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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ARTICLE INFO

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 eco-system 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 inter-actions are important to the population dynamics of plants. Spatial influences such as plant competition or the distribu-tion of safe sites for germination result in temporally-variable spatial patterns of plant distribution (Kenkel, 1988). If spatial

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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.