Original article

Woody dominance in a semi-arid savanna rangeland — Evidence for competitive self-thinning

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ABSTRACT

Self-thinning has been considered an important mechanism facilitating species coexistence in nature. The purpose of this study was to examine the role of self-thinning in regulating the density of woody plants in semi-arid savannas. Previous models (e.g. the 'honeycomb rippling model') have postulated that, as trees grow older (inferred by size), the interplant distance, taken to reflect competition-induced mortality, becomes greater and more even. Therefore, the opening of canopies in the long-run promotes species coexistence. To study the role of self-thinning in a semi-arid savanna we selected four savanna patches and sampled the plant density, size, and distance between the tallest woody plant and its nearest conspecific and heterospecific neighbors, along with other environmental variables. Interplant distance was positively influenced by species, tree size, woody species diversity, and nearest neighbor type (conspecific vs. heterospecific). Distances did not increase evenly with increasing size of the tallest tree or shrub, however. We conclude that self-thinning is evident in woody encroached semi-arid savanna patches, as suggested by the honeycomb rippling model. The mechanism may play a significant role for the long-term stability of the savanna by opening dense canopies and facilitating tree–grass coexistence.

1. Introduction

The structure of a savanna vegetation is partitioned between woody and herbaceous layers (Scholes and Archer, 1997). The balance between these two layers is maintained primarily by competition for scarce environmental resources, such as water and nutrients, and factors such as fire, herbivory and precipitation that buffer the dominance of any one life form in the landscape (Sankaran et al., 2004, 2005). Nevertheless, over the past few decades, increasing dominance by woody plants and a corresponding decline in herbaceous production has been widely reported from many arid and semi-arid savannas (Ward, 2005; Scheiter and Higgins, 2009; Lunt et al., 2010). This phenomenon, referred to as woody encroachment, is regarded as a serious threat to livestock production (Archer, 1990; Hudak, 1999; Shackleton and Gambiza, 2008) and to the overall integrity of these ecosystems (Biederman and Boutton, 2009; Ratajczak et al., 2012). Although several models have been developed to explain how the phenomenon happens in different rangelands (e.g., Walker and Noy-Meir,

1982; Westoby et al., 1989), its causes are not well understood (Ward, 2005).

Despite limited knowledge of the driving factors, ecologists have questioned what the long-term implications of woody encroachment might be for species coexistence and whether the process could be reversed naturally through local competition and density-dependent mortality. This process of competitive self-thinning was originally proposed to describe the influence of plant density on the biomass or size of individual trees in even-aged monoculture plantations (Yoda et al., 1963; Westoby and Howell, 1986). Various models have been developed subsequently to predict how self-thinning affects individual tree biomass or size in mixed-size stands (e.g., Tome and Burkhart, 1989; Reynolds and Ford, 2005). More recently, a wide perspective on self-thinning has been developed and used to predict density-dependent mortality in natural ecosystems (Wiegand et al., 2006). Few studies, however, have provided evidence of the process in natural rangeland ecosystems that are composed of diverse species and mixed age groups (e.g., Enquist and Niklas, 2001; Midgley, 2001; Meyer et al., 2007; Sea and Hanan, 2012).

Some authors (e.g., Wiegand et al., 2006; Sea and Hanan, 2012) suggest that self-thinning is a potent natural mechanism stabilizing the density of woody vegetation in savanna rangelands. Woody encroachment is accordingly considered to be a natural phenomenon triggered by irregular rare events, such as periods of high

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rainfall, the resulting dense woody patches persisting only temporarily until self-thinning mortality emerges (Wiegand et al., 2006). Through time, the ecosystem gradually returns to a more open state and stabilizes, a process described as the 'honeycomb rippling model of patch dynamics' (Ward, 2005; Wiegand et al., 2006).

The honeycomb rippling model is based on the assumption that growth, inferred from tree size, and mortality, inferred from distance between the nearest neighboring trees, are strongly influenced by intra- and interspecific competition between woody plants for scarce environmental resources, principally water and soil nutrients in savannas (Wiegand et al., 2006). The model describes the process of self-thinning in arid savannas, which are characterized by highly variable rainfall, as follows. After any favorable event, for example, suitable rainfall, many equal-sized seedlings germinate in patches. Suppose these equal-sized seedlings are spatially distributed in a hexagonal pattern, forming a series of circular rings (like a honeycomb), with roots and branches touching each other. As the seedlings grow larger, they start competing with their immediate neighbors because of increasing demand for environmental resources. Competition becomes particularly intense during unfavorable (e.g. drought) years. If one of the seedlings in the center of the hexagon (first ring) outcompetes its immediate neighbors (second ring), causing them to die, this mortality provides an opportunity for individuals in the first and the third rings to access more resources and grow bigger, gradually occupying more space and subsequently coming to compete with each other. Another round of mortality ensues. Thus, the mortality of every second seedling benefits the surviving neighbors in the ring. This thinning process continues successively, rippling through the community, until maximum tree size has been attained and the distance between neighboring trees is wide enough to minimize resource competition (Wiegand et al., 2006). Eventually, with increasing tree size through time, the distance between the trees becomes more even (Fig. 1). According to this model, therefore, opening up the tree canopy through self-thinning, in the long run, is expected to facilitate grass recovery and the restoration of the entire rangeland system.

