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Multi-proxy evidence for competition between savanna woody species

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Abstract

Coexistence of trees and grasses in savannas should be possible if competition between the woody and the grassy components is less intense than the competition within each component. Although several studies have investigated competition between trees and grasses, little is known about tree–tree interactions. We used a multi-proxy approach to examine the spatial pattern of *Acacia mellifera* and other savanna woody species in a semi-arid savanna in South Africa. Spatial analysis of the point patterns of young and reproductively mature shrubs detected decreasing aggregation with size/age over all spatial scales. This indicated the prevalence of competition although the overall spatial shrub pattern was aggregated. In contrast to point pattern statistics that detect changes only when competition has led to the death of the inferior competitor, we also applied methods identifying the competitive effect on sizes of individual trees. Competition should lead to a negative spatial autocorrelation in size, which we observed in half of the studied cases. Quantile regressions show that nearest-neighbour distance increased steeply with combined size of the target shrub and its neighbours indicating strong competitive effects. The medians of the distributions of maximum root lengths of *A. mellifera*, of the scale of regular patterns, and of negative autocorrelations were not significantly different, suggesting that overlapping root systems mediate competitive interactions. A competitor removal experiment did not lead to increased shrub sizes, which may be due to the limited duration of the experiment. From the nearest neighbour and autocorrelation analyses, we conclude that competition had a strong impact on growth rates of savanna woody species. Competition-induced mortality only becomes obvious when analysing the shift towards less aggregated spatial patterns when shrubs become reproductively mature. As the overall clustered spatial pattern masks the perceptible effect of competition, a time component should always be included in spatial pattern-based inference of competition.

Keywords: *Acacia mellifera*; Competitor removal experiment; Nearest-neighbour distance; Quantile regression; Spatial autocorrelation; Spatial point pattern analysis

Introduction

Clements et al. (1929) postulated that the composition of any mature stand of vegetation is shaped by competition (see also Wilson and Tilman, 1991; Silvertown, 2004). Theoretically, coexistence of life forms

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within a mature stand of vegetation is possible if competition within life forms is stronger than competition between life forms (Scholes and Archer, 1997). Through time, a multitude of approaches has been developed to infer competition from physiological and morphometric relationships, and, more recently, from spatial patterns (e.g., Clements et al., 1929; Pielou, 1962; Welden and Slauson, 1986; Shackleton, 2002; Wiegand and Moloney, 2004). However, there have been only few attempts to apply different approaches to data from the same study area to compare results from inferential and experimental methods (e.g., Goldberg et al., 1999; Freckleton and Watkinson, 2000; Kint et al., 2003).

Savannas constitute classic examples of a vegetation type maintained through the coexistence of two dominant life forms, namely woody species and grasses. Thus far, the relationship between these life forms has been more often in the focus of savanna research than intra-life form interactions (e.g., Brown et al., 1998; Fetene, 2003). Little emphasis has been placed on positive and negative interactions among trees in determining their spatial pattern and density despite the fact that tree density defines savannas as open or closed (Couteron and Kokou, 1997; Scholes and Archer, 1997). Facilitation is a positive interaction leading to the aggregation of plants, thereby increasing densities (Scholes and Archer, 1997; Bruno et al., 2003). Worldwide, increasing densities of woody species often unpalatable to livestock pose growing ecological and economic problems to tree–grass coexistence in savannas. This intensifying shrub encroachment supports the assumption that aggregated spatial patterns of woody species prevail in many savannas and are maintained by facilitative interactions or other mechanisms causing aggregation. On the other hand, competition among trees may limit the density and spatial pattern of trees to the extent that savannas do not become woodlands (Jeltsch et al., 2000). This is particularly true for savannas with a mean annual precipitation of less than 650 mm where maximum woody cover is increasing with increasing mean annual precipitation (Sankaran et al., 2005) indicating the prevalence of competition for soil moisture. Hence, tree–tree competition may be an important driving factor in maintaining the existence of the savanna biome.

