at 25% and 75% canopy radius) to mean grass growth in open grassland areas (g ; tree removal plots), where $y = (s - g)/(s + g)$. Because open grassland measurements were not experimentally linked with specific tree transects, averages of grass biomass from each 25 m² subplot were used to calculate y , resulting in two replicates per site (rainfall level). This formulation of tree effects on grass growth follows that of a meta-analysis performed by Dohn et al. (2013), allowing direct comparison between grass production trends along the SSDE rainfall gradient to those observed across global savannas.

4.2.9 *Generalized linear models*

Linear regression analyses investigating the relationships among abiotic factors and plant growth were performed using generalized least squares (GLS) and generalized linear mixed models (GLMM). Mixed effects models account for correlation among observations stemming

from temporally or spatially replicated datasets. The random effects structure in mixed models allowed us to identify variation in the dataset attributable to repeated measures and grouping structures in the sampling design, and to calculate unbiased linear predictors for fixed effects. A qualitative factor identifying individual trees (treeID) was included as a random effect for all models with measurements taken along tree transects to account for lack of independence among observations within transects. Models with soil moisture as the response variable included an additional random effect accounting for timing of data collection (i.e. early, mid or late season sampling).

Model assumptions of normality and homogeneity were evaluated by visual inspection of model residuals; initial model fits indicated a violation of homogeneity. Generalized linear models account for heterogeneous data through explicit modeling of variance components. In the context of this study, variance in response variables and predictors differed substantially among sites. Site was thus included as a variance covariate in all linear regression analyses. Models including soil moisture factors further required a variance structure accounting for heterogeneity among temporal replicates.

After accounting for random effects and unequal variances, models were evaluated for parsimony by stepwise deletion of parameters based on Akaike's Information Criterion (AIC). Reduced models were further evaluated by likelihood ratio tests on model variants excluding predictors one a time, thus generating probability values for individual model parameters. All models were fit using the *nlme* package in R version 3.0.2 (Pinheiro et al. 2013; R Core Team 2013). Variance structures were modeled with *varIdent* (site-level variance) and *varPower* (variance due to temporal replication) in *nlme*, chosen based on likelihood ratio tests on model variants differing in the form of the variance structure. Models were initially fit using maximum

likelihood estimation to allow for model comparison by likelihood ratio tests. Final model coefficients were estimated using restricted maximum likelihood estimation. Tukey's HSD post-hoc analyses were conducted to detect differences among groups using the *lsmeans* package in R (Lenth 2014). Model fit was estimated using a measure of goodness of fit (R^2) developed for linear mixed models (Nakagawa and Schielzeth 2013).

4.2.10 Modeling savanna plant-environment dynamics

We used GLMMs to model the effects of distance to the nearest tree (i.e. tree transect location) and rainfall (i.e. site) on abiotic response variables: soil moisture, soil N availability and leaf N concentrations. For each of these models, open grassland measurements were given a unique treeID in accordance with the random effects structure and assigned a distance of 225% canopy radius, the minimum distance at which open grassland sampling occurred relative to trees in areas adjacent to tree removal plots. Light availability was similarly modeled but lacked an open grassland (225% canopy radius) component because canopy interceptance values along tree transects were relative to measurements taken in open grassland regions (i.e. tree removal plots had uniform DIFN values of 1.0).

The above analyses were then combined into one multivariate GLMM aimed at examining the relative influence of light and soil moisture in determining the effect of tree canopies on grass production at each rainfall level. Because soil moisture measurements were replicated randomly throughout tree removal plots (i.e. not directly linked with specific biomass samples), open grassland data were omitted from this model. Open grassland production estimates were instead included in a subsequent GLMM for the effects of light availability on grass production. Soil N availability and plant leaf N concentrations were also excluded from this model because of large

differences in available sample size and experimental design. An analysis of a subset of the data coinciding with available soil N measurements revealed no effect of soil N on grass production (results not shown). Final model coefficients following model reduction are presented in standardized and unstandardized forms. Scaling continuous predictors (i.e. subtracting factor mean and dividing by standard deviation) allows for comparisons between model parameters in the presence of interactions, thereby providing an approximation of effect size in the units of standard deviations (Shielzeth 2010).

Finally, we used a GLS model to assess the impact of grass presence on tree growth and a GLMM to examine grass effects on soil moisture. A random effects structure (treeID) was not needed in analyzing tree circumference increments due to data independence (i.e. one measurement per tree, no temporal replication). Soil moisture in the presence (control plots) and absence (grass removal plots) of grasses was evaluated as a function of distance to trees and rainfall.

4.3 Results

4.3.1 Light

Light availability increased (i.e. decreased light interceptance by canopy foliage) with increasing distance to the nearest tree and decreasing mean annual rainfall ($P < 0.0001$; GLMM; Fig. 4.2A). Average light availability differed significantly for all pairwise comparisons of sites ($P < 0.05$), except between the two driest sites (D & E; $P = 0.991$) and between two of the relatively mesic sites (A & C; $P = 0.623$; Tukey's HSD). Larger slopes for light availability regressions found in the arid sites likely reflect differences in light interceptance attributable to leaf density within the canopies of small trees (drier sites) relative to larger trees (wetter sites)

and lower density of trees in drier sites, resulting in negligible shading effects by neighboring trees.

4.3.2 *Soil moisture*

Annual rainfall had a strong positive effect on soil VWC ($P < 0.0001$; GLMM; Fig. 4.2B). Average VWC differed significantly for pairwise comparisons between all sites ($P < 0.0001$), except between the two arid sites D and E ($P = 0.994$), and between two of the relatively mesic sites (C & A; $P = 0.931$; Tukey's HSD), matching site-level pairwise differences detected in the light availability analysis. The distance-to-tree main effect and its interaction with rainfall both had weak but marginally significant effects on soil VWC ($P = 0.068$ and $P = 0.058$ respectively), suggesting that the effects of trees on subcanopy soil water availability depend on regional climatic factors. Indeed, site-level regressions suggest increasing soil moisture with distance from trees in arid regions (sites D and E) and an opposite tree-distance effect in mesic sites (A, B and C), though only the negative slope for Site B was significant ($P = 0.035$; Table 4.2).

4.3.3 *Available nitrogen*

Generalized linear mixed effects analyses revealed significant site ($P = 0.0019$) and distance-from-tree ($P < 0.0001$) effects on soil nitrogen availability (Fig. 4.3A; Table 4.2). Soil N was higher in Site E than in Site C ($P = 0.036$), which in turn was higher than Site A ($P = 0.042$; Tukey's HSD), indicating higher nutrient availability with decreasing MAP. The observed differences were largely driven by a substantial increase in soil N directly beneath trees (25% canopy radius) in Site E.

Generalized linear mixed effects analyses on grass leaf nitrogen concentrations found rainfall and distance effects consistent with soil nitrogen results, i.e. increasing N with decreasing MAP and increasing distance to trees ($P = 0.002$ and $P = 0.0001$, respectively; Fig. 4.3B). In particular, grass leaf N was higher in the driest site (E) than in the other four sites ($P < 0.0001$; Tukey's HSD).

4.3.4 *Tree effects on grass production*

The normalized ratio of sub-canopy to open grassland grass production decreased with increasing rainfall ($P < 0.0001$, $R^2 = 0.427$; Fig. 4.4). The observed switch from a net-positive tree effect ratio in arid regions to a negative ratio in the three mesic sites indicates increased facilitation in dry regions, consistent with the predictions of the SGH. Patterns found along the rainfall gradient at SSDE sites are generally consistent with those observed for tropical savannas on coarse-textured soils in a meta-analysis by Dohn et al. (2013).

To assess the relative influence of soil moisture and light availability in shaping observed effects of tree canopy and rainfall on grass production, we tested a GLMM with distance to the nearest tree, growing season rainfall, sub-canopy DIFN and soil VWC as fixed effects. Beginning with a maximal model that included the four main effects and all possible interactions, model evaluation by AIC selection resulted in the removal of the four-way and all three-way interactions. Remaining model structure was evaluated for parsimony by likelihood ratio tests on model variants with and without each predictor ("leave-one-out" model selection, $\alpha = 0.05$; Table 4.3, higher-order interactions were not significant and are not shown). The final model included distance to trees, rainfall and light as main effects, as well as rainfall x distance and rainfall x light interaction terms ($R^2 = 0.277$). Standardized coefficient estimates presented in

Table 4.3 provide approximate effect sizes of model parameters; unstandardized coefficients estimate effect on grass biomass in the original units of the respective predictor.

Notably, soil moisture and all related interaction terms were removed during model evaluation, suggesting a primary influence of light availability, mediated by canopy characteristics and regional climate, on grass growth. In general, light had a strong positive effect on biomass production, particularly in wet systems. Grass biomass also increased with increasing distance to the nearest tree, particularly in high rainfall sites, evidenced by a strong positive rainfall x distance interaction term. The final model retained distance as a main effect and in an interaction with rainfall, suggesting either that 1) tree canopies influence grass production through mechanisms unrelated to effects on light and water availability, or 2) our measurements of sub-canopy resource availability inadequately captured temporal and spatial fluctuations in plant-available resources. Given the model output, the latter consideration seems particularly likely for the highly light-limited environments typical of mesic savannas. We found a substantial suppressive effect of rainfall on grass biomass, most plausibly linked with lower average light availability associated with high woody cover and densely-foliated crowns in wet regions. However, examination of the rainfall : distance and rainfall : light interaction terms (Table 4.3) suggests that distance effects are particularly strong at high rainfalls, while light effects are comparatively diminished. Thus, trees do indeed appear to significantly impact grass growth in mesic sites, although we cannot affirmatively attribute canopy shading effects as the primary mechanism in this analysis.

Site-level regressions further investigating the mechanistic link between light availability and grass productivity are shown in Fig. 4.5, including open-grassland measurements (excluded from multi-factorial GLMM described above due to differences in sampling design between tree

transects and tree-removal plots). We found a significant decrease in biomass in Site D (583 mm MAP) with increasing sub-canopy light ($P < 0.0001$), and no correlation in Site E (448 mm MAP; $P = 0.560$). The three mesic sites showed significant increases in grass production with light availability ($P < 0.0001$), further emphasizing the interactions among climate, light and distance to trees observed in the multi-factorial model.

4.3.5 *Grass effects on tree growth*

The presence of grasses had no significant effect on tree circumference growth over one growing season ($P = 0.170$; generalized least squares model; Fig. 4.6). Average tree growth was higher in Site B than in the three driest sites ($P < 0.05$; Tukey's HSD). We expected grass presence to affect tree growth through hydrological impacts on surface runoff and belowground water availability. However, the presence of grasses had no effect on soil VWC at 20 cm across all sites ($P = 0.769$; GLMM; results not shown).

4.4 Discussion

We found evidence that the net effect of trees on grasses shifted from positive to negative with increasing mean annual rainfall, consistent with findings at global scales within savannas (Dohn et al. 2013) and, more broadly, with prevailing theory predicting the response of neighboring organisms to abiotic stress gradients (Bertness and Callaway 1994; Brooker et al. 2008). While empirical evidence supporting general SGH predictions is extensive (He et al. 2013; He and Bertness 2014), it is evident that the mechanisms that generate observed patterns are unique to specific ecosystems and the nature of the stress gradient (Maestre et al. 2009; He et al. 2013). The functionality and predictive value of vegetation models built on SGH principles

therefore depends on understanding the interplay of species interactions and the abiotic environment. With this study, we aimed to improve our understanding of drivers of savanna tree-grass responses to environmental stress through quantification of plant available resources and plant growth in the presence and absence of neighbors along a water stress gradient.

Of the factors examined in this study, we found that the amount of light reaching the herbaceous layer and the distance to the nearest tree bole best explained site-level subcanopy grass production. Surprisingly, we found no effect of tree canopies on soil moisture in the top 20 cm, and, correspondingly, no correlation between plant-available water and grass production. Strong light limitation observed in wet savannas, coupled with the neutral or negative response to light in arid savannas, suggests a fundamental shift in the primary resource limiting grass growth along the climatic gradient. It is unlikely that photoinhibition of photosynthetic pathways contributed directly to the negative impacts of light on grasses in arid savannas given the preference of C₄ plants for high light conditions in warm climates (Ehleringer 1978; Long 1999). Furthermore, higher plant available nitrogen in the soil under trees did not consistently correspond with an increase in herbaceous growth, suggesting nitrogen was not a primary limiting resource to plant growth. We propose that these findings strongly point to a growth response to differences in plant available water along tree transects at the dry end of the gradient, despite our inability to measure these effects empirically in this study. Our soil moisture measurements represent snapshots in time of the hydrological properties of the soil. Soil VWC at a given point in time is a function of numerous interacting factors, including time since last precipitation event, evapotranspiration rates as influenced by temperature and relative humidity, spatial variability of vegetation and throughfall, and physical properties of the soil affecting pore size and drainage rates (Breshears et al. 1997; Huxman et al. 2005; Holdo and Mack 2014; Zhu

et al. 2014). Accordingly, soil water content varies markedly at fine scales through time and space. We sought to overcome a highly heterogeneous soil layer and the variable nature of soil moisture measurements through large sample sizes and repeated measurements over the course of the growing season. Our results highlight the need for continuous monitoring of soil hydrology prior to and following rain events to study the differential responses of grasses beneath tree canopies and in open grassland to water inputs.

Gauging soil moisture availability may additionally be complicated by feedbacks with grass standing biomass and resource uptake rates. Soil patches with high moisture due to soil hydraulic properties and/or overhead canopy effects likely augment herbaceous production, leading to increased root density and plant transpiration rates. Thus, while water availability may be higher following a rain event in a grass-dominated patch, rapid depletion of upper soil layers may lead to decreased soil water availability over time relative to bare or sparsely-vegetated patches, especially late in the growing season when standing biomass is high. However, we detected no effect of grass presence on soil moisture, suggesting production-transpiration feedbacks were likely not the primary mechanism generating observed patterns of soil moisture.

