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# Analysis of long-term dynamics of crowns of sessile oaks at the stand level by means of spatial statistics

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**Abstract**

We analysed crown dynamics at the stand level in three plots of an even-aged sessile oak stand (one unthinned reference plot and two plots of different thinning intensities) of a long-term experiment in Rhineland Palatinate, Germany. Crown projections and stem locations were recorded in 1977, 1994 and 2004. Spatial structures of stems and crowns were analysed using the index of Clark and Evans and Ripley's *K*-function. In the unthinned plot, despite crowns being highly asymmetric, it was shown that crowns did not expand in a way that makes their distribution more regular. In this dense plot with slender trees, the stability constraint was probably more important than the search for light. In the thinned plots, spatial distributions of both stems and crowns were found to be regular, in general with more regular distributions for crowns than for stems. The more regular spatial distributions of crowns were attributed to the effect of thinning and to the subsequent plastic reaction of the crowns of the remaining trees. The plastic reaction of crowns toward more regular distributions was stronger in the case of moderate thinning than in the case of intensive thinning. In the latter case, the lower plot density was probably less limiting for the access to light. Finally, the benefit of the plasticity of crowns in the thinned plots was quantified in terms of canopy cover at the stand level. Crown plasticity enabled a higher space occupation by the canopy and a reduction of overlaps between neighbouring crowns. The results of this study suggested that trees of a stand can adapt to their environment in order to find a trade-off between different functions like mechanical stability, access to light and the physiological cost associated with adaptive growth.
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*Keywords:* Crown plasticity; Index of Clark and Evans; Ripley's *K*-function; Spatial pattern; Canopy closure; *Quercus petraea*

## 1. Introduction

Despite their apparently fixed position of rooting, trees show remarkable capacities to forage for water and nutrients in the soil and for light at the crown level, by developing their root system and their branches, respectively. The present study is based on the hypothesis that trees take advantage of this plasticity to adapt to their environment and to occupy efficiently the surrounding space. Such a behaviour of trees is supposed to make their access to resources easier, especially under the competitive pressure of neighbouring trees. This suggests that trees expand preferentially in a given direction only if they can find a benefit in doing so.

About crown plasticity, a tree can modify its access to light by developing its branches preferentially on one side or another of the stem (Sumida et al., 2002). Exploration of the aerial space toward a preferred direction is also possible by adaptive growth leading to bending or leaning of trees. As a result of this plasticity, centres of gravity of crown projections are not at the same locations as stem bases, and spatial distributions of crowns and stems are different. Pretzsch and Schütze (2005) report that the capacity of crown plasticity depends on the tree species with, for instance, a greater capacity of space occupation for European beech (*Fagus sylvatica* L.) than for Norway spruce (*Picea abies* (L.) Karst.).

Crown plasticity is often analysed at the individual tree level based on crown projections. Seifert et al. (unpublished data) report a significant influence of the compass direction on the plasticity of crowns of European beech. In many other studies, intensity and direction of crown displacements (i.e. the vectors from the stem bases to the centres of gravity of crown projections) are studied as functions of tree characteristics (e.g. diameter at breast height, total tree height) and of the locations of neighbouring trees compared with the location

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of the target tree (Gavrikov et al., 1993; Rouvinen and Kuuluvainen, 1997; Brisson, 2001; Muth and Bazzaz, 2002, 2003). Besides, there are few spatially explicit model approaches to simulate the plastic reaction of crowns to competition in three dimensions (Seifert, 2003; Boudon and Le Moguédec, 2007).

Hence, an individual crown grows under the influence of neighbouring crowns, and in turn the neighbouring crowns also react (Muth and Bazzaz, 2003). This process of space sequestration at the stand level probably slows down and almost ceases when an optimum in space occupation is approached. The balance of the system is disturbed by events like mortality and thinning of trees, so that the system must adapt to changing distributions of crowns. Big changes in crown distributions occur after thinning, for instance. As trees of a stand interact, it appears important to consider the stand level for the investigation of crown displacements and for the comprehension of underlying growth strategies of trees within stands. Analyses at the stand level are necessary to answer questions about light interception by the stand canopy, biomass production of the stand and regeneration processes, for instance. In the present study, we focused on the spatial structure of stands.

