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

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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.

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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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1995; Berezovskaya 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*

[Mirb.] Franco; 71%) and Norway spruce (*Picea abies* [L.] Karst.; 29%). Douglas-fir had been planted in a regular grid 53 years ago and spruce in irregular groups. This plot has not been thinned during the last four decades. Plot 4 (P4) is located at 50°36′N, 10°32′E on a relatively steep slope (22°) in westerly (270°) direction. P4 is a monoculture of Douglas-fir, which have been planted in a regular grid 41 years ago. P3 and P4 contain only gymnosperms. All four plots have not been thinned during several decades.

2.2. Data collection

Data were collected in summer 2004. For each plot, we established a rectangle and adjusted its dimension to record at least 100 dead or live trees with a diameter at breast height (dbh) ≥ 4 cm at 1.4 m above ground. Since average distances among trees varied between sites, plot dimensions varied from 45 m × 30 m (P1) to 20 m × 19 m (P4). Within the plots, x–y-locations of all trees with a dbh ≥ 4 cm were mapped using a laser-based rangefinder (Leica DISTO^{TM} classic 5) and the ''Interpoint method'' of Boose et al. (1998). Smaller trees or seedlings were not recorded. Tree height and status (live/dead) were recorded and individuals identified to species. If trees had only very weak remains of green foliage, they were considered as dead. The slenderness coefficient (Rudnicki et al., 2003) was calculated as the ratio of tree height (m) to dbh (cm). To map the horizontal crown extent, we divided its projected area into the four points of a compass and within each quarter (e.g. within N to E) we selected the two most cantilevered branches. For each branch we measured the distance of the perpendicular of its tip to the trunk with the rangefinder and recorded the exact angle of that branch relative to north. These readings from the laser-based rangefinder overestimate accuracy (resolution 0.01 m) since we did not use technical aid to determine the vertical projections from branch tips to the ground. However, the determination of the crown centre is considered accurate because we used eight polar coordinates to measure the crown projection. The mean distance of these eight polar coordinates to the crown centre was used to calculate the crown radius. The computed crown vector length from the crown centre to the x–y-coordinates of the stem-base position was done with trigonometric calculations.

2.3. Statistical analysis

All analyses in this study refer to crown centres and their respective trunk locations of only live trees in a plot. For the purpose of point pattern analysis we investigated all trunks and all corresponding crowns in a plot, and additionally only ''upper crowns'' to separate overstory trees from the three-dimensional canopy layer. We classified all those crowns as upper crowns whose height exceeded two thirds of the mean of the 10 highest trees in a plot. Due to limited numbers of live trees in lower height classes, these were not analysed separately.

Second-order point pattern analyses of trunks, crowns and upper crowns were conducted using the univariate pair-correlation function $g(r)$. The g-function is the expected density of points at a given distance r of an arbitrary point, divided by the intensity λ of the pattern (Stoyan and Stoyan, 1994). It is closely related to the K-function, i.e., $g(r) = (2\pi r)^{-1} dK(r)/dr$. We used $g(r)$ because this non-cumulative probability density function is more sensitive to specific scales r and hence more suitable for exploratory data analysis than the cumulative K-function (Stoyan and Penttinen, 2000; Wiegand and Moloney, 2004). Under complete spatial randomness (CSR), $g(r) = 1$ and values of $g(r) < 1$ indicate regularity, and values of $g(r) > 1$ indicate aggregation. For example, if $g(r) = 2$, inter-tree distances r are twice as frequent as under CSR, if $g(r) = 0.5$, inter-tree distances r are half as frequent, and if $g(r) = 0$, no inter-tree distances r exist. The latter is called a hard-core distance because the physical expansion of tree crowns, a regular planting scheme or the outcome of self-thinning do not allow two points to come closer than $2r$. To assess whether the spatial pattern identified was significantly different from random, we used Monte Carlo techniques to construct approximate confidence envelopes (Dale et al., 2002; Wiegand and Moloney, 2004). Approximate 95% confidence envelopes were determined using the 5th-lowest and 5th-highest value of 199 Monte Carlo simulations of the CSR null model. Note that this is not a goodness-of-fit test with exact confidence intervals (Stoyan and Stoyan, 1994, pp. 300–302; Loosmore and Ford, 2006). We used the grid-based software *Programita* (Wiegand and Moloney, 2004) for all spatial point pattern analyses.

