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Changes of woody plant interaction and spatial distribution between rocky and sandy soil areas in a semi-arid savanna, South Africa

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ABSTRACT

We examined the impact of shrub–shrub interactions and soil type (rocky or sandy) on growth and spatial distribution of the two savanna shrub species *Tarchonanthus camphoratus* and *Acacia mellifera*. To explore plant interactions, we compared the size of juvenile and mature *T. camphoratus* shrubs between different locations (under the subcanopy of *A. mellifera* and in the open). Juvenile *T. camphoratus* shrubs had similar sizes regardless of location; however, in rocky soil, mature shrubs in the open were larger than those near *A. mellifera*, implying an inter-specific competitive effect of *A. mellifera* on *T. camphoratus*. Juvenile *T. camphoratus* shrubs grew faster in the sandy than in the rocky area. Furthermore, we used the Wiegand–Moloney *O*-ring statistics to explore the spatial distribution of *T. camphoratus*. *T. camphoratus* showed spatial aggregation, but in the rocky area *T. camphoratus* juveniles were positively associated with *A. mellifera* (indicating facilitation as the pattern-creating process), whereas in the sandy area they were positively associated with mature *T. camphoratus* shrubs (indicating seed dispersal as the pattern-creating process). *T. camphoratus* exhibited encroachment potential in the sandy area. We showed how spatial pattern analysis can help to explore processes determining woody plant spacing and recommend its further use.

1. Introduction

Savanna ecosystems are characterized by the co-dominance of woody plants (shrubs and trees) and grasses (Scholes and Archer, 1997; Scholes and Walker, 1993). Many studies have been conducted to investigate the mechanisms that allow the co-dominance of these two different life-forms (Jeltsch et al., 2000; Sankaran et al., 2004; Scholes and Archer, 1997; Skarpe, 1992; Wiegand et al., 2006). Researchers focused on the impact of disturbances such as grazing, fire, and the interactions between woody plants and understorey species (grasses or herbs; Vetaas, 1992; Higgins et al., 2000; Jeltsch et al., 2000).

There are only a few investigations of interactions within a life-form, especially on how woody plant species influence one another (Mahall and Callaway, 1992; Midgley and Bond, 2001; Smith and Goodman, 1986; Smith and Walker, 1983). The fine-scale spatial distribution of woody plants in arid and semi-arid environments has been investigated in recent years (Barot et al., 1999; Bucini and Hanan, 2007; Dean et al., 1999; Smet and Ward, 2006; Strand et al., 2007), often finding spatial associations between woody plants (e.g. Dean et al., 1999; Meyer et al., 2008; Milton and Dean, 1995; Skarpe, 1991), although a spatial repulsion of woody plants is expected in water-limited ecosystems due to competition. A spatial association of woody plants can be caused by several processes, e.g. a facilitative effect of one plant on the other (nurse plant syndrome), directed seed dispersal, or a heterogeneous environment. If the association is caused by inter-specific facilitative interactions, the association between the heterospecific plants constitutes a nurse–protégé interaction (Flores and Jurado, 2003; Malkinson and Jeltsch, 2007). A nurse plant has an established canopy beneath which conditions for seed germination and seedling survival are improved, e.g. due to increased water availability, more nutrients in the soil, or reduced grazing pressure (Flores and Jurado, 2003). The protégé plants are seedlings of the other species benefiting from the nurse plant, presumably with little effect on their benefactor. However, this commensal relationship may turn into competition once the protégé-seedlings grow into established plants (Flores-Martinez et al., 1994; McAuliffe, 1988; Miriti, 2006).

Directed seed dispersal results in spatial plant associations similar to those caused by nurse plant effects when wind-dispersed

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seeds are trapped beneath (apparent nurse) plants or when animal-dispersed seeds are preferentially defecated beneath (apparent nurse) plants (Dean et al., 1999; Maclean, 1970; Milton and Dean, 1995). In the case of environmental heterogeneity, external factors cause environmental variables to be unevenly distributed in space and/or time. If local environments (e.g. soil nutrient concentrations) are favorable to the investigated species, these species will tend to co-occur even in the absence of mutualistic or commensalistic interactions (Barot et al., 1999; Maestre et al., 2003).

Knowledge about the drivers of vegetation structure and dynamics in savannas are important for the management of tree or shrub encroachment, i.e. an increase of woody vegetation associated with a reduction of the grass layer (Roques et al., 2001). Shrub encroachment is a process with considerable consequences for ecology (e.g. loss of habitat diversity) and economy (e.g. reduced productivity) in savannas worldwide (Dalle et al., 2006; Kaphengst and Ward, 2008; Meik et al., 2002). To investigate how woody plants interact should be a useful approach to improve our understanding of processes and dynamics in savannas, and may provide possibilities for management of shrub-encroached areas. Two dominant shrub species, *Tarchonanthus camphoratus* and *Acacia mellifera*, are the focus of our work in the arid Northern Cape province of South Africa. The shrub vegetation in this area, with a focus on *A. mellifera*, was studied by Meyer et al. (2005, 2008); they found that *A. mellifera* is an important encroaching species. However, the role of *T. camphoratus* as a potential encroacher is not well understood.

We evaluated the growth and the spatial distribution of *T. camphoratus* and its interactions with *A. mellifera* in two different soil areas. The composition, structure, and spatial arrangement of vegetation are influenced by the amount of available soil moisture and nutrients. These factors in turn are influenced by soil characteristics (Cole, 1982), such as soil depth or the proportion of soil rock fragments (Fournier and Planchon, 1998; Maestre and Cortina, 2002; Picard et al., 2005). We studied the growth and spatial distribution of woody plants in an area with a high amount of rock fragments and in a sandy soil area without rocks. Surface rock fragments can improve soil conditions for plant growth by protecting soil for crust development, by slowing down surface run-off of water, and by decreasing the loss of water by evaporation (Cerdà, 2001; Poesen and Lavee, 1994). Rock fragments may increase the infiltration of water into soil, but they can also transport heat more rapidly and deeper into the soil (Poesen and Lavee, 1994). Based on the positive effects of rock fragments we expect a greater density of shrubs in areas with a greater amount of rock fragments (Britz and Ward, 2007).