We found some evidence of a canopy enrichment effect on nitrogen in our analyses of soil N availability and grass leaf N concentrations, though there was a high degree of variability along tree transects and among sites, likely due to low sample sizes. Previous studies have shown nutrient enrichment of subcanopy soils and grasses is fairly ubiquitous for savanna trees (see Dohn et al. 2013 for a review). However, the effects of higher nutrient availability on herbaceous production likely depend on regional bioclimatic factors. For example, increased soil N is likely to have a large effect on biomass accumulation when other resources are bountiful, such as in patches further from tree boles (high light) in mesic sites (high soil moisture). In addition to

increasing production, higher N availability can lead to increases in forage quality, with implications for the distribution and abundance of herbivores throughout the landscape (Belsky 1992; Ludwig et al. 2008).

In addition to elucidating mechanisms driving tree effects on grasses, we also sought to quantify grass effects on tree growth. We did not detect any effect of grass presence on tree circumference increments, suggesting either that facilitative effects of increased water infiltration and increased competition for resources in the presence of grasses offset, or that grasses have negligible effects on plant-available resources for adult trees in these systems. It is also plausible that grasses do indeed influence tree growth by way of altering water infiltration and resource availability, but these effects may be too small to detect over the course of one growing season for large, slow-growing trees. Furthermore, dendrometer bands installed at the beginning of the growing season may require time to uniformly align with tree stems, increasing variability for first-year measurements (Keeland and Sharitz 1993). Further monitoring of tree growth in the absence and presence of grasses is needed to draw general conclusions on the magnitude of grass effects on woody growth.

4.4.1 Conclusions

In a controlled experiment replicated along a savanna rainfall gradient, we observed suppression of grass growth beneath tree canopies in sites with high mean annual precipitation, but an opposite trend (i.e. net facilitative effects of canopies on herbaceous production) in arid sites. We observed no effect of grasses on woody growth. We also measured abiotic variables in direct proximity to biomass sampling sites to better understand the underlying mechanisms driving tree-grass interactions along the rainfall gradient. Light availability and distance to tree

boles were closely linked with grass growth, but we found no effect of soil moisture, despite circumstantial evidence that plant-available water is likely important in determining observed patterns of herbaceous production.

Our results contribute to a growing body of empirical data describing savanna community dynamics and to our understanding of drivers of savanna vegetation structure. Though our understanding of the role of top-down drivers of savanna dynamics has improved substantively in recent years (e.g. Smit et al. 2010; Hoffman et al. 2012; Lehmann et al. 2014), *in situ* data isolating interactions among trees and grasses remains relatively rare, particularly from West Africa (Tagesson et al. 2014). We provide data on ecosystem properties and biotic responses that may be used to refine models that do not explicitly consider interactions among vegetative life forms, or those that utilize simple competition coefficients. Clearly, positive interactions among trees and grasses and complex feedbacks between vegetation, the abiotic template and local climate variables are integral components of savanna ecosystems. From a theoretical standpoint, a robust understanding of the mechanisms that determine the relative distribution and primary productivity of trees and grasses throughout a landscape is critical to predict the response of savanna vegetation to changing climatic regimes, particularly shifts in rainfall amount and seasonality. Within a landscape, knowledge in this regard may help inform managers looking to optimize the yield and sustainability of ecosystem services essential to adjacent populations, namely herbaceous biomass for livestock fodder and woody biomass for fuel. Our results contribute to this understanding, and we hope to stimulate further investigations into mechanisms governing savanna tree-grass interactions along climatic gradients, particularly with respect to relationships among tree canopies, grass production and soil moisture.

4.5 Tables

Table 4.1. Characteristics of study sites situated along a mean annual precipitation gradient* (MAP) in Mali, West Africa.

	Latitude (N)	Longitude (W)	MAP (mm yr ⁻¹)	Study year rainfall (mm)	Soil % sand	Woody cover (%)	Dominant woody species
Site A	11.039	-6.835	1132	1098	60.4	60.3	<i>Deterium microcarpum</i>
Site B	11.612	-7.067	1044	990	36	61.3	<i>Terminalia macroptera</i>
Site C	12.882	-8.477	869	786	39.2	47.5	<i>Combretum glutinosum</i>
Site D	14.549	-9.975	583	637	84.6	12.4	<i>Combretum glutinosum</i>
Site E	15.217	-9.542	448	481	90.4	5.4	<i>Acacia seyal</i> & <i>Balanites aegyptiaca</i>

*MAP values derived from CRU high-resolution gridded datasets (Harris et al. 2014)

Table 4.2. Linear regression coefficients estimating sub-canopy resource availability as a function of distance to the nearest tree (% canopy radius) for 5 sites situated along a rainfall gradient. *P*-values represent probability values for a t-test on slope coefficients; bold values indicate a significant ($P < 0.05$) distance effect.

	Light (% sky visibility)						Soil moisture (% volumetric water content)					N mineralization (nmol N day⁻¹)				
	Intercept			Slope			Intercept		Slope			Intercept		Slope		
	MAP	Estimate	SE	Estimate	SE	<i>P</i>	Estimate	SE	Estimate	SE	<i>P</i>	Estimate	SE	Estimate	SE	<i>P</i>
Site A	1132	29.17	2.92	0.15	0.02	< 0.001	15.42	0.68	-0.004	0.003	0.185	0.04	0.05	-0.0003	0.0004	0.445
Site B	1044	22.44	2.63	0.05	0.01	0.002	19.82	0.59	-0.005	0.003	0.038	NA	NA	NA	NA	NA
Site C	869	22.81	3.11	0.17	0.02	< 0.001	15.15	0.70	-0.003	0.004	0.381	0.12	0.05	-0.0004	0.0004	0.373
Site D	583	28.62	3.73	0.41	0.03	< 0.001	5.37	0.65	0.002	0.002	0.402	NA	NA	NA	NA	NA
Site E	448	27.50	4.90	0.40	0.04	< 0.001	4.87	0.74	0.004	0.003	0.144	0.50	0.06	-0.0028	0.0004	< 0.001

SE = standard error; MAP = mean annual precipitation (Harris et al. 2014)

Table 4.3. Generalized linear mixed model estimating the effects of abiotic factors on herbaceous growth as a function of distance to the nearest tree ($R^2 = 0.xxx$, AIC =). P -values represent probability values for t -tests on model coefficients; P_L represent probability values for model parameters based on likelihood ratio tests on leave-one-out model variants, with associated change in Akaike's Information Criterion (AIC). Parameters with $P_L > 0.05$ (*) were excluded from the final model; main effects contributing to significant interactions were not tested (NT).

	P_L	ΔAIC	Original model		Standardized model			
			Estimate	SE	Estimate	SE	t	P
Distance	NT	NT	-3.436	0.866	7.25	5.62	1.29	0.199
Rainfall	NT	NT	-0.381	0.092	-40.81	12.36	-3.30	0.001
Light	NT	NT	3.704	215.8	31.64	10.30	3.07	0.003
Soil moisture*	0.321	-1.01	-	-	-	-	-	-
Rainfall : Light	0.007	5.24	-0.241	0.250	-11.46	11.90	-0.96	0.337
Rainfall : Distance	0.028	2.84	0.004	0.001	39.33	9.10	4.32	<0.001
Distance : Light*	0.064	1.43	-	-	-	-	-	-
Light : Soil moisture*	0.695	-1.85	-	-	-	-	-	-
Distance : Soil moisture*	0.742	-1.89	-	-	-	-	-	-
Rainfall : Soil moisture*	0.233	-0.58	-	-	-	-	-	-

4.6 Figures

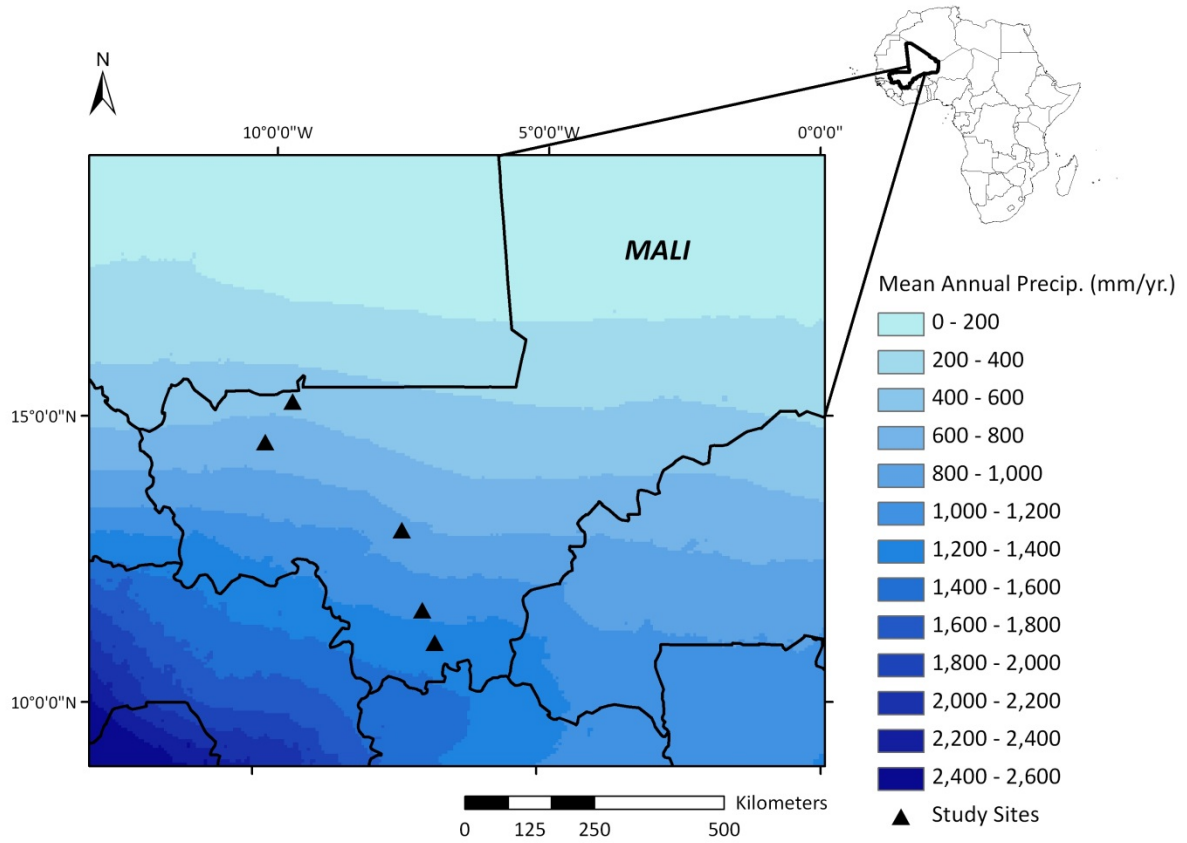


Fig. 4.1. Locations of five experimental sites (triangles) situated along a north-south mean annual rainfall gradient in Mali, West Africa.

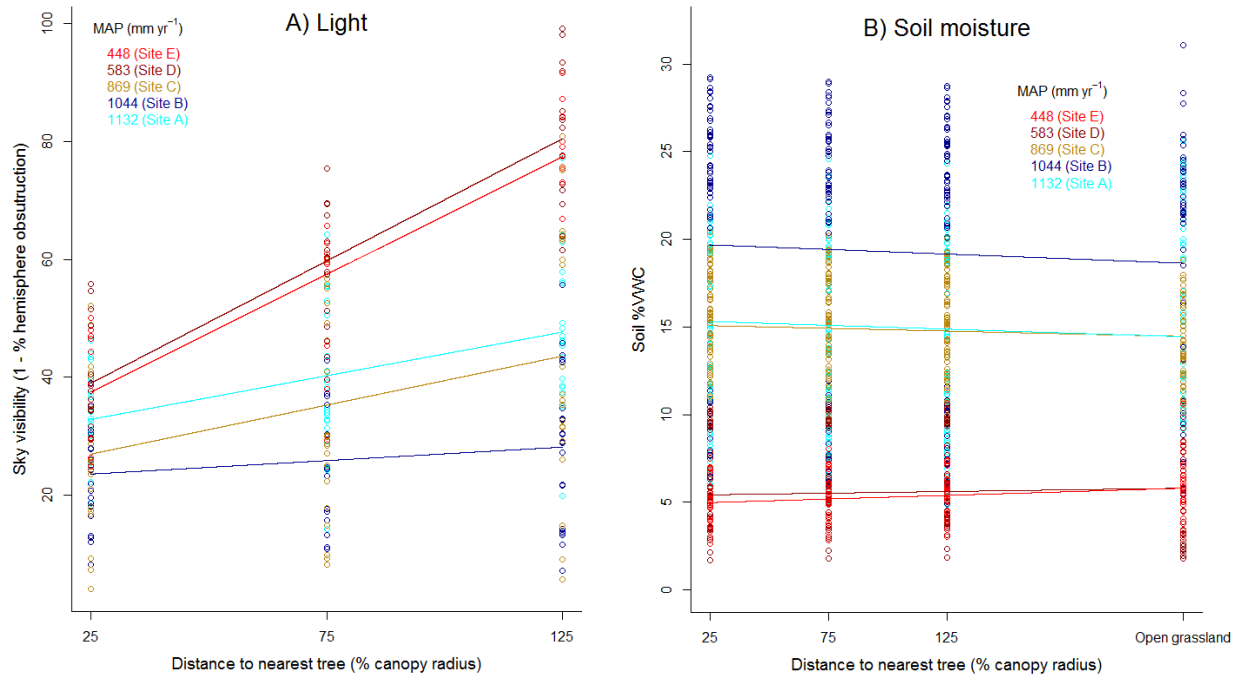


Fig. 4.2. Resource availability as a function of distance to the nearest tree at five sites along a mean annual precipitation (MAP) gradient. A) Light availability estimated by diffuse non-interceptance, a measure of the fraction of sky visible to understory plants. Light propagation to the herbaceous layer increased with distance to trees in all sites ($P < 0.0001$; generalized linear mixed model) but sparse canopies and low tree densities increase light availability in arid relative to mesic savannas. B) Soil volumetric water content (VWC) differs among sites ($P < 0.0001$; GLMM), with a general increase in VWC in mesic savannas. Soil VWC did not differ significantly along tree transects except for a slight decrease with increasing distance from trees in Site B (1044 mm MAP; $P = 0.038$). Rainfall values represent mean annual rainfall since 1980 for each site (Table 1).

