Ecology, 98(2), 2017, pp. 478–488
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Spatial vegetation patterns and neighborhood competition among woody plants in an East African savanna

Justin Dohn,[1,2,7] David J. Augustine,[3] Niall P. Hanan,[4] Jayashree Ratnam,[5] and Mahesh Sankaran[5,6]

[1]*Natural Resource Ecology Laboratory and Graduate Degree Program in Ecology, Colorado State University, Fort Collins, Colorado 80523 USA*
[2]*Arcadis, Denver, Colorado 80246 USA*
[3]*Rangeland Resources Research Unit, USDA Agricultural Research Service, Fort Collins, Colorado 80526 USA*
[4]*Geospatial Sciences Center of Excellence, South Dakota State University, Brookings, South Dakota 57006 USA*
[5]*National Centre for Biological Sciences, Tata Institute of Fundamental Research, GKVK Campus, Bellary Road, Bangalore 560065 India*
[6]*School of Biology, University of Leeds, Leeds, LS2 9JT United Kingdom*

Abstract. The majority of research on savanna vegetation dynamics has focused on the coexistence of woody and herbaceous vegetation. Interactions among woody plants in savannas are relatively poorly understood. We present data from a 10-yr longitudinal study of spatially explicit growth patterns of woody vegetation in an East African savanna following exclusion of large herbivores and in the absence of fire. We examined plant spatial patterns and quantified the degree of competition among woody individuals. Woody plants in this semiarid savanna exhibit strongly clumped spatial distributions at scales of 1–5 m. However, analysis of woody plant growth rates relative to their conspecific and heterospecific neighbors revealed evidence for strong competitive interactions at neighborhood scales of up to 5 m for most woody plant species. Thus, woody plants were aggregated in clumps despite significantly decreased growth rates in close proximity to neighbors, indicating that the spatial distribution of woody plants in this region depends on dispersal and establishment processes rather than on competitive, density-dependent mortality. However, our documentation of suppressive effects of woody plants on neighbors also suggests a potentially important role for tree-tree competition in controlling vegetation structure and indicates that the balanced-competition hypothesis may contribute to well-known patterns in maximum tree cover across rainfall gradients in Africa.

Key words: Acacia; *aggregation; pair correlation function; patchiness; pattern formation; semiarid savanna; spatial ecology; woody plant interactions.*

Introduction

Understanding 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 advances 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, Bond 2008, Murphy and Bowman 2012, Tredennick and Hanan 2015). 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*a*, van Langevelde et al. 2011). Relatively little work has focused on interactions among woody plants, despite mounting empirical evidence that tree-tree interactions may be as important as tree-grass interactions in constraining savanna structure (Riginos et al. 2005, Wiegand et al. 2006, Meyer et al. 2008*b*, Moustakas et al. 2008, Calabrese et al. 2010, Kambatuku et al. 2011, Belay and Moe 2012, Sea and Hanan 2012).

Woody plants may positively or negatively affect the establishment and growth of other woody neighbors. Trees can facilitate seed germination and seedling recruitment by improving subcanopy microsite conditions through litter inputs and decreased evapotranspiration rates (O'Connor 1995, Hoffman 1996, Salazar et al. 2012), or by capturing run-off from adjacent bare patches (Franz et al. 2012). However, expansive lateral root systems typical of many savanna tree species can result in belowground competition for water and nutrients, reducing plant available resources (Belsky 1994, Schenk and Jackson 2002, Sternberg et al. 2004). Plant interactions at local scales can, in turn, influence landscape-scale productivity and the relative distribution of trees and grasses in the landscape (Riginos et al. 2009, Calabrese et al. 2010). For example, competition among trees can promote competitive self-thinning through density-dependent mortality and regularly spaced stands, a phenomenon well documented in monospecific stands and forested ecosystems

Manuscript received 21 January 2016; revised 22 October 2016; accepted 31 October 2016. Corresponding Editor: Truman P. Young.

[7] E-mail: jdohn3@hotmail.com

(e.g., Laessle 1965, Kenkel 1988, Stoll and Bergius 2005, Wiegand et al. 2008). Direct empirical evidence of competition among savanna woody species is comparatively rare (Calabrese et al. 2010), particularly studies evaluating the growth performance of multi-age and multi-species assemblages. Instead, competition in mixed woody-herbaceous systems has generally been inferred from spatial distribution of woody plants, with studies reporting spatial arrangements ranging from clumped to over-dispersed (Skarpe 1991, Couteron and Kokou 1997, Barot et al. 1999, Jeltsch et al. 1999, Caylor et al. 2003, Moustakas et al. 2008, Pillay and Ward 2012, Browning et al. 2014). As such, we have a poor understanding of the relative importance of woody competition in shaping savanna vegetation structure, and studies that empirically evaluate the effect of woody plants on neighboring plant growth in savannas represent a clear research need.