The aim of this study was to evaluate factors that determine the structure of the two savanna woody plant species by describing growth and spatial distributions of these species on different soil types. In doing this, we focused on possible size-/age-related differences in growth and spatial distribution of *T. camphoratus* shrubs. In addition, we examined the relationships of the spatial distribution of *T. camphoratus* to those of *A. mellifera* shrubs. To explore processes determining the spatial distribution of woody plants, we applied spatial pattern analysis.

We made the following predictions (see Table 1):

I) *T. camphoratus* plants growing near *A. mellifera* are smaller than plants in the open matrix due to inter-specific competition between the two woody species.
II) Shrubs of *T. camphoratus* exhibit improved growth in areas with a high amount of rock fragments due to improved soil conditions for plant growth.
III) A regular distribution of *T. camphoratus* shrubs is expected due to intra-specific competition.
IV) Juveniles of *T. camphoratus* are associated with mature *T. camphoratus* or *A. mellifera* shrubs due to facilitation. With growth of the juveniles, competition increases between juvenile and mature plant, so that the association disappears in the larger size classes.

2. Methods

2.1. Study site

Field data were collected in three plots in a semi-arid savanna in the Kimberley Thorn Bushveld (Mucina and Rutherford, 2006), South Africa, from September to November 2007. The plots were situated at Pniel Estates (28°35′ S, 24°29′ E), 35 km northwest of Kimberley. The mean annual rainfall is 388 mm and occurs mainly in the summer months between November and April, but with a high interannual variation (C.V. = 39%; Kraaij and Ward, 2006). The soil of the study area is deep red Kalahari sand (Smet and Ward, 2006) and in some regions a high amount of surface and below-ground rock fragments occurs, with a predominance of andesite rocks near the Vaal river. Pniel Estate has an area of about 230.2 km^2, rocky soil is about 40% (91.8 km^2) of the total area and sandy soil is about 32% (73.6 km^2). Fire frequency for the whole area was calculated as 0.006 per year (Meyer et al., 2007). The area is grazed by game (912 LSU^{-1}, Britz and Ward, 2007), e.g. *Raphicerus campestris* (steenbok), *Antidorcas marsupialis* (springboks), *Hippotragus equinus* (roan), *Connochaetes gnou* and *Connochaetes taurinus* (wildebeest), *Oryx gazella* (gemsbok), and *Tragelaphus strepsiceros* (kudu). All plots were laid out in a fenced game ranch (14 000 ha), in which the woody cover ranges between 30% and 50%. The woody vegetation is dominated by *A. mellifera* (Vahl) Benth. and *T. camphoratus* L. Other shrub species in the area include *Grewia flava*, *Acacia tortilis*, and *Ziziphus mucronata*. In the sandy area of the game ranch, *Acacia erioloba* trees are dominant. Grass cover ranges between 30% and 45% and frequent species are *Schmidtia pappophoroides*, *Eragrostis lehmanniana*, *Aristida congesta* and *Cynodon dactylon* (Britz and Ward, 2007).

We located three plots in regions with specific soil conditions: plot 1 (20 m × 20 m) was laid out in an area with sand but a high amount of rock fragments (hereafter referred to as “rocky plot”), plot 2 (20 m × 20 m) in an area with sandy soil (referred to as “sandy plot”), and plot 3 (20 m × 21 m) in an area with sandy soil but with a small amount of small and medium stones (referred to as “rocky–sandy plot”). The position of each plot was located by design to each of the three soil types and to cover representative stands of the vegetation in the area. The rocky plot was 6.5 km from the sandy plot and 1.9 km from the rocky–sandy plot and the sandy and rocky–sandy plots were 4.6 km apart.

2.2. Field methods

In each plot, we measured the *x*- and *y*-coordinates of every woody plant. For single-stemmed individuals, we measured the coordinates of the stem base, whereas for multi-stemmed individuals, we estimated the stem center by visual approximation and determined the coordinates thereof. Stems separated by a distance of <20 cm were considered as belonging to one individual. The height, maximum canopy diameter, and the canopy diameter perpendicular to the maximum were recorded for all woody plants in the plot. For *T. camphoratus* individuals we counted the number of stems belonging to one individual.

To be able to evaluate differences in growth and spatial distribution with plant size (assumed to be correlated with plant age), we divided all *T. camphoratus* plants into two size classes. Plants

Table 1
Overview of tests, their results, and explanations. The first column gives the number of the tested hypothesis explained in the introduction section (see above).

Hypothesis number	Null hypothesis	Test statistics	Results	Explanation
	Size			
I	No differences in the size-frequency distribution of *T. camphoratus* shrubs between locations (under the subcanopy of *A. mellifera*, in the open) within a soil area.	Kolmogorov–Smirnov test	Juveniles have similar size distributions within an area. The canopy size distribution of mature shrubs near *A. mellifera* plants is different to shrubs in the open in the rocky plot. In the other two plots, mature shrubs differ not between the locations (Fig. 2).	Differences in the size distribution of plants under the subcanopy of *A. mellifera* may be caused by e.g. an impact of interactions on growth.
		Mann–Whitney *U*-test (Bonferroni adjustment)	Mature shrubs in the open have larger canopies than shrubs under the subcanopy of *A. mellifera* in the rocky soil area (Fig. 2).	In the rocky soil area, mature shrubs near *A. mellifera* may suffer from competition.
	Growth			
II	No difference of growth of *T. camphoratus* juveniles between sandy and rocky soil.	Multiple response permutation procedure	Juveniles in the sandy grew faster than in the rocky area (Fig. 3).	Greater growth rate of juveniles in the sandy area can be caused by better conditions for *T. camphoratus* plants on sandy soils. However, the high density of *A. mellifera* shrubs in the rocky area may decrease the resources for growth of juvenile *T. camphoratus* shrubs.
	Spatial distribution			
III	Univariate *T. camphoratus* analysis: plants are randomly distributed.	Spatial data analysis with null model: complete spatial randomness	Aggregation of *T. camphoratus* shrubs in all plots (Fig. 4).	Aggregation of plants can be caused by e.g. directed seed dispersal, vegetative reproduction, facilitation, or environmental heterogeneity.
IV	No differences in the spatial distribution of juveniles and mature *T. camphoratus* shrubs.	Random labeling	No differences (Appendix C).	Juveniles and mature shrubs are distributed in the same way.
	1) No spatial association between *T. camphoratus* size classes (juveniles/mature shrubs). 2) No spatial association between *T. camphoratus* and *A. mellifera*.	Toroidal shift	1) Spatial association of juveniles and mature *T. camphoratus* shrubs in the sandy soil plot (Fig. 5a). 2) Spatial association between juveniles and *A. mellifera* shrubs in the rocky soil plot (Fig. 5b).	1) The association in the sandy plot may be caused by seed dispersal. 2) The association in the rocky plot may be caused by a positive effect of *A. mellifera* on the establishment or survival of juvenile *T. camphoratus* shrubs (nurse plant syndrome).
	1) No spatial association between *T. camphoratus* size classes (juveniles/mature shrubs). 2) No spatial association between *T. camphoratus* juveniles and *A. mellifera*.	Antecedent conditions	1) Spatial association of juveniles and mature shrubs in the sandy soil plot (Appendix B). 2) Spatial association between juveniles and *A. mellifera* in all three plots (Appendix B).	See above (explanation toroidal shift null model).