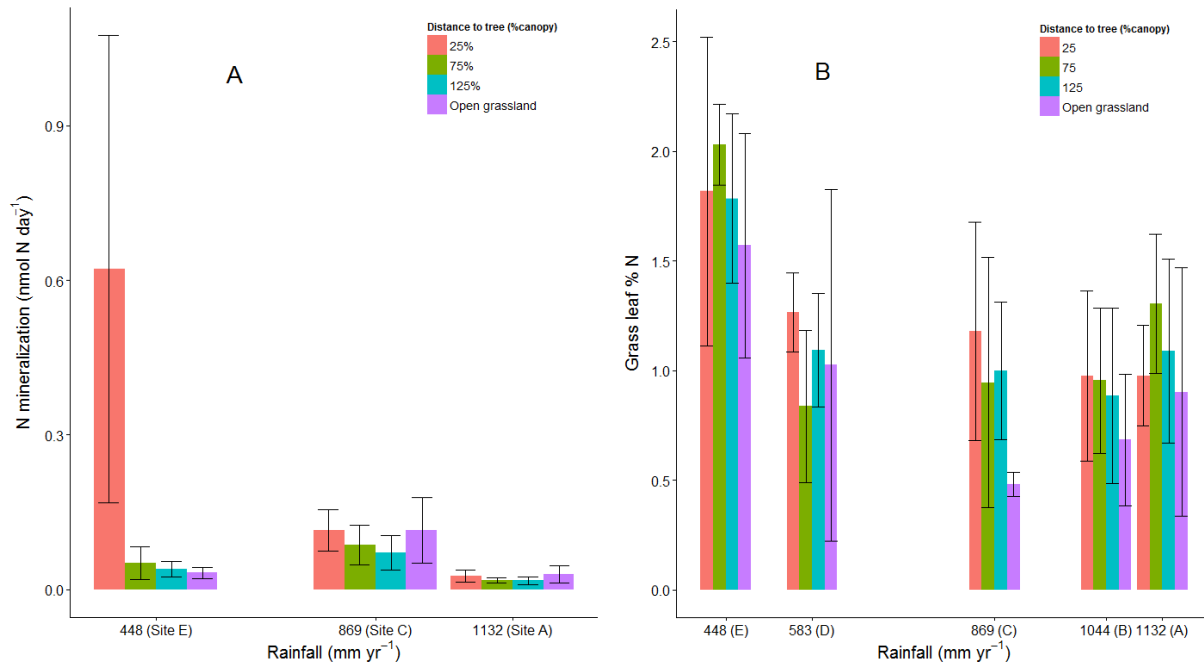


Fig. 4.3. Nitrogen concentrations at sites situated along a mean annual precipitation (MAP) gradient. A) Soil nitrogen mineralization rates estimated using ion exchange resin bags. Soil nitrogen availability was higher beneath tree canopies (25% canopy radius) in the driest site (448 mm mean annual precipitation [MAP]) than at other locations at that site and at all locations in the two relatively mesic sites ($P < 0.0001$; 869 and 1132 mm MAP, respectively). Soil N was higher in the intermediate site than in the wettest site ($P = 0.042$), suggesting a general decline in mean N availability with increasing rainfall. B) Nitrogen concentrations in grass leaves. Grass N declined with increasing distance from trees and with increasing MAP ($P = 0.002$ and $P = 0.0001$, respectively). Specifically, grass N was significantly higher on average in the driest site (300 mm MAP) than in any of the other sites ($P < 0.0001$, Tukey's HSD). Rainfall values represent mean annual rainfall since 1980 for each site (Table 1). Error bars represent 95% confidence intervals of the mean.

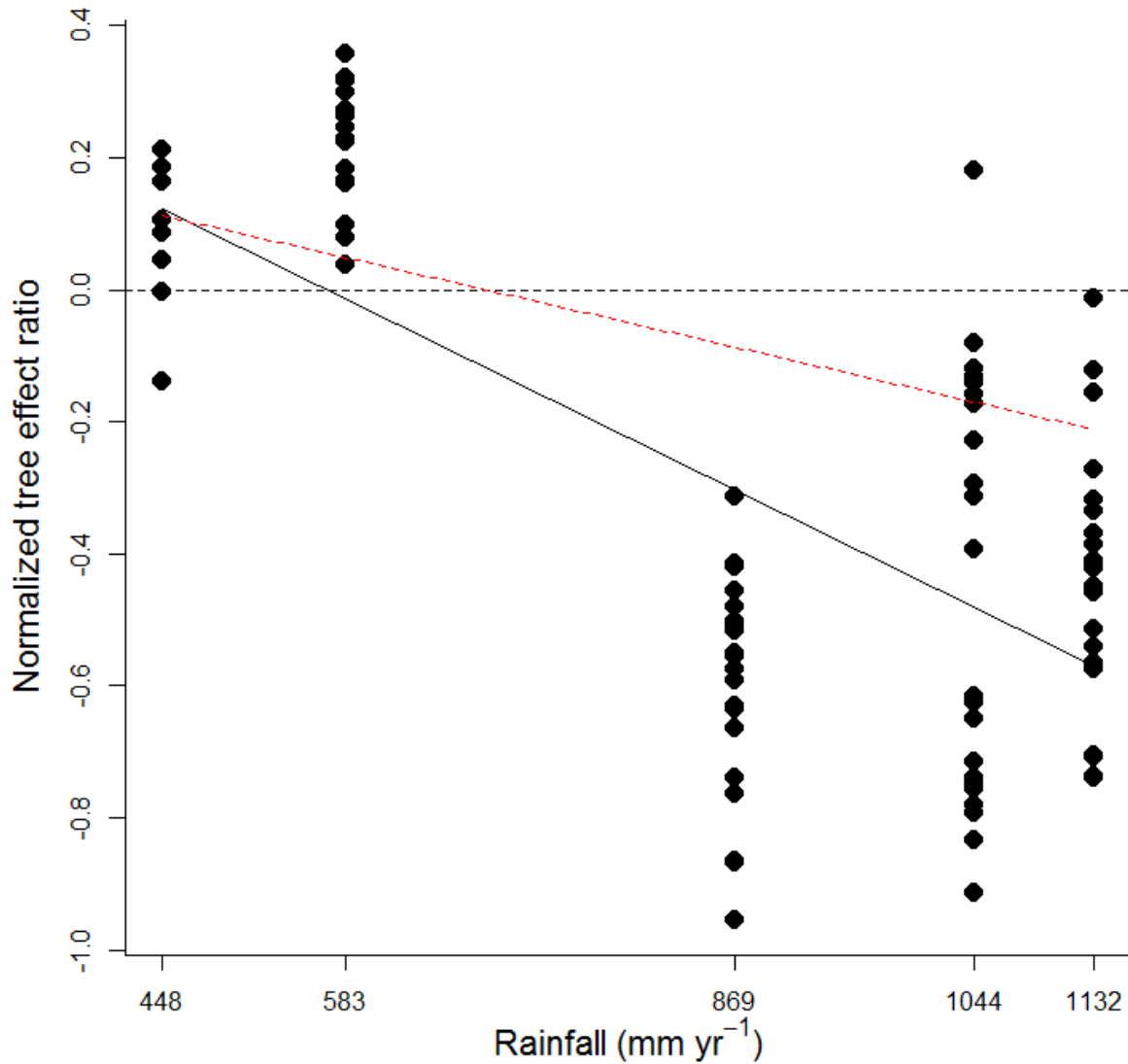


Fig. 4.4. Normalized ratio of subcanopy to open-grassland herbaceous biomass for five sites in Mali, West Africa situated along a gradient of mean annual precipitation. Tree canopies in arid savannas (MAP < 600 mm) enhance sub-canopy grass growth, while in mesic regions trees suppress herbaceous production ($P < 0.0001$, $R^2 = 0.427$). Points represent ratio of subcanopy (mean biomass at 25% and 75% canopy radius) to open-grassland (site-level mean biomass in tree removal plots) grass production. Black line shows regression line for normalized tree effect ratio as a function of MAP for experimental sites used in this study; dotted red line represents regression line from Dohn et al. (2013) for the normalized tree effect ratio of tropical savannas on coarse-textured soils. Rainfall values represent mean annual rainfall since 1980 for each site (Table 1).

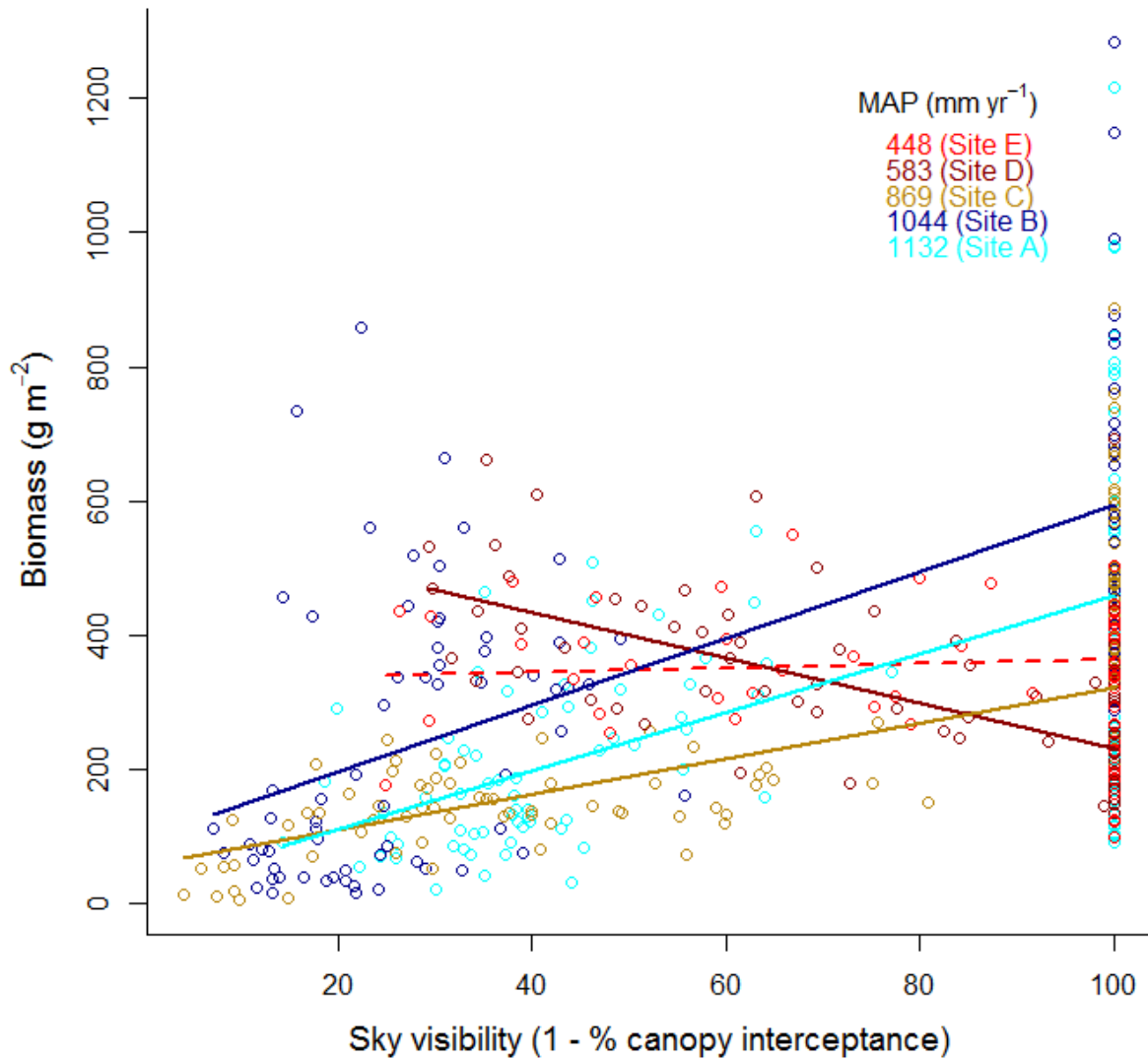


Fig. 4.5. Grass production as a function of sub-canopy light availability at five sites along a mean annual precipitation (MAP) gradient. Light limitation was evident in the three mesic sites ($P < 0.0001$), while in arid regions light had a neutral (Site E, 448 mm MAP; $P = 0.560$, dashed line) or negative effect (Site D, 583 mm MAP; $P < 0.0001$) on grass productivity. Samples taken at 100% sky visibility represent open grassland measurements (i.e. beyond canopy shading effects).