The main objective of this study was to examine whether self-thinning, as suggested by the honeycomb rippling model, is evident in a semi-arid savanna, and to assess its potential for inducing long-term stability in the woody encroached savanna patches. Compared with arid areas, semi-arid savannas receive relatively better, but still highly variable rainfall. Frequent droughts, which are typical of the lower Omo region (Carr, 1998), can increase moisture stress in the soil, thereby triggering intense competition between woody plants (Chesson, 2000). We were specifically interested in exploring the relationship between interplant distance, implicated in competition-induced mortality, and tree or shrub size, associated with growth, as predicted by the honeycomb rippling model. We asked the following questions:

1) Does the distance to nearest conspecific and heterospecific neighbors increase with increasing size of the tree or shrub? If self-thinning is a natural mechanism regulating the density of woody plants in savannas, we would expect a strong positive association between woody plant size and distance to the nearest neighbor (Wiegand et al., 2005).

2) Is self-thinning influenced by (a) whether the nearest neighbor is conspecific or heterospecific; (b) the diversity of woody species present in the vicinity; (c) the identity of the woody plant species and their attributes, such as its nitrogen-fixing ability and growth-form; and (d) some measure of environmental stress? The intensity of self-thinning increases with the level of environmental stress (Grime, 1979; Chu et al., 2010). More fertile soils and higher rainfall should lower environmental stress, thereby reducing the level of competition. Consequently, interplant distance is expected to decline with increasing rainfall, and between nitrogen-fixing woody plants.

3) Does interplant distance become more even with increasing woody plant size? Within a plot, we would expect a strong negative association between the coefficient of variation (CV) of interplant distance and mean tree size. That is, as the size of woody plants increases, interplant distance should become more uniform (reflected in a lower CV), compared to plots with small-sized trees or shrubs.

2. Material and methods

2.1. Study area

The study was conducted in the western part of Hamer district in the lower Omo region, Southwestern Ethiopia (4.92–5.33° N, and 36.17–36.37°E). It is surrounded by Mago National Park to the north, the Omo River to the west, and the Bethesda and Gemballa plateaus to the east (Fig. 2). The area has mostly arid to semi-arid climate. Long-term rainfall data recorded at the Turmi and Erbore meteorological stations, obtained from the Southern Ethiopian Meteorology office, shows average annual rainfall to be 581 mm, with high inter-annual variability (CV = 33.7%). The elevation ranges between 398 and 550 m above mean sea level, and higher elevation areas are largely dominated by savanna vegetation, with *Acacia* spp. and other broad-leaved trees and dwarf shrubs prominent. Areas in the lowlands, closer to the Omo R, are dominated by tall grasses and dwarf shrubs. Although the area is traditionally a communal grazing land for the Hamer and Kara people, it has been partly administered by the Murule Control Hunting Area Management Unit since the mid-1970s. In recent years, most of these rangelands have become encroached by woody species that suppress grass growth and adversely affect livestock production and wildlife conservation. Although the vegetation is adapted to fire and herbivory, such disturbances have been suppressed for the past few decades as a result, primarily, of frequent droughts occurring in the region (Carr, 1998).

2.2. Site selection and sampling method

Following a preliminary survey conducted in 2009, we selected four rangeland sites with similar elevation, landforms and soil types. Site 1 (Murle) was located adjacent to Murle headquarter; whereas Site 2 (Gudre), Site 3 (Zewgella) and Site 4 (Lochuba) were located approximately 15 km south, 20 km north, and 30 km southeast of Murle headquarter, respectively (Fig. 2). The 1980 land-cover map of the region showed all the sites as open savannas, at which time they were important grazing areas for both wild and domestic herbivores. Site 1 still retains its open savanna structure, but sites 2, 3 and 4 have recently become, respectively, slightly,
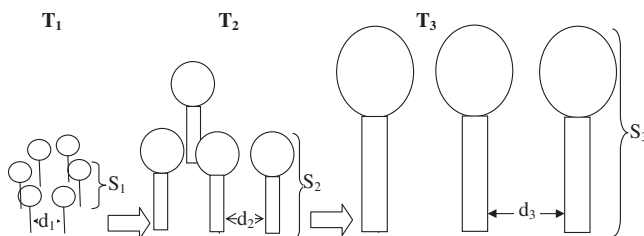