smaller than 80 cm in height and less than 10 stems were classified as juveniles, plants larger than 80 cm or with $\geq$10 stems per plant were classified as mature shrubs. We chose 80 cm as the limit for juvenile plants because the minimum height of *T. camphoratus* plants with flowers found in the three plots was 82 cm. The limitation of $<$10 stems for juvenile plants was chosen based on the observation that in 1 year plants do not produce more than 10 stems. More specifically, we chose 10 stems as a limit because the mean number of new stems developed between September and November 2007 was 1.12 (SD 1.73) in the rocky area and 2.78 (SD 3.53) in the sandy area.

To get an estimate of the growth of *T. camphoratus* juveniles, we measured all juveniles in the rocky and sandy plot and around the plots on two occasions (end of September and end of November 2007). We recorded their height, maximum canopy diameter, and counted the number of stems. Furthermore, we recorded the location of the juvenile plant as either under the subcanopy of *A. mellifera*, under the subcanopy of another woody plant species, or in the open matrix (i.e. not surrounded by any other woody plant).

2.3. Analysis of plant size and growth

All data were tested for normality using a Shapiro–Wilks test. In each plot, the distributions of height and maximum canopy diameter of juvenile and mature *T. camphoratus* shrubs under the subcanopy of *A. mellifera* shrubs were compared to plants growing in the open matrix with the Kolmogorov–Smirnov test. If the test showed differences between the size-frequency distributions ($p < 0.05$), we used the Student's *t*-test (normally distributed values) or the Mann–Whitney *U*-test (if values were not normally distributed) to examine the difference in height and/or canopy size between plants nearby *A. mellifera* shrubs and in the open. Because of the multiple comparisons we used the Bonferroni adjustment of α, resulting in a realized significance level of 0.0167.

For all *T. camphoratus* juveniles in the open and beneath *A. mellifera* canopy that were measured twice in 2007 (see above; rocky area: $n = 41$, sandy area: $n = 41$), we calculated the differences in height and in maximum canopy diameter. We compared the growth of *T. camphoratus* juveniles between the rocky and the sandy areas to determine growth differences between the two areas. We used a multiple response permutation procedure (MRPP) with 999 permutations because the data were not normally distributed and variance was heterogeneous. All non-spatial statistics were done with the software package R (version 2.10.1).

2.4. Spatial pattern analysis

We used the information about the position of the shrubs in each plot to examine (1) the spatial dependence between *T. camphoratus* shrubs and *A. mellifera* shrubs and (2) the spatial dependence between different size classes of *T. camphoratus*. The spatial data analyses were performed with the software Programita (Wiegand and Moloney, 2004). The position of a plant in a plot is represented by a point and the analysis of the spatial point pattern exhibits whether the points are distributed randomly. If the pattern shows a non-random distribution, aggregation or repulsion of the points is possible (under- or overdispersion). In spatial pattern analyses, one has to distinguish between first-order and second-order effects, but in nature a mix of both types often occurs. On the one hand, the spatial pattern could result from an underlying process (e.g. imposed by the environment), which affects the distribution of the points (first-order effect, described by the intensity $\lambda(x, y)$) and/or the pattern could be produced by an attraction or repulsion of the points themselves (second-order effect; Bailey and Gatrell, 1995). The intensity λ is defined as the number of plants per area and should be homogeneous in the plot if second-order effects were investigated. We focused on the second-order processes determining the spatial distribution of the species investigated; therefore we evaluated each plot for its homogeneity by using the *L*-function (Besag, 1977; Ripley, 1976). The *L*-function has a memory effect, so that in a plot with a "virtual aggregation" of points due to first-order effects the *L*-function increases with larger scales (Wiegand and Moloney, 2004). Whenever the intensity is heterogeneous, we adjusted the null model to account for $\lambda(x, y)$ and to focus on second-order effects (see methods Section 2.5 below).

To describe the spatial distribution and second-order effects of *T. camphoratus* and *A. mellifera*, we used the Wiegand and Moloney (2004) *O*-ring statistic. The *O*-ring statistic is similar to Ripley's (1976) *K*-statistic, but uses annuli instead of circles, so that the spatial relation between points can be related to a certain scale (Wiegand and Moloney, 2004). The *O*-ring statistic of a univariate point pattern counts the number of points in a ring around an arbitrarily chosen point at a specific distance h and width δh. This is done for all points of the pattern. The O_{12}-ring statistic for a bivariate analysis (point pattern 1: species 1, point pattern 2: species 2) is similar to the univariate function but counts the number of points of pattern 2 in a ring of distance h from an arbitrary point of pattern 1.

Confidence envelopes for the *O*-ring statistic were estimated from 999 Monte-Carlo simulations of the point patterns using a specific null model (defined below; Bailey and Gatrell, 1995). In each simulation, the points were redistributed according to the null model and the *O*-ring statistic was calculated for the simulated point pattern. From all simulations, the upper and lower confidence envelopes were estimated using the 5th lowest and 5th highest value for each distance h, representing a significant level of approximately $p = 0.01$.