To facilitate the interpretation of the analysis of trunk and crown patterns, we also analysed the effects of neighbourhood density on individual trees. Linear regressions between the mean of the distances of the three nearest neighbours to a focal tree were used as independent variable. The dbh, the crown radius and the crown vector length, respectively, of the focal tree were used as dependent variable. The coefficient of determination r^2 of this regression reveals competitive effects in local tree neighbourhoods, provided that the analysis is based on more than two nearest neighbours (Shackleton, 2002; Getzin et al., 2006).

To also account for the concentration of directionality in neighbourhood competition, we determined the variance in the angles of the three nearest neighbours to a focal tree. A low variance would indicate strong directionality. Here, we used circular statistics (Batschelet, 1981) based on unit vectors where the mean vector length r approaches 1 under strong directedness but 0 under circular uniformity. As response variable of focal trees, we used the crown vector length (as above) and the angle of asymmetric growth α. The angle α was the difference between the direction of asymmetric growth of the focal tree and the mean vector angle $\bar{\phi}$ of the three nearest neighbour trunks to the focal tree trunk. Under strong directional influences from nearest neighbours, we would expect values of the independent variable r to approach 1 and focal trees to bend in opposite direction ($\alpha = 180°$).

The direction of asymmetric tree growth at the stand level was examined with three consecutive tests of circular statistics (Batschelet, 1981) because conventional statistics, e.g. based on

the normal distribution and a linear scale, is not applicable to examine the directional dispersion of angular data. These tests are based on unit vectors and the mean vector length r. As a prerequisite for the subsequent tests for randomness, we used Watson's U^2 test to check whether the angular data fit the null hypothesis of a von Mises distribution, i.e. the sample is fairly unimodal and symmetric. The Watson test calculates the mean square deviation U^2 between data and the fitted distribution. If the deviation U^2 is too high, H_0 is rejected. We applied Rayleigh's uniformity test to calculate whether the circular dispersion of crown centres around trunks differs significantly from the H_0 of randomness. A significant deviation from H_0 is statistical evidence of one-sidedness or directedness. However, this direction remains unspecified in this test. The test statistic is Rayleigh's $Z = nr^2$, where r is the mean vector length and n the sample size. The larger Z, the more are the data concentrated around the mean and thus, the less likelihood exists of the data being uniformly distributed around the circle. If crowns in a plot were directed, we used the V test, to examine whether (1) crowns would cluster in southerly direction around $180°$ (towards incoming solar radiation), or (2) in the direction down the slope. In the V test, the hypothesised mean direction is specified a priory. If data tend to be clustered around a hypothetical direction, the V test is more powerful in rejecting randomness than Rayleigh's uniformity test (Batschelet, 1981). The formula is $V = r\cos(\bar{\phi} - \theta_0)$, where r is mean vector length, $\bar{\phi}$ is mean vector angle and θ_0 is the hypothetical direction. V ranges between -1 and $+1$. If the observed angles ϕ_i do not differ much from θ_0, V approaches 1, and H_0 is rejected. Then the data cluster around the hypothetical direction. We surveyed the orientation of asymmetric crown development with R-software (package CircStats; http://www.R-project.org/).

3. Results

Both in deciduous and coniferous forests, we had each a low density and a high-density plot (Table 1). In both forest types, mortality was lower in the respective low-density plot than in the high-density plot. In comparison with the coniferous stands (P3, P4), mortality was lower in the deciduous stands (P1, P2). The range in tree height was smallest in P4, since all planted Douglas-fir were of the same age. The mean crown radius was

only 1.1 m in P4 but 2.3 m in P1. The coefficient of variation for the mean crown radius was lowest in P1 but highest in P3 and P2. The most slender trees occurred in P4 (Table 1).