Fig. 1. The two main predictions of honeycomb rippling model: first, the inter-distance between woody plants (d) increases with tree or shrub age predicted by size (S); second, in the process of successive thinning with time (T), density declines and the interplant distance gradually becomes more even (i.e. the variability of interplant distance between individual trees or shrubs is $T3 < T2 < T1$).
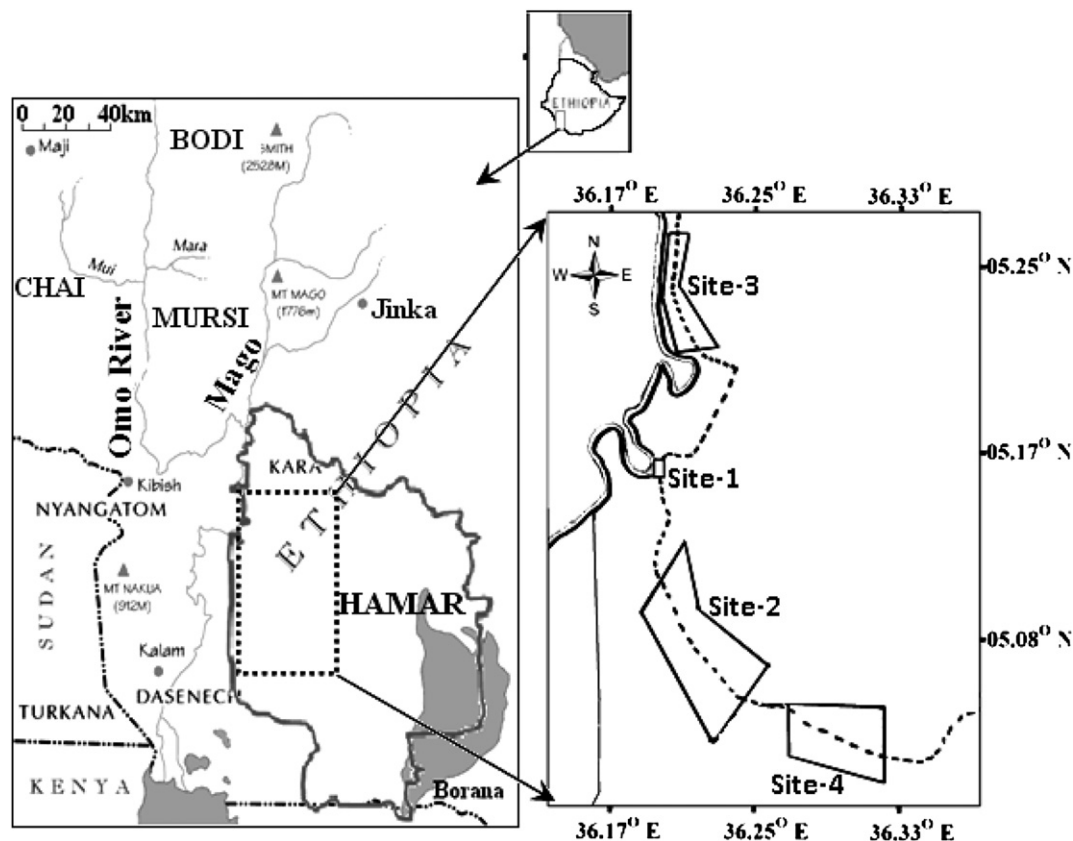
Fig. 2. Location of the study area: the position of Hamer district in the lower Omo region of southwestern Ethiopia (left), and the location of the four study sites in the western part of Hamer district (right). The broken lines indicate track trails.

moderately and highly encroached by woody plants. To assess the degree of similarity in soils organic matter among the sites, we collected 24—35 topsoil samples (0—10 cm depth) from each site, and analyzed using the loss-on-ignition technique (Schulte and Hopkins, 1996). The soil organic matter, which is the main source of carbon and nitrogen, ranges between 1.3 and 1.6%, with no significant variation between the four sites ($F_{(3, 70)} = 0.420$, $p = 0.739$).

The vegetation sampling followed a systematic random sampling protocol in which plots were systematically placed at regular intervals along the length of the line transects. At each site, we selected a straight track running across the length of the site along the elevation gradient. Parallel to the track, we marked two straight 6—8 km long line transects, one to the left and the other to the right of the trail, approximately 1000 m apart. In order to identify waypoints along each transect; we placed visible flags, approximately every 200 m. We used a GPS (Garmine GPS III) tracking system to establish distances and directions, and to mark the waypoints.