In the univariate case, if the *O*-ring function exceeds the upper confidence envelope it indicates a spatial aggregation of the species (e.g. caused by positive effects or seed dispersal). However, if the function is below the lower confidence envelope, it indicates a spatial regularity of the plants (e.g. caused by intra-specific competition). If the function is between both limits, the distribution of plants does not deviate from the assumption of the chosen null model.

In the bivariate analysis, values above the upper confidence envelope indicate significant association between the two point patterns, whereas values below the lower confidence envelope indicate significant repulsion. As in the univariate case, values within the two confidence envelopes do not differ significantly from the null model.

2.5. Null models of the spatial pattern analysis

We calculated the univariate *O*-ring statistic for the *T. camphoratus* pattern of each plot and compared it to the null model of complete spatial randomness (CSR; homogeneous Poisson process; Wiegand and Moloney, 2004). On the basis of the *L*-function, we concluded that the intensity λ in the rocky plot varies with location (x, y) within the plot. Therefore, we estimated the first-order intensity $\lambda(x, y)$ in the plot applying a moving window (Wiegand and Moloney, 2004) with a bandwidth of 8 m. The bandwidth of 8 m is based on knowledge about the shrubs, assuming a mean shrub–shrub interaction radius of this distance. The heterogeneous Poisson process in the rocky plot was established by randomly distributing all plants within an 8 m radius around their original position (Wiegand and Moloney, 2004). Consequently, the spatial pattern of the shrubs in the rocky plot and their deviation from random distribution can be interpreted up to 8 m only.

To test for spatial independence between the two size classes, we examined the spatial distribution of *T. camphoratus* juveniles in relation to mature plants with the toroidal shift null model by fixation of the points of mature shrubs and random movement of the whole juvenile pattern relative to the first pattern but without changing the relative positions (Wiegand and Moloney, 2004). To account for the fact that mature shrubs were established before juvenile shrubs developed, we also used a null model which incorporates antecedent conditions (Wiegand and Moloney, 2004) to analyze the spatial distribution of juveniles in regard of the distribution of mature shrubs. This additional test was performed by fixation of the pattern of mature shrubs and the redistribution of juveniles according to a heterogeneous Poisson process within an 8 m circle around the original position of the juveniles in the rocky plot (see above) and according to a homogeneous Poisson process in the sandy and in the rocky–sandy plot.

Contrary to the last two spatial approaches, in which we investigated the spatial relation between the distributions of juveniles and mature shrubs, the random labeling null model was used to detect possible differences in the spatial distribution of juveniles compared to the distribution of mature shrubs regardless of the underlying first-order process (Wiegand and Moloney, 2004). In this spatial analysis we used the bivariate pair-correlation function $g_{12}(h)$, which is related to Ripley's bivariate K_{12}-function, but uses annuli instead of circles: $g_{12}(h) = (\mathrm{d}K'_{12}(h)/\mathrm{d}h)/2\pi h$ (Stoyan and Stoyan, 1994; Strand et al., 2007). The idea behind random labeling is the following: If both patterns have the same spatial distribution, each pattern can be considered as random thinning of the combined pattern. As a result, the pair-correlation function is invariant and $g_{12}(h) = g_{21}(h) = g_{11}(h) = g_{22}(h)$ (Getzin et al., 2008; Wiegand and Moloney, 2004). Consequently, we can use the differences between pair-correlation functions (Bailey and Gatrell, 1995; Dixon, 2002) to evaluate the spatial distribution of juveniles in relation to the spatial distribution of mature shrubs. We used the case-control design with mature shrubs as pattern 1 (control pattern) and juveniles as pattern 2 (cases) (Getzin et al., 2008; Wiegand and Moloney, 2004). Thus, a difference of $g_{12}(h)$

and $g_{11}(h)$ provides insights into the spatial distribution of juveniles around mature shrubs in relation to the spatial distribution of mature shrubs to each other (Getzin et al., 2008). The second comparison, $g_{21}(h) - g_{22}(h)$, can be used to evaluate the spatial distribution of juveniles. For example, a positive deviation would mean that juveniles exhibited a clumped spatial distribution in comparison to mature shrubs (Getzin et al., 2006, 2008). To perform the random labeling analysis, the spatial position of all plants in the plot remained fixed, but the labels of the points (mature or juvenile) were randomly assigned to the overall pattern (Bailey and Gatrell, 1995).

A possible effect of *A. mellifera* on the spatial distribution of juvenile or mature *T. camphoratus* was tested with the toroidal shift null model. We applied toroidal shift to a) the juvenile *T. camphoratus* pattern and b) to the mature *T. camphoratus* pattern, both relative to the *A. mellifera* pattern. To complement the evaluation of a spatial impact of *A. mellifera* on juveniles of *T. camphoratus* a null model with respect to antecedent conditions was performed by fixation of the *A. mellifera* pattern and a redistribution of the position of juveniles according to a heterogeneous Poisson process with an 8 m radius around the original position of the juveniles in the rocky plot (see above) and according to a homogeneous Poisson process in the sandy and in the rocky–sandy plot.

3. Results

In total, we recorded 179, 25, and 31 *A. mellifera* plants and 52, 85, and 51 *T. camphoratus* plants in the rocky, sandy, and rocky–sandy plots, respectively (see Fig. 1 for basic description). Furthermore, we recorded 38 plants of other woody species in the rocky plot, and 31 plants in each of the other two plots.

3.1. Plant size and growth

Within any given plot, the size-frequency distribution of height and maximum canopy diameter of *T. camphoratus* juveniles growing near *A. mellifera* individuals showed no significant differences to juveniles in the open matrix (Fig. 2; Kolmogorov–Smirnov test: $p > 0.1$). In the rocky plot, mature shrubs of *T. camphoratus* growing in the open had a different distribution of maximum canopy and larger maximum canopy diameters than shrubs growing near *A. mellifera* (Fig. 2; Kolmogorov–Smirnov test, Mann–Whitney test: $p < 0.0167$), but the shrub height was similar in both locations (Kolmogorov–Smirnov test: $p > 0.2$). In the sandy plot and in the rocky–sandy plot, the size-frequency distributions of height and maximum canopy diameter of mature shrubs were similar for the shrubs located near *A. mellifera* and the shrubs in the open matrix ($p > 0.2$).