The trunk pattern was mainly random in P1 (Fig. 1). In P2, trunks were regularly spaced at the smallest scale of 0.25 m, but random at larger scales. In P3, the trunk pattern was regular only up to 0.5 m (hard-core distance) and between 1.5 and 1.75 m otherwise it was predominantly random. In P4, the trunk pattern reflects the regular planting scheme. Trunks were regularly spaced up to 1.25 m with a hard-core distance up to 0.5 m.

Corresponding crown centres were randomly distributed in P1 and P2 (Fig. 1). In P3, crowns had a hard-core distance of 0.75 m. The crown pattern was random from 1.25 m onwards. In P4, crowns had a hard-core distance of 0.25 m, but their pattern was random above this scale. These patterns were very similar for the crown centres of overstory trees. Upper crowns were mainly randomly distributed in P1, P2 and P4. In P3, upper crowns had a hard-core distance of 0.75 m but their pattern was random from 1.25 m onwards (Fig. 1).

We also compared crown and trunk patterns at a radius of 1 m and expressed their relation as multiples of the g-function values: at a comparative reference scale of $r = 1$ m, inter-crown distances were 1.5, 1.2, 0.3 and 2.0 times as frequent as inter-trunk distances in P1, P2, P3 and P4, respectively. Thus, crowns were more regular than trunks at $r = 1$ m in P3. But in P4 with regular planting distances, trunks were more regular than the relatively narrow crowns in this high-density stand.

The crown vector length was normally distributed in all stands (Kolmogorov–Smirnov test). The extent of asymmetric growth was greatest in the two deciduous stands, with a maximum of 3.29 m in P2 (Table 2; Fig. 2). The mean crown vector length of all combined angiosperms from P1 and P2 was significantly larger than that of all combined gymnosperms from P3 and P4.

The crown vector length was in none of the plots significantly correlated with the mean of the distance of the three nearest neighbours or the variance of the angles of these neighbours to the focal tree (Table 3). Nor was there a significant correlation between the direction α of bending focal trees, relative to the direction of the mean angle $\bar{\phi}$ of the three nearest neighbours, and the variance of the angles of the neighbours. Hence, the extent and direction of asymmetric

Table 1
Stand structure of the four plots

Stand structural variables	Deciduous forest		Coniferous forest	
	Plot 1	Plot 2	Plot 3	Plot 4
Number of live trees	103	98	76	41
Proportion of dead trees in plot (%)	6.4	17.6	28.3	59.0
Density of live and dead trees (N/ha)	814.8	2458.7	952.5	2631.6
Mean dbh of live trees (cm) [CV (%)]	21.6 [29.7]	14.2 [46.4]	31.3 [42.5]	25.1 [29.5]
Mean crown radius (m) [CV (%)]	2.3 [35.7]	1.4 [40.4]	1.8 [51.8]	1.1 [37.3]
Min, max height of live trees (m)	8.0–32.0	3.0–12.0	7.5–35.0	18.0–32.0
Min, max height of upper canopy trees (m)	20.0–32.0	8.0–12.0	22.5–35.0	21.0–32.0
Mean slenderness coefficient (m/cm)	1.0	0.6	0.9	1.1