In the light of increasing aggregation of woody species in savannas, the identification of parallel competitive interactions is a growing challenge for the methodological tool set of a spatial ecologist. In general, the use of spatial methods is favoured over non-spatial methods because they retain more information. Spatial pattern analysis is an indirect approach to evaluating interaction among plants (Couteron and Kokou, 1997) without the need for costly long-term demographic censuses. A shift towards less aggregated distributions of plants indicates density-dependent mortality, possibly caused by intraspecific competition for an evenly distributed resource (Wolf, 2005). Aggregation can result from vegetative reproduction, clumped seed dispersal, heterogeneity of soil resources, temporary local release from recruitment limitation, disturbances, facilitation, or a combination of these factors (Ford, 1975; Phillips and MacMahon, 1981; Skarpe, 1991). Plants are randomly spaced either due to the absence of processes causing regularity or aggregation or because processes causing regularity and aggregation are balancing each other, e.g. in a transient state between aggregation and regular distribution (Skarpe, 1991). Competition also leads to a negative spatial autocorrelation in plant size, so that taller plants have smaller neighbours (Cannell et al., 1984; Purves and Law, 2002). Spatial point pattern statistics can be used to identify at which scales a spatial pattern is significantly clustered or regular and at which scales individual size measures are spatially autocorrelated. Point pattern statistics incorporate more information from a fully mapped spatial pattern than most other spatial methods.

However, if the aim is to differentiate between intensity and importance of competition, nearest-neighbour analysis is the method of choice (Welden and Slauson, 1986). As competition may control the size and density of savanna trees (Smith and Walker, 1983), competition has also been inferred by nearest-neighbour analysis of *Acacia* stands (Gutierrez and Fuentes, 1979; Smith and Goodman, 1986; Benshahar, 1991). The combined size of a plant and its nearest neighbour is generally positively correlated with the distance between them (Gutierrez and Fuentes, 1979; Smith and Walker, 1983). Nearest-neighbour analysis has been criticised to underestimate the prevalence of competition because the nearest neighbour may not have the greatest competitive impact on a target plant if the nearest neighbour is very small compared to other plants in the vicinity (Shackleton, 2002). This limitation can be overcome by using more than one nearest neighbour (Shackleton, 2002). It is a simple and rapid method which can be very insightful in combination with other methods such as the scale-dependent spatial point pattern analysis used here (see application in, e.g., Grundy et al., 1994 (three nearest neighbours); Shackleton, 2002; Ward, 2005). Spatial point pattern analysis is particularly effective when the effects of competition are sufficiently strong to result in differential mortality, whereas nearest-neighbour analysis may also detect weaker competitive effects among living individuals.

While inference of competition from spatial patterns is indirect, experimental competitor removal is a direct method and should be preferred when the focus lies on the isolation of the effects of competition. The disadvantage of experimental approaches is that it may be much more time consuming than spatial pattern analysis.

The aim of the present study is to investigate whether the prevalence of competition among *Acacia mellifera* (Vahl) Benth. and other woody components of a semi-arid savanna in South Africa can be inferred with different spatial pattern analysis methods and an experimental approach in the presence of spatial aggregation and time constraints. We do not separate inter-shrub competition further into intra- and inter-specific competition because our focus was on inter-shrub competition, regardless of species identity. If we assume that inter-shrub competition is the major driver in the shrub community investigated, we can derive the following predictions:

1. Spatial point patterns of young and old woody species will show less aggregation with age.
2. There will be a negative spatial autocorrelation in shrub sizes.
3. The combined size of four neighbours will increase with the sum of the distances to the four nearest neighbours.
4. Competitor removal will lead to increases in shrub size.

Methods

Study area

The study was conducted in semi-arid savanna in the Kalahari thornveld at Pniel Estates (S28°35′, E24°29′), 30 km north of Kimberley, South Africa, in January and February 2004 and in January 2005. Mean annual precipitation is 377 mm and mostly occurs as thunderstorms throughout the summer months (September–March). *A. mellifera* is the dominant plant species in the study area; *Tarchonanthus camphoratus* and *Acacia tortilis* are the other important woody species. Typically, woody cover ranges between 15% and 30%.