The growth of juvenile *T. camphoratus* shrubs differed between the rocky and the sandy area. Juvenile plants grew larger (height and maximum canopy diameter) in the sandy area than in the rocky area over the two months (pooled under canopy and matrix plants; Fig. 3, $p < 0.013$).

3.2. Spatial pattern analysis

The univariate spatial analysis of the overall pattern of *T. camphoratus* plants revealed an aggregation at distances of 0.4 m in the rocky plot (Fig. 4). In the sandy plot, aggregation was observed at 0.2–1.8 m, at 2.6 m, and at 3.2–4.0 m (Fig. 4). In the rocky–sandy plot aggregation was found at distances of 0.2–1.0 m (Fig. 4). Repulsion was found in the rocky–sandy plot at distances of 4.4–4.8 m (Fig. 4).

The spatial analysis of mature shrubs and juveniles with the toroidal shift null model revealed an association between both size classes of *T. camphoratus* in the sandy plot only (Fig. 5a), but not in the other two plots (Appendix A Fig. a, b). This result was supported by the analysis with the null model accounting for antecedent conditions: in the sandy plot there was an association at 0.4–1.8 m and at 3.6–4.0 m (Appendix B Fig. a), but not in the other two plots (Appendix B Fig. b, c). The analysis of the random labeling null model also showed no deviation from the null hypothesis of 'random thinning' (Appendix C) and juveniles of *T. camphoratus* exhibited no

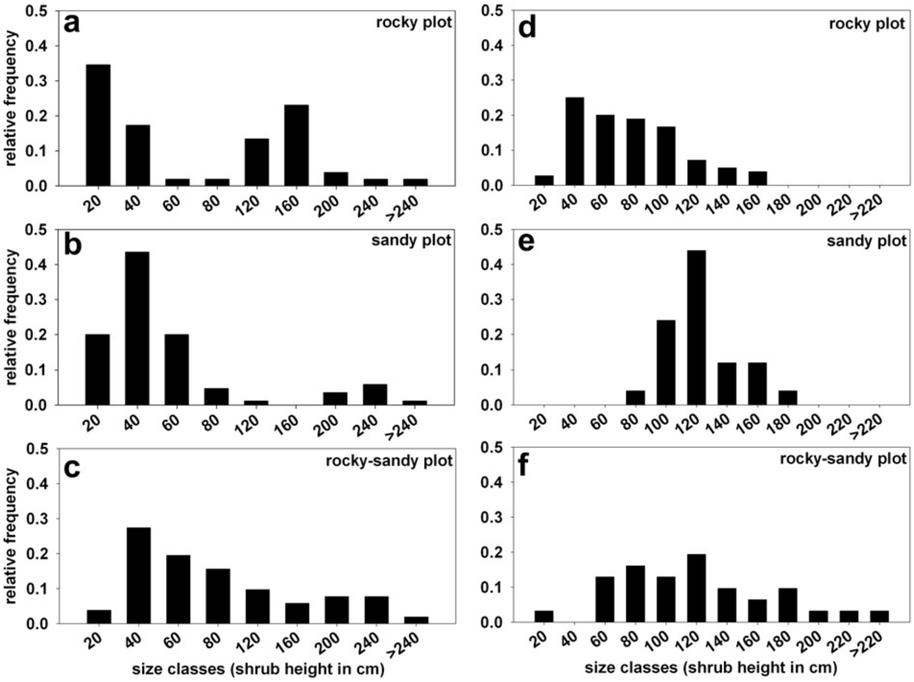

Fig. 1. Size-frequency distributions of height of *T. camphoratus* shrubs (a–c) and *A. mellifera* shrubs (d–f) in the three study plots. Mature shrubs of *T. camphoratus* (height > 0.8 m and more than 10 stems) were separated into larger size classes due to greater variability in size with age (see Wiegand et al., 2005).

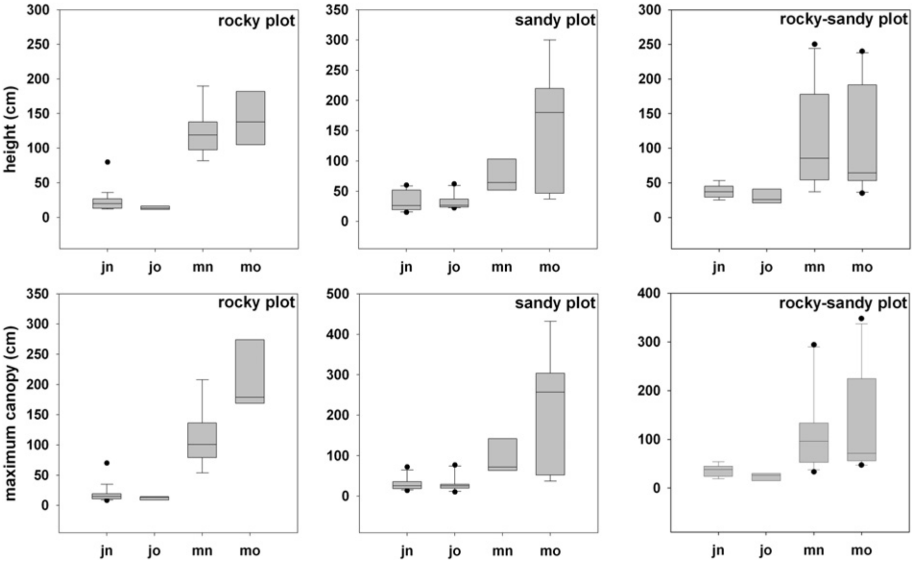

Fig. 2. Comparison of size of *T. camphoratus* plants between different locations. Box plots of height (upper row) and maximum canopy diameter (lower row) of *T. camphoratus* juveniles (*j*) and mature shrubs (*m*) growing near *A. mellifera* plants (*n*) and in the open (○), respectively, are shown. Horizontal lines are the medians and the boxes span the first and third quartile, whiskers show the non-outlier range, whereas points are outliers.

additional clustering compared to the spatial pattern of mature *T. camphoratus* plants (Appendix C) in all plots.