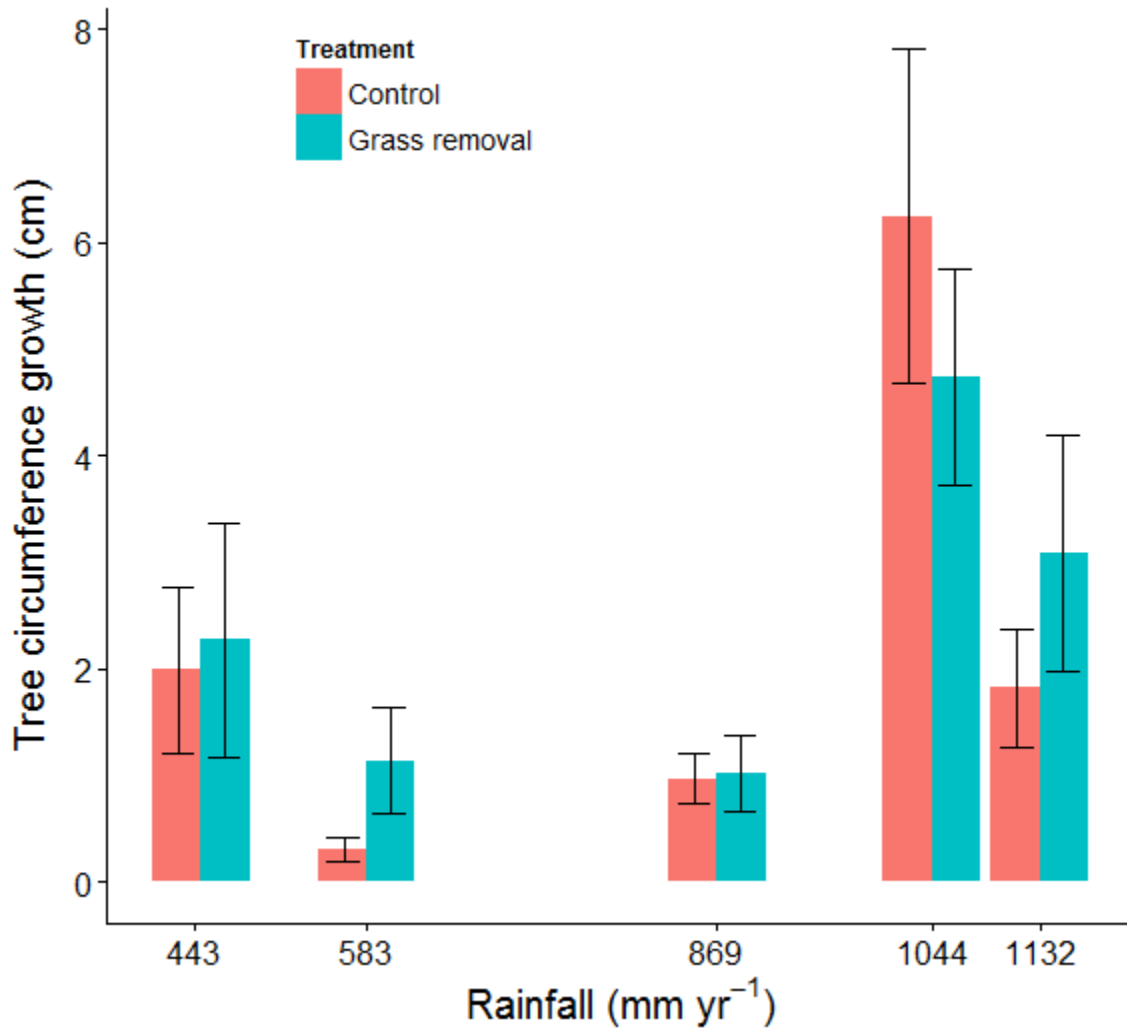


Fig. 4.6. Tree circumference increments over one growing season in the presence and absence of grasses at five sites along a mean annual precipitation gradient. Grass removal had no effect on tree growth ($P = 0.170$). Rainfall values represent mean annual rainfall since 1980 for each site (Harris et al. 2014). Error bars represent ± 1 standard error of the mean.

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Chapter 5: Spatial vegetation patterns and neighborhood competition among woody plants in an East African savanna

Summary

The vast majority of research focusing on plant dynamics in savannas examines tree-grass interactions; interactions among woody species remain relatively poorly understood but may represent a major component of savanna structure and function. Here I present results from an East African savanna estimating tree growth as a function of the size and distance of neighboring woody competitors. In three sites located within fire and herbivore exclosures at Mpala Research Centre in Kenya, we monitored spatially explicit growth patterns of woody vegetation at three time steps over a ten year period. In so doing, we quantified the magnitude of inter-tree competition and inferred its impact on stand spatial structure through spatial point pattern analysis. We found that shrubs suppressed the growth of woody neighbors at a scale of 4 m, despite significant spatial aggregation of shrubs in the landscape. We also observed conspicuous shifts in the dominance hierarchy of woody species over the course of the study, perhaps related to differences in growth rates and competitive abilities associated with divergent responses to herbivore pressure. Our results suggest that competition among woody plants influences production and relative species abundance, but dispersal and establishment bottlenecks are likely more important for landscape-scale spatial structure in this system, particularly in the absence of fire and herbivory.

5.1 Introduction

Discerning the drivers and dynamics of vegetation structure remains a fundamental pursuit of savanna ecology. A clear understanding of the processes that underpin savanna

community assembly is integral to our ability to explain the distribution of global savannas and forecast their response to a changing global climate and highly variable land-use. Recent theoretical advancements have seen the integration of demographic and stochastic processes (i.e. disturbance pressures, primarily fire and herbivory) with plant coexistence and niche theory to explain the persistence of savanna systems in regions where climatic conditions may otherwise support forests or grasslands (Sankaran et al. 2005, Scheiter and Higgins 2007; Bond 2008; Murphy and Bowman 2012; Tredennick et al. In Press). The majority of this research has examined mechanisms governing the coexistence of woody and herbaceous vegetation, a defining characteristic of the savanna biome (e.g. Sankaran et al. 2004, Meyer et al. 2008; van Langevelde et al. 2011). Relatively little work has focused on interactions among woody plants, despite mounting empirical evidence that tree-tree interactions are an important component of savanna structure and functioning (Riginos et al. 2005; Meyer et al. 2008b; Calabrese et al. 2010; Kambatuku et al. 2011; Belay and Moe 2012; Sea and Hanan 2012).

Trees may positively or negatively affect the establishment and growth of woody neighbors. Trees can increase germination and recruitment by improving microsite conditions through litter inputs and decreased subcanopy evapotranspiration rates (O'Connor 1995; Hoffman 1996; Salazar et al. 2012). However, expansive lateral root systems typical of many savanna tree species drive belowground competition for water and nutrients, reducing plant available resources (Belsky 1994; Schenk and Jackson 2002; Sternberg et al. 2004). Plant interactions at individual scales influence landscape-scale productivity and the relative distribution of trees and grasses throughout the landscape (Riginos et al. 2009; Calabrese et al. 2010; Sea and Hanan 2012). For example, strong competition among trees promotes competitive self-thinning through density-dependent mortality and may prompt a tendency towards regularly

spaced stands, a phenomenon well documented in monospecific stands and forested ecosystems (e.g. Laessle 1965; Kenkle 1988; Stoll and Bergius 2005; Wolf 2005). Direct empirical evidence of competition among savanna woody species is comparatively rare (Calabrese et al. 2010), particularly studies evaluating the growth performance of multi-species assemblages. Instead, competition in mixed woody-herbaceous systems has generally been inferred from spatial point pattern analyses of the distribution of woody plants in a landscape, and existing studies report spatial arrangements ranging from highly clumped to dispersed (Smith and Goodman 1987; Skarpe 1991; Couteron and Kokou 1997; Barot et al. 1999; Jeltsch et al. 1999; Caylor et al. 2003; Moustakas et al. 2008, Schleicher et al. 2011; Pillay and Ward 2012; Browning et al. 2014). As such, we have a poor understanding of the degree of woody competition in savannas and its relative importance in shaping vegetation structure.

Distinct spatial patterns consisting of vegetated patches alternating with areas of bare soil have been described for savanna ecosystems worldwide (Aguiar and Sala 1999; Tongway et al. 2001; Franz et al. 2011). Analytical models have shown that surface runoff, local plant density, and water infiltration rates, both by themselves and in concert with each other, can create and maintain the irregular vegetation patterns that typify savanna ecosystems (Klausmeier 1999, HilleRisLambers et al. 2001, Pueyo et al. 2008). Hence, patches of bare soil and plant cover in these systems may largely be an expression of abiotic controls on moisture availability, possibly augmented by positive local interactions among closely-spaced individuals which more effectively hold soil moisture. Where such patterns are generated by the patchy distribution of woody plants, as in our study system, both facilitation and competition may be operating, the former through clusters of shrubs more effectively trapping moisture inputs, and the latter

operating within clusters depending upon shrub density, size class distribution, and species composition.

Although many studies have documented spatial patterns of woody vegetation in savannas, few have quantified the spatial scale and intensity of competitive interactions among woody plants. Furthermore, because fire and herbivory are important drivers of savanna woody cover (Sankaran et al. 2005; Bond 2008; Staver and Bond 2014), general predictions for the role of competition in structuring savannas may require studies examining stand structure in low-disturbance situations (Calabrese et al. 2010). We present data from a 10-year longitudinal study monitoring spatially explicit growth patterns of woody vegetation at three sites in an East African savanna in the absence of fire and herbivory. Our objectives are to assess the magnitude of competition among woody plants in this system, quantify the spatial scale of plant competition and discuss its relative influence in determining landscape-scale woody distribution. We seek to expand upon studies that infer competition intensity and importance from spatial patterns alone by presenting spatial point-pattern analyses of shrub distribution at each site alongside analyses of growth performance in the presence of neighbors. Study plots are located in sites with long-term fire suppression, and herbivores were excluded at the onset of the study. Thus, our study also represents an opportunity to understand spatial patterns of woody vegetation dynamics in the absence of large mammalian herbivores, particularly with respect to shifts in stand spatial structure and implications for competition as a driver of community structure. Finally, we explicitly consider species-specific responses to competition intensity, including effects of conspecific and heterospecific neighbors, in order to make inferences on mechanisms governing woody species diversity.

5.2 Methods

5.2.1 Study area

The study was conducted at the Mpala Research Centre and associated Mpala Ranch (MRC) in north central Laikipia, Kenya (37°53'E, 0°17'N). Study sites were underlain by well-drained, moderate to very deep, friable sandy loams developed from metamorphic basement rocks (Ahn & Geiger 1987) and occurred at elevations of ~1700 m. Long-term mean annual rainfall (1972-2009) for a gauge located near the center of our study area was 514 mm, and for the period 1999 to 2009 averaged 493 mm. However, our 3 study sites were distributed along a precipitation gradient (Augustine 2003), with a gauge located near the most mesic study site recording an average of 593 mm annually during 1999 – 2009. Rainfall in the area typically occurs in a tri-modal fashion with a consistent dry season between January – March, and wet seasons during April-May, August and October. Vegetation in the area is characterized by an *Acacia*-dominated bushland community and a discontinuous layer of perennial grasses (Augustine 2003). The shrub layer is dominated by *A. mellifera*, *A. etbaica*, *A. brevispica* and *Grewia tenax* (Augustine & McNaughton 2004). The herbaceous layer is discontinuous, with the understory of shrub clusters dominated by perennial bunchgrasses and inter-shrub patches consisting of bare soil or patches of stoloniferous grasses (Augustine 2003). Analyses of aerial photos from 1961 and 1969 combined with reports from long-term residents of the district indicate shrub cover has increased over the past half century, reaching an average cover of 28% in north-central Laikipia in 1998 (Augustine 2003).

Herbivore exclosures (70 m x 70 m) were established at each of three study sites at MRC in 1999. Exclosures consisted of a 11-strand, 3-m tall electrified fence with additional mesh and electrified wires from 0 – 0.5m height and excluded large herbivores ranging in size from dik-

diks to elephants (Sankaran et al. 2013). At the time of fence establishment in 1999, we mapped all individual trees and shrubs >0.5 m tall within a 50 m x 50 m area in each exclosure and measured their basal diameter (at 15 cm above ground level, including all stems on multi-stemmed individuals), canopy dimensions (maximum length and width in the cardinal directions) and maximum plant height. Woody plants were censused again in 2002 and 2009, with all shrubs and trees >0.5 m in height mapped and re-measured in terms of basal area, canopy dimensions, and height. Site-level averages of shrub density and size are shown in Table 1.

The dataset includes a number of shrubs with negative growth rates, likely due either to partial death and re-growth of individuals or to changes in stem counts at 15 cm height of multi-stemmed individuals. While these may represent unrealistic estimates of shrub growth over time, we have chosen not to exclude them from the final model because the factors producing these estimates were also likely present on many shrubs with positive values.

5.2.2 *Spatial analysis*

To examine the spatial organization of shrubs within each plot, we implemented the univariate pair correlation function $g(r)$ (Stoyan and Stoyan 1994). The pair correlation function estimates point density within a circular ring at distance r from a representative focal point, normalized by dividing by the intensity of the pattern to facilitate interpretation. Thus, $g(r)$ represents a non-cumulative alternative to the widely used Ripley's K function (Ripley 1976) without the confounding effects of patterns at short distances from the focal point obscuring patterns at longer distances, allowing for a more accurate estimation of the spatial extent of point aggregation or dispersal (Stoyan and Stoyan 1994; Wiegand and Moloney 20013). Pair correlation functions for each site were evaluated relative to a null model of complete spatial

randomness (CSR), which describes a homogenous poisson point process that assumes no interaction among points and constant plot intensity. Under the assumption of CSR, $g(r) = 1$; values of $g(r) > 1$ signify clustered patterns (i.e. increased point density than expected under CSR at distance r), while values of $g(r) < 1$ signify point dispersion. Confidence envelopes for the null model were estimated by extracting the 5th and 95th quantiles from 199 Monte Carlo simulations of CSR, corresponding to a significance level of $\alpha = 0.05$ for a two-tailed test (Wiegand and Moloney 2013). We also computed bootstrap confidence intervals for the true value of the pair correlation functions for each site based on 1000 pointwise simulations (Loh 2008). Homogeneity of plot intensity was evaluated by visual assessment of first-order intensity and the second-order pair correlation and L-functions, as described by Wiegand and Moloney (2013); no significant departures from homogeneity were detected. Spatial analyses were conducted using the R package *spatstat* (Baddeley and Turner 2005) with an isotropic edge correction.

