Original article

Spacing patterns of an *Acacia* tree in the Kalahari over a 61-year period: How clumped becomes regular and *vice versa*

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ABSTRACT

Nearest tree neighbour distances and the tree spatial formation on a large scale over time and space replicates were examined. The study was conducted in a natural savanna ecosystem in the Southern Kalahari, South Africa. Nearest tree neighbour and point pattern analysis methods were used to investigate changes in the spatial pattern of trees in two plots. Trees larger than 2 m canopy diameter were mapped. We used aerial photographs of the study area from 1940, 1964, 1984, 1993, and a satellite image from 2001 to follow two plots over time. Field work was carried out too for classification accuracy. We were able to identify and individually follow over 2400 individual trees from 1940 until 2001. Nearest neighbour analysis results indicate that dead trees were on average closer to their nearest neighbouring trees than living trees were to their neighbours. Most dead trees were on average 6 m from their nearest neighbours, while most living trees were about 20 m apart. Point pattern analysis results show a cyclical transition from clumped to random and sequentially to regular tree spacing. These transitions were not correlated across two plots. Generally, decreases in small-scale clumping coincided with periods of high mortality. Our findings show that regular, clumped, and random tree pattern can occur, pending on time, location, and scale within the location.

1. Introduction

Understanding and explaining the underlying processes of the observed spatial patterns of plant individuals has long been an interesting question in plant ecology (Sterner et al., 1986; Wiegand and Moloney, 2004). Spatial heterogeneity and interactions are important to the population dynamics of plants. Spatial influences such as plant competition or the distribution of safe sites for germination result in temporally-variable spatial patterns of plant distribution (Kenkel, 1988). If spatial

processes have a strong influence on spatial patterns of plant distribution, then these spatial patterns necessarily contain information on population dynamics. Therefore, it should be possible to learn about population processes by investigating spatial patterns of plant distribution (Wiegand and Moloney, 2004).

Tree spacing can be random, regular, or clumped. Regular patterns can be the result of density-dependent mortality when tree–tree competition for one or more limiting resources takes place. The regular pattern is created by competition between clumped neighbouring individuals and death of some of them (Ward et al., 1996; Wolf, 2005). Clumped distributions can be formed by management history (Drew and Flewelling, 1979), soil and soil patchiness (Picard et al., 2005), vegetative reproduction (Peterson and Squiers, 1995), limited dispersal capabilities (Peterken and Jones, 1989), as well as gap regeneration (Stewart, 1989). Theoretically, assuming spatial homogeneity, the spatial distribution that provides optimal growth opportunities for all trees is achieved by equal tree spacing, i.e. regular tree distribution (Wolf, 2005). At a smaller spatial scale (up to 30 m), direct inter-tree competition with neighbouring trees has been recorded (Coomes et al., 2002), but there were also cases where neighbourhood-dependent competition was not important (Shackleton, 2002).

Savannas cover about 13% of the global land surface and about half of the area of Africa, Australia, and South America (Scholes and Archer, 1997; Sankaran et al., 2005). Trees in the savanna are critical for providing shade and shelter to animals (Belsky et al., 1989), and they influence plant communities by altering soil moisture and nutrient concentration (Belsky et al., 1989). Tree cover in arid woodlands is lower than tree cover in mesic or humid woodlands; therefore land use of arid woodlands is more prone to desertification (Shepherd, 1991). In addition, arid and semi-arid ecosystems are usually far less managed, and therefore more natural, than northern hemisphere hardwoods (Gourlay, 1995).

Long-term data are difficult to find in ecology due to the difficulties involved in collecting them (Menges, 2000). This problem is particularly acute in the case of long-lived organisms such as trees, whose lifetimes are usually considerably longer than those of researchers (Franklin et al., 1987; Menges, 2000). As a result, most studies that analyze tree spatial distributions mainly refer to even-aged stands of coniferous forests (e.g. Kenkel, 1988; Leemans, 1991). Fewer studies refer to natural deciduous forests (e.g. Szwagrzyk and Czerwczak, 1993) or to savanna ecosystems (e.g. Barot et al., 1999). However, all the abovementioned studies apply pattern analysis at a study area without any time replicate. There are very few field studies referring to any tree ecosystem that cover also the temporal aspect of spatial pattern dynamics (but see Ward et al., 1996; Wolf, 2005).