Only live trees were used to investigate crown–trunk relations and asymmetric growth. CV: coefficient of variation.
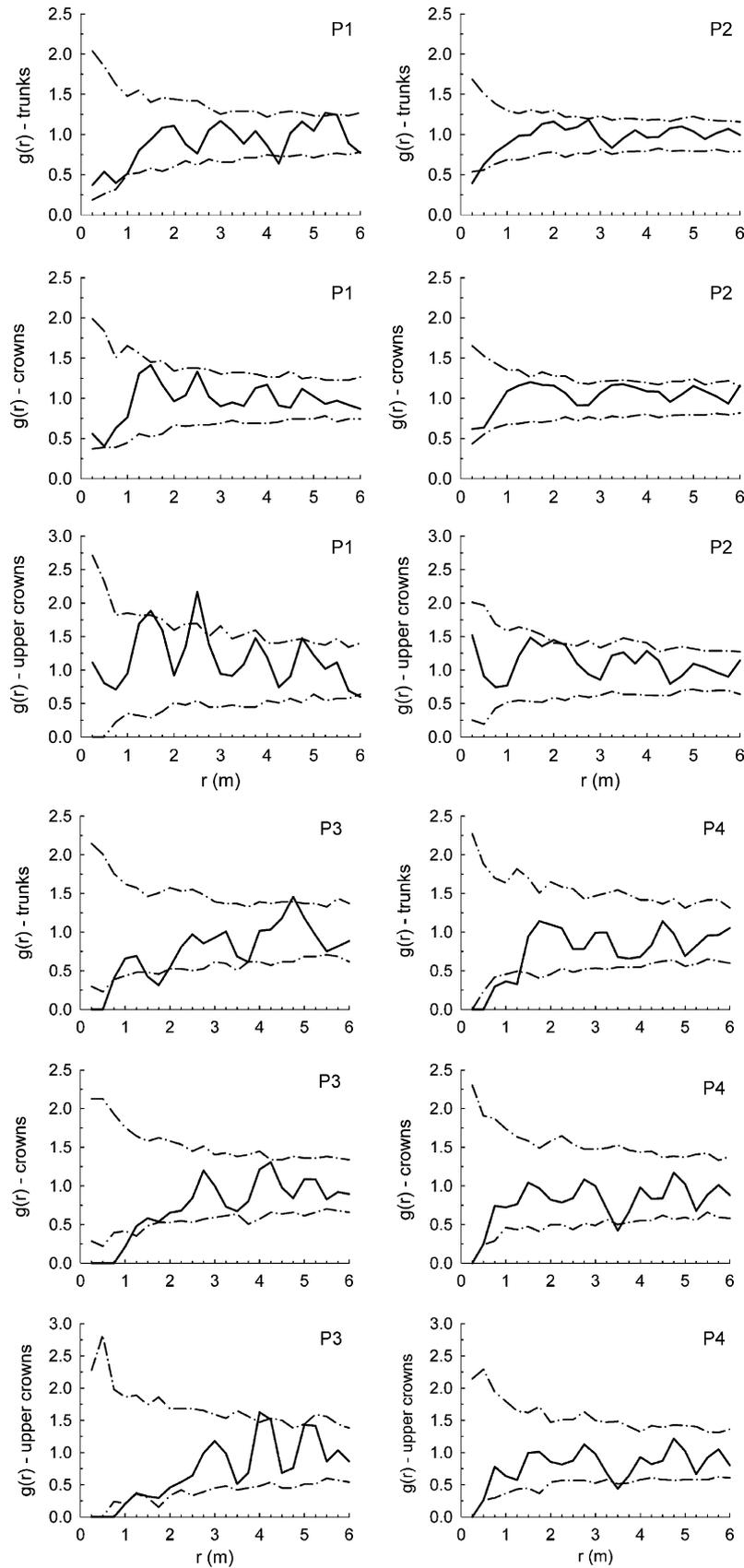
Fig. 1. Point pattern analysis of trunks, crown centres, and only upper crown centres in deciduous forest (P1, P2) and coniferous forest (P3, P4). We used the univariate *g*-function (solid line) and approximately 95% upper and lower confidence envelopes of the null model CSR (broken line) to analyse the patterns. Solid lines below the CSR null model indicate regular patterns (repulsion), *g*(*r*)-values above indicate significant clumping (attraction).

Table 2
The extent of asymmetric growth

Extent of asymmetric growth	Deciduous forest		Coniferous forest	
	Plot 1	Plot 2	Plot 3	Plot 4
Mean crown vector length (m), separately	1.18	0.93	0.71	0.36
−95%, +95% confidence limits of mean (m)	1.04–1.32	0.82–1.05	0.62–0.80	0.29–0.43
Min, max crown vector length (m)	0.05–3.05	0.13–3.29	0.05–1.81	0.03–1.14
Mean crown vector length (m), combined	1.06[***]		0.59	

Crown vector length is the horizontal distance between the centroid of the projected crown area and the stem-base position. We calculated the mean crown vector length for the four plots *separately* and for deciduous and coniferous trees *combined*. The difference between the mean crown vector length of combined deciduous and combined coniferous trees was tested for significance using a *t*-test for independent samples.
[***] $p < 0.001$.