5.2.3 Neighborhood competition model

Shrub growth was estimated using relative growth rate (RGR; y) calculated as a function of basal area in the first (basal area BA_1 at year t_1 ;) and last (basal area BA_2 at year t_2) year in which the individual was recorded, where $y = (\ln BA_2 - \ln BA_1) / (t_2 - t_1)$. To evaluate the effects of neighboring shrubs on focal shrub RGR we used a linear mixed effects regression model. Mixed effects models account for correlation among observations due to grouping structures in the study design, allowing for best linear unbiased predictions without violating the assumption of observation independence (Pinheiro and Bates 2000). Because our study was replicated in three locations, site was included as a random effect in order to avoid confounding the effects of

neighborhood competition with variation attributable to inter-site environmental and biotic heterogeneity. A random effects structure allowing both slope and intercept terms to vary within each site was evaluated with ANOVA-based likelihood tests. A random intercept model (i.e. disregarding random slopes) was found to have the strongest fit. We also included a rational quadratic spatial correlation structure to account for spatial autocorrelation of shrub growth estimates within each site, selected based on model comparison between various forms of correlation structures (Pinheiro and Bates 2000).

The primary objective of the fixed effects structure of the model is to describe the effects of neighboring shrubs on focal shrub RGR. There are two fundamental considerations in characterizing a shrub's competitive neighborhood: the size of the neighborhood (i.e. the distance at which neighbors are considered competitors), and the quantitative summation of the effects of those competitors. We tested a number of model structures to find an optimal method for the latter, the simplest of which sums size of heterospecific and conspecific neighbors within a set radius from focal shrubs. We compared the performance of this model to one utilizing a distance-dependent competition index (CI1):

$$CI1_i = \sum [D_j / (dist_{ij} + 1)], \quad (1)$$

where neighborhood influence on the i th shrub is a function of the size of neighboring shrubs (D_j) and the distance between the neighbor and focal shrub ($dist_{ij}$). Similar indices have been used effectively in previous plant growth studies (e.g. Zhao et al. 2006). A square-root transformation on $dist_{ij}$ (CI1-SQRT) was evaluated separately to test whether decreasing the relative influence of shrubs in close proximity to the focal shrub improved model fit. We also tested another estimate of competition intensity commonplace in plant growth studies, Hegyi's

CI (CI_h; Hegyi 1974), which is similar to (1) but implements a distance-weighted ratio of neighbor to focal shrub size (D_i):

$$CI_{h_i} = \sum [(D_j / D_i) / (dist_{ij} + 1)]. \quad (2)$$

The large range of shrub sizes in our dataset (ranging from saplings of 0.5 m height to adult trees) resulted in a large skew in the distribution of CI_h, producing distorted estimates of individual neighbor contribution and biologically unrealistic approximations of neighborhood size. Thus, we discarded CI_h as a candidate model in order to maintain normality of predictor variables and produce meaningful model coefficients. The CIs for heterospecific and conspecific neighboring shrubs were estimated independently and included as separate predictors in the mixed model along with a qualitative identifier representing the species of the focal shrub to test for differential within- and between-species responses. Species with low shrub counts (N<15) in the final dataset (i.e. after edge corrections) were grouped into one bin to ensure sufficient sample size for model coefficient estimates. Initial shrub size was also included as a fixed effect to account for the decline in RGR with increasing size observed in most organisms (Rees et al. 2010). Shrub height, basal area, basal diameter and canopy area at each data survey timestep as well as averaged over the study period were all tested as proxies for initial shrub size. Models with and without log transformations of the shrub size predictor were considered to address the assumption of normality.

All eligible model variants, including all combinations of CI forms and shrub size estimates, were ranked based on Akaike Information Criterion (AIC). Because varying the neighborhood size necessitated sub-sampling the data to account for edge effects, these models were initially compared with a set neighborhood size of 4.5 m radius to allow for AIC

comparisons of models fit to the same response vector. The 4.5 m neighborhood was chosen based on preliminary tests of CI models and inspection of spatial point pattern analyses. After determining the optimal form of the fixed effects, we compared models of varying neighborhood sizes to discern the distance at which competitive neighborhood best explains variation in focal shrub RGR. Beginning with a large neighborhood radius (>15 m), models with sequentially smaller neighborhood sizes (0.5 m intervals) were ranked based on AIC. We also tested models with size-dependent neighborhood radii, where each shrub is given a “zone of influence” as a linear or power function of the size of that shrub, and two shrubs are counted as neighbors if these zones overlap. In the present study, static neighborhood sizes compared favorably to zone of influence models in all cases (see Bella 1971 and Corral Rivas et al. 2005 for examples of applications of zone of influence models).

After selecting a shrub neighborhood size, the model was evaluated for extraneous predictors and interactions. Beginning with a maximal model that included all fixed effects and interactions, covariates were removed based on stepwise AIC deletion until model parsimony was achieved. Remaining model parameters were evaluated for significance ($\alpha = 0.05$) by likelihood ratio tests comparing the AIC-selected model and models excluding highest-order parameters one at a time. Interactions between the heterospecific and conspecific competition indices were not included in the maximal model to exclude extraneous parameters with little ecological significance. To reduce collinearity among intercept and slope terms and produce meaningful intercept and main effect coefficients, initial shrub size values were centered by subtracting population mean (Schielzeth 2010). Models were initially fit with maximum likelihood estimation to allow for comparisons among models that differed in their fixed effects structures, and coefficients for the final model were estimated with the preferred restricted

maximum likelihood estimation (Pinheiro and Bates 2000). Only individuals located a minimum distance set at the chosen neighborhood size from plot edges were included as focal shrubs in all analyses to avoid bias introduced by edge effects. Model residuals were evaluated visually for homogeneity and normality, and model fit was estimated using a measure of goodness of fit (R^2) developed for linear mixed models (Nakagawa & Schielzeth 2013). All modelling efforts were conducted in the *nlme* package in R version 3.0.2 (Pinheiro et al. 2013; R Core Team 2013).

5.3 Results

5.3.1 Shrub aggregation

Spatial point pattern analysis revealed significant shrub aggregation at short distances from focal shrubs in all three sites ($g(r) > 1$), with a tendency towards random or dispersed distributions at greater distances ($g(r) \leq 1$; Fig. 5.1). The size of shrub clusters increased over time in sites B and C, from approximately 4 – 5 m in 1999 and 2002 to ~8 m in Site B and ~11 m in Site C in 2009. This increase in aggregation occurred concurrently with a substantial increase in shrub density in all sites, suggesting that new recruitment occurs within or at the edges of existing patches (Table 5.2).

5.3.2 Modelling shrub competitive neighborhoods

Model comparison based on AIC selection found models fit with CII superior to other candidate models. Comparisons among models that differed in the estimator for shrub size in the competition indices revealed a significant improvement of models using basal diameter over models based on basal area, canopy area, or height. Initial basal area and initial basal diameter had nearly identical fits when evaluated as a proxy for a focal shrub size fixed effect; basal area

was chosen due to the direct link with the response variable (shrub basal area RGR). Thus, CII partitioned into hetero- and conspecific contributions, log-transformed initial shrub basal area, and a qualitative predictor identifying the species of the focal shrub constituted the four fixed effects evaluated for inclusion in the final model. Under this model structure, a neighborhood size of 4.0 m resulted in the best model performance. A representation of the stepwise process of model selection is presented in Table 5.3.

Model evaluation based on AIC selection and likelihood ratio tests resulted in a model that retained all four main effects and their interactions. Visual assessment of model residuals initially found a violation of the assumption of normality, which we addressed by evaluating and excluding outliers (N=16) based on a two-sided outlier test on the normalized residuals ($\alpha = 0.001$). The final model explained 53.5% of the variation in focal shrub RGR. Only 5.8% of the variation was attributed to the site random effect (marginal $R^2 = 0.477$; Nakagawa and Schielzeth 2013), suggesting factors affecting shrub growth rates are relatively consistent across sites. Model output with species-level coefficient estimates is presented in Table 5.4. Intercepts represent RGR estimates for a shrub of mean basal area ($\mu = 27.3 \text{ cm}^2$) in the absence of competition (CII = 0).

Shrub RGR declined with increasing shrub size for all species ($P < 0.01$ for *Croton dichogamous* and *Rhus* spp., $P \leq 0.005$ for all others) except for *Lycium europaeum* ($P = 0.982$). Increases in the magnitude of heterospecific and conspecific competition indices generally suppressed shrub growth, although these effects were only significant in select species (Table 5.4). A significant negative interaction between shrub size and conspecific neighbors observed in two species (*Acacia etbaica* and *Rhus* spp.; $P < 0.01$) and marginally in *Acacia mellifera* ($P = 0.07$) suggests stronger effects of competitive neighborhood on smaller shrubs, an intuitive

result. However, *A. etbaica* showed the opposite effect of heterospecific neighbors (i.e. stronger effects of neighbors on larger shrubs; $P < 0.001$). *A. etbaica* also deviated from trends observed for other species in showing a positive effect of conspecific neighbors on growth ($P = 0.018$).

5.4 Discussion

The role of woody plant competition in structuring savanna ecosystems is poorly understood, in part due to a dearth of empirical studies measuring the intensity of shrub-shrub competition and assessing its relative influence on community dynamics. In this study, we quantify the magnitude and spatial scale of inter-shrub competition through longitudinal surveys of shrub morphological characteristics. We also analyze shrub spatial distribution and infer the relative influence of observed patterns of competition on stand structure through spatial point pattern analysis.

5.4.1 Shrub spatial distribution

We found marked shrub aggregation in all three sites, with increasing shrub cluster size over the course of the study in two of the sites. Shrub density also increased substantially in all sites (129% increase in shrub count across sites), attributable to a release from browsing pressure following the construction of herbivore exclusion fences in 1999. In a previous study on these sites, Augustine and McNaughton (2004) found a nearly 6-fold increase in shrub recruitment relative to control plots following exclusion of browsers and mixed feeders, primarily dik-dik (*Madoqua kirkii*), impala (*Aepyceros melampus*) and elephant (*Loxodonta africana*).

In the absence of browsing pressure, the parallel increases in shrub density and cluster size suggest that shrub recruitment events occur with increasing frequency in close proximity to

established shrubs relative to open areas. Spatial aggregation by woody plants may be driven by several candidate mechanisms, including limited propagule dispersal, underlying environmental heterogeneity, and facilitative effects of neighbors on establishment and growth operating through increased capture of moisture inputs in patches with high plant density. Dispersal limitation can occur if seed banks in herbaceous-dominated patches or bare ground are insufficient to respond quickly to the absence of browsing. There is evidence that seed dispersal throughout the landscape may indeed be a limiting factor in some savanna systems, with far fewer seeds found in open areas than under tree canopies (Smith and Shackleton 1988; Tybirk et al. 1994; Argaw et al. 1999; Witkowski and Garner 2000; Wilson and Witkowski 2003). Alternatively, seed germination may occur with relative regularity throughout the landscape, suggesting establishment (i.e. sapling to adult transition) is the primary bottleneck to woody dispersal (Walker et al 1986; O'Connor 1995; Witkowski and Garner 2000, Midgley and Bond 2001). Under this framework, differences in resource availability attributable to edaphic heterogeneity or patterns of soil moisture retention govern microclimate suitability for persistence beyond the seedling stage, creating a matrix of favorable and unfavorable sites for shrub establishment within the landscape. Shrubs thrive on patches where surface topography and edaphic properties increase soil moisture availability, but suffer high mortality in areas of low moisture or high stress, leading to landscape-scale woody aggregation around suitable microsites. Finally, existing shrub clumps may promote aggregation through beneficial modification of the abiotic environment. Surface runoff from adjacent bare patches is captured by shrub clumps, resulting in increased infiltration and soil moisture availability (Franz et al 2012). Established canopies further improve microsite conditions by reducing evaporative water losses due to light interceptance (O'Connor 1995; Salazar et al. 2012) and by increasing

subcanopy nutrient concentrations through litter decomposition (Belsky et al. 1989; Ludwig et al. 2004; Hagos and Smit 2005). Shrubs may also indirectly facilitate establishment by suppressing grasses, thus reducing resource competition in upper soil layers. However, the effects of woody plants on herbaceous production vary predictably with mean annual precipitation such that trees in dry regions generally promote subcanopy grass growth (Dohn et al. 2013), suggesting this may be an important facilitative mechanism only in mesic savannas. Indeed, shrub clusters at MRC typically have greater grass biomass than inter-shrub spaces (Augustine 2003).

In the present study, propagule dispersal limitations may have been augmented by herbivore exclusion. Though seed production increases in the absence of herbivores for many species (Young and Augustine 2007), consumption and subsequent excretion of seeds by browsers can represent an important dispersal mechanism by providing a means of transport beyond the capacity of passive seed fall and wind dispersal (Brown and Archer 1987), evidenced in savannas by the presence of seeds often found beneath heterospecific canopies (Tybirk et al. 1994; Witkowski and Garner 2000). Herbivore dispersal may also improve seed viability through scarification of the seed coat during digestion and the provision of essential nutrients and water in the form of dung deposited with the seeds. Thus, seeds that otherwise may remain dormant or are rendered inviable from exposure away from canopy shelter show increased germination rates (Miller 1994, 1995; Loth et al. 2005; but see Hauser 1994; O'Connor 1995). Given that shrubs were aggregated at the start of the study (i.e. prior to herbivore exclusion), it is likely that edaphic heterogeneity and/or shrub facilitative processes also contributed to observed aggregation patterns.

While we lack direct evidence necessary to positively identify the mechanisms responsible for increased woody aggregation observed at our sites, it is noteworthy that

aggregation occurred in the absence of fire. Clumped arrangements of vegetation are often proposed to be a consequence of frequent fire disturbance (e.g. Skarpe 1991; Kennedy and Potgieter 2003; Calabrese et al. 2010). Heterogeneous fire percolation throughout a landscape results in a mosaic of burnt and unburnt patches with distinct shrub demographics attributable to differential fire-induced mortality of woody seedlings. Shrub clumps in unburnt patches disrupt the herbaceous fuel layer, potentially impacting future fire dynamics and promoting further landscape-scale aggregation by physically impeding fire spread. Our results show that irrespective of benefits incurred in the presence of fire, aggregation of savanna vegetation persists in its absence, indicating alternate driving mechanisms in this system.