The spatial analyses of *A. mellifera* and *T. camphoratus* patterns with the toroidal shift null model revealed independence between both species in most cases (Appendix A Fig. c–j). Only in the rocky plot there was an association between *T. camphoratus* juveniles and the *A. mellifera* distribution at distances of 0.8–1.0 m (Fig. 5b). The analysis with the antecedent conditions null model exhibited an association at 0.8–1.0 m in the rocky plot (Appendix B Fig. d), in the sandy plot at 0.2 m (Appendix B Fig. e), and in the rocky–sandy plot at 1.2 m (Appendix B Fig. f).

4. Discussion

We investigated how woody plant interactions and soil type affect growth and spatial distribution of the two savanna woody plant species *T. camphoratus* and *A. mellifera*. The greatest number of woody plants was recorded in the rocky plot (total number of woody plants: rocky plot – 269, sandy plot – 141, rocky–sandy plot – 113), probably due to improved soil conditions caused by the high content of soil rock fragments in this area (Britz and Ward, 2007; for a review see Poesen and Lavee, 1994). However, Ward and Esler (in press) revealed that a low grass density, such as caused by grazing, exerted a greater influence on seedling recruitment of *A. mellifera* than rocky substrate. The number of plants per species differed considerably in our plots, with *T. camphoratus* being most abundant in the sandy area, whereas *A. mellifera* was more abundant in the rocky area. This difference in density of the shrub species can be caused by (1) niche differences, with *T. camphoratus* preferring sandy soil and *A. mellifera* preferring soils with higher rock fragment content and/or (2) a competitive effect, in which *A. mellifera* may be a stronger competitor on rocky soils than *T. camphoratus*.

In an experimental removal of *A. mellifera* plants, *T. camphoratus* shrubs reached larger sizes and more juvenile shrubs were found in the plots without *A. mellifera* plants, indicating that inter-specific competition occurs (Schleicher, unpublished data). To further evaluate the competitive impact of *A. mellifera* on *T. camphoratus*, we compared the size of *T. camphoratus* juveniles under the subcanopy of *A. mellifera* to juveniles growing in the open matrix within our rocky and sandy soil plots. Under both rocky and sandy soil conditions, the location of juvenile *T. camphoratus* shrubs within a plot had little effect on its size. Hence, contrary to our hypothesis 1, no competitive effect of *A. mellifera* on the size of nearby *T. camphoratus* juveniles could be identified. Although seedling recruitment of *T. camphoratus* occurred after the removal of *A. mellifera* shrubs in a removal experiment (Schleicher, unpublished data), the size of *T. camphoratus* juveniles seems unaffected by *A. mellifera* shrubs.

Furthermore, the growth of juveniles was compared between the two soil types. Contrary to our hypothesis 2, we found that *T. camphoratus* juveniles in the sandy area grew larger than juveniles in the rocky area. Therefore, soil conditions seem to play an important role in the growth of woody plants, but a negative effect of *A. mellifera* shrubs in the rocky area cannot be excluded. Although we found no effect of *A. mellifera* on the size of nearby juveniles, the very high density of *A. mellifera* shrubs in the rocky area may deplete the water and nutrient resources of the soil beyond their canopy areas. The shallow soil in the rocky area does not allow a vertical separation of root systems to prevent belowground competition for water and nutrients (see also Wiegand et al., 2005). Thus, a belowground negative effect of *A. mellifera* on *T. camphoratus* plants may occur in the whole area. Support for this hypothesis is given by root excavations, which revealed a large root system of *A. mellifera* shrubs in savannas. Meyer et al. (2008) found root lengths up to 15 m of *A. mellifera* shrubs in sandy soils and we also observed root lengths of *A. mellifera* plants greater than 9 m in sandy soil (October 2007, Pniel Estates, Schleicher, unpublished data). Because of the shallow soil in the rocky area, we expect a greater root system extent on this soil type. With such a large root system, even *T. camphoratus* shrubs not directly surrounded by *A. mellifera* shrubs may be negatively affected. These could explain the similarity in size of juveniles regardless of an open or a subcanopy location. In conclusion, further studies are necessary to determine whether there is a competitive effect of *A. mellifera* on *T. camphoratus* juveniles or, respectively, an impact of soil conditions on juvenile growth.

Contrary to the similarity of juvenile size within a plot, the size of mature shrubs of *T. camphoratus* differed with regard to the location of the plant. In the rocky plot, the maximum canopy diameter of mature shrubs in the open matrix was greater than that of shrubs growing near *A. mellifera* shrubs. Because we could not

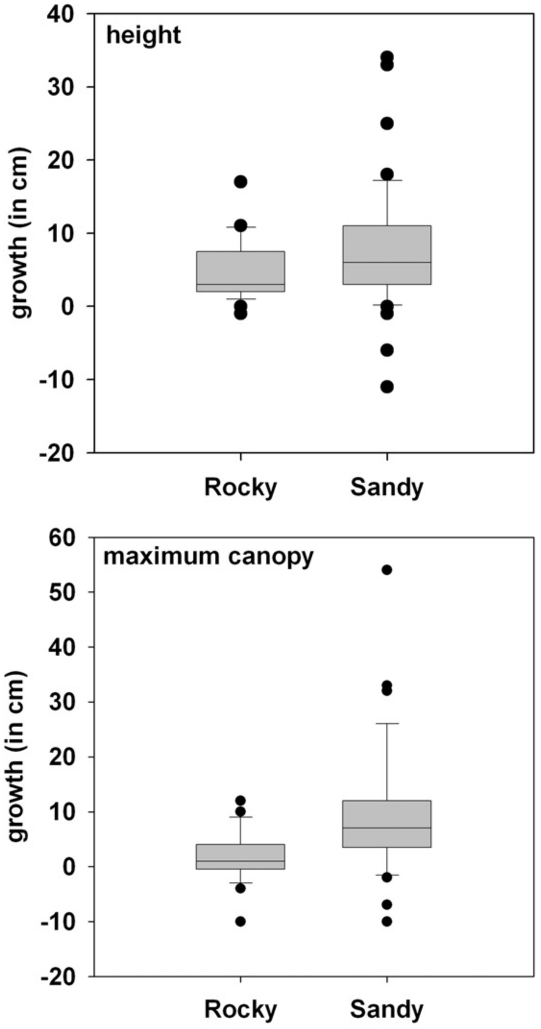

Fig. 3. Growth of *T. camphoratus* juveniles in different plots. The height and maximum canopy diameter growth of *T. camphoratus* juveniles between September and November 2007 in the rocky area and in the sandy area are presented. Horizontal lines are the medians and the boxes span the first and third quartile, whiskers show the non-outlier range, whereas points are outliers.

find such a size difference in the other two plots, it can be assumed that only in the rocky plot do *T. camphoratus* shrubs, from a certain minimum size, suffer from competition from the surrounding *A. mellifera* plants.