In order to detect the underlying processes of tree spatial formations, mathematical techniques such as nearest neighbour analysis and area of influence have been proposed (Coomes et al., 2002). The definition of the area of influence is a circle of arbitrary radius centered on each plant and individuals falling within its bounds are deemed competitors (Kenkel, 1988). Nearest neighbour techniques examine an arbitrary number of nearest individuals of each plant (Shackleton, 2002). Using nearest neighbour techniques one can examine whether trees are competing with their nearest neighbours. However, competitive influence of neighbours reflects highly complex cross-correlations between the individuals making up a population (Fowler, 1984). Thus, nearest neighbour analysis offers insights into the underlying competitive inter-tree interactions on a small spatial scale only. Another available technique is point pattern analysis (Wiegand and Moloney, 2004). This technique is the summary statistics of all plant-to-plant distances in a mapped area and offers the potential for detecting both different types and scales of patterns. However, results of spatial pattern analysis for evidence of competition are often masked by environmental heterogeneity, restricted seed dispersal, and random input via germination (Kenkel, 1988). Thus, while a regular pattern usually infers competition, failure to detect such a pattern cannot be used as evidence that competition is unimportant (Kenkel, 1988).

Given the absence of long-term tree data, we used aerial photographs and satellite images covering 61 years to provide long-term spatial data on tree spatial distribution. We have aerial photographs of two study plots from 1940, 1964, 1984, 1993, and a satellite image from 2001. We were able to identify and follow every individual tree from 1940 to the next available photo till 2001. Doing so, we created a database containing over 2000 trees during a 61-year period.

Questions that we addressed in this study are:

1. Are trees competing directly with their nearest tree neighbours on a small scale?
2. What is the spatial tree distribution on a large scale and what are the underlying processes formatting the spatial distribution of trees as deduced from the pattern analysis?
3. Is the tree pattern formation consistent over time and space replicate?

2.   Study area and methods

2.1.   Study area

Our two study plots are located in semi-arid savanna in the Kalahari on Dronfield Ranch, near Kimberley, South Africa. The plots are rectangular and their size and locations are: Plot 1 – 149 ha, 28°38′43″S and 24°51′19″E, Plot 2 – 197 ha, 28°37′48″S and 24°50′7″E. The distance between the centers of the two plots is 2.592 km. Rain falls mainly during summer months, namely December–February. Mean annual precipitation is 411 mm (SD = 132), summer mean maximum daily temperature is 32 °C, and winter mean minimum daily temperature is 3 °C (South African Weather Forecast Service, unpublished data). In both plots, soil consisted of mainly Hutton (haplic arenosol) soil type and was >2 m deep (Anonymous, 1974; and soil samples taken by us in the field, unpublished data).

The land was bought by the *De Beers Consolidated Mines Ltd.* in 1870 to serve as rangeland for horses, donkeys, and oxen used as draft animals in the diamond mines of Kimberley. Initially, the ranch was managed with cattle and wild mammalian herbivores. The wild ungulates were gradually removed from the land and the ranch was turned into a cattle ranch, which it still is today.

In our two study plots, *Acacia erioloba* (E. Mey) is the only tree species present. Cattle do not browse *A. erioloba* but wild ungulates do (Barnes 2001). Therefore, there was little browsing of *A. erioloba*. There were no tree diseases (A. Anthony, Dronfield farm manager, pers. comm.). There was no tree cutting in any of our plots with the exception of Plot 1 between 1940 and 1964. The trees cut in Plot 1 could be identified with the help of the farm manager and were excluded from the analysis.

2.2. *A. erioloba characteristics*

Acacia erioloba is a keystone tree species in the Kalahari Desert and in African savannas (Milton and Dean, 1995). It is an appropriate species to carry out a long term study on tree spatial dynamics because it is a long-lived tree; individuals older than 200 years have been recorded (Timberlake, 1980). The fact that individuals of this species have very deep roots (maximum recorded = 68 m) allowing them access to permanent groundwater sources (Jennings, 1974) makes *A. erioloba* less affected by climatic variations than other trees (Barnes et al., 1997). Its mortality decomposition takes a minimum period of 3 years (Milton and Dean, 1995). *Acacias* in the Negev desert, Israel need on average 10 years to decompose (Ward and Rohner, 1997). Therefore a small bias is possible in our analysis due to the fact that some trees appearing in the photos could already have been dead.

