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ScienceDirect
Forest Ecology and Management 242 (2007) 165–174
Forest Ecology and Management
www.elsevier.com/locate/foreco

Asymmetric tree growth at the stand level: Random crown patterns and the response to slope

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Received 8 June 2006; received in revised form 25 October 2006; accepted 11 January 2007

Abstract

Asymmetric tree growth is an adaptation to maximise photosynthesis by growing in response to gaps and neighbours, topographical site conditions or incoming solar radiation. Whereas spatial statistics have been widely used to study the distribution of trunk locations, less research has been undertaken to analyse the distribution of crown centres and asymmetric growth at the stand level. It is generally assumed that trees optimise light harvesting via more regular crown patterns. In this study, we primarily ask whether random crown patterns can be found in deciduous and coniferous forests located in continental Europe. Here, we analysed the spatial patterns of trunks, crowns and crowns of overstory trees in different deciduous and coniferous stands, using the scale-dependent *g*-function and Monte Carlo simulations. We also tested whether the extent of asymmetric growth, that is the crown vector length between the stem-base position and the centroid of the projected crown area, would be greater in angiosperms than in gymnosperms. Finally, we applied circular statistics to test whether trees preferentially bend in slope direction or towards incoming solar radiation. In the deciduous stands, patterns of crowns and upper crowns were random. Response to large-scale heterogeneity in light was strong, because trees bent significantly in downward direction of the slopes. The extent of asymmetric growth was significantly greater in angiosperms than in gymnosperms. The patterns of crowns and upper crowns were regular in a mixed coniferous stand but random in a dense stand with regularly planted Douglas-fir. Mechanical instability caused mutual crown support and attraction between the crowns in this dense stand. The even-aged, slender Douglas-fir clustered significantly in downward direction of the slope. In none of the four stands, trees clustered in southerly direction towards incoming solar radiation.

Keywords: Coniferous/deciduous stands; Crown vector; Douglas-fir; *g*-Function; Light heterogeneity; Slope

1. Introduction

Over the past 20 years, spatial analysis of tree trunks has become an established method to infer tree population dynamics such as self-thinning or gap recruitment in forest communities (e.g. Sterner et al., 1986; Kenkel, 1988; Batista and Maguire, 1998; He and Duncan, 2000; Wiegand et al., 2000; Gratzer and Rai, 2004; Wolf, 2005; Getzin et al., 2006). Since stem positions are fixed to the ground, high neighbourhood densities may result in density-dependent mortality or may be compensated by shifting the crown centres away from the trunks. The latter, known as crown asymmetry, develops through plastic response to a heterogeneous light environment because canopy structure is mainly built to maximise photosynthesis (Berezovskava et al., 1997). Given that heterogeneous light conditions prevail in local neighbourhoods of most trees and that interactions between trees are primarily mediated through light, crown centres are considered more important than trunks for defining the representative positions of trees (Umeki, 1995a; Bravo et al., 2001).

So far, the main proximate causes for asymmetric crown development have been well researched at the individual tree level. Trees expand branches preferentially on the side of gaps (Brisson, 2001; Muth and Bazzaz, 2002) and morphological plasticity in lateral growth is needed to resist asymmetric competition from neighbours that are larger, too close, more shade-tolerant, or mechanically more robust (Umeki, 1995b; Rouvinen and Kuuluvainen, 1997; Bravo et al., 2001; Brisson, 2001; Rudnicki et al., 2001; Paulo et al., 2002; Muth and Bazzaz, 2003; Rock et al., 2004). At the stand level, however, information on resulting crown patterns and their ultimate relation to underlying trunk patterns is still insufficient (Song et al., 1997). Such information is needed to improve the simulation of individual tree growth (Pacala and Deutschman,

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doi:10.1016/j.foreco.2007.01.009

1995; Berezovskava et al., 1997; Busing and Mailly, 2004), to predict stand biomass or tree regeneration from GIS-derived canopy data (Clark et al., 2004; Koukoulas and Blackburn, 2005), to assess stand resistance to damage by wind (Mason, 2002; Rudnicki et al., 2003) or to improve the accuracy of radiation penetration measurements (Kucharik et al., 1999). For stand productivity, the advantage of asymmetric over symmetric crown development increases with increasing initial aggregation of trunks because a horizontal distribution with more widely spaced crowns enhances interception of light above them (Sorrensen-Cothern et al., 1993; Umeki, 1997). Despite vertical stratification in canopy architecture, the two-dimensional pattern of crown centres may therefore become more regular relative to the aggregated pattern of stem-base positions. The horizontal pattern of crowns becomes of increasing importance in remotely sensed forest inventory because photo-derived crown extent is a suitable measure of the trees ‘functional growing space’ (Gougeon and Leckie, 2003; Popescu et al., 2003).