Analyses of spatial structures are increasingly used in forest ecology to characterise tree distributions (usually as regular, random or aggregated) and to enhance our understanding of dynamic processes at the stand level. Numerous methods exist and are described on the basis of studies in forest ecology (Radtke and Burkhart, 1998; Goreaud and Pélissier, 1999, 2003; Goreaud, 2000; Pommerening, 2002; Perry et al., 2006; Pommerening and Stoyan, 2006). Most of the studies focus on stem base locations. They compare forests or sub-groups of trees (analysed by species or by classes of diameter or height) with respect to their spatial structure (Song et al., 2004) or follow changes of spatial structure over time in relation to thinning and natural processes like growth, regeneration and mortality (Vacek and Lepš, 1996; Ward et al., 1996; Goreaud, 2000; Montes et al., 2004).

Fewer studies are reported that characterise crown displacements at the stand level. Empirical studies aiming at describing this dynamics still remain rare due to difficulties in acquiring suitable data about trees. Indeed, long-term measurements of tree crowns are required for such analyses. Most of the existing studies focus on the characterisation of the spatial structure of crowns and on its comparison with the spatial structure of stems at one given date. Ishizuka (1984) showed, in six stands of a natural mixed forest of Hokkaido, Japan, that crowns were more regularly distributed (uniform or random distributions for upper layer trees, and random distributions for all trees together) than stem bases (usually contagious distributions). Umeki (1995b) performed a similar analysis but based on simulated crown locations obtained though a model established at the individual tree level. Simulated crowns were more regularly distributed than stems as the model was developed in a way that crowns repel each other. In a pure stand of *Atherosperma moschatum*, Olesen (2001) also found that crowns were more regularly distributed than stems. In contrast, in a dense and regularly planted monoculture of Douglas-fir (*Pseudotsuga menziesii*), Getzin and Wiegand (2007) found that stems were more regularly distributed than crowns. Thus, regular distributions of crowns may not always be optimal in terms of stand productivity, for instance. An optimal crown distribution is likely a trade-off between different functions such as light interception and mechanical stability, and it depends probably on the type of stand (pure or mixed), species, age of trees and stand density. About crown development over time, we did not find any study based on repeated measurements of tree crowns. Gavrikov et al. (1993) report that distributions of stems and crowns become more and more regular over time. However, they analysed three different stands representing three age classes, but not repeated measurements of the same stand. Umeki (1995a) used another approach based on a fast growing annual plant, *Xanthium canadense*, but not on trees. After a few months of monitoring, the plants showed a more regular spatial structure of crowns than of stems, and an increase in regularity of the spatial structure of crowns over time.

In the present study, we used repeated measurements of stem base locations and of crown projections of sessile oaks (*Quercus petraea* (Matt.) Liebl.) from a permanent experiment in Germany, that represented a relatively rare database. The aim was to analyse the dynamic response of crowns under different thinning intensities at the stand level by means of spatial analysis techniques. The aspect of crown plasticity studied here was the radial expansion of crowns in preferential directions estimated from crown projections. ‘‘At the stand level’’ means that in the present study we were not interested in the individual crown displacements, but rather in the consequences of the interactions between trees for the whole stand in terms of crown distribution and canopy closure. We investigated three hypotheses:

**Hypothesis 1.** Crowns are always more regularly distributed than stems suggesting that crowns expand toward an increase in regularity of their spatial distribution.

**Hypothesis 2.** The regularity of crown distributions increases over time. The underlying idea was that a process that makes crown distributions more regular is in progress as long as a steady-state is not reached. The system is considered as steady when a local optimum is achieved regarding the regularity of the crown distribution.

**Hypothesis 3.** One benefit of this crown plasticity is an increase of the canopy cover at the stand level suggesting a better light interception by the stand.

## 2. Materials and methods

### 2.1. Study area

The permanent experiment Waldleiningen 88 is located near the city of Kaiserslautern (Germany) on a north-facing slope at an altitude of about 420 m. The main species is oak with beech trees in the under storey. In this work, the assumption was made

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