2.3. *Remote-sensing methods*

For the identification and multi-temporal analysis of *A. erioloba* we used black-and-white aerial photographs of the area taken in 1940, 1964, 1984, and 1993, and an Ikonos satellite image taken in 2001. We were able to identify and follow every individual tree from 1940 to the next available photo till 2001. Our classification accuracy was 1 m. We included trees with canopy diameter T of at least 2 m to ensure high classification reliability. The minimum projected canopy surface (canopy area) recorded is $St = \pi \cdot (T/2)^2 = \pi \cdot (2/2)^2 = 3.14 \, m^2$. Thus all trees used in the analysis of this paper have a minimum canopy surface of 3.14 m². During ground truth verification of tree classification, the positions of 500 randomly selected trees were obtained based on GPS readings in the field, and compared with the tree positions given by the classification. No objects that were not trees were found to be classified as trees. However, the error mainly consisted of a few cases of two or more adjacent trees with overlapping canopy being classified as one tree. This was not a common problem though, because the maximum percentage of tree cover observed on the plots during the years of available remotely sensed imagery was 6% at most. For further details concerning the remote-sensing methods see Moustakas et al. (2006).

We identified trees on the 2 plots in years 1940, 1964, 1984, 1993, and 2001. In each plot, and for each year, we numbered each tree vector (the contour of tree canopy surface area as seen on the remotely-sensed imagery) and we extracted its projected canopy area in m² (henceforward referred to as canopy area) and its central coordinates using MapInfo Professional (Anonymous, 1998). A tree was classified as dead when: (a) at the location of the canopy (using *X, Y* coordinates) of a tree in the previous photo there was no tree; or (b) at the previous location of the canopy there was a tree that was at least 25% smaller than the previous canopy size of the tree. We recorded the period during which the death of the tree took place and the canopy area of the dead tree, and we determined when this dead tree had first appeared in our database. Doing so, we derived an age estimate (interval) for dead trees. Thereafter, we recorded the *X, Y* coordinates of dead trees, the plot they appeared in, the year that they were first established, the year that they were last seen, and the first photo year in which they were absent. The *X, Y* coordinates of dead trees refer to the last photo they were found alive. Dead trees refer to the interval between the period that the trees were last seen and the first available image that they are not seen. For example, the 1940 deaths derive from the trees seen in 1940 but not seen in 1964. An overview of tree canopies, as they appear after the remote sensing processing and classification, in Plot 2 during 1940 is given in Fig. 1.

2.4. *Nearest neighbour analysis*

We examined whether trees are directly competing with their nearest neighbouring trees. If this is valid then the mean distance to the nearest neighbouring trees should be smaller for dead trees than for living trees. In order to examine the validity of this hypothesis, we summed for each tree present on our two plots, the distance to its four nearest neighbouring trees. Sequentially we divided the sum of the distance to the four nearest neighbouring trees by four, resulting in the average distance to the four nearest neighbours of each tree. We repeated the above described procedure for the dead trees exclusively; thus for each dead tree we summed the distance to its four nearest neighbouring trees (regardless if the nearest trees were dead or alive) and divided it by four. Dead trees were included in the total tree analysis (e.g. trees that died

Fig. 1 – Overview of projected tree canopies in Plot 2 during 1940.

between 1940 and 1964 are included in the total trees analysis of 1940). We calculated the average of the distances to the 4 nearest neighbouring trees, based on the centre coordinates of each tree (i.e. the centre of mass of the tree canopy). The use of 4 nearest neighbour analysis is a well established technique in order to detect competition (Shackleton, 2002) though often canopy diameter distances rather than tree center distances are used (Shackleton, 2002).

2.5.   Spatial pattern analysis

A commonly used characterisation of spatial point patterns is the expected density of points at radius r around a randomly chosen point (in our case around each tree). The pair-correlation function $g(r)$ (Stoyan and Stoyan, 1994) viewed as a function of radius (spatial scale r) and multiplied with the intensity λ of the pattern is known as the O-ring statistic, $O(r) = \lambda g(r)$ (Wiegand and Moloney, 2004). The O-ring statistic is a neighbourhood density function (Wiegand and Moloney, 2004). Furthermore the O-ring statistic is an appropriate method for detecting patterns across scales as it can isolate specific distance classes while cumulative statistical methods of point pattern analysis (such as Ripley's K-function) confound effects at larger distances with ones at shorter distances (Wiegand and Moloney, 2004).

Based on point-to-point distances, the O-ring statistic describes clumping ($O(r) > \lambda$) and regularity ($O(r) < \lambda$) at a given radius r, using a simulated density creating an upper and a lower confidence limit for the null model. Consequently, values of $O(r)$ above the upper confidence limit indicate significant aggregation, while $O(r)$ below the lower confidence limit indicates significant regularity. Values of $O(r)$ within the confidence interval cannot be distinguished from randomness and thus characterise spatially uncorrelated points at scale r. Significant departure from an underlying null model was tested by 99 Monte Carlo simulations of the null model. The highest and lowest values of these simulations represent approximately 99% upper and lower confidence limits, respectively, of the null model.