Field methods

To explore the spatial pattern of the woody species in the study area, we set up 20 fenced 15 m × 15 m plots. Within the plots, we determined the x- and y-coordinate and the maximum canopy diameter of all *A. mellifera* ($n = 880$), *A. tortilis* ($n = 89$), and *T. camphoratus* ($n = 108$) individuals (total $n = 1077$ shrubs, minimum $n = 10$ shrubs/plot, maximum $n = 167$ shrubs/plot). There were no other woody species present in the plots.

To investigate the effect of competitive release on shrub growth, we set up a competitor removal experiment. All aboveground parts of all woody species within a radius of 7.5 m around 15 *A. mellifera* "target" shrubs were cut and poisoned in February 2004. In the vicinity of each target shrub, a control shrub of similar size was marked. The maximum canopy diameter, the canopy diameter perpendicular to the maximum canopy diameter, and three shrub heights were determined for every target and control shrub directly before the poisoning and 11 months later.

In a set of ten 10 m × 10 m plots, we determined the length of the regrowth of the present season at the tips of up to 10 branches per *A. mellifera* shrub in 2004 ($n = 309$ shrubs) and 2005 ($n = 281$ shrubs). To determine the adult mortality rate, we counted the number of *A. mellifera* shrubs that died between 2004 and 2005 in these plots.

We excavated 16 lateral roots of 10 *A. mellifera* shrubs and determined their maximum lengths. We restricted the excavations to the shallow lateral roots due to logistic constraints and because the small taproot of *A. mellifera* is of minor importance for water and nutrient uptake compared to the lateral roots in *A. mellifera* (D. Ward, pers. obs.).

Spatial pattern analyses

We analysed the spatial distribution of woody individuals in the 20 15 m × 15 m plots in two approaches, the "split approach" and the "overall approach": We split the *A. mellifera* shrubs in the 20 15 m × 15 m plots into those with a canopy diameter of less than 145 cm ("small") and those with a greater canopy diameter ("large") to test the hypothesis that originally aggregated shrub seedling patterns become less aggregated with individual life time due to the action of competition (split approach). This canopy diameter represents the threshold for seed production and therefore reproductive maturity in *A. mellifera* (D. Ward, unpublished data). As a rule of thumb, a pattern to be analysed with spatial point pattern statistics should comprise at least about 30 points (T. Wiegand, personal communication), which was fulfilled by only 12 plots in the split approach. We also analysed the spatial distribution of the individuals of all shrub species occurring in all 20 15 m × 15 m plots to be able to compare it with the *A. mellifera* patterns (overall approach).

In both approaches, we applied the univariate Wiegand–Moloney O-ring statistic with the null-hypothesis of complete spatial randomness (CSR, Wiegand and Moloney, 2004). The Wiegand–Moloney O-ring statistic is used to analyse the second-order properties of fully mapped spatial point patterns and is similar to Ripley's K statistic (Ripley, 1976, 1981; Besag, 1977). In contrast to Ripley's K, the O-ring function measures interaction at distance h only, without a memory effect from integration over all distances up to h (Wiegand and Moloney, 2004; for a description of the statistic see Appendix A). Wiegand–Moloney's O-ring function is equal to Stoyan and Stoyan's pair-correlation function (Stoyan and Stoyan, 1994) multiplied with the intensity of the pattern λ. Upper and lower confidence envelopes were generated from 99 simulations resulting in a confidence level of $p = 0.01$. The point pattern analyses were carried out with the *Programita* software (Wiegand and Moloney, 2004) which also offers a function to combine replicates to obtain a general picture of the spatial patterns in a study area. Hence, we analysed the 12 plots in the split approach combined as well as all 20 plots in the overall approach. In the overall approach, we determined the frequency distribution of significantly regular patterns at scales from 0 to 500 cm over all plots separately with a grid cell size of 10 cm.

Spatial autocorrelation

To examine the average similarity or dissimilarity in size of neighbouring shrubs, we investigated the spatial autocorrelation of the shrub canopy diameters at different spatial scales h in the 15 m × 15 m plots: Based on the point pattern of the stem locations of the shrubs, we calculated Pearson's correlation coefficient between the canopy diameter at point i and the mean of the canopy diameters at points within a ring centred on i with radius h and width δh. The frequency distribution of plots with significant negative autocorrelation was determined at scales from 0 to 590 cm. The null-model for the assessment of significance was complete spatial randomness. The autocorrelation analyses were carried out with the *Programita* software (Wiegand and Moloney, 2004).