To sample the vegetation representatively at each site, we placed a 20 × 20 m plot every 400 m along the length of each line transect. A total of 114 plots were sampled across all sites combined: 24 at Site 1; 29 at Site 2; 35 at Site 3; and 26 at Site 4. Individual woody plants present in each plot were identified to species and categorized into one of three age categories (Dalle et al., 2006): adult (diameter at breast height > 2.5 cm); sapling (diameter at stump height < 2.5 cm and height > 100 cm); or seedling (height < 100 cm).

From each woody plant species recorded in a plot, we selected the largest adult-sized individual, assumed to be the superior competitor to its neighbors, and measured its height and diameter

at breast height (dbh). We also measured the distance from the center of its stem, at soil level, to the nearest conspecific and heterospecific neighbor, respectively. Plant height and interplant distances were measured to the nearest cm using calibrated poles, whereas dbh was measured to the nearest mm using a vernier caliper. We also recorded elevation at each plot using a GPS. The plot-level mean annual rainfall was extracted from the world climate database (www.worldclim.org) using the DIVA-GIS program. The program provides average climatic data for any point on the globe by interpolating the long-term meteorological records from the nearest stations (see Hijmans et al., 2004). Given the small distances between sites (i.e., 15—20 km), we expect minor rainfall variation, spatially.

2.3. Statistical analysis

To compare woody plant density between plots and across sites with different species and mixed age groups, we standardized the density of all woody plants into Tree Equivalents (TE) based on height measurements. One TE corresponds to a 1.5 m tall tree or shrub (Dalle et al., 2006). The plot level woody plant species diversity was calculated using Shannon—Wiener index (H') given by $-\Sigma\, p_i \cdot \ln(p_i)$, where p_i is the relative proportion of the ith species.

A strict test of the honeycomb rippling model requires having temporal data. Because we did not sample the vegetation over time, we used "space-for-time substitution" (*sensu* Pickett, 1989). In our study, the temporal dynamics of woody plants were deduced from the size (a proxy for age or time) and spacing pattern (a proxy for mortality) of these woody assemblages. Such proxies have been commonly used in ecological studies. A similar approach was used

by Wiegand et al. (2006) when testing the honeycomb rippling model using a one-time vegetation survey conducted by Wiegand et al. (2005) in Namibia. Nevertheless, this method provides only qualitative information. In our case, we did not set out to quantify competitive self-thinning *per se*, but rather to estimate its effect on woody plant mortality, based on the size-spacing relationship.

To examine the evidence for competitive self-thinning and assess if it is influenced by species type and other variables, we used linear mixed-effect models. Our response variable, interplant distance, was regressed against eight explanatory variables considered as fixed effects: tree size (dbh); woody plant species diversity; nearest neighbor type (i.e. conspecific or heterospecific); N_2 fixing ability (yes or no); growth form (tree or shrub); species type; rainfall; and elevation. To simplify the model, we included only the eight most abundant plant species (i.e. 4 trees and 4 shrubs: Table 1). These constitute more than 85% of woody vegetation density in the area. We also included plots and sites as random effects (see Table 2 for list of variables). To normalize the covariance structure and error distribution, a condition for linear mixed regression models, we log-transformed interplant distances and dbh.

Since N_2 fixing ability is highly correlated with species type, we developed four models, two using N_2 fixing ability and two using species type as explanatory variables. We followed standard model-fitting and adequacy checking procedures to fit each of the four models. To select the best explanatory variables in each model, we started running the full model by including all of the variables of interest. Those that were not significant at the 0.05 probability level, based on the *F*-test, were sequentially excluded. After fitting each of the four reduced models, we used multi-model inference to assess the candidate models (Burnham and Anderson, 2002). The model with the lowest ΔAICc or the highest Akaike weight (*Wi*) among the four candidate models was selected as the most parsimonious one (Burnham and Anderson, 2002). In a further analysis, to explore if the species differentially influence the self-thinning process, we performed a multiple-comparisons test (Post-hoc Tukey's HSD test) based on this parsimonious model.

To examine if the interplant distance becomes more even with increasing size, we calculated the mean interplant distances, mean dbh, and their coefficients of variation (CV) for each plot. CV has been used previously to measure the relative evenness or homogeneity of interplant distances at a plot level (Goncalves and Batalha, 2011). If the CV is low, the interplant distances are taken

Table 2
Description of response and explanatory variables included in the model to explain interplant distances.

Variable	Mean	SE
Response variables		
Interplant distance (m)	2.84	0.11
Fixed effect variables		
Size (dbh) (cm)	6.86	0.22
Woody species diversity	1.12	0.01
Elevation (m.a.s.l)	487.19	2.77
Rainfall (mm)	501.75	0.79
Nearest neighbor type (conspecific vs. heterospecific)	–	–
Growth form (Tree/shrub)	–	–
Nitrogen fixation ability (yes/no)	–	–
Species (see Table 1)	–	–
Random effect variable		
Sites (*n* = 4)	–	–
Plots (*n* = 114)	–	–

to be relatively evenly distributed within a plot. To test the significance of this association we employed Pearson's correlation analysis. Based on the honeycomb rippling model, we expect a negative linear association between the mean tree or shrub size and the CV. All the statistical analyses were performed using R-software (R Development Core Team, 2010).