Instead of using a constant intensity the heterogeneous Poisson null model is appropriate in this study because the overall intensity λ varies across the study plot with the location x, y due to heterogeneous topography (Wiegand and Moloney, 2004; Getzin et al., 2006). Thus the intensity is denoted as $\lambda(x, y)$. We used a circular moving window with a fixed bandwidth R = 40 m to estimate $\lambda(x, y)$. The moving window with radius R assumes a random distribution of trees only within this window. So it is assumed that the landscape is homogeneous within the radius of 40 m and we test for deviation from this random distribution of trees which could be due to facilitation or underground competition. The fixed 40 m radius was chosen based on visual observation of spatial heterogeneity in our study plots. We chose 40 m to account for all possible negative interactions between trees (underground) but to also exclude all larger scale effects from landscape heterogeneity. Hence, patterns and their deviation from random distributions may be interpreted up to a radius of R = 40 m only.

We compared the pattern of surviving trees against the pattern of living and dead trees at older stages of the

chronosequence (Wolf, 2005) but thereby excluded pattern effects from wide-ranging landscape heterogeneity. For the abovementioned point pattern analysis of tree spatial distributions, Programita software was used (Wiegand and Moloney, 2004). Programita is a grid-based software. Each cell of the grid was chosen to be 2×2 m since that corresponds to the minimum tree canopy diameter used in our analysis.

3.   Results

3.1.   Nearest neighbour analysis

In Plot 1 most trees that died had average distances to their 4 nearest neighbour trees between 4 and 6 m (Fig. 2). Due to our classification accuracy (2 m), the nearest neighbour distance recorded was 4 m. In the same plot, there were very few dead trees with nearest neighbour distances greater than 4 m. In Plot 1, the most frequent nearest neighbour distance was 8–10 m until 1993. In 2001, where no data on tree death are available (see Section 2), nearest neighbor distance peaked at distances between 20 and 25 m. However, if the size-class of 20–25 m is omitted, the nearest neighbour distance frequency graph is unimodal with a peak at the 14–16 m size-class (Fig. 2). In Plot 2, most dead trees had average nearest neighbour distances of 4–6 m in all years but 1984 (Fig. 2). However, there is a moderate number of dead trees with distance to nearest neighbours >6 m. During 1984, dead trees had on average larger distances to their nearest neighbours peaking at 10–12 m. Most living trees consistently had 20–25 m distance to their nearest neighbours in Plot 2. However, if the size-class of 20–25 m is omitted, the nearest distance frequency graph is unimodal with a peak at around 18 m in all years but 2001 (Fig. 2). The mean size of dead trees on each plot and year is listed in Table 1.

Overall, in all years and plots, most dead trees had on average up to 6 m distance to their nearest neighbours. The number of dead trees plotted against the distance of the nearest neighbours monotonically declines thereafter (Fig. 3). Most living trees had 20–25 m distance to their nearest neighbouring trees in Plot 2. However, if the size-class of 20–25 m is omitted, the nearest distance frequency graph peaks at around 18 m and declines thereafter.

3.2.   Spatial pattern analysis

Overall, in both plots there is a high temporal variation of tree spatial distribution, especially in Plot 2. In Plot 1, at small distances, tree spatial distribution was initially clumped (1940; at 2 m & 1964; at 2 m) then random (1984 & 1993) and finally, in 2001; at 2 and 4 m, regular (Fig. 4). At intermediate and large scales, tree spacing was random (1940) then regular (1964; at 12 m, 1984; at 18 m, & 1993; at 18 and 32 m) and finally in 2001 random again (Fig. 4).