Nearest-neighbour analyses

For all shrubs in the 15 m × 15 m plots, we investigated the relationship between the sum of the distances to the four nearest neighbours and the sum of the canopy diameters of the target shrub and its four nearest neighbours. As variance was not homogeneous across the range of x values, we used quantile regression instead of conventional linear regression (Goldberg and Scheiner, 1993; Thomson et al., 1996). In quantile regression, different parts of the variance are captured by different quantiles (Koenker and Bassett, 1978). Quantile regression functions are estimated as the minimised asymmetrically weighted sum of absolute residual errors (Koenker and Bassett, 1978; Cade et al., 1999; Cade, 2003). The τth quantile regression function, $Q(\tau)$, describes a linear or nonlinear fit through the data so that τ proportion of the data is less than $Q(\tau)$ and $1-\tau$ proportion is greater than $Q(\tau)$. The upper quantile is a more appropriate representation of the limiting factor than the central estimate of a conventional regression (Thomson et al., 1996). The greater the similarity in slope of the upper quantiles, the smaller is the proportion of the sample that is affected by the interaction with unmeasured factors (see also Meyer et al., 2005). Nearest-neighbour and quantile regression analyses were carried out with the software package S-PLUS 6.1.

Morphometric analyses

In the competitor removal experiment, the relative growth rates

$$\mathrm{RGR} = \ln(\text{final size}/\text{initial size})/(\text{final time step} - \text{initial time step})$$

(Larcher, 2003) of height and canopy diameter of control and target shrubs were compared using t-tests with Welch's correction for unequal variances.

Results

In the split approach, the spatial pattern of the small shrubs in the 12 combined 15 m × 15 m plots was significantly clustered relative to the null model of CSR at virtually all scales up to 500 cm ($p<0.01$, Fig. 1a). Contrarily, the spatial pattern of large shrubs in the 12 combined 15 m × 15 m plots of the split approach was random at virtually all scales with a significant deviation to regularity at 350 cm ($p<0.01$, Fig. 1b). In the overall approach, the combined analysis of all shrubs in the 20 15 m × 15 m plots produced similar results to the small shrub pattern analysis: significant aggregation at virtually all scales ($p<0.01$). When the plots of the overall approach were analysed separately, the rare occurrence of a significant regular pattern was most probable at scales around 330 cm (= mode in Fig. 2a).

In the 15 m × 15 m plots, negative spatial autocorrelation in the canopy diameter of all woody species occurred approximately as often as positive autocorrelation (see Table 1 for mean canopy diameters). We obtained non-significant autocorrelation results in a few cases only. The mode of the frequency distribution of the scales at which negative autocorrelation occurred was 370 cm (Fig. 2b).

There was a significantly positive relationship between combined nearest-neighbour distance and combined canopy diameters in the 15 m × 15 m plots (Fig. 3a) because the lower 90% confidence intervals of the slopes of all quantile regression lines were greater than 0 (Fig. 3b). The 0.999-quantile had a very steep slope (slope = 1.51, Fig. 3b), corresponding with a high intensity of competition (cf. Welden and Slauson, 1986). Because the quantiles did not have similar slopes (Fig. 3b), unmeasured factors played an important