5.4.2 Quantifying woody competition

We found strong evidence of competition among woody plants within a 4 m radius neighborhood. At this scale, our results indicate a decrease in shrub growth rates with increasing neighbor size and decreasing distance to neighbors. Basal stem size of neighbors better predicted RGR of focal shrubs compared to height and crown area metrics of neighbors. This finding strongly points to below-ground competition for water as the likely mechanism generating competitive suppression of growth rates, as has generally been suggested by other models of woody plant spatial patterns in the region (Franz et al. 2011, 2012). Studies of competition among trees in forests generally show increased performance of models utilizing crown area to describe tree size, reflective of size-asymmetric competition for light typical in closed-canopy systems (e.g. von Oheimb et al. 2011; Fraver et al. 2014). Lower woody cover characteristic of savannas shifts the primary limiting factor in photosynthetic reactions to belowground resources. Thus, it follows that morphological characteristics reflective of below-ground resource capture

and water transport are more intimately linked with variation in savanna plant growth rates. The 4 m spatial extent of competition we detected may reflect average lateral range of primary root biomass across species, though we lack root distribution data to test this directly.

The magnitude of a shrub's response to a neighbor varied with the size of the focal shrub and the species of the neighbor and focal shrubs. Species also differed in their relative responses to heterospecifics and conspecifics, suggesting distinct differences in competitive abilities, potentially driving shifts in community composition. Interestingly, the three most abundant species (all *Acacia* spp.) at the onset of the study exhibited the largest shifts in relative abundance over the study period. Of these, species that were suppressed by heterospecific neighbors more than conspecifics (namely *A. etbaica* and *A. mellifera*) increased in abundance (5.6% and 7.6%, respectively), while *A. brevispica*, which showed strong suppression by conspecifics, decreased in abundance over the study period (-10.8%). Notably, decreases in community abundance were also associated with low growth rates. Three species decreased in relative abundance (*A. brevispica*, *C. dichogamous* and *L. europaeum*), representing the three lowest mean RGRs. These results suggest that in the absence of browsing, species that can effectively compete for water are at a competitive advantage relative to slow-growing, unpalatable species that invest heavily in herbivore defenses. Over time, differences in species' abilities to acquire resources contribute to decreases in abundance and potentially eventual competitive exclusion from the system.

Though suppression of growth through competition for resources was the predominant neighborhood interaction we detected, facilitative effects were likely also contributing to the net effect of neighbors in shrub clumps. Positive effects of woody neighbors are not unprecedented (e.g. Zhao et al. 2006), and are often attributed to microclimate modification by neighbor shrubs

or intermediate species. Indeed, a positive effect of conspecific neighbors on focal shrub growth rates detected for one species (*A. etbaica*) suggests facilitative processes may be a particularly important factor contributing to long-term increases in the abundance of this species.

5.4.3 Implications for savanna vegetation structure

These results demonstrate the importance of inter-shrub competition in savanna ecosystems. Many studies have made inferences concerning the impact of herbivores and fire based on vegetation patterns, but few explicitly consider biotic interactions among woody plants. Our documentation of strong neighborhood effects at the 4 m scale indicates that belowground competition is playing an important role in determining community structure.

While all species increased in absolute number of shrubs, we observed a conspicuous shift in the dominance hierarchy of the community, with some species increasing in relative abundance (notably, *A. etbaica* and *A. mellifera*) at the expense of others (*A. brevispica* and *L. europaeum*). Decreases in abundance corresponded with high levels of conspecific competition. A possible explanation for this trend lies in differential species' responses to the exclusion of herbivores. Species that perform poorly in high densities of conspecifics may depend on dispersal far from seed sources for persistence in the community. In the absence of herbivore-mediated dispersal, strong seed limitation in open areas may shift the competitive balance in favor of species that perform well in conspecific clumps. This result suggests a key role of browsers in maintaining community diversity in this system. Changes in herbivore density have previously been shown to affect plant diversity, but variable results across studies suggest a high degree of dependency on climatic conditions and the composition of constituent herbivore and plant communities (e.g. Olff and Ritchie 1998; Bakker et al. 2006; Jacobs and Naiman 2008;

Levick and Rogers 2008; Young et al. 2013). Studies that rigorously analyze seed dispersal and shifts in community composition in the presence and absence of herbivores are needed to gain insight on the effects of herbivore dispersal on savanna woody communities.

Shifts in vegetation structure detailed in this study occurred immediately following herbivore exclusion. Thus, it is plausible that observed trends may be temporary responses to an altered disturbance regime. Over time, as new shrub cohorts established in the absence of browsing pressure mature, aggregation processes may give way to processes promoting random or dispersed spatial arrangements (i.e. competitive self-thinning). However, similar aggregated patterns have been found in other systems with co-dominant woody and herbaceous layers. For example, in a study on a North American shrubland, Browning et al. (2014) found woody aggregation in the long-term absence of herbivores, contrary to their hypotheses predicting trends towards randomness or dispersion. The authors speculated that herbicide applications or negligible competition intensity among woody plants contributed to observed patterns. On our sites, we can rule out the former consideration, and we demonstrate here that inter-shrub competition is a significant biotic interaction. Thus, it appears that processes governing germination (e.g. seed dispersal) and seedling establishment (e.g. capture of runon by shrub patches) are more important than woody competition in determining distribution of vegetation, at least in some savannas.

5.4.4 Conclusion

We found spatial aggregation of woody plants, despite significant decreases in growth rates with decreasing distance to neighbors. Savannas are highly dynamic ecosystems often characterized by high herbivore density and frequent fires (Scholes and Archer 1997; Bond

2008). Browsing and fire likely represent major evolutionary drivers in African savannas, translating into a competitive advantage for species that can develop strategies to minimize their impact or respond quickly following disturbance events. Indeed, empirical work in savannas suggest analogous browsing and fire ‘traps’, whereby woody plants must reach an escape height to avoid topkill by fires (Bell 1984; Higgins et al. 2000; Hoffman et al. 2009) or terminal browsing by herbivores (Augustine and McNaughton 2004; Staver and Bond 2014). With high growth rates seemingly important for plant survival, why then do we see clumped spatial arrangements when dispersed or random arrangements might improve fitness by allowing plants to quickly surpass escape height bottlenecks? The clumping patterns we documented could arise from several mechanisms operating alone or in concert, including 1) dispersal limitation (e.g. greater seed deposition beneath existing shrub canopies), 2) an establishment bottleneck imposed by limited available favorable microsites corresponding to edaphic and environmental heterogeneity, and 3) spatial variation in surface runoff and runoff patterns, with increased capture of both rainfall and runoff in patches with greater shrub density. It is unclear the extent to which facilitative moderation of the abiotic environment by existing shrub clumps enhanced aggregation processes, although increased water availability in close proximity to shrub canopies is plausible (Franz et al. 2011). Additional benefits to clumped spatial patterns may be realized in the presence of fire and/or herbivory, but our results suggest that 1) endogenous abiotic components of savanna systems are sufficient to produce aggregated arrangements, and 2) both interspecific and conspecific competition become important determinants of growth rates within shrub clusters.

These findings have broad empirical and theoretical implications for our understanding of savanna community dynamics. Existing studies of savanna vegetation interactions focus

disproportionately on interactions between the woody and herbaceous layers; interactions among woody plants are relatively poorly understood and may represent a gap in our ability to predict future savanna structure and distribution with dynamic global vegetation models (DVGMs). Our results provide empirical support for the occurrence of competition among woody plants in savannas and may be used to parameterize future iterations of DGVMs. We also observed shifts in the spatial organization and abundance of woody species during a decade of growth in the absence of herbivores, suggesting a strong role of top-down drivers in determining community composition. This finding has important management implications regarding the potential for species-specific declines in abundance leading to local competitive exclusion, particularly in areas undergoing land use change or where herbivore densities are predicted to change.

5.5 Tables

Table 5.1. Shrub density and median shrub basal area (BA) and height (h) at three data survey time-steps for experimental sites in Mpala Research Centre, Kenya.

Year	Site A			Site B			Site C		
	Density (shrubs ha ⁻¹)	BA (cm ²)	h (m)	Density (shrubs ha ⁻¹)	BA (cm ²)	h (m)	Density (shrubs ha ⁻¹)	BA (cm ²)	h (m)
1999	2408	3.1	1.4	1292	2.3	1.3	988	4.5	1.9
2002	2740	3.7	1.5	1728	2.3	1.3	1456	2.0	1.1
2009	3908	3.6	1.9	3196	3.4	1.8	2768	3.9	2.4

Table 5.2. Species-level summary statistics for shrub populations at final data survey (2009). Growth estimates represent basal area increment (BA) and relative growth rate (RGR) means with associated standard deviations (SD). Only species with N > 10 shown here.

Species	N° Shrubs				Shrub height		Shrub growth		
	Site A	Site B	Site C	Total	Mean (m)	Maximum (m)	BA	(cm ² yr ⁻¹)	RGR (cm ² cm ⁻² yr ⁻¹)
<i>Abutilon mauritianum</i>	9	2	0	11	1.2 (0.7)	2.7	1.18 (1.30)		0.29 (0.13)
<i>Acacia balanites</i>	2	7	17	26	1.6 (1.1)	4.2	3.50 (4.57)		0.23 (0.14)
<i>Acacia brevispica</i>	251	25	2	278	2.0 (1.0)	5.9	0.60 (1.43)		0.06 (0.13)
<i>Acacia etbaica</i>	67	121	89	277	1.4 (0.9)	5.4	1.79 (4.15)		0.17 (0.14)
<i>Acacia mellifera</i>	99	90	130	319	1.8 (1.4)	9.1	3.89 (11.28)		0.11 (0.11)
<i>Boscia angustifolia</i>	7	8	0	15	1.7 (1.1)	4.6	2.71 (5.27)		0.11 (0.10)
<i>Commiphora</i> spp.	12	7	0	19	0.9 (0.5)	2.2	1.67 (5.9)		0.11 (0.14)
<i>Croton dichogamous</i>	56	0	1	57	1.6 (0.6)	4.1	0.41 (0.98)		0.04 (0.10)
<i>Euclea divinorum</i>	11	0	7	18	2.0 (1.3)	6.0	1.38 (2.73)		0.16 (0.12)
<i>Grewia tenax</i>	113	65	59	237	1.1 (0.6)	3.9	0.42 (0.61)		0.15 (0.12)
<i>Lycium europaeum</i>	0	84	25	109	1.2 (0.6)	3.7	0.09 (0.69)		0.05 (0.11)
<i>Rhus</i> spp.	22	2	16	40	0.9 (0.4)	2.9	0.69 (1.51)		0.14 (0.14)

Table 5.3. Performance of alternate models explaining growth in shrub basal area as a function of neighborhood model (column 1), maximum neighborhood distance used (column 2) and initial shrub size (column 3). Shrub counts represent sample size after adjusting for edge effects (i.e. discarding individuals within a distance of plot edges determined by the neighborhood radius). Model comparison based on Akaike's Information Criterion (AIC); model performance was evaluated using the same number of shrubs for all models to allow for AIC comparison. Best model highlighted in bold.

Competitive neighborhood description	Neighborhood radius (m)	Shrub size parameter	N° Shrubs	AIC	R ²
None (null model)	4.5	BA	860	-1567.3	0.382
Sum neighbor BA	4.5	BA	860	-1720.7	0.528
CI1-SQRT	4.5	BA	860	-1736.3	0.538
CI1	4.5	CA	860	-1734.6	0.542
CI1	4.5	height	860	-1709.9	0.535
CI1	4.5	diam	860	-1741.8	0.545
CI1	4.5	BA	860	-1745.5	0.544
CI1	5.0	BA	808	-1730.5	0.534
CI1	4.0	BA	913	-1748.2	0.547
CI1	3.5	BA	970	-1743.3	0.546
CI1	3.0	BA	1026	-1734.0	0.540

BA = basal area; CA = canopy area; diam = basal diameter. See section 2.4 for full description of competition indices (e.g. CI1) and model comparison methods.

Table 5.4. Parameter estimates for common species (N > 20) derived from the best linear mixed model predicting the effects of a neighbor competition index (CI1) on shrub relative growth rate. Shrub size values are centered around factor mean. *P*-values represent probability values for a *t*-test on coefficient estimates; bold values represent *P* < 0.05.