In Plot 2, at small spatial scales, tree spatial distribution was clumped (1940; at 2 m), regular (1964; at 4 m), then clumped (1984; at 2 m), and finally regular (1993; at 6 m & 2001; at 6 m) (Fig. 4). At intermediate and large distances, tree spacing was initially random (1940), then regular
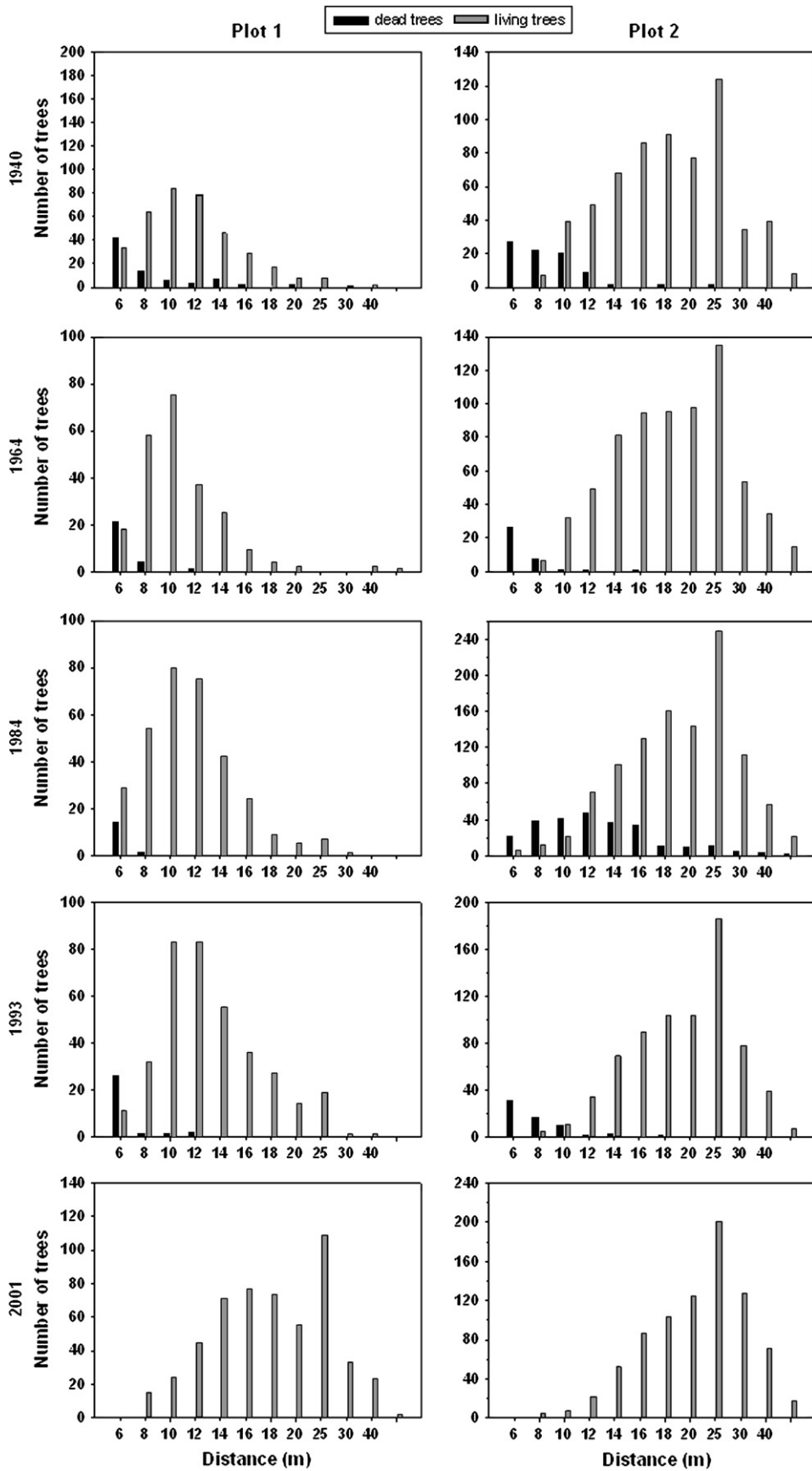
Fig. 2 – Mean inter-stem distances (in m) to four nearest neighbours of trees. The first bin starts at 4 m, because the smallest tree recorded by our remote-sensing methods had a canopy diameter of 2 m. Bin size increases linearly up to 20 m, and non-linearly thereafter (approximating a logarithmic increase). In 2001 there were no data on tree death (see Section 2).