Table 3
The coefficients of determination (r^2) of nearest neighbour regressions

Linear regression	Deciduous forest		Coniferous forest	
	Plot 1	Plot 2	Plot 3	Plot 4
Mean of 3 NN distances				
Dbh	0.0457[*]	0.0321	0.0789[*]	0.1587[**]
Crown radius	0.0422[*]	0.1953[***]	0.1821[***]	0.2111[**]
Crown vector length	0.0152	0.0002	0.0113	0.0729
Variance in angles of 3 NN				
Crown vector length	0.0151	0.0224	0.0384	0.0112
Difference in growth angle α to $\bar{\phi}$ of 3 NN	0.0331	0.0001	0.0109	0.0192

Regressions are linear regressions between dependent variables (dbh, crown radius, crown vector length, difference in growth angle α to mean angle $\bar{\phi}$ of 3 NN) of focal trees and the mean of the three nearest neighbour (NN) distances, and the variance in angles of the three nearest neighbours to the focal tree (independent variables), respectively.
[*] Significance level of correlations is $p < 0.05$.
[**] Significance level of correlations is $p < 0.01$.
[***] Significance level of correlations is $p < 0.001$.

Table 4
The direction of asymmetric growth analysed with circular statistics

Circular statistics	Deciduous forest		Coniferous forest	
	Plot 1	Plot 2	Plot 3	Plot 4
Mean vector angle	0.8°	264.2°	343.1°	271.2°
Watson's U^2 test (U^2, von Mises)	0.025	0.044	0.009	0.06
Rayleigh's uniformity test (Z)	8.382[***]	15.009[***]	0.689	6.064[**]
V test				
V, hypothetical mean = 180°, sunlight	−0.285	0.040	–	−0.008
V, hypothetical mean = slope direction	0.245[***]	0.357[***]	–	0.384[***]
Slope direction	330°	240°	260°	270°

For Plot 3, the null hypothesis of uniformity could not be rejected, making *V* tests unnecessary.
[**] Significance level is $p < 0.01$.
[***] Significance level is $p < 0.001$.

growth of focal trees was not directly dependent on neighbourhood density or the directionality of nearest neighbour influence. However, neighbourhood density had significant effects on the crown radius and dbh of focal trees. Although r^2-values were low, these significant effects on crown radius were strongest in the two high-density stands P2 and P4.

Except for P3, crown centres were not randomly distributed around their stem-base positions, as indicated by Rayleigh's uniformity test (Table 4; Fig. 2). In P1, P2 and P4 asymmetric crown development clustered significantly in downward

direction of slopes. The mean vector angle was most similar to the slope direction in P4, but least in P3. Trees did not bend significantly towards the southern direction of incoming solar radiation.

4. Discussion

The main aim of this study was to determine if random crown patterns exist in deciduous and coniferous forests located in continental Europe. We chose stands differing in composi-
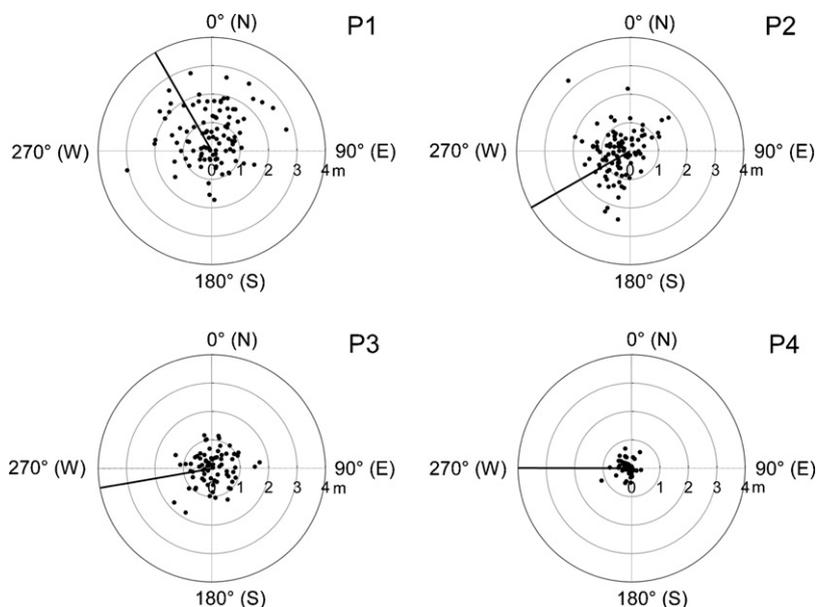
Fig. 2. Extent and direction of asymmetric growth in deciduous forest (P1, P2) and coniferous forest (P3, P4). Black dots show the individual locations of crown centres in relation to their stem-base position (centre of cross). Black lines within polar plots indicate the downward direction of slopes.