Although second-order analyses of canopy distributions are still scarce, it is thought that regular crown patterns with even-spaced crown centres would be optimal to maximise light harvesting (Kuuluvainen and Pukkala, 1987; Umeki, 1995a,c; Olesen, 2001). For example, in a pure stand of evergreen Tasmanian forest, there is a tendency towards regularity of crowns (Olesen, 2001) and in a chronosequence of pine trees in Siberia, regularity of crowns increases with stand age (Gavrikov et al., 1993). Unfortunately, both Gavrikov et al. (1993) and Olesen (2001) did not assess the statistical significance of the difference between measured regular crown patterns and the null hypothesis that they were random. For mixed coniferous and mixed deciduous forests in Japan, Ishizuka (1984) found that regular crown patterns prevailed in the overstory. However, since lower, middle and all crown layers combined were dominated by random distributions, he proposed that random crown patterns would be optimal for light harvesting. The phenomenon of mutual crown support is even more contradicting the general assumption of dominating regular crown patterns. This has been shown for high-density stands with slender coniferous trees, where frequent crown collisions may cause clumped canopy structures (Rudnicki et al., 2003).

Other variables of crown displacement are the extent and direction of asymmetric growth. The extent is the two-dimensional vector length between the stem-base position and the centroid of the projected crown area. This extent is closely related to the magnitude to which spatial crown patterns may deviate from trunk patterns. It has been hypothesised that plastic response would be generally smaller in gymno- than in angiosperms because coniferous trees dominate in marginal areas with fewer competitors and more frequent fires. Both would lead to more homogeneous light intensities around coniferous trees, making asymmetric crown development less necessary (Waller, 1986). This hypothesis has been supported in Japan (Umeki, 1995b) and North America (Muth and Bazzaz, 2002).

Also, knowledge on directional preferences of bending trees is still insufficient at the stand level. Umeki (1995a) found that aspect of slope was more important for the direction of asymmetric growth than influences from nearest neighbouring trees. Crown displacement at the stand level may be further influenced by the interacting effects of slope topography and sunlight (Olesen, 2001). Some studies from higher latitudes found evidence that crowns predominantly grow towards incoming solar radiation in southerly direction (Rouvinen and Kuuluvainen, 1997; Skatter and Kucera, 1998) whereas studies from 50° to 55° northern latitude did not find this alignment (Gavrikov et al., 1993; Frech et al., 2003). However, asymmetric growth towards south has been found in the Mediterranean, too (Paulo et al., 2002).

In this study, we investigate if random crown patterns can be found in deciduous and coniferous forests located in continental Europe. We use four different forest stands in central Germany which do not have aggregated trunks and which have not been thinned for decades. These plots include two deciduous stands, a mixed coniferous stand and a high-density stand with slender Douglas-fir. More explicitly, we analyse at what spatial scales patterns of trunks, crowns and upper crowns deviate significantly from a random distribution. Furthermore, we test the hypothesis that the extent of asymmetric growth (crown vector length) is greater in angio- than in gymnosperms. Finally, we analyse the directional preferences of bending trees in relation to slope topography and sunlight at the stand level.

2. Materials and methods

2.1. Study areas

The two plots with deciduous trees are on calcareous soils in central Thuringia/Germany, with a mean annual precipitation of around 550 mm. Plot 1 (P1) is located near the city of Erfurt (50°57′N, 11°01′E) on a moderate slope (8°) in north-west-northerly (330°) direction. The plot is dominated by ca. 50-year-old common ash (*Fraxinus excelsior* L.; 48% of live trees) and wild cherry (*Prunus avium* L.; 18%). Less common species include hornbeam (*Carpinus betulus* L.; 11%) or sycamore maple (*Acer pseudoplatanus* L.; 10%). All species in P1 have been naturally regenerated. Plot 2 (P2) is close to the city of Jena (50°57′N, 11°39′E) on a moderate slope (10°) in west-south-westerly (240°) direction. It is a copse-like low forest of ca. 80 years age. Trees in P2 had been coppiced for firewood until the forest became a protected nature reserve in the 1950s. The plot is dominated by durmast oak (*Quercus petraea* [Matt.] Liebl.; 38%) and wild service tree (*Sorbus torminalis* [L.] Crantz; 38%), which both show strong phototropic response. Less common species are European cornel (*Cornus mas* L.; 15%) or field maple (*Acer campestre* L.; 8%). P1 and P2 contain only angiosperms.

The two plots with coniferous trees are in the Thuringian Forest on acidic soils with an annual precipitation ranging between 900 and 1100 mm. Plot 3 (P3) is located at 50°33′N, 10°45′E on a moderate slope (10°) in westerly (260°) direction. The micro-topography of the plot is partly uneven with two or three meter wide grooves running parallel to the slope. P3 is dominated by Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*