3. Results

We investigated a total of 988 individual woody plants that belong to 16 different species. *Acacia nilotica*, *Acacia brevispica*, *Maerua crassifolia*, *Ormocarpum trichocarpum*, *Teclea nobilis*, *Lannea triphylla*, *Grewia tenax* and *Grewia villosa* were the most frequent woody species comprising more than 85% of the woody plant density in the entire study area (Table 1). Mean dbh of the adult trees and shrubs was 6.86 cm (SE = 0.22) whereas, mean interplant distance was 2.84 m (SE = 0.11) (Table 2). The plot-level woody species diversity (*H′*) ranged from 0.17 in the open savanna sites to 2.03 in relatively dense woody patches (Table 2).

In line with the general hypothesis, our results, explained by the parsimonious model (Table 3), showed evidence of self-thinning in this semi-arid savanna. We found a strong positive association between tree or shrub size and interplant distances, inferring self-thinning (Table 4). This strong positive association between tree or

Table 1
Attributes of woody plant species recorded in the lower Omo region of southwestern Ethiopia.

Species name[a]	Growth-form	N_2 fixing ability	Relative frequency (%)	Interplant distance (mean ± SD) between nearest neighbors (meters)	
				Con-specific	Hetero-specific
Acacia nilotica[a]	Tree	Yes	67.5	4.9 ± 4.7	2.4 ± 2.0
Acacia brevispica[a]	Tree	Yes	34.2	4.9 ± 4.0	2.0 ± 1.7
Acacia melifera	Shrub	Yes	23.7	4.6 ± 3.3	2.3 ± 1.7
Acacia senegal	Tree	Yes	14.0	5.6 ± 5.2	1.8 ± 1.4
Balanitus rotundifolia	Tree	No	22.8	6.8 ± 5.5	2.5 ± 3.2
Cadaba farinosa	Shrub	No	30.7	5.1 ± 4.6	1.3 ± 0.9
Combretum paniculatum	Tree	No	21.1	2.6 ± 2.1	1.0 ± 0.9
Grewia tenax[a]	Shrub	No	62.3	3.1 ± 2.7	2.1 ± 1.9
Grewia villosa[a]	Shrub	No	54.4	2.7 ± 2.4	1.3 ± 1.1
Lannea triphylla	Tree	No	11.4	1.9 ± 2.8	1.3 ± 0.9
Lycium shawii[a]	Tree	No	38.6	4.3 ± 4.0	1.8 ± 1.2
Maerua crassifolia[a]	Tree	No	92.1	3.8 ± 3.1	2.8 ± 2.2
Maerua oblongifolia	Shrub	No	38.6	5.7 ± 4.0	2.0 ± 2.0
Ormocarpum trichocarpum[a]	Tree	Yes	27.2	1.7 ± 1.8	1.6 ± 1.1
Premna resinosa	Tree	No	17.5	4.3 ± 3.9	1.9 ± 2.0
Teclea nobilis[a]	Tree	No	43.9	3.8 ± 4.0	1.2 ± 2.2

[a] The eight most abundant plant species included in the mixed regression model.

Table 3
Comparison of the four candidate linear mixed effect models with plots within sites included as random effect accounting for repeated measurements. Model 1 was selected as parsimonious model for its low AIC and deviance scores.

Model	Global model	K	AICc	ΔAIC	Wi	Deviance
1	Distance ~ dbh + nearest neighbor type + diversity + species	22	2017.75	0.00	0.570	1973.76
2	Distance ~ dbh + nearest neighbor type + diversity + elevation	15	2018.35	0.60	0.420	1988.36
3	Distance ~ dbh + nearest neighbor type + diversity + elevation + N_2_fix	16	2028.02	10.27	0.000	1996.02
4	Distance ~ dbh + nearest neighbor type + diversity	17	2028.63	10.88	0.000	1994.64

K is number of parameters in the regression model.
Wi (AICc weight) is the relative likelihood of model i.
% dev. is the % deviance explained by the fixed effects of the model, which is give by two times the negative of logLik (logarithm of likelihood).

shrub size and interplant distance (Fig. 3) affirms the potential of self-thinning to regulate the dominance of woody plants in woody encroached semi-arid savanna patches, as suggested by the honeycomb rippling model.