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 characterize savanna ecosystems (Klausmeier 1999, HilleRisLambers et al. 2001, Pueyo et al. 2008). Where such patterns are generated by the patchy distribution of woody plants, both facilitation and competition may be operating (Schleicher et al. 2011), the former through plant clusters effectively trapping moisture inputs or increasing resource availability through hydraulic lift, litter fall and nitrogen fixation, and the latter operating within clusters depending upon woody plant 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 require examination of stand structure in low-disturbance situations (Calabrese et al. 2010). We present data from a 10-yr 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 were to assess the magnitude of competition among woody plants in this system, quantify the spatial scale of plant competition and infer its role in determining landscape-scale woody distribution. We expand on studies that infer competition intensity and importance from spatial patterns alone by combining spatial point-pattern analyses of woody plant distribution at each site with analysis of growth performance in the presence of varying densities of neighbors. Finally, we explicitly considered species-specific responses to competition intensity, including effects of conspecific and heterospecific neighbors, in order to make inferences about the mechanisms governing woody species diversity.

METHODS

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 are underlain by well-drained, moderate to very deep, friable sandy loams and occur 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. Vegetation in the area is characterized by an *Acacia*-dominated bushland community and a discontinuous layer of perennial grasses (Augustine 2003). The woody plant canopy layer is dominated by *Acacia (Senegalia) mellifera*, *Acacia (Vachellia) etbaica*, *Acacia (Senegalia) brevispica* and *Grewia tenax* (Augustine and McNaughton 2004).

Herbivore exclosures (70 × 70 m) were established at each of three study sites at MRC in 1999. Exclosure fences exclude mammalian 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 × 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 remeasured. Woody plant sizes varied widely with some individuals >9 m in height. Some dominant species such as *A. mellifera* could be considered either shrubs, due to their spherical, multi-branched growth form, or trees, due to their height. Site-level averages of woody plant density and size are shown in Table 1. A more detailed description of the study area and experimental design can be found in Appendix S1.

Spatial analysis

To examine the spatial organization of woody plants within each plot, we implemented the univariate pair correlation function $g(r)$, which estimates the probability of finding a point at distance r from a representative focal point, normalized by dividing by the intensity of the pattern (i.e., the mean number of points per unit area) to facilitate interpretation (Stoyan and Stoyan 1994). 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),

Table 1. Woody plant density and median basal area (BA) and height (*h*) on three survey dates at experimental sites in Mpala Research Centre, Kenya.

Year	Site A			Site B			Site C		
	Density (individuals/ha)	BA (cm^2)	*h* (m)	Density (individuals/ha)	BA (cm^2)	*h* (m)	Density (individuals/ha)	BA (cm^2)	*h* (m)
1999	2,408	3.1	1.4	1,292	2.3	1.3	988	4.5	1.9
2002	2,740	3.7	1.5	1,728	2.3	1.3	1,456	2.0	1.1
2009	3,908	3.6	1.9	3,196	3.4	1.8	2,768	3.9	2.4

while values of $g(r) < 1$ signify point dispersion. Confidence envelopes for the null model were estimated by extracting the 2.5 and 97.5 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). Because use of prediction envelopes for statistical testing of spatial point patterns underestimates Type 1 error (Loosmore and Ford 2006), the Diggle-Cressie-Loosmore-Ford test was used to determine if the observed spatial pattern differed from the null hypothesis of CSR and to evaluate goodness-of-fit for the computed confidence envelopes (Cressie 1991, Diggle 2003, Loosmore and Ford 2006). Bootstrap confidence intervals for the true value of the pair correlation functions for each site were estimated based on 1000 pointwise simulations (Loh 2008). Spatial analyses were conducted using the R package spatstat (Baddeley and Turner 2005) with an isotropic correction, which adjusts for edge effects in rectangular plots. Further details on the spatial analysis can be found in Appendix S1.

Neighborhood competition model

Woody plant 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 $y = (\ln BA_2 - \ln BA_1)(t_2 - t_1)^{-1}$. Linear mixed effects models were used to evaluate the effects of neighboring woody plants on focal plant RGR, with site 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. Spatial autocorrelation of woody plant growth estimates was evaluated through model comparison utilizing various forms of correlation structures available in the nlme package in R (Pinheiro and Bates 2000, Pinheiro et al. 2013).