Table 1 – Tree characteristics for each different plot and period (data from Moustakas et al., 2006). For each plot and for each period (*year*), we list the relative area covered by tree canopies (*Relative tree cover* in %), the total number of trees (*Total trees*), the number of dead trees (*Dead trees*), the mean canopy area of the dead trees (*Dead size* in m^2), and the number of new trees (*New trees*). Dead trees refer to the interval; for example, the 1940 deaths derive from the dead trees between 1940 and 1964. The other statistics refer to the year the picture was taken. Thus, we always refer back to the last time that the dead trees were seen. In Plot 1 during 1940–1964, 89 trees were cut by the farm manager

Year	1940	1964	1984	1993	2001
Plot 1					
Relative tree cover (%)	0.78	0.72	0.75	0.84	0.91
Total trees	370	230	325	361	526
Dead trees	74	25	14	29	
Dead size (m^2)	41.7	31.9	23.6	26.0	
New trees	23	120	50	194	
Plot 2					
Relative tree cover (%)	0.95	1.40	2.65	2.02	1.36
Total trees	621	691	1078	855	817
Dead trees	80	35	253	60	
Dead size (m^2)	30.3	36.6	31.2	31.0	
New trees	150	422	30	22	

(1964; at 22 m, 1984; at 14 and 22 m, 1993; at 12 and at 22 m, & 2001; at 18 m). Particularly in 1993, regular tree spacing was observed at two different distances.

4. Discussion

Overall, results from our nearest neighbour analysis indicate that dead trees were on average more closely located to their nearest neighbours than living trees were to their neighbours. Tree individuals compete against other trees for the limiting

Fig. 3 – Cumulative plot of mean inter-stem distances (in m) to four nearest neighbours of all trees (all plots and years). The first bin starts at 4 m (cf. Fig. 2).

factor (water, nutrients, or to a lesser extent in savannas, light). Combining nearest neighbour and point pattern analysis results, the tree mortality that we recorded is not random given that dead trees are much closer on average to their nearest neighbours than living ones. This is in accordance with the findings of Sterner et al. (1986) and Kenkel (1988).

There is a strong bias in the nearest neighbour analysis (Shackleton, 2002), which is not as important in single-species studies as in multi-species studies due to niche differentiation. This bias occurs because the nearest neighbour is not necessarily the major competitor. It is often found that the nearest neighbour to a tree can be a very small-sized tree while a near but not the nearest neighbour can be a large-sized tree and the major competitor (Shackleton, 2002). For this reason, Shackleton (2002) proposed the use of more than one neighbour. In the same study, Shackleton (2002) found that competition was less important than previously thought for tree spacing in savannas, though intra-specific competition was more prevalent in *Acacia* communities than broad-leaved savannas. However, according to our results, competition is very important. This is mainly due to the fact that our results derive from long-term, time-replicated data. "Although some information can be deduced from a single snapshot of an ecological pattern, one should be careful not to over-interpret a single snapshot in attempting to identify the underlying processes driving the system" (Jeltsch et al., 1999). In fact, arid ecosystems are characterized by slow rates of changes and thus need on average longer time periods to conclude processes than northern hemisphere hardwoods (Sankaran et al., 2005).

In a different environment with much higher tree density, Kenkel (1988) found a mean "area of influence" of a 3.5 m radius, suggesting that trees may compete directly only with their immediate neighbours. In our case, and in most arid environments, the percentage of tree cover is very low; maximum percentage of tree canopy cover in our plots was 3% (Moustakas et al., 2006). Note that field based tree canopy cover should be somewhat higher because our canopy cover is derived from images, i.e. underestimates the number of small trees. Couteron and Kokou (1997) found that the mean tree density around dead trees was lower than around surviving ones. Our results suggest that in arid environments trees also compete with their immediate neighbours, even though their immediate neighbours are statistically further than in more humid environments. Thus, inter-tree competition can be important in terms of tree neighbourhood formation in arid environments.