Interplant distance was positively influenced by woody species diversity. Greater interplant distance, and hence a stronger self-thinning effect, was evident in areas with more diverse communities. We also found significantly higher interplant distances between conspecific neighbors compared to heterospecific neighbors (Fig. 4) suggesting a tendency for stronger competitive interaction between individuals within species than between species (Table 4). Self-thinning was also influenced by the species identity of woody plants. The post-hoc Turkey's HSD test showed that T. nobilis has significantly smaller interplant distance than G. tenax ($z = -3.023$, $p = 0.048$) and M. crassifolia ($z = -3.943$, $p = 0.002$). O. trichocarpum, similarly, has significantly lower interplant distance than M. crassifolia ($z = -3.907$, $p = 0.002$), but all the other pair-wise comparisons between species were not significant at 0.05 level (Fig. 4). Other potential explanatory variables including, elevation, rainfall, N_2-fixing ability, and growth-form did not significantly influence interplant distances.

The relationship between tree or shrub size and the CV of interplant distances did not match the predictions of the honeycomb rippling model. The Pearson's correlation analysis showed no strong negative association between CV of interplant distances and mean size of the tree or shrub ($r = 0.045$, $p = 0.641$; Fig. 5). Thus the strength of self-thinning did not increase evenly with tree size.

4. Discussion

We found evidence of self-thinning in semi-arid savanna patches in the lower Omo region, an area of moderate but erratic rainfall. The positive association between size and the distance to the nearest neighboring woody plants suggests a potential role for

competitive self-thinning in regulating the density of encroaching woody plants in this savanna, as predicted by the honeycomb rippling model. The model was originally developed for arid rangelands having a low and patchy annual rainfall (100−200 mm), the basic assumption being that growth (estimated by size) and mortality (estimated by interplant distance) are influenced by competitive interactions between neighboring woody plants (Wiegand et al., 2006).

The second prediction of the honeycomb rippling model, that interplant distances would become more even with increasing tree size (Wiegand et al., 2006) was not supported by our data. The discrepancy might result from differences in species composition and the patchy nature of their distribution. Unlike most arid rangelands, which are dominated by a single dominant woody plant
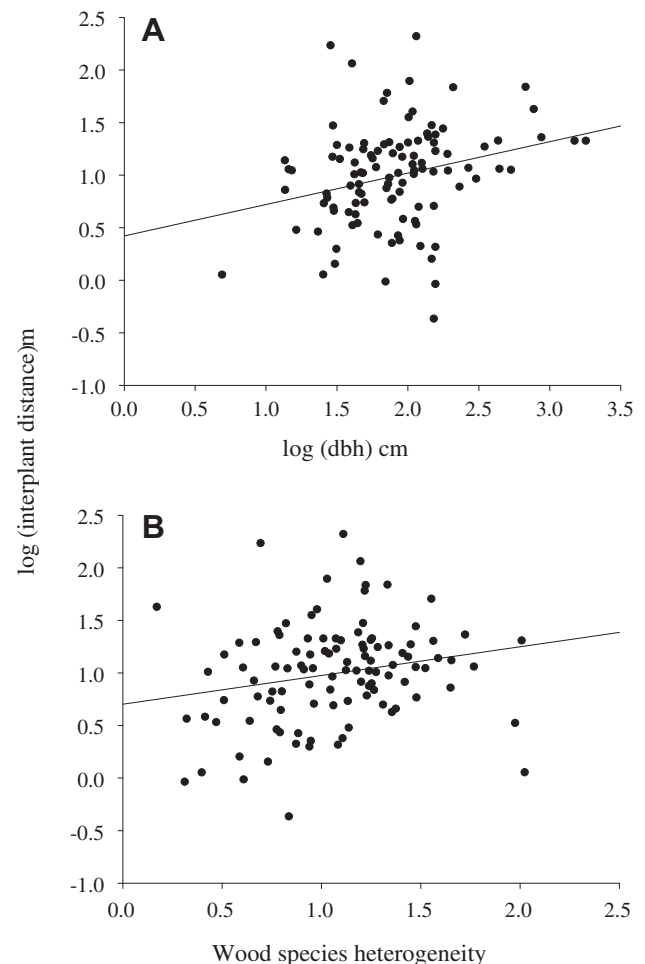

Table 4
Linear mixed effect model showing the effects of tree or shrub size, nearest neighbor type, woody species diversity and species on interplant distances. Growth-form, N_2 fixing ability and elevation were not included in the final model. Plots within sites were included in the model as a random effect.