The comparison of shrub sizes between those occurring beneath other shrubs and in the open is one way to investigate woody plant interactions, but spatial pattern analysis can also give insights into factors influencing the vegetation structure of savannas. Contrary to our expectation of a regular distribution of *T. camphoratus* shrubs (hypothesis 3), we found spatial aggregation of *T. camphoratus* shrubs in all three plots. Moreover, a spatial aggregation of *A. mellifera* shrubs was exhibited by Meyer et al. (2008). An aggregation of individuals of the same species can be caused, for example, by directed seed dispersal or vegetative reproduction and/or a positive effect of large plants on the establishment and survival of juveniles (Callaway, 1995; Harper, 1977; Skarpe, 1991). Seeds of *T. camphoratus* are wind-dispersed and it can be expected that the majority of seeds fall below the parent plant (Okubo and Levin, 1989), so that we would expect an association of juveniles around larger shrubs of the same species. However, a spatial association of juveniles and mature shrubs could only be found in the sandy soil plot. This spatial association on sandy soil was supported by the null model accounting for antecedent conditions.

An aggregation of shrubs of the same species can also occur due to a positive effect of one plant species on the establishment of seedlings of the other species (nurse plant syndrome; Callaway, 1992; Flores and Jurado, 2003). For example, the canopy of a large shrub of one species reduces solar radiation or moderates temperature extremes by canopy shade (review Bertness and Callaway, 1994; Callaway, 1995; Turner et al., 1966) and therefore provides good conditions for germination. Hence, a further explanation for the spatial aggregation of *T. camphoratus* shrubs may be a positive effect of *A. mellifera* shrubs on seedling establishment, leading to clustering. To investigate this possibility, we used a spatial analysis with the toroidal shift null model to evaluate the spatial relation between *A. mellifera* and *T. camphoratus* shrubs. We found no spatial association between both woody plant species with one exception, viz. an association of *A. mellifera* shrubs and juveniles of *T. camphoratus* in the rocky plot. The null model accounting for antecedent conditions also showed a spatial association at 0.8–1.0 m in the rocky plot. However, in the sandy plot and the rocky–sandy plot we found a positive spatial association of *A. mellifera* and juvenile *T. camphoratus* at short distances, which was not visible with the toroidal shift analysis. The

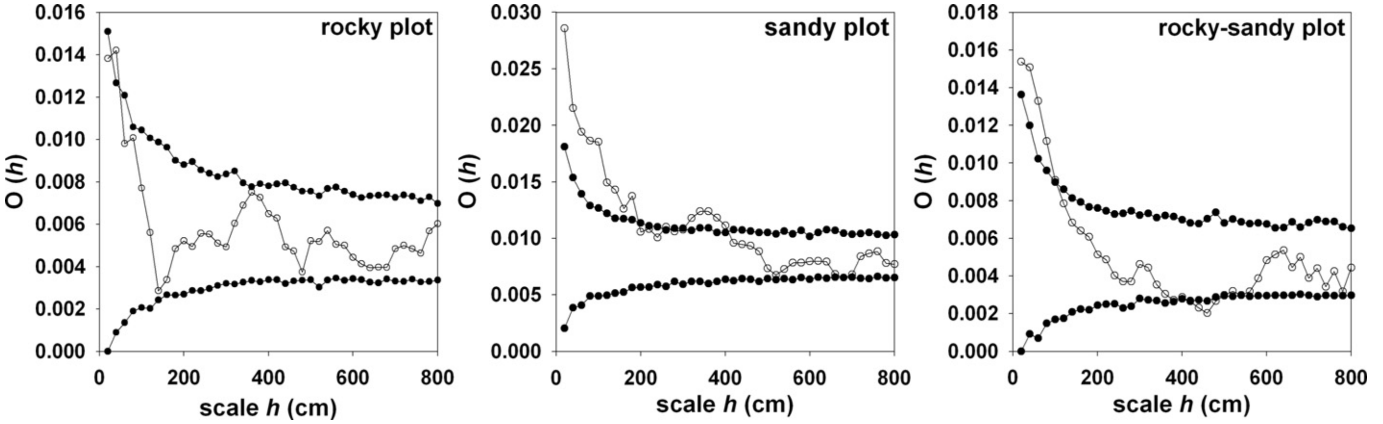

Fig. 4. Spatial distribution of *T. camphoratus* shrubs. The univariate *O*-ring function (-○-) was calculated from the *T. camphoratus* pattern. The spatial positions of plants were redistributed according to a homogeneous Poisson process (null model of CSR) and the 5th lowest and highest values of 999 Monte-Carlo simulations (representing a significant level of approximately $p = 0.01$) were used to estimate the confidence envelopes (-●-). The redistribution of shrubs in the rocky plot was based on a heterogeneous Poisson process because of heterogeneity (also see text) i.e. shrubs were redistributed within 8 m around their original location. If the *O*-ring function exceeds the upper confidence envelope it indicates a spatial aggregation of the species. If the function is below the lower confidence envelope, it indicates a spatial regularity of the plants. If the function is between both limits, the distribution of plants does not deviate from a randomly distributed pattern.