The primary objective of the fixed effects structure of the model is to describe the effects of neighbors on focal plant RGR. There are two fundamental considerations in characterizing a woody plant's competitive neighborhood: the size of the neighborhood (i.e., the distance at which neighbors are considered to be 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 plants. We compared the performance of this model to one utilizing a distance-dependent competition index (CI1)

$$\mathrm{CI1}_i = \sum [D_j(dist_{ij}+1)^{-1}] \qquad (1)$$

where neighborhood influence on the *i*th individual is a function of the size of neighbors (D_j) and the distance between the neighbor and focal plant (dist_{ij}). Because it appeared that neighboring plants at very close distances were having disproportionate effects, we evaluated a square-root transformation on dist_{ij} (CI1-SQRT). We also tested another index of competition intensity commonplace in plant growth studies, Hegyi's CI (CIh; Hegyi 1974), which is similar to Eq. 1 but implements a distance-weighted ratio of neighbor to focal plant size (D_i)

$$\mathrm{CIh}_i = \sum [(D_j D_i^{-1})(dist_{ij}+1)^{-1}]. \qquad (2)$$

The CIs for heterospecific and conspecific neighbors were estimated independently and included as separate predictors in the mixed model. These models performed better than models with a single competition index that combined heterospecific and conspecific neighbors. Initial size was also included as a fixed effect to account for the decline in RGR with increasing size observable in most organisms (Rees et al. 2010). Height, basal area, basal diameter and canopy area at each date, as well as averaged over the study period, were all tested as indices of focal plant size. Models with and without log transformations of the size predictor were considered to address the assumption of normality.

All eligible model variants, including all combinations of CI forms and size estimates, were ranked based on Akaike information criterion (AIC). 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 plant RGR. Beginning with a large neighborhood radius (>15 m), models with sequentially smaller neighborhood sizes (0.5 m intervals) were ranked based on AIC. After selecting a neighborhood size, the model was evaluated for extraneous predictors and interactions. Beginning with a maximal model that included all fixed effects (i.e., hetero- and conspecific CIs and focal plant size) and their interactions, covariates were removed based on stepwise AIC deletion until model parsimony was achieved. Model residuals were visually evaluated for homogeneity and normality, and model fit was estimated using a measure of goodness of fit (R^2) developed for linear mixed models (Nakagawa and Schielzeth 2013). The model selection process was repeated in its entirety independently for all abundant species in the plots ($N > 25$ at two or more data survey time steps). Model coefficients, AIC and model fit (R^2) for the species-specific models were compared to a species-neutral model that does not explicitly account for species-level effects, and to a single mixed model with species as a categorical fixed effect. Separate models distinguished by the size class of the focal individual (0.5–1.5, 1.5–2.5, and >2.5 m height) were evaluated to test for an ontogenetic shift in the effects of neighboring plants on focal individuals (Lessin et al. 2001, Miriti 2006). All modelling efforts were conducted in the *nlme* package in R version 3.0.2 (Pinheiro et al. 2013, R Development Core Team 2013). Further details on the neighborhood competition model and model selection process can be found in Appendix S1.

RESULTS

Woody plant aggregation

Spatial point-pattern analysis revealed significant aggregation at short distances from focal shrubs in all three sites ($g(r) > 1$), with a tendency toward random or dispersed distributions at greater distances ($g(r) \leq 1$; Fig. 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 2). To test whether spatial processes shift over the life cycle of shrubs, we ran point-pattern analyses for woody plants separated into three size classes (0.5–1.5, 1.5–2.5, and >2.5 m height). Results of these size-class analyses were qualitatively similar to the community-scale analysis (i.e., aggregation at all size classes), and thus only the latter is shown here.

Modelling woody plant competitive neighborhoods

Model comparison based on AIC indicated that models using the CI1 index of competitive neighborhood were generally superior to the other candidate indices (see Appendix S1 for tables detailing AIC model comparison for all steps in the model selection process). In the case of equivalent models with different competition indices ($\Delta AIC < 2$), CI1 was used for consistency across species. The best estimator of neighbor size in the calculation of CI1 varied among species between basal area and basal diameter (Table 3). With the exception of the model describing *Croton dichogamous* growth rates*,* initial basal area and initial basal diameter had nearly identical fits when evaluated as a proxy for focal plant size. We adopted basal area to represent initial size as this metric was more directly linked with the response variable (woody plant basal area RGR). In the case of *C. dichogamous*, initial canopy area was found to better explain focal plant growth. Thus, the full models test variations in RGR as a function of hetero- and conspecific competition (CI1) and log-transformed initial basal area. Visual assessment of model residuals initially found a violation of the assumption of normality, which we addressed by evaluating and excluding outliers based on a two-sided outlier test on the normalized residuals ($\alpha = 0.001$).