Species	Intercept			Heterospecific CI1			Conspecific CI1			Shrub size			Het CI1 : Shrub size			Con CI1 : Shrub size		
	Estimate	SE	<i>P</i>	Estimate	SE	<i>P</i>	Estimate	SE	<i>P</i>	Estimate	SE	<i>P</i>	Estimate	SE	<i>P</i>	Estimate	SE	<i>P</i>
<i>Acacia brevispica</i>	0.1437	0.0227	0.000	0.0002	0.0007	0.803	-0.0044	0.0012	0.000	-0.0308	0.0084	0.000	0.0001	0.0004	0.893	0.0001	0.0006	0.900
<i>Acacia etbaica</i>	0.2171	0.0206	0.000	-0.0050	0.0007	0.000	0.0017	0.0007	0.018	-0.0429	0.0067	0.000	0.0015	0.0004	0.000	-0.0013	0.0004	0.001
<i>Acacia mellifera</i>	0.2045	0.0202	0.000	-0.0021	0.0006	0.000	-0.0016	0.0008	0.042	-0.0340	0.0051	0.000	0.0004	0.0003	0.199	-0.0007	0.0004	0.073
<i>Croton dichogamous</i>	0.2547	0.0831	0.002	0.0015	0.0052	0.775	-0.0113	0.0062	0.069	-0.0853	0.0487	0.080	-0.0004	0.0030	0.907	0.0038	0.0037	0.311
<i>Grewia tenax</i>	0.1749	0.0311	0.000	-0.0023	0.0008	0.007	-0.0004	0.0029	0.889	-0.0555	0.0150	0.000	0.0004	0.0004	0.385	-0.0002	0.0015	0.900
<i>Lycium europaeum</i>	0.1339	0.0442	0.003	-0.0016	0.0012	0.169	-0.0205	0.0062	0.001	-0.0007	0.0321	0.982	-0.0007	0.0010	0.469	-0.0040	0.0047	0.397
<i>Rhus</i> spp.	0.1568	0.0553	0.005	0.0006	0.0014	0.654	-0.0364	0.0151	0.016	-0.1013	0.0552	0.067	0.0014	0.0011	0.190	-0.0251	0.0083	0.003
uncommon spp.	0.1894	0.0266	0.000	-0.0008	0.0007	0.274	-0.0032	0.0034	0.351	-0.0309	0.0109	0.005	-0.0003	0.0003	0.330	0.0008	0.0021	0.700

SE = standard error; See section 2.4 for description of competition index (CI1)

5.6 Figures

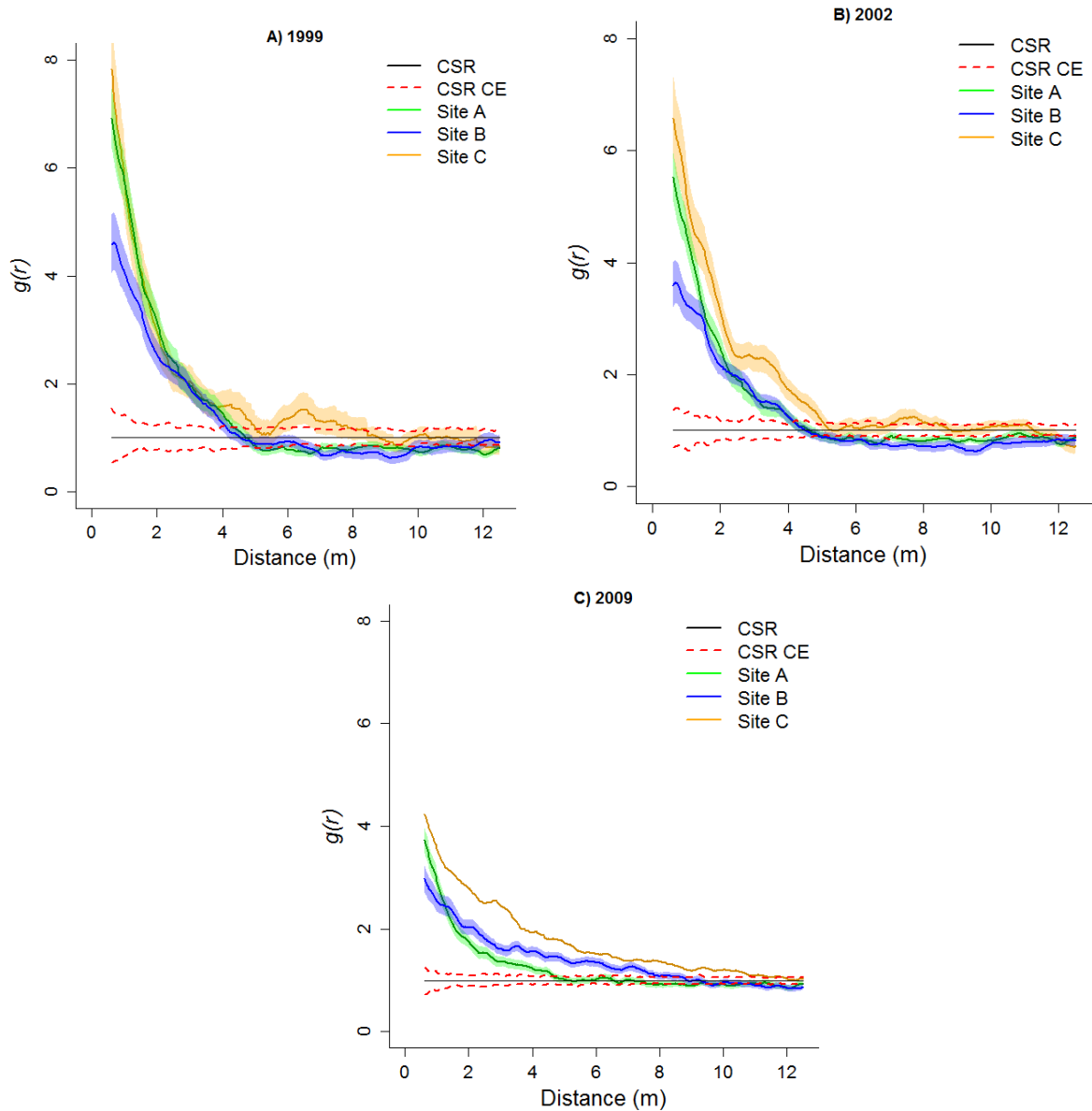


Fig. 5.1. Univariate pair correlation functions $g(r)$ detailing shrub distribution in three sites at Mpala Research Centre mapped in 1999, 2002 and 2009. Shrub communities at these sites aggregated ($g(r) > 1$) at increasing distances over time, concurrent with increasing population densities in each site. Dotted red lines represent 95% confidence envelopes (CE) calculated by 199 Monte Carlo simulations of the null model of complete spatial randomness (CSR). Shaded areas represent 95% confidence intervals for the true value of $g(r)$ for each site based on 1000 pointwise bootstrap simulations.

5.7 References

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Chapter 6: Summary and conclusions

This dissertation advances our understanding of interactions among woody and herbaceous vegetation in savannas. By analyzing existing empirical studies, implementing two neighbor removal experiments in North America and West Africa, and analyzing woody competition and spatial structure in East Africa, I addressed four questions designed to increase knowledge of the interplay of biotic interactions among trees and grasses and the abiotic template across global savannas (see Chapter 1). In a meta-analysis presented in Chapter 2, we found that the effect of trees on subcanopy herbaceous production varies predictably with climate, such that trees in arid savannas generally promote grass growth and trees in mesic regions suppress growth. This finding is consistent with a general theoretical model predicting the relative importance of facilitative processes for species coexistence. Termed the stress gradient hypothesis (SGH), the theory predicts an increasing importance of facilitation with increasing environmental stress, such as high water-stress typical of arid savannas (Bertness and Callaway 1994).

In Chapters 3 and 4, we experimentally tested the predictions of the SGH and inferred mechanistic drivers by relating abiotic covariates to plant growth in the presence and absence of neighbors. In the shortgrass steppe (SGS) in northeastern Colorado, we found a net-neutral effect of shrubs on grasses, contrary to expected facilitation. We suggested shrub morphology and interactive effects of topography and soil texture were primarily responsible for observed patterns of growth. At five savanna field sites situated along a rainfall gradient (i.e. water-stress gradient) in Mali, West Africa, we found a net suppressive effect of trees on grass growth in mesic savannas, and a net beneficial effect in arid savannas. Light availability and distance to

tree boles best explained shifts in herbaceous production along the rainfall gradient. These results indicate that the effects of savanna trees on subcanopy grass production generally conform to the predictions of the SGH, and appear to be mediated by microclimate modification by tree canopies related to light availability and water balance. The effects of grasses on trees along environmental gradients are less clear, though we found net neutral effects on woody growth over one growing season in tropical and temperate shrub-grass systems, suggesting that operative competitive and facilitative mechanisms largely offset, or that the effects of grasses on plant-available resources for woody species are negligible. In Chapter 5, shrubs suppressed the growth of woody neighbors at a scale of 4 m in an East African savanna, despite significant spatial aggregation of shrubs in the landscape. These results suggest that competition among woody plants influences production and relative species abundance, but dispersal and establishment bottlenecks are likely more important for landscape-scale spatial structure in this system.

Savannas encompass a hugely diverse array of ecosystems unified by the coexistence of woody and herbaceous vegetation. Accordingly, savannas occur on a continuum of woody cover ranging from arid systems with very few, isolated trees similar in structure and function to grasslands, to mesic systems with nearly full canopy closure, similar to forests. A primary challenge for researchers studying savannas is to derive general theory on the processes that maintain the coexistence of trees and grasses across the structural diversity of global savannas, i.e. the mechanisms that prevent a transition to tree-less or closed canopy systems. Decades of empirical work have greatly improved our ability to address this central ‘savanna problem’ and predict the response to perturbations or long-term changes in disturbance regime, climate, anthropogenic land use, or ecosystem properties (e.g. faunal extinctions, nutrient deposition). A key finding in this regard is that the stabilizing mechanisms for savannas are likely

fundamentally different depending on climate (Sankaran et al. 2005). In arid and semi-arid savannas (mean annual precipitation [MAP] < 650 mm), maximum woody cover is constrained by water availability. In mesic savannas (MAP > 650 mm), precipitation is generally sufficient to support closed canopy ecosystems, and savannas are maintained by disturbance (fire, herbivory). Thus, we see a shift with increasing MAP from ‘stable’ systems where tree-grass coexistence is maintained by regional climatic conditions to ‘unstable’ systems, maintained by stochastic disturbances.

Though these patterns are evident at global scales, there is a great degree of variability in woody cover for discrete ecosystems at similar rainfall levels (Sankaran et al. 2005; Hirota et al. 2011; Staver et al. 2011). Much of this variability is attributed to differences in land use and disturbance intensity, where factors such as fire frequency (Murphy and Bowman 2012; Dantas et al. 2013) and herbivore density (Holdo et al. 2013; Staver and Bond 2014) further impact the relative abundance of trees and grasses. Largely missing from ecosystem models, however, is explicit consideration of biotic interactions among savanna vegetation, and how these interactions might affect the stability and distribution of savannas along the rainfall gradient. This dissertation advances our understanding of the net outcome and underlying mechanisms of savanna plant interactions, and grants insight into their relative importance for savannas at meta-scales. For example, suppression of subcanopy grass growth by trees in very wet savannas may reduce fuel load and fire intensity, promoting a positive feedback between increasing woody cover and decreasing fire frequency, thus accelerating transitions to forested ecosystems. However, tree-grass interactions have different implications for savannas in areas with climates close to the 650 mm MAP benchmark that approximates the transition from climatically-determined savannas to systems maintained by disturbance. Depending on edaphic and

environmental properties, the switch from net facilitation to net competition for the effects of trees on grasses occurs at a similar point along the rainfall gradient (~650-950 mm MAP; Chapter 2). Therefore, in savannas where trees promote grasses, increased fire intensity and spread due to larger fuel loads may strengthen savanna maintenance by suppressing woody establishment.

The research described in this dissertation contributes significantly to our understanding of interactions among savanna plants, but it is also evident that significant gaps remain. Woody establishment (i.e. transition from juvenile to adult) represents a key demographic bottleneck affecting the relative distribution of trees and grasses in a landscape (Sankaran et al. 2004; Werner and Prior 2013). We found strong support for SGH predictions in the effects of adult trees on grass production, but we did not explicitly consider effects at multiple life stages. Thus, investigations of competitive and facilitative interactions between grasses and woody plants throughout the life history of trees are needed. Furthermore, we found competitive effects among trees in an East African semi-arid savanna, but the degree and importance of inter-tree competition at other points along the rainfall gradient is poorly understood. Lastly, we found negligible effects of grasses on woody growth over the course of one growing year, but multi-year studies may be necessary to detect effects on slow-growing woody plants. The results of this dissertation, supplemented by future investigations of savanna plant interactions, represent significant improvements to theory on the coexistence between woody and herbaceous vegetation. Savanna trees and grasses are vital to a large portion of the human population as a source of fuelwood and grazing fodder (Le Houerou 1989). Thus, a robust understanding of the mechanisms that maintain woody-herbaceous assemblages can help inform the management of savanna systems in order to optimize the yield and sustainability of ecosystem goods and

services critical to the livelihoods of local communities. Furthermore, we provide empirical data that can be used to refine and parameterize vegetation models predicting savanna ecosystem processes and the global distribution of mixed tree-grass systems.

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Appendix

A2: Appendix for Chapter 2

Table A2.1 Data sources for sub-canopy to open grassland herbaceous biomass ratios

Authors	Publication Year	Location	Rainfall	Sub-canopy : open grassland biomass*	N
Abdallah et al.	2008	Tunisia	218	0.414	24
Abule et al.	2005	Ethiopia	446	0.094	20
Abule et al.	2005	Ethiopia	446	0.155	20
Abule et al.	2005	Ethiopia	446	0.179	20
Abule et al.	2005	Ethiopia	446	0.282	20
Amévor et al.	UPD†	Mali	244	-0.028	3
Amévor et al.	UPD	Mali	244	0.076	16
Amévor et al.	UPD	Mali	379	-0.025	3
Amévor et al.	UPD	Mali	429	0.174	3
Amévor et al.	UPD	Mali	509	0.057	3
Amévor et al.	UPD	Mali	540	-0.052	3
Amévor et al.	UPD	Mali	554	0.166	16
Amévor et al.	UPD	Mali	555	-0.147	3
Amévor et al.	UPD	Mali	707	-0.103	3
Amévor et al.	UPD	Mali	776	0.084	16
Amévor et al.	UPD	Mali	868	-0.064	3
Amévor et al.	UPD	Mali	941	-0.336	3
Amévor et al.	UPD	Mali	966	-0.451	3
Amévor et al.	UPD	Mali	966	-0.325	3
Amévor et al.	UPD	Mali	1037	0.010	16
Amévor et al.	UPD	Mali	1112	-0.100	16
Anderson et al.	2001	Texas, USA	853	-0.264	13
Belsky et al.	1989	Kenya	494	0.294	3
Belsky et al.	1989	Kenya	494	0.356	3
Belsky et al.	1993a	Kenya	509	0.138	2
Belsky et al.	1993a	Kenya	509	0.273	2
Belsky et al.	1993a	Kenya	659	0.039	3
Belsky et al.	1993a	Kenya	659	0.159	3
Belsky et al.	1993b	Kenya	620	0.039	4
Belsky et al.	1993b	Kenya	620	0.212	3
Engle et al.	1987	Oklahoma, USA	841	-0.303	8
Engle et al.	1987	Oklahoma, USA	1436	-0.326	64