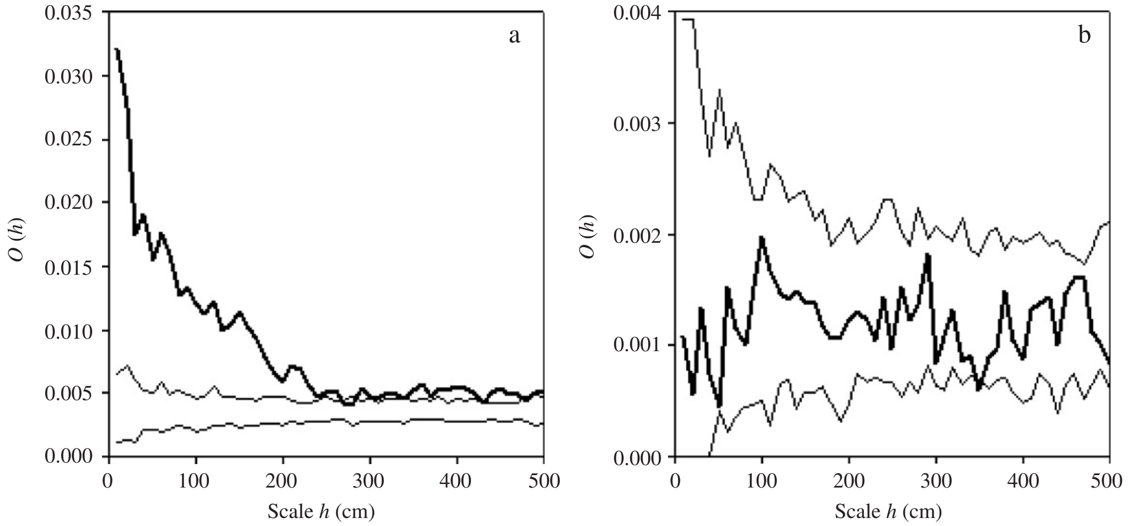

Fig. 1. The univariate *O*-ring statistic $O(h)$ at different scales h (bold lines) with upper and lower confidence envelopes (thin lines) representing the maximum and the minimum value from 99 simulations with the null-hypothesis of CSR combined for small (a) and large (b) *A. mellifera* shrubs in 12 15 m × 15 m plots (split approach). The threshold separating small and large shrubs was a canopy diameter of 145 cm, which is the size at reproductive maturity. If $O(h)$ is above the upper confidence interval, the pattern is significantly clustered, if $O(h)$ is below the lower confidence interval, the pattern is significantly regular at the considered scale ($p < 0.01$).

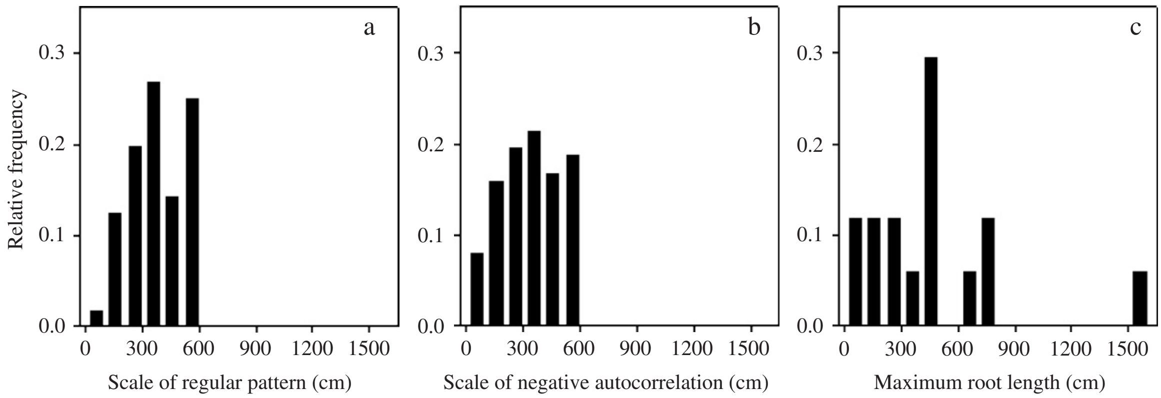

Fig. 2. Relative frequency distributions of (a) regular patterns at different scales, (b) negative autocorrelation at different scales, and (c) of the maximum root length. (a) Point pattern analysis was carried out for all woody plants in 20 15 m × 15 m plots at scales from 0 to 590 cm on a plot basis with the null model of CSR (overall approach). Only the relative frequencies of the significantly regular patterns over all plots are presented. (b) Autocorrelation analysis of the canopy diameter of all woody species in 20 15 m × 15 m plots was performed at scales from 0 to 590 cm with Pearson's correlation index. Only the relative frequencies of the significantly negative autocorrelations over all plots are presented. (c) Maximum root length was determined for 16 roots of 10 *A. mellifera* shrubs.

interactive role in the relationship between combined canopy diameters and nearest-neighbour distances.