Model evaluation based on AIC stepwise deletion resulted in the removal of select covariates in nearly all cases (Table 3). Notably, the conspecific CI and in many cases its interaction with focal plant size were generally

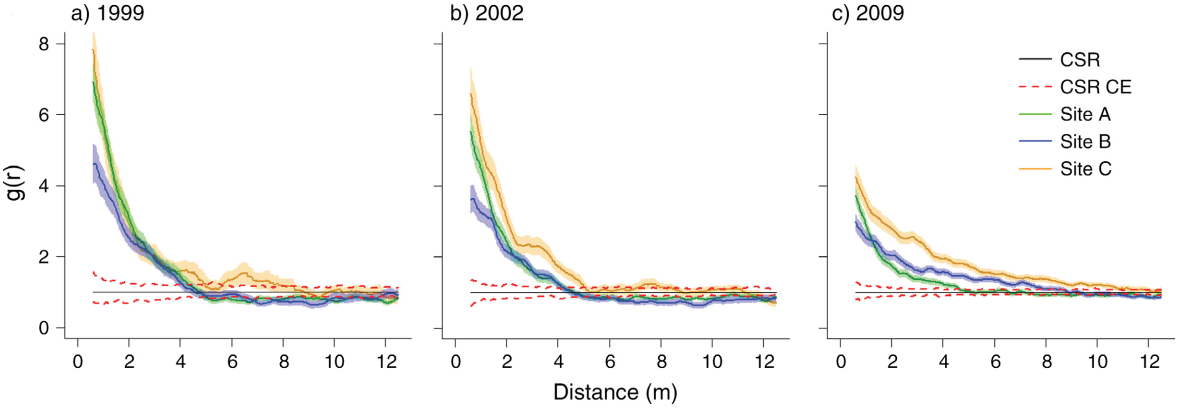

FIG. 1. Univariate pair correlation functions $g(r)$ detailing woody plant distribution in three sites at Mpala Research Centre, Kenya, mapped in 1999, 2002, and 2009. Woody plant communities aggregated ($g(r) > 1$) at increasing distances over time, particularly at sites B and C, concurrent with increasing population densities in each site (Table 1). 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 bootstrap simulations. [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 2. Species-level summary statistics for woody plant populations at initial (1999) and final (2009) data surveys across all sites.

Species	Density (individuals ha^{-1})		Relative abundance (%)		Height (m)		Growth	
	1999	2009	1999	2009	Mean	Maximum	BA (cm^2·yr^{-1})	RGR (cm^2·cm^{-2}·yr^{-1})
Acacia brevispica	361	404	23.97	12.61	2.0 (1.0)	5.9	0.60 (1.43)	0.06 (0.13)
Acacia etbaica	303	821	20.12	25.62	1.4 (0.9)	5.4	1.79 (4.15)	0.17 (0.14)
Acacia mellifera	312	908	20.72	28.34	1.8 (1.4)	9.1	3.89 (11.28)	0.11 (0.11)
Balanites aegyptiaca	23	51	1.53	1.59	1.6 (1.1)	4.2	3.50 (4.57)	0.23 (0.14)
Boscia angustifolia	16	27	1.06	0.84	1.7 (1.1)	4.6	2.71 (5.27)	0.11 (0.10)
Commiphora spp.	13	45	0.86	1.40	0.9 (0.5)	2.2	1.67 (5.9)	0.11 (0.14)
Croton dichogamous	80	137	5.31	4.28	1.6 (0.6)	4.1	0.41 (0.98)	0.04 (0.10)
Euclea divinorum	15	39	1.00	1.22	2.0 (1.3)	6.0	1.38 (2.73)	0.16 (0.12)
Grewia tenax	247	533	16.40	16.64	1.1 (0.6)	3.9	0.42 (0.61)	0.15 (0.12)
Lycium europaeum	111	164	7.37	5.12	1.2 (0.6)	3.7	0.09 (0.69)	0.05 (0.11)
Rhus spp.	25	75	1.66	2.34	0.9 (0.4)	2.9	0.69 (1.51)	0.14 (0.14)

Notes: Individual height estimates are for 2009. Growth estimates represent basal area increment (BA) and relative growth rate (RGR) means with associated standard deviations in parentheses. Only species with number of individuals $N > 10$ in the survey plots are shown here.