tion, height and origin and that appeared likely to exhibit such random patterns. In three out of four plots we could not reject the null hypothesis of randomly distributed crowns, which agrees with Ishizuka's (1984) findings. However, due to the high stand-to-stand variation, we cannot conclude that random crown patterns would generally be optimal for light harvesting. But due to our solid statistical pattern confirmation with Monte Carlo simulations and due to the fact that even upper crowns may be randomly spread, our results suggest that random crown patterns may exist more often than is commonly believed. For example, Gavrikov et al. (1993) and Olesen (2001) did not statistically show that crowns were evenly distributed. In the study of Gavrikov et al. (1993), crown centres of 55- and 90-year-old Scots pine trees have fairly low g-function values of 0.4–0.5 at a radius of 0.5 m but no confidence limits are indicated for the g-function. In our study, crown centres of deciduous and coniferous stands (Fig. 1) had comparable g-values at this scale of $r = 0.5$ m, but the crown pattern was still within the confidence envelope of the Poisson-null model and hence, not significantly different from random. Despite the similarity of the low g-function values in the two studies, statistical conclusions are not transferable because confidence envelopes depend on underlying patterns. This demonstrates their importance for supporting conclusions on crown patterns.

Information on two-dimensional crown patterns requires careful interpretation, because in reality, canopy architecture is three-dimensional (Song et al., 1997). In Ishizuka's (1984) study, lower, middle and all crown layers combined were random but, except for one plot with random overstory crowns, upper crowns had regular patterns. Since his spatial analysis was based on nearest neighbour statistics, the regularity of upper crowns could well reflect a hard-core distance and thus merely the physical expansion of large crown diameters. Instead, spatial analysis based on scale-dependent correlation functions may show that hard-core distances disappear at larger

scales to reveal random patterns of upper crowns (Koukoulas and Blackburn, 2005). We have shown this for the overstory in P4, but not for P3 where the hard-core distance turned into regularity of upper crowns. Overall, our surprising result is that upper crowns in the two deciduous plots did not show a hard-core distance and that random crown patterns dominated in P1, P2 and P4. These findings on the two-dimensional distribution of crown centres are considered robust. This is because with the separate analysis of upper crowns we have largely excluded problems with the fact that maximal crown extent and patterns may vary with different height strata (Frech et al., 2003; Song et al., 2004).

One reason for the dominating random crown patterns in the two deciduous stands could be the greater extent in asymmetric growth (mean crown vector length) in angiosperms as compared to gymnosperms. Also, it is known from similar mixed deciduous forests in central Germany that tree crowns at the same height level may overlap considerably (Frech et al., 2003). In combination with phototropic opportunism to gaps in space (especially of Q. petraea and S. torminalis in P2), this lateral plasticity in crown development could be the central mechanism in forming the observed random crown patterns in the deciduous stands. Such a strategy would also explain the comparatively low mortalities in the low and high-density stands. Furthermore, competition as inferred from correlation between neighbourhood density and crown radius or dbh was very low in P1, probably leading to random trunk patterns (Getzin et al., 2006). In contrast, competition in the high-density stand P2 was higher and could have caused the regular trunk pattern at the smallest scale of $r = 0.25$ m. However, the random crown pattern does not reflect this stronger competition. Also, the density and directionality of nearest neighbours had no significant effects on the crown vector lengths or the direction of asymmetric growth. For our stands with random or regular trunk patterns, we assume that competition from local

tree neighbours is compensated more by plasticity in crown radius than by plasticity in asymmetric growth. This means that higher neighbourhood densities will lead to smaller crowns but not to larger crown vector lengths. These results and our findings on crown patterns could have been different if aggregated trunks had dominated our stands (Sorrensen-Cothern et al., 1993; Umeki, 1997). But in this study, we looked for random crown patterns and hence avoided stands with aggregated trunks.