Predictor	Value	Std. error	t-Value	p-Value
(Intercept)	−0.07	0.22	−0.32	0.750
Tree or shrub size (dbh) in cm	0.14	0.05	2.61	0.009
Conspecific neighbor (vs. heterospecific)	0.54	0.07	8.06	0.000
Diversity	0.27	0.12	2.22	0.029
Species (A. brevispica vs.)				
A. nilotica	−0.12	0.16	−0.76	0.450
G. tenax	0.02	0.18	0.12	0.908
G. villosa	−0.10	0.19	−0.53	0.598
L. shawii	−0.08	0.19	−0.41	0.682
M. crassifolia	0.09	0.15	0.58	0.561
O. trichocarpum	−0.51	0.18	−2.74	0.006
T. nobilis	−0.47	0.18	−2.54	0.011

Fig. 3. Association between interplant distance and: (A) tree or shrub size, (B) Woody species diversity in lower Omo region of southwestern Ethiopia.
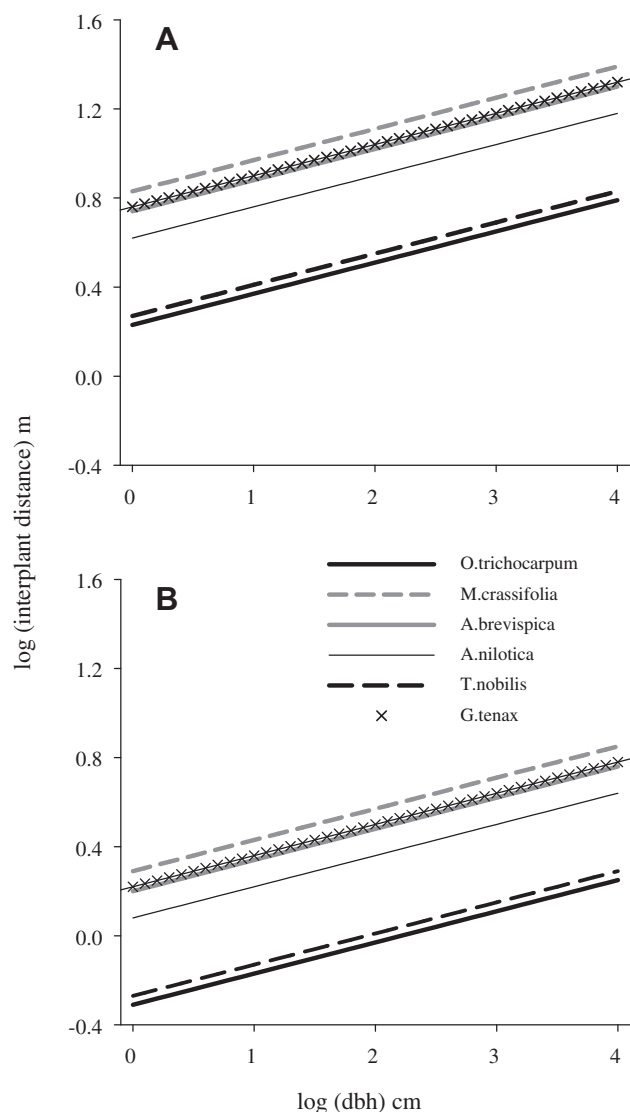
Fig. 4. The association between tree or shrub size, measured as stem diameter, and interplant distance between conspecific neighbors (A); and heterospecific neighbors (B), as influenced by the type of woody plant species. *Ormocarpum trichocarpum* and *T. nobilis* vary significantly from other species (see Table 4). The fitted value was calculated from the most parsimonious model (Table 4), using mean dbh and diversity.
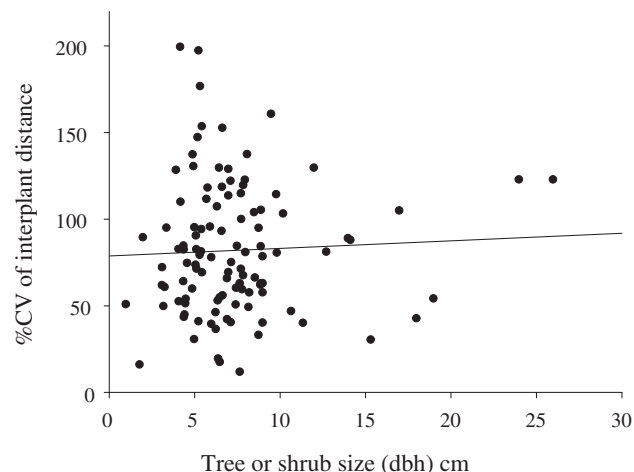

Fig. 5. Association between tree or shrub size (dbh) and CV of interplant distance. The slope of the regression line was not different from 0 ($r = 0.045$, $p = 0.641$), showing no significant association between the two.

species (Wiegand et al., 2006), the vegetation in our study area was composed of diverse assemblages of woody species with different spatial distribution patterns.