retained in the models, while the effects of heterospecific neighbors were far more variable. Conspecific neighbors suppressed focal plant growth for all species except for *G. tenax,* where no effect of conspecifics was observed, and *A. etbaica*, where a facilitative effect was observed. In all cases where the heterospecific CI was retained in the model, heterospecific neighbors suppressed focal plant growth. Woody plant RGR decreased with increasing size for all species. Competitive neighborhood sizes ranged from 2.5 to 5 m radius. For many species, multiple neighborhood sizes within this range offered statistically indistinguishable model fits (see Appendix S1), in which case the smallest neighborhood size was selected. Model outputs with species-level coefficient estimates are presented in Table 3. Intercepts represent RGR estimates for a woody plant of mean basal area (see Table 4 for species-specific mean values) in the absence of competition (CI1 = 0). Separate models distinguished by focal shrub size classes were qualitatively similar (i.e., same direction and general magnitude of competitive neighborhood and

TABLE 3. Model output for species-specific models predicting focal woody plant relative growth rate as a function of a neighborhood competition index (CI) and focal plant basal area (cm^2) at the onset of the experiment.

Neighbor size estimator and species	Neighborhood size (m)	N	R^2	Model coefficients					
				Intercept	Heterospecific CI	Conspecific CI	Initial size	Het CI size	Con CI size
Basal area									
Acacia brevispica	3.5	186	0.51	0.114		−0.0010	−0.029		
Acacia mellifera	2.5	240	0.45	0.145	−0.0003	−0.0005	−0.025		
Lycium europaeum	5.0	66	0.57	0.076		−0.0003	−0.012		−0.0027
Rhus spp.	3.0	25	0.49	0.184		−0.0148	−0.042		−0.0177
Basal diameter									
Acacia etbaica	2.5	195	0.51	0.209	−0.0070	0.0021	−0.040	0.0015	−0.0022
Croton dichogamous	3.5	31	0.73	0.202		−0.0079	−0.090†		0.0028
Grewia tenax	3.0	162	0.36	0.231	−0.0031		−0.043		
All species‡	4.0	913	0.55	0.178	−0.0002	−0.0037	−0.033	0.0003	−0.0001
Species neutral§	3.0	1,008	0.30	0.182	−0.0025	−0.0019	−0.028		−0.0007

Notes: Models differed in the optimal estimator for neighbor size in the CIs, chosen based on Akaike information criterion (AIC) model comparison. Neighborhood size (radius) was determined based on AIC model comparison among models with sequentially smaller neighborhood sizes. *N* represents sample size after subsampling data set to adjust for edge effects and outliers. For main effects, more negative values represent greater negative relationships between the focal plant and the density of neighbors. Missing values show covariates removed during the AIC model simplification process (see Appendix S1).

† Canopy area used as initial size estimator for *C. dichogamous.*

‡ All species included in one model, represented as a categorical fixed effect.

§ All species included in one model, with no explicit consideration of species effects.

Table 4. Average size (initial basal area; cm^2) and neighborhood competition intensity for abundant species on three sites at Mpala Research Centre, Kenya.

Species	Heterospecific CI		Conspecific CI		Basal area	
	Mean	SE	Mean	SE	Mean	SE
All species	163.7	6.9	36.8	1.7	27.3	4.0
Acacia brevispica	142.0	11.6	41.6	2.0	11.8	1.4
Acacia etbaica	65.2	5.9	47.3	4.6	27.0	8.1
Acacia mellifera	51.0	6.8	62.8	5.0	72.3	15.1
Croton dichogamous	217.8	20.8	55.1	5.0	5.2	1.2
Grewia tenax	274.3	19.6	13.3	1.0	1.7	0.2
Lycium europaeum	339.6	28.8	5.6	0.7	3.5	0.9
Rhus spp.	417.1	68.3	3.9	0.9	5.3	2.0

Notes: Values represent means across all three sites with associated standard errors (SE). Competition intensity is a function of the size and distance of heterospecific and conspecific neighboring woody plants within 4.0 m radius, estimated with a competition index (CI; see *Methods* for CI description).

initial size effects); thus, only the model including all mapped woody individuals is presented here.