In the two deciduous stands, influences of local neighbourhood competition on the extent and direction of asymmetric growth and resulting crown patterns seem to be masked by more important mechanisms such as large-scale heterogeneity in light induced by slope topography. The aspect of slope determines the average direction of the gradient in availability of light for tree individuals. Umeki (1995a) has shown that this large-scale heterogeneity in light was more important for asymmetric growth than small-scale heterogeneity in light induced from nearest neighbouring trees. The crowns of neighbours on the upper side of the slope are situated at higher positions than those of the same-sized neighbours on the lower side. Availability of light is higher on the lower side hence all tree individuals will grow more rapidly to the lower side of the slope. We observed this joined response in the two deciduous stands and also in the coniferous stand P4 because trees bent significantly in downward direction of the slopes. This response seems to be independent of the direction of incoming solar radiation, because trees in P1 bent even towards north.

The reason for not finding downhill bending in the mixed coniferous stand with Douglas-fir and Norway spruce could be the micro-topography of P3. The grooves running parallel to the incline did probably cancel out systematic growth response to slope direction. In addition, smaller flexibility in lateral growth of gymnosperms is probably the main reason that regular crown patterns reflect regular trunk patterns in P3. Evenly spaced crown centres appear to be more frequent in coniferous than in deciduous stands because the homogenizing effects of slope topography relative to the effects of local neighbourhood seem less important for asymmetric growth of coniferous trees, as compared to deciduous trees (Umeki, 1995b). This would explain the stronger correlation between dbh or crown radius and neighbourhood density in the two coniferous stands. Still, also in the coniferous stands neighbourhood density or directionality had no significant effects on the extent or direction of bending trees. In the mixed coniferous stand, this could have been a result of the less dense planting scheme. However, this does not apply for our unusual high-density stand with planted Douglas-fir, P4.

In P4, the trunk pattern was regular and due to the high mortality, light gaps were present. One could expect that crowns grow straight upright and thereby reflect the same regular pattern as the trunks at $r \leq 1.25$ m. One could also expect that crowns would bear the costs of growing asymmetrically (Spicer and Gartner, 1998; Muth and Bazzaz, 2003), but would compensate these costs by growing away from each other towards more beneficial light conditions in tree-fall gaps. In the latter case, crown locations would be

evenly spaced beyond scales of 1.25 m, and hence would be more regular than trunks (as in P3). Surprisingly, we found the opposite: crowns were randomly but trunks regularly spaced. At the comparative reference scale of $r = 1$ m, inter-crown distances were twice as frequent as inter-trunk distances. Hence, crowns must have grown towards each other, as was also confirmed by our visual inspection of the pattern. This was possible, because the mean crown radius in P4 was comparatively small and the hard-core distance of regularly planted trunks was twice as high as the hard-core distance of crowns or upper crowns.

If crowns of P4 had all the space to maximise photosynthesis in a regular growth pattern, what other mechanism has caused attraction between them and finally a random pattern? We assume that mechanical constraints, i.e. instability problems, were more important than phototropic mechanisms in determining the nature of the crown pattern. Trees of P4 were the most slender ones and the high mortality rate of almost 60% caused many tree-fall gaps within the stand. These Douglas-fir were also growing on the steepest slope and showed least resistance to bending in downward direction. Slope direction and the mean vector angle of trees were nearly equal (Table 4). Evidently, trees of P4 were strongly dependent on stabilizing each other, which explains the attraction among crown centres. Rudnicki et al. (2003) found similar characteristics in high-density stands of boreal forest where crown overlap increased in a stand with more distant neighbours. They proposed that slender trees would rely on a strategy of mutual crown