In our point pattern analysis, clumped trees occur at a scale of 2 m only. However, due to remote-sensing limitations, trees of a minimum of 2 m canopy diameter were analyzed and thus scales 0–2 m were not investigated. Given that *A. erioloba* seedlings were observed to germinate in patches (Skarpe, 1991), trees could also be clumped at scales smaller than 2 m, a scale not investigated by us. Skarpe (1991) found a random distribution of mature *A. erioloba* trees at all scales up to 50 m, using Ripley's *K*-function. The explanation given was that this pattern was the trade-off between competition, promoting regular pattern and fire, promoting clumping. Jeltsch et al. (1999) found that "a random pattern may only represent a transitory phase … promoting clumping or even distribution
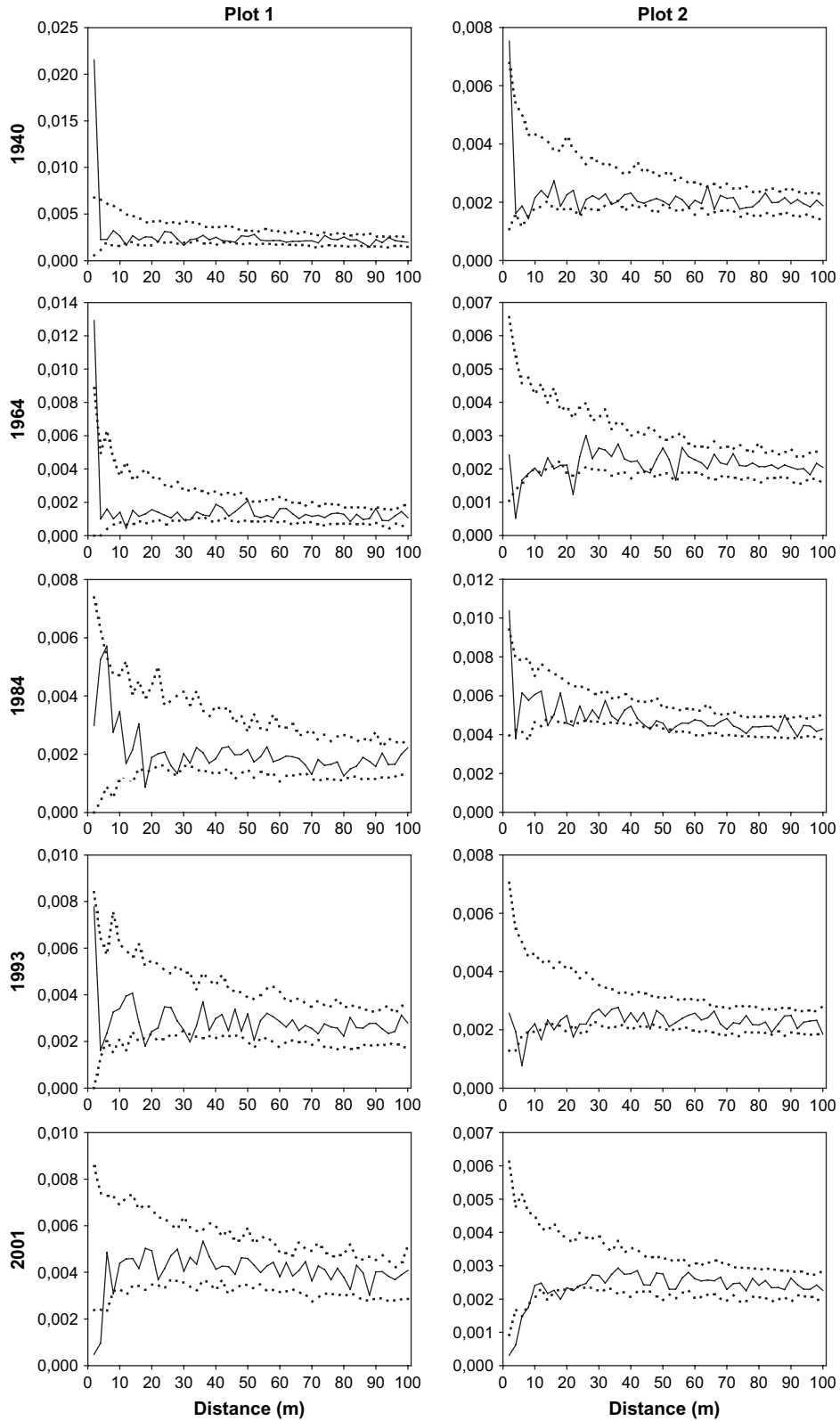
Fig. 4 – Temporal change in spatial pattern for all trees larger than 2 m (canopy diameter). Solid lines represent the observed O-ring statistics. The dotted lines represent approximate upper and lower 99% confidence intervals. All results between the two dotted lines cannot be distinguished from a random tree distribution. Values above and below the envelopes indicate significant clumping and regularity, respectively. As we used the heterogeneous Poisson null model, deviation from randomness is only detectable within a distance of $r = 40$ m (see Section 2).

across a range of scales''. Our findings show that regular, clumped, and random pattern can occur, pending on the time and location. Thus, our findings are in agreement with the conclusions of Jeltsch et al. (1999).