In general, increasing neighborhood competition decreased woody plant RGR, with a decline from ~0.18 $\text{cm}^2\cdot\text{cm}^{-2}\cdot\text{yr}^{-1}$ in the absence of competition to ~0.13 $\text{cm}^2\cdot\text{cm}^{-2}\cdot\text{yr}^{-1}$ under community-wide mean competition intensity for young saplings in the species-neutral model. However, the results of the species-specific models indicate stark differences among species in their potential growth rates and in their response to neighborhood competition. We illustrate this by comparing modeled RGR for each species as a function of initial basal area: first, in the absence of competition (CI1 = 0; simulating isolated woody plants with no neighborhood effects; Fig. 2A), second, in the presence of species-specific mean levels of competition (i.e., CI1 is set at mean levels for each respective species; Fig. 2B, see Table 4 for mean CI values), and third, in the presence of community-wide mean levels of competition (i.e., CI1 is set at average levels found for all woody species, allowing direct comparisons of species growth rates under a set competition intensity; Fig. 2C). Notably, *Lycium europaeum* and *A. brevispica* grew most slowly and *G. tenax* and *A. etbaica* grew most rapidly, irrespective of neighborhood competition intensity (Fig. 2). Conversely, *C. dichogamous* responded significantly to shifts in its competitive neighborhood, with a relatively high potential growth rate under low competition (Fig. 2A), but distinctly low RGR under the high levels of competition typically found for this species (Fig. 2B, Table 4). *Rhus* also performed poorly under community-mean competition intensity due to substantially higher levels of conspecific competition relative to average levels found for this species (Fig. 2B, C; Table 4) and the strong suppressive effect of conspecific neighbors on *Rhus* individuals (Table 3).

Discussion

The role of woody plant competition in structuring savanna ecosystems is poorly understood, in part due to a dearth of empirical studies examining how the complex spatial distributions of woody plants found in many savannas are related to individual growth rates. We found that woody plants in this semiarid savanna exhibit strongly clumped spatial distributions at scales of 1–5 m. However, analyses of woody plant growth rates relative to their conspecific and heterospecific neighbors revealed evidence for competitive interactions at similar scales for most woody plant species. In other words, woody plants are far more aggregated than expected by chance, but such aggregation is associated with reduced growth rates for individuals in size classes ranging from saplings to mature individuals. This finding suggests that processes leading to aggregation operate at earlier demographic stages than processes controlling growth of saplings and larger individuals. In particular, controls over seed dispersal, seed germination, and the survival of seedlings to the sapling stage (i.e., survival to 0.5 m height, at which point an individual would begin to be mapped and monitored in our dataset) appear to lead to the clumped distribution of woody plants in this savanna. Once a sapling is established, however, competitive interactions outweigh potential facilitative effects of neighbors on resources, controlling growth of larger size classes. Such ontogenetic shifts from facilitation to competition have been demonstrated in other woody systems (e.g., Miriti 2006). Woody plant density also increased substantially over time, attributable to a release from browsing pressure following the exclusion of large herbivores from the study sites in 1999. In the absence of browsing pressure, the parallel increases in woody plant density and cluster size suggest that recruitment events occur with increasing frequency in close proximity to established individuals relative to intervening open areas.

We suggest that spatial aggregation of woody plants in this savanna may be driven by three candidate mechanisms: propagule dispersal, underlying environmental heterogeneity, and facilitative effects of neighbors on seedling establishment and growth. Dispersal processes could influence long-term spatial patterns in several