Relative growth rates in height ($t = -0.80$, df $= 42.77$, $p = 0.43$) and canopy diameter ($t = -1.72$, df $= 54.97$, $p = 0.09$) were not significantly different for control and target *A. mellifera* shrubs in the competitor removal experiment (Table 1). Total rainfall between poisoning and data collection (230 mm) was lower than the long-term mean for those 11 months of the year (320 mm, Zucchini and Adamson, 1984).

Over the two study years, *A. mellifera* showed an annual growth rate of 2.63 cm/year (Table 1). From 2004 to 2005, two out of 309 *A. mellifera* shrubs died in the 10 m × 10 m plots, giving an annual adult mortality rate of 0.0065 (Table 1).

The location of the frequency distribution of maximum root lengths (Fig. 2c) was not significantly different from the frequency distributions of the scale of regular patterns (Fig. 2a) and of autocorrelation (Fig. 2b) in the 15 m × 15 m plots ($p = 0.50$ and 0.24,

Table 1. Mean and standard deviation (S.D) of parameters estimated from the competitor removal experiment, the 15 m × 15 m plots, and the 10 m × 10 m plots[a]

Species	*n*	Parameter	Mean	S.D.
Competitor removal experiment				
A. mellifera	15	RGR in target height	0.06	0.10
A. mellifera	15	RGR in control height	0.05	0.05
A. mellifera	15	RGR in target canopy diameter	0.07	0.11
A. mellifera	15	RGR in control canopy diameter	0.02	0.10
15 m × 15 m plots				
A. mellifera	880	Canopy diameter	112.79	104.73
A. tortilis	89	Canopy diameter	79.88	67.16
T. camphorates	108	Canopy diameter	119.72	81.97
10 m × 10 m plots				
A. mellifera	309	Annual regrowth length	3.38	3.43
A. mellifera	309	Adult mortality	0.0065	0.0803

[a] In the competitor removal experiment, relative growth rate (RGR) was investigated for control shrubs and target shrubs, whose woody competitors where removed within a radius of 7.5 m, over a 1-year period. No treatments were applied to the 10 m × 10 m plots and the 15 m × 15 m plots. All parameter units are cm, except year^{-1} for adult mortality and RGR which is dimensionless. *n* = sample size, *A. mellifera* = *Acacia mellifera*, *T. camphoratus* = *Tarchonanthus camphoratus*.

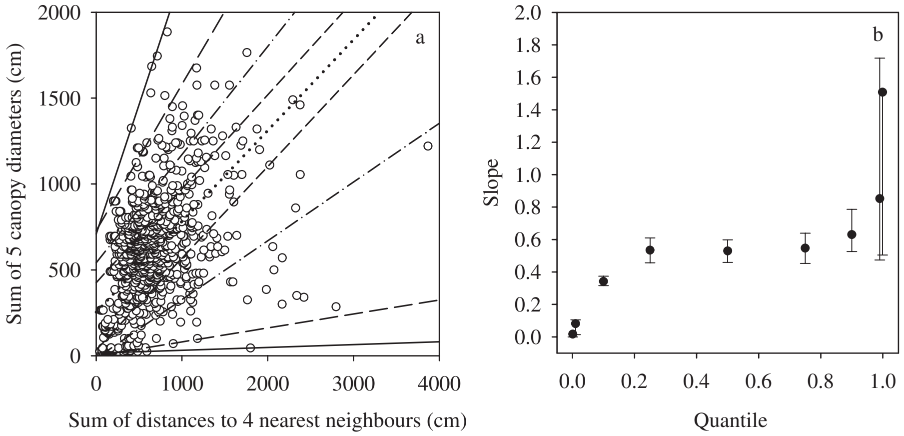

Fig. 3. Relationship between the sum of the canopy diameters of the target shrub and its 4 nearest neighbours and the sum of the distances to the 4 nearest neighbours in the 15 m × 15 m plots ($n = 1077$). The plots consisted of the shrub species *A. mellifera*, *A. tortilis*, and *T. camphorates*: (a) Quantile regression estimates. Quantiles from top to bottom: solid line: 0.999 – quantile, long-dashed: 0.99 – quantile, dot-dashed: 0.9 – quantile, short-dashed: 0.75 – quantile, dotted: 0.5 – quantile, short-dashed: 0.25 – quantile, dot-dashed: 0.1 – quantile, long-dashed: 0.01 – quantile, solid line: 0.001 – quantile. (b) Slopes of the quantile regression lines in (a) (solid circles) with upper and lower 90% confidence intervals.

respectively) although the power of these tests was very low ($1-\beta<0.03$).