Generally, pending the time observation snapshot and the scale of reference, our results show a cyclical transition from clumped tree spacing to random and sequentially to a more regular one. Using tree data from an aerial photo as input to a model, Jeltsch et al. (1999) predicted the existence of these cycles in time. Using simulations, it was found that periods of slightly increasing tree numbers were characterized by an increase in tree clumping whereas periods of slightly decreasing tree numbers showed a tendency towards random or even tree spacing (Jeltsch et al., 1999). According to our results, periods of high mortality are characterized by a decrease in small-scale clumping (Plot 1: 1940–1964 and 1964–1984; Plot 2: 1940–1964 and 1984–1993) (Fig. 4; Table 1). While these conclusions are based on visual interpretation of the results, no significant results were found using statistical analyses (results not shown here). In the same study, Jeltsch et al. (1999) found clumping at intermediate to large scales, which contradicts our findings. This is partly due to the heterogeneous Poisson process that we incorporated in our point pattern analysis. When tree spatial randomness is assumed, (i.e. homogenous Poisson) and Ripley's K-function is applied, our results show clumping at intermediate scales over some snapshots (results not shown here). However assuming complete spatial randomness (using K-function or g-function without inhomogeneous Poisson) would significantly bias results in our case. Trees obviously have fewer chances growing on the top of a hill than in the plain. Thus the statistical method applied is very important for the interpretation of point pattern analysis results.

There is a small bias in our results due to the fact that in Plot 1, presumably the 89 trees that were cut were among the largest ones and this is expected to slightly underestimate both nearest total trees neighbour distances as well as dead tree distances in the plot in 1964. However, in general, the mean dead tree sizes (Table 1) do not exhibit high variation through time with the exception of Plot 1 in 1940. This is due to the fact that the *A. erioloba* size mortality distribution recorded by Moustakas et al. (2006) has a consistently inverted U shape through time and plots, where the death of middle-sized trees is more likely than small or large-sized tree individuals.

Despite the general interest in non-linear dynamics in animal populations, plant populations are supposed to show a stable equilibrium that is attributed to fundamental differences compared with animals. While there is a debate on whether savannas are in equilibrium or not (Walker et al., 1981; Belsky, 1994), some studies find more complex dynamics, but empirical studies usually are far too short and models are built with short-term data. Thus the existence of possible vegetation cycles is often omitted (Bauer et al., 2002). There are several cases of cyclical transitions observed in different cases in ecology (nutrients-perennial plants interactions: Loreau, 1997; grasses: Bauer et al., 2002; behavioural ecology: Crespi, 2004). In savannas particularly there is evidence of cyclical changes (Gillson, 2004b; Wiegand et al., 2005). Vegetation ecologists have found that effects of plants on

microclimate and soils can cause a microscale positive feedback, implying that critical precipitation conditions for colonization of a site may differ from those for disappearance from that site (Scheffer et al., 2005). Our data support the existence of savanna cycles reported by Gillson (2004b) and Wiegand et al. (2005). Our study plots are located less than 3 km from each other and thus climatic differences are very small. However, recruitment, percentage of tree cover and total number of trees on each plot do not peak at the same time on each plot (Table 1). Therefore, even though savanna vegetation follows cycles, these vegetation cycles peak at different times depending on location (patch size). As a result, our study supports that savannas are patch dynamic systems (Levin, 1992), as expressed by Gillson (2004a) and Wiegand et al. (2006).

Most studies so far would believe that climate is a major factor for tree mortality, which is globally valid in the sense that extreme weather phenomena do influence the total numbers of dead trees. However in a previous study in the same area and tree species, Moustakas et al. (2006) found that the *A. erioloba* size-class mortality distribution (and not the total number of deaths) was consistent across years and thus across different climatic regimes. The role of intra-specific competition in such semi-arid savanna environments has not been carefully examined thus far (but see Meyer et al. (2008). Even though there is evidence of strong below-ground competition (Coomes and Grubb, 1998), trees are not necessarily competing with neighbouring trees (Brisson and Reynolds, 1994). Relationships between competition for access to nutrient-rich soil, tree age, tree location and patch characteristics that perhaps explain pattern variations among savanna vegetation characteristics are reported to be important (Barot et al., 1999). When one makes a single hypothesis it is easier to become attached to it (Platt, 1964). However, we are unable to find an explanatory factor other than intra-specific competition for the nearest neighbour distances recorded. In many classic biological studies, the role of competition in extreme habitats is supposed to be very weak. Braun-Blanquet (1932) states that competition in deserts is weak and Darwin (1859) says ''… when we reach deserts the struggle for life is almost exclusively with the elements''. While in our analysis we did not include soil properties and nutrients as explanatory variables, the fact that nearest neighbour distances of dead trees were much closer than total trees provides strong evidence for intra-specific competition. We are also aware that there were no tree diseases or parasites present in the area that could spatially bias our results (i.e. if dead trees were closer to infected areas).

of BIOTA-Africa. The comments of 2 anonymous reviewers significantly improved an earlier version of this paper.

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