Given differences in canopy shape and rooting structure among the species in this region, we should expect variation in competitive performance (Callaway and Walker, 1997) and hence in interplant distances. Some species, for example, *O. trichocarpum*, have narrow crowns and are better able to tolerate shade or drought. They can, therefore, grow closer to their neighbors, whereas others, like *A. nilotica*, grow sparsely, perhaps to avoid competition. Furthermore, a facilitative interaction between woody plants is apparent in arid and semi-arid savannas, with some trees and shrubs facilitating the growth of others under their canopies (Callaway and Walker, 1997; Schleicher et al., 2011). *Grewia* species, for example, grow better under the canopies of large *Acacia* trees (Schleicher et al., 2011). In these situations, the interplant distance will not be much influenced by the size of the nurse tree. In mixed-species

communities, therefore, it is debatable whether a pattern of homogenous distances between individual woody plants in a given age class should be expected.

We also observed variation in apparent self-thinning between conspecific and heterospecific neighbors. Although intra- and interspecific competitive interactions have influenced the density of woody plants in our study area, interplant distances were higher among conspecific neighbors than to heterospecific neighbors. This suggests stronger intraspecific competition (Fig. 4), in support of previous studies (e.g. Chesson, 2000; Chesson et al., 2004; Kambatuku et al., 2011). When two individual woody plants with similar resource requirement occupy the same environment, competition is likely to be more intense, eventually resulting in the mortality of the less competitive individual. Thus, this intense intraspecific competition could be the basis for species coexistence and community stability in savannas (Chesson, 2000; Chesson et al., 2004).

Contrary to our expectation, self-thinning was not influenced by nitrogen-fixing ability. As nitrogen is a limiting factor for plant growth in most savannas (Kraaij and Ward, 2006), we expected non-leguminous woody plants to experience more self-thinning than leguminous species. In theory, nitrogen fixing woody plants should be able to tolerate more competition for nitrogen by taking advantage of their symbiotic association with nitrogen-fixing rhizobia (Cramer et al., 2010). However, we did not find any significant differences between the two functional groups, possibly because soil nutrients were not limiting. The soil organic matter in the study area, which is the principal source of carbon and nitrogen, was fairly good compared to most East African rangeland soils that are regarded as having low fertility (Coppock, 1994), and therefore not likely to be the main stress factor inducing competition.

Applying the concept of self-thinning in natural savanna ecosystems has been criticized because of the problem of distinguishing the effects of self-thinning from those of various other factors that can modify plant–plant interactions in these systems. Interactions between woody savanna plants can be influenced not only by self-thinning, but also by factors such as fire, herbivory and competition from herbaceous plants (Scholes and Archer, 1997; van Langevelde et al., 2003). As suggested by Bertness and Callaway (1994), increasing abiotic stress and herbivore pressure diminish the importance of competition between woody plants. The intensity of competition increases along gradients of increasing abiotic stress, whereas it declines along gradients of disturbances (Grime,

1979). Fire and browsers can also reduce the level of competition between woody plants by directly impacting biomass accumulation, growth and survival. Under intense disturbance, the density of woody plants is always likely to be below the maximum carrying capacity of the land, making self-thinning unlikely. Goncalves and Batalha (2011), for example, reported difficulty in detecting self-thinning in fire-adapted seasonal savannas in Brazil, where plant density is frequently checked by fire before populations reach carrying capacity. Conversely, competition from the herbaceous layer could exaggerate the effect of self-thinning by intensifying level of stress for environmental resources.

However, our study system had relatively low grass cover and few disturbances, making it more suitable for detecting evidence of self-thinning. The magnitude of animal herbivory, the main disturbance in this pastoral area, was substantially reduced because of prolonged droughts that caused high mortality among the animals of the region (Fratkin, 2001). Fire has also been suppressed for the past few decades, partly because of low herbaceous fuel loads and partly as a function of management policies discouraging wildfires (Carr, 1998). Although episodes of high rainfall are thought to be the main driver behind the proliferation of woody plants in most savanna systems (Vetter, 2005), moisture stress during prolonged intervening drought years is a likely to be an ideal situation for detecting self-thinning in these rangelands, with the intensity of competition increasing along a gradient of increasing moisture stress (Grime, 1979).

5. Conclusion

In conclusion, this study supports the notion that self-thinning can operate in woody encroached semi-arid savannas. By regulating the density of trees and shrubs, self-thinning can be regarded as a natural mechanism promoting the long-term stability of these ecosystems. Our data suggest that the phenomenon of woody encroachment in semi-arid savannas could potentially be reversed through natural self-thinning. In a long-run, opening up of the canopy could promote tree–grass coexistence, although whether this mechanism can ensure the recovery of the natural tree–grass balance in already altered savanna ecosystems is not clear. It may take many decades before woody-encroached sites return to open savanna, a process that will depend on the competitive ability and longevity of individual woody plants. In the meantime, native grass species may disappear from the local landscape due to the long-term effects of woody encroachment. In such cases, to ensure grass persistence and to restore species diversity, management might consider limiting the process of natural self-thinning by selectively removing smaller woody plants.

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