Discussion

Spatial point pattern analysis showed that the overall spatial pattern of woody species in the study area was clustered. However, the separate analysis of small and large shrubs revealed that this was due to the strong aggregation of small plants that had not reached reproductive maturity. The spatial pattern of the reproductively mature *A. mellifera* shrubs was random at all scales except 350 cm where it was significantly regular. Age and size do not have to be related in savanna shrubs but in *A. mellifera*, height and shape have been shown to be reliable indicators of age (Adams, 1967). It follows that over the life time of an individual, patterns become less aggregated in the study area which provides evidence for competitive interactions in the individuals' past. Hence, we can corroborate prediction 1. However, the competitive effect is masked by the overall aggregation of shrubs. Several earlier studies also reported clustered or random distributions for *Acacia* and other savanna woody species (Skarpe, 1991; Couteron and Kokou, 1997; Barot et al., 1999; Wiegand et al., 2000a). This underlines the importance of explicit consideration of time when inferring processes from spatial patterns. Only when time is included, prevailing competitive effects can be distinguished from a possibly much stronger effect of aggregation early in the life time of individuals (Wolf, 2005; Getzin et al., 2006). If chronosequences are not available, the age of plants or proxies for the age as in this study can be used to include a time component into the analysis.

The distinct aggregation that we found for young woody savanna species may have many reasons. Although vegetative reproduction is often considered to be the proximate mechanism that leads to aggregation in woody species (Phillips and MacMahon, 1981), we did not find any evidence for vegetative reproduction in *A. mellifera* during the root system excavations of the present study. Scholes and Archer (1997) suggest topography (e.g., termite mounds), soil depth, and fire patchiness as potential factors that may generate aggregated spatial patterns in savanna plants. In the study area, topography is relatively homogenous, few termite mounds were observed, soil depth was similar in all plots, and fuel loads are too low to support many fires. Nevertheless, fire has been suggested to cause clustered growth patterns of *A. mellifera* by preventing field layer vegetation from entering the *A. mellifera* thickets (Skarpe, 1991). However, it is more probable that aggregated seed dispersal caused the observed patterns of small shrubs. At the study site, field observations indicate that seedling density declines almost exponentially with distance from the rooting point of the parent shrub (K. Meyer, unpublished observations of two reproducing shrubs). This aggregated dispersal could be enhanced by a facilitative effect of the parent shrub or other large shrubs in the vicinity. In facilitative interactions, ‘‘nurse plants’’ create nutrient and soil moisture-rich patches under their canopy promoting germination and establishment of other (mostly smaller) plants (Belsky, 1994; Holzapfel and Mahall, 1999; Münzbergova and Ward, 2002). This can lead to a temporary local release from recruitment limitation during periods of favourable environmental conditions, e.g. overlapping local rainfall events. A combination of facilitation and aggregated seed dispersal is also consistent with the observation of less aggregated larger shrubs that may act as nurse plants for their own clustered progeny.

However, also in the overall approach, regular spatial patterns were detected in some cases. Additionally, negative autocorrelation in canopy diameter was observed in half of the cases indicating competitive action in the past (Prediction 2). Here, competition may act in a way that competitively superior trees impair the viability or the growth of their neighbours. This was supported by the fact that the most frequent scale of regular patterns and of negative autocorrelation matched the average maximum root length. Maximum root length can be taken as a simple surrogate for the maximum extension of the zone of influence of a plant (Casper et al., 2003). Two plants compete with each other when their zones of influence overlap. The greater the overlap, the more intense is the competition. Hence, in our case, the regular pattern and negative autocorrelation may result from zones of influence whose maximum degree of overlap is restricted by the intensity of competition: As soon as the edge of a zone of influence of one plant reaches the centre of the zone of influence of another plant, the competitively inferior plant dies (regular pattern) or at least grows less in diameter (negative autocorrelation). Those cases where we did not find regular spatial patterns or negative autocorrelation can be attributed to the early phase in the transition from an originally clustered pattern via a random to a regular pattern. This indicates that small aggregated plants are present at greater densities in the study area than large plants that have survived the increased competitive pressure at greater individual shrub sizes.