Engle et al.	1987	Oklahoma, USA	1436	-0.325	96
Frost & McDougald	1989	California, USA	283	0.143	40
Frost & McDougald	1989	California, USA	283	0.180	40
Frost & McDougald	1989	California, USA	283	0.250	40
Frost & McDougald	1989	California, USA	305	0.004	40
Frost & McDougald	1989	California, USA	305	0.234	40
Frost & McDougald	1989	California, USA	305	0.244	40
Grouzis & Akpo	1997	Senegal	172	0.400	7
Grouzis & Akpo	1997	Senegal	250	0.188	15
Grouzis & Akpo	1997	Senegal	250	0.328	20
Grouzis & Akpo	1997	Senegal	250	0.389	20
Grouzis & Akpo	1997	Senegal	250	0.394	15
Haworth & McPherson	1994	Arizona, USA	410	-0.196	10
Haworth & McPherson	1994	Arizona, USA	415	-0.211	10
Holland	1980	California, USA	401	0.321	3
Holland	1980	California, USA	242	0.347	3
Holland	1980	California, USA	450	0.231	3
Holland	1980	California, USA	304	0.231	3
Jackson et al.	1990	California, USA	640	0.055	2
Jackson et al.	1990	California, USA	980	0.138	2
Jackson et al.	1990	California, USA	1060	-0.046	2
Jeddi & Chaieb	2009	Tunisia	263	0.183	18
Jeddi & Chaieb	2009	Tunisia	263	0.196	18
Jeddi & Chaieb	2009	Tunisia	263	0.241	18
Ko & Reich	1993	Wisconsin, USA	615	-0.390	7
Ko & Reich	1993	Wisconsin, USA	615	-0.239	3
Ludwig et al.	2004	Tanzania	798	-0.021	4
McClaran & Bartolome	1989	California, USA	176	-0.068	3
McClaran & Bartolome	1989	California, USA	275	-0.109	3
McClaran & Bartolome	1989	California, USA	351	0.038	3
McClaran & Bartolome	1989	California, USA	357	-0.460	3
McClaran & Bartolome	1989	California, USA	481	-0.298	3
McClaran & Bartolome	1989	California, USA	543	0.060	3
McClaran & Bartolome	1989	California, USA	593	-0.282	3
McClaran & Bartolome	1989	California, USA	618	-0.348	3
McClaran & Bartolome	1989	California, USA	848	-0.131	3
McClaran & Bartolome	1989	California, USA	1120	-0.451	3
Mordelet & Menaut	1995	Cote d'Ivoire	1200	-0.197	6
Moustakas et al.	UPD	South Africa	496	0.145	17
Moustakas et al.	UPD	South Africa	544	0.258	28
Moustakas et al.	UPD	South Africa	550	0.115	28
Moustakas et al.	UPD	South Africa	737	-0.046	21
Ratliff et al.	1991	California, USA	483	-0.215	NA†

Ratliff et al.	1991	California, USA	483	-0.119	NA
Ratliff et al.	1991	California, USA	483	-0.093	NA
Ratliff et al.	1991	California, USA	483	-0.041	NA
Ratliff et al.	1991	California, USA	483	0.099	NA
Ratliff et al.	1991	California, USA	483	0.155	NA
Simmons et al.	2008	Texas, USA	427	0.136	8
Simmons et al.	2008	Texas, USA	614	-0.013	8
Stuart-Hill & Tainton	1989	South Africa	577	0.081	NA
Stuart-Hill et al.	1987	South Africa	422	0.114	NA
Treydte et al.	2007	South Africa	450	0.068	9
Treydte et al.	2007	South Africa	450	0.091	9
Treydte et al.	2007	South Africa	540	0.000	10
Treydte et al.	2007	South Africa	540	0.027	13
Treydte et al.	2007	Tanzania	900	0.045	6
Treydte et al.	2007	Tanzania	900	0.162	9
Treydte et al.	2008	South Africa	500	0.058	13
Treydte et al.	2008	South Africa	500	0.168	12
Treydte et al.	2008	South Africa	500	0.179	13
Treydte et al.	2008	South Africa	500	0.478	12
Weltzin & Coughenour	1990	Kenya	395	0.361	15

*Tree effect ratio calculated as normalized ratio $y=(s-g)/(s+g)$; †UPD = unpublished data; ‡NA = not available

Table A2.2 Data sources for calculated sub-canopy to open grassland soil and leaf nutrient ratios

Author(s)	Year Published	Location	Rainfall	Nutrient	Soil or Leaf	Sub-canopy : open grassland nutrients	N
Abdallah et al.	2008	Tunisia	218	N	S	0.097	6
Abdallah et al.	2008	Tunisia	218	P	S	0.249	6
Abule et al.	2005	Ethiopia	446	N	S	0.152	10
Abule et al.	2005	Ethiopia	446	N	S	0.163	10
Abule et al.	2005	Ethiopia	446	N	S	0.165	10
Abule et al.	2005	Ethiopia	446	N	S	0.172	10
Anderson et al.	2001	Texas, USA	853	N	S	-0.177	7
Anderson et al.	2001	Texas, USA	853	P	S	0.153	7
Belsky et al.	1993a	Kenya	494	P	S	0.270	6
Belsky et al.	1993a	Kenya	509	P	S	0.469	4
Belsky et al.	1993a	Kenya	620	P	S	0.398	7
Belsky et al.	1993b	Kenya	494	N	L	0.553	3
Belsky et al.	1993b	Kenya	494	N	L	0.654	3
Belsky et al.	1993b	Kenya	494	N	S	0.333	3
Belsky et al.	1993b	Kenya	494	N	S	0.356	3
Belsky et al.	1993b	Kenya	620	N	L	0.190	3
Belsky et al.	1993b	Kenya	620	N	L	0.569	4
Belsky et al.	1993b	Kenya	620	N	S	0.232	3
Belsky et al.	1993b	Kenya	620	N	S	0.238	4
Jackson et al.	1990	California, USA	640	N	L	0.235	2
Jackson et al.	1990	California, USA	980	N	L	0.323	2
Jackson et al.	1990	California, USA	980	N	S	0.118	2
Jackson et al.	1990	California, USA	980	P	S	0.644	2
Jackson et al.	1990	California, USA	1060	N	L	-0.094	2
Jeddi & Chaieb	2009	Tunisia	263	P	S	0.071	18
Jeddi & Chaieb	2009	Tunisia	263	P	S	0.081	18
Jeddi & Chaieb	2009	Tunisia	263	P	S	0.110	18
Jeddi & Chaieb	2009	Tunisia	263	N	S	0.224	18
Jeddi & Chaieb	2009	Tunisia	263	N	S	0.248	18
Jeddi & Chaieb	2009	Tunisia	263	N	S	0.370	18
Ko & Reich	1993	Wisconsin, USA	615	P	S	-0.109	2
Ko & Reich	1993	Wisconsin, USA	615	P	S	0.140	4
Ludwig et al.	2004	Tanzania	798	P	L	-0.014	5

Ludwig et al.	2004	Tanzania	798	N	L	0.188	5
Ludwig et al.	2004	Tanzania	798	P	S	0.383	5
Ludwig et al.	2004	Tanzania	798	N	S	0.609	5
Ludwig et al.	2004	Tanzania	1368	P	L	-0.211	5
Ludwig et al.	2004	Tanzania	1368	N	L	0.123	5
Treydte et al.	2007	South Africa	450	N	L	0.032	9
Treydte et al.	2007	South Africa	450	P	L	0.046	9
Treydte et al.	2007	South Africa	450	N	L	0.055	9
Treydte et al.	2007	South Africa	450	P	L	0.061	9
Treydte et al.	2007	South Africa	450	P	S	0.116	9
Treydte et al.	2007	South Africa	450	P	S	0.153	9
Treydte et al.	2007	South Africa	450	N	S	0.229	9
Treydte et al.	2007	South Africa	450	N	S	0.319	9
Treydte et al.	2007	South Africa	540	N	L	0.095	10
Treydte et al.	2007	South Africa	540	N	L	0.124	13
Treydte et al.	2007	South Africa	540	P	L	0.182	13
Treydte et al.	2007	South Africa	540	P	L	0.187	10
Treydte et al.	2007	South Africa	540	P	S	-0.004	13
Treydte et al.	2007	South Africa	540	N	S	0.061	13
Treydte et al.	2007	South Africa	540	P	S	0.136	10
Treydte et al.	2007	South Africa	540	N	S	0.250	10
Treydte et al.	2007	Africa	900	P	L	0.039	6
Treydte et al.	2007	Tanzania	900	N	L	0.061	9
Treydte et al.	2007	Tanzania	900	N	L	0.072	6
Treydte et al.	2007	South Africa	900	P	L	0.200	9
Treydte et al.	2007	South Africa	900	N	S	-0.123	6
Treydte et al.	2007	Africa	900	P	S	0.033	6

Treydte et al.	2007	South Africa	900	N	S	0.238	9
Treydte et al.	2007	South Africa	900	P	S	0.362	9
Treydte et al.	2008	South Africa	450	P	L	-0.088	9
Treydte et al.	2008	South Africa	450	N	L	0.019	9
Treydte et al.	2008	South Africa	450	P	L	0.035	10
Treydte et al.	2008	South Africa	450	N	L	0.048	9
Treydte et al.	2008	South Africa	450	P	L	0.063	9
Treydte et al.	2008	South Africa	450	N	L	0.102	13
Treydte et al.	2008	South Africa	450	N	L	0.102	10
Treydte et al.	2008	South Africa	450	P	L	0.151	13
Treydte et al.	2008	South Africa	500	P	L	-0.063	13
Treydte et al.	2008	South Africa	500	P	L	0.080	12
Treydte et al.	2008	South Africa	500	N	L	0.084	13
Treydte et al.	2008	South Africa	500	N	L	0.123	12
Weltzin & Coughenour	1990	Kenya	395	N	S	0.456	15

A2.3 Results of linear regression analyses used to identify correlations between precipitation over percent evapotranspiration (PPT/PET) and the normalized ratio of sub-canopy to open-grassland herbaceous biomass in tropical African and temperate North American savannas.

The results of our linear regression analyses using PPT/PET mirror the results of the analyses with annual rainfall as the explanatory variable. These results suggest a shift from net facilitation in dry, water-limited savannas to net competition in mesic regions, consistent with the SGH (Fig. A2.1).

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 PPT/PET, bioclimatic zone, and soil texture. The simplified model included only the main effects of PPT/PET, with similar sensitivity to PPT/PET (i.e. slope) across all sites ($P = 0.154$), but distinctly different intercept values between tropical and temperate bioclimatic zones ($P = 0.0008$), and between the coarse and fine soil textures in tropical regions ($P = 0.013$) (Fig. A2.1; 23.86 on 91 degrees of freedom, adjusted $r^2=0.422$, $P < 0.0001$).

This analysis revealed no difference in which factors constitute the optimally simplified model when compared to the annual rainfall model (Fig. 2.2). Furthermore, the PPT/PET analysis revealed no statistical convergence among intercepts of the tropical and temperate climate groups, contrary to what would be expected if climatic factors related to temperature strongly influenced the observed difference between tropical and temperate interactions.

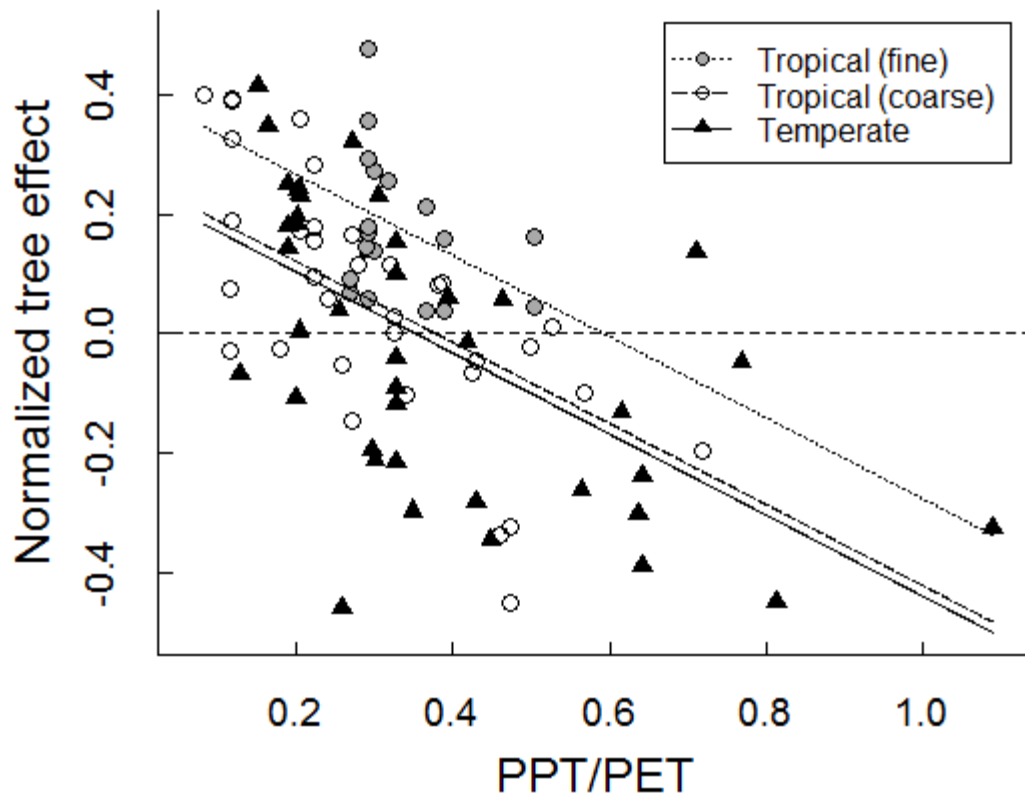


Fig. A2.1. Normalized ratio of sub-canopy to open-grassland herbaceous biomass along a gradient of precipitation over percent evapotranspiration (PPT/PET) for temperate and tropical savannas on coarse and fine soils (adjusted $r^2=0.422$, $P < 0.0001$).

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