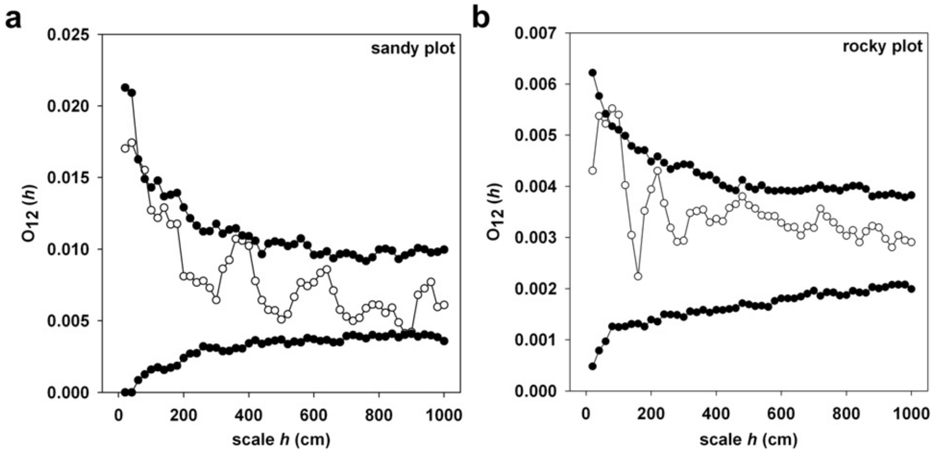

Fig. 5. Test of spatial dependence between size classes of *T. camphoratus* and *A. mellifera* with the toroidal shift null model. Only results deviating from a random distribution are shown (see Appendix A for the analyses showing a random distribution): The *O*-ring function (-○-) of (a) mature shrubs and juveniles of *T. camphoratus* in the sandy plot and (b) the *A. mellifera* pattern and juveniles of *T. camphoratus* in the rocky plot. The points of pattern 1 were fixed and the whole pattern of juveniles was moved randomly relative to the first pattern but without changing the relative positions of the points of the juvenile pattern towards each other. The sides of the model plot were connected to each other, so that points which left one side during simulation reappeared on the opposite site. The 5th lowest and highest values of 999 Monte-Carlo simulations (representing a significant level of approximately $p = 0.01$) were used to estimate the confidence envelopes (-●-).

toroidal shift analysis is more convincing than the antecedent conditions analysis because the second-order structure of the point pattern is preserved. Hence, considering the analysis with the toroidal shift null model, *A. mellifera* seems not to have an effect on the distribution of *T. camphoratus* in the sandy and the rocky–sandy plot, but did have an effect in the rocky plot. However, the observed association in the rocky plot may either result from the co-occurrence of the two species due to a shared preference for certain specific environmental conditions (which are patchily distributed in the rocky area) or it may be caused by a positive effect of *A. mellifera* shrubs on the establishment and/or survival of *T. camphoratus* juveniles.

Despite a high number of *T. camphoratus* juveniles under the subcanopy of *A. mellifera* shrubs in the rocky plot and the spatial association in the rocky plot, we found no evidence for a positive influence of established *A. mellifera* plants on the size of *T. camphoratus* juveniles. As mentioned earlier, the size of juveniles growing under *A. mellifera* subcanopies is similar to the size of juveniles in the open matrix. However, it is possible that juveniles growing under the subcanopy of *A. mellifera* are positively influenced at another time of the year. For example, this may occur by protection from herbivory during the rainy season (*A. mellifera* is very thorny while *T. camphoratus* is not) or by protection from heat during the dry season. A longer observation period is necessary to decide whether there is a positive effect of *A. mellifera* on *T. camphoratus* establishment and survival.

Regardless, the association between juveniles and *A. mellifera* shrubs in the rocky plot vanishes with the growth of *T. camphoratus* plants, because we found spatial independence between *A. mellifera* and mature shrubs of *T. camphoratus*. This observation can be explained in two ways: either (1) there is a negative effect of one species on the other at a certain size of the *T. camphoratus* shrub, resulting in the death of one of the two plants, or (2) *T. camphoratus* plants have a longer lifespan, which allows them to outlive *A. mellifera* shrubs, so that the spatial association between both shrub species is lost in time. With our data we could not examine the process causing the loss of spatial association between these two species.

The last spatial analysis we performed was random labeling, which should give insights into the spatial pattern of juveniles compared to the distribution of mature shrubs. If, for example, juveniles are clumped (as would be the case following the hypothesis of a positive effect of *A. mellifera* on *T. camphoratus* juveniles) and mature shrubs are randomly or regularly distributed due to a self-thinning process (Wiegand et al., 2008), the differences in the spatial arrangement of both size classes should occur by a deviation from the random labeling null model. Indeed, we found no differences between the distributions of both size classes in all three plots, so that juveniles seem to be distributed in the same way as mature shrubs. This is in contrast to other studies which found a self-thinning effect in the spatial distribution of woody plants (Meyer et al., 2008; Ward, 2005; Wiegand et al., 2008). However, Wiegand and Moloney (2004) recommended that the number of controls should be greater than the number of cases for random labeling. In our study, the number of cases was greater than the number of controls in the rocky and the sandy plot. Consequently, the results of the spatial analysis with the random labeling null model have to be evaluated with caution.

In sum, despite the limitation of just one plot per soil type, at our study site we found clear differences in the spatial distribution of *T. camphoratus* with regard to the soil conditions, that are also connected with changes in plant–plant interactions. Although an aggregation of *T. camphoratus* shrubs was found in each plot, the cause of this aggregation is different in the soil areas. In the rocky plot, a spatial association of *A. mellifera* and *T. camphoratus* juveniles seems to reflect a positive woody plant interaction, contrary to the competitive effect of *A. mellifera* shrubs on mature *T. camphoratus* shrubs. On the other hand, in the sandy soil area, the association between mature and juvenile *T. camphoratus* shrubs reflects the seed dispersal process. In the sandy area of our study site we revealed the recruitment potential of *T. camphoratus* and therefore its potential for encroachment on sandy soil. To more firmly establish this connection and to evaluate the influence of *A. mellifera* shrubs on *T. camphoratus* juveniles in the rocky area, further replications are necessary. In conclusion, we showed how spatial point pattern analysis can help to explore processes determining the spatial distribution of woody plants. Thus, we recommend including this technique in investigations of vegetation structure and in further evaluations of the encroachment potential of woody savanna plants.

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Appendix. Supplementary material

Supplementary material related to this article can be found online at doi:10.1016/j.jaridenv.2010.10.003.

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