Supporting prediction 3, the results from the nearest-neighbour analyses are consistent with several studies inferring the existence of competition in *Acacia* species (Gutierrez and Fuentes, 1979; Smith and Walker, 1983; Smith and Goodman, 1986). Wiegand et al. (2005) have shown that inter-trees distances increase with age/size and Ward (2005) has shown that trees become more evenly spaced with age/size. For the study area, the nearest-neighbour analyses did not only show the existence of competition but also the high intensity thereof (inferred from the steep slope of the upper limiting quantile in Fig. 3a; Welden and Slauson, 1986). Nevertheless, our analyses also support the hypothesis of Welden and Slauson (1986) that the intensity of competition and its importance relative to other factors are independent of each other: The similar slopes of the quantile regression lines (Fig. 3a) lead to the conclusion that unmeasured factors other than nearest-neighbour distance also had an important (interactive) effect on shrub size. These other factors could be, for instance, nutrient heterogeneities or water stress. This result may enhance the view that, in arid savannas, aboveground competition for light (as revealed by nearest-neighbour analyses) is of minor importance compared with belowground competition for water and nutrients (Vila, 1997). However, only long-term studies can generate reliable conclusions on the relationship between growth and space (cf. Wiegand et al., 2000b).

The experimental removal of competitors did not have a significant positive effect on shrub size, which is inconsistent with prediction 4. This is even more surprising as shrub removal is expected to have a fertilising effect on target shrubs through the decomposition of the roots of the removed competitors. However, some of the "removed competitors" were able to produce viable regrowth in spite of having been poisoned. Hence, viability and especially belowground competitive strength may not have been completely impaired by the poisoning treatment. Rainfall was below the long-term average in the period between competitor removal and data collection. This may be the reason for the generally low growth rates of *A. mellifera* observed in this study. Growth may have been too slow to cause a significant difference in relative growth rates of targets and controls (see also Wiegand et al., 2005). In general, demographic processes were very slow in *A. mellifera* because mortality and growth rate were very low in the study period; we found only two dead trees and a growth rate of annual regrowth at the tips of the branches of 3.4 cm/year.

Overall, the existence of competition in the study area was inferred by spatial point pattern analysis and autocorrelation analysis, as well as nearest-neighbour analysis (with high intensity). The competitor removal experiment did not support an explanation involving competition but this may be due to an insufficient duration of the treatments.

Although an experimental approach may be more powerful in general, we showed that if demographic processes are slow – as it is commonly the case in arid areas – inferential methods such as spatial point pattern statistics or nearest-neighbour analyses are more time efficient and still provide similarly satisfying answers compared with experiments. In spatial analyses, it is important to include a time-related component that allows inference of competition if patterns become less aggregated over time. From the spatial analyses, we conclude that competition acts after the onset of individual reproductive maturity turning the originally aggregated shrub pattern into a less aggregated pattern. Only then, the overlap of root systems may be strong enough to lead to perceptible changes in growth and spatial patterns of savanna woody species that can be detected in spite of overall aggregated spatial patterns.

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Appendix A

The basic idea behind Wiegand–Moloney's O is to construct concentric rings with radius h and width δh around each point in the study area, to count the number of points within these rings, to take the average across all rings of the same radius, and to compare it to the number of points expected at scale h assuming a random process (Wiegand and Moloney, 2004). The O-ring function is given as

$$O(h) = \frac{1/N\sum_{i=1}^{N} p_i(h, \delta h)}{1/N\sum_{i=1}^{N} \mathrm{area}_i},$$

where h is the radius of the ring, N the number of points in the study area, $pi(h,\delta h)$ the number of points within the ring of radius h and width δh around the point i, and area_i is the area of the ring around point i.

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