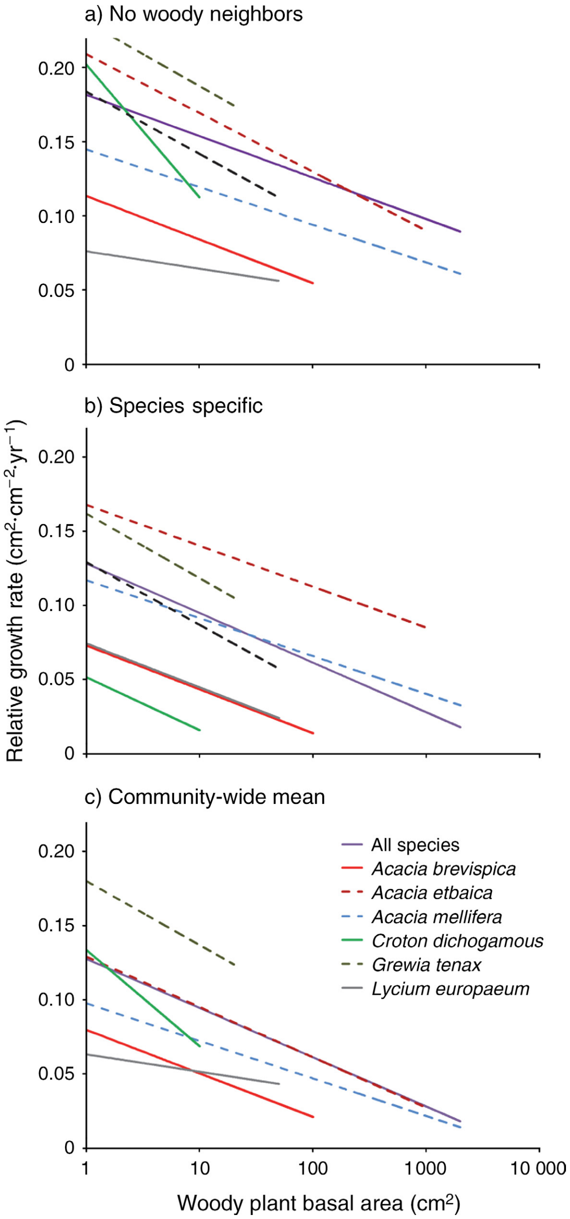

FIG. 2. Modeled relative growth rate of woody plants as a function of initial basal area (log scale) under three competitive neighborhood scenarios (see *Methods* for description of competition index [CI]): (A) no competition (CI1 = 0; simulating isolated individuals with no neighborhood effects), (B) species-specific mean CI (i.e., CI1 is set at mean levels for each respective species, simulating growth rates under average competition intensity for each species; see Table 4 for mean CI values), and (C) community-wide mean CI (i.e., CI1 is set at average levels found for all woody species, allowing direct comparisons of species growth rates under a set competition intensity). *Rhus* is excluded from panel C to improve figure visibility (strongly negative relative growth rate [RGR] under community-wide mean CI for *Rhus* obscures other species differences). [Color figure can be viewed at wileyonlinelibrary.com]

ways. First, seed rain may be greater in the immediate vicinity of mature individuals. Given the scale of woody plant aggregation (1–5 m) and the fact that intervening spaces between individuals were as small as the height of mature plants (e.g., 5–9 m), this mechanism could potentially contribute to our documented spatial patterns. In addition, some species with strongly clumped distributions (e.g., *Rhus, Grewia*) are dispersed by birds, which could contribute to greater seed deposition beneath rather than between canopies.

Alternatively, seed deposition and germination may occur with relative regularity throughout the landscape, while establishment and long-term survival vary with edaphic and microclimate heterogeneity (Walker et al. 1986, O'Connor 1995, Witkowski and Garner 2000, Midgley and Bond 2001). Our study system is characterized by gently rolling topography, with all study sites on slopes of 2–3 degrees. Surface soil texture was relatively homogenous across the study plots; we did not quantify spatial variation in the soil profile or depth to bedrock. However, the regularity in spatial clustering of woody plants at the scales we quantified seems unlikely to be associated with a similar regularity in edaphic heterogeneity. A third possibility is that existing woody plant clumps promote aggregation through facilitation of seedlings. For example, studies in this savanna have shown that surface runoff from upslope patches with low plant density can be trapped in clumps, resulting in increased infiltration and soil moisture availability (Franz et al. 2012). Established woody plant canopies may also improve microsite conditions by reducing evaporative losses due to light interceptance (O'Connor 1995, Salazar et al. 2012), and by increasing subcanopy nutrient concentrations through litter deposition (Belsky et al. 1989, Ludwig et al. 2004, Hagos and Smit 2005). Furthermore, the effects of woody plants on understory herbaceous production vary predictably with mean annual precipitation such that woody plants in dry regions generally promote subcanopy grass growth (Dohn et al. 2013). Indeed, clusters at MRC typically have greater grass biomass than inter-plant spaces (Augustine 2003). We suggest that facilitative processes leading to aggregated distributions may primarily operate in surface soil layers where moisture is accessed by woody seedlings and grasses, because our neighborhood analyses indicate competitive interactions among neighboring woody plants in the sapling and larger size classes, and such competition is likely to occur in deeper soil layers. Most importantly, our findings indicate that processes governing seed dispersal, seed germination and seedling establishment are more important than competition among established woody plants in determining plant distribution, at least in some savannas.

We also note that woody plant aggregation, including new establishments, 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 in a landscape can result in a mosaic of burnt and unburnt patches when woody plants reduce herbaceous fuel load, promoting higher seedling survival near established clumps. Though fire may have contributed to clumped distributions observed at the onset of the study, our results show that aggregation of woody plants persist and increase in the absence of fire, suggesting that aggregated spatial patterns are not induced by fire alone.

We found strong evidence of competition among woody plants within a 2.5–5.0 m radius neighborhood depending on the species of the focal plant, with a community-scale neighborhood of 3.0 m. At this scale, our results indicate a decrease in growth rates with increasing neighbor size and decreasing distance to neighbors. Basal stem size of neighbors better predicted RGR of focal plants compared to height and crown area metrics. This finding strongly points to belowground competition for water as the likely mechanism generating competitive suppression of growth rates, as has been suggested by other studies 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 wetter systems (e.g., von Oheimb et al. 2011, Fraver et al. 2014). Water limitations and drought seasonality characteristic of tropical savannas shift the primary limiting factor to belowground resources. Thus, it follows that morphological characteristics reflective of below-ground resource capture are linked with variation in savanna plant growth rates. The spatial extent of competition we detected may reflect species-specific average lateral range of primary root biomass, though we lack root distribution data to test this directly.

The magnitude of a woody plant's response to neighbors varied with the size of the focal individual and the species of the neighbor and focal plant. Species also differed in their relative responses to hetero- and conspecifics, indicating distinct differences in competitive abilities. In addition to differential responses of species to hetero- and conspecific competition, we observed conspicuous shifts in community composition over the duration of the study, with some species increasing in relative abundance at the expense of others. Three species that decreased in relative abundance were associated with low mean RGR (particularly in their species-specific competitive neighborhoods; *A. brevispica, C. dichogamous* and *L. europaeum*), large neighborhood sizes (≥3.5 m), and high mean levels of competition with heterospecific neighbors. Two dominant species that increased dramatically in relative density exhibited balanced effects of hetero- and conspecific neighbors on their growth rates; both *A. etbaica* and *A. mellifera* appear to be effective competitors for belowground resources. Notably, these two *Acacias* also displayed the lowest levels of mean competition intensity of all surveyed species, suggesting an increased ability to colonize interplant patches due to high dispersal ability or enhanced establishment success away from clumps. For a given plant size, RGR was greater for *A. etbaica* than *A. mellifera*, both in the presence and absence of competition, which was surprising given that *A. etbaica* invests to a greater degree in structural defense (straight and recurved thorns) than *A. mellifera* (recurved thorns only). Understanding above- and belowground traits that allow species such as *A. etbaica* to compete effectively in dense neighborhoods while also allocating resources to structural defenses against herbivores is a key research need.

The observed increase in tree density following the removal of herbivores demonstrates the degree to which disturbances, in this case, browse-induced seedling mortality and growth suppression (Sankaran et al. 2013), can impact landscape scale woody density and cover in savannas. However, our documentation of suppressive effects of woody plants on neighbors demonstrates an important role for tree–tree competition in limiting woody plant growth rates. These results provide support for the balanced competition hypothesis, which suggests that trees in mixed woody-herbaceous systems become self-limiting as densities increase (Scholes and Archer 1997, Sankaran et al. 2004). Thus, competition among woody plants may contribute to observed patterns in maximum woody cover across rainfall gradients in Africa (Sankaran et al. 2005).

Conclusion

We found spatial aggregation of woody plants, despite significant decreases in growth rates when plants are growing in competition with neighbors. African savannas are highly dynamic ecosystems characterized by substantial seasonal variation in moisture availability combined with high herbivore density and frequent fires (Scholes and Archer 1997, Bond 2008). Browsing, fire and water limitation likely represent major evolutionary drivers in African savannas, translating into a competitive advantage for species adapted to 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, Sankaran et al. 2013, 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, but not limited to, (1) dispersal limitation (e.g., greater seed deposition beneath existing canopies), and (2) spatial heterogeneity in seed germination and survival associated with edaphic variability and surface run-off/run-on patterns influenced by plant clusters. In particular, we suggest that facilitative moderation of the abiotic environment by existing woody clumps that trap surface runoff (Franz et al. 2011) and improve resource availability may be an important mechanism contributing to spatial patterns in woody plant distribution. Additional beneficial or detrimental effects of clumped spatial patterns may be realized in the presence of fire and/or herbivory, but our results in plots not subject to either fire or large mammalian herbivory suggest that (1) endogenous abiotic components of savanna systems combined with soil–plant feedbacks are sufficient to produce aggregated arrangements, and (2) both interspecific and conspecific competition become important determinants of growth rates within woody plant clusters. This suggests a potentially important role for tree-tree competition in controlling patterns in maximum tree cover across rainfall gradients in Africa.

Acknowledgments

We thank J. Ekiru, F. Lomojo, Lokwye, and Lokken for assistance in the field, the Office of the President of the Republic of Kenya for permission to conduct the research, and the Mpala Research Centre for logistical support. We also thank T. Young and two anonymous reviewers for helpful comments that greatly improved this manuscript. This manuscript is based upon work supported by the National Science Foundation under NSF Graduate Research Fellowship Grant DGE-0822211 to J. Dohn, grants DEB-1139096 and DEB-0919078 to N. Hannan, grants from NERC (NE-E017436-1) and UKPopNet to M. Sankaran, a grant from the Earth & Biosphere Institute (EBI), University of Leeds, Leeds, UK to J. Ratnam, and support from the USDA-Agricultural Research Service to D. J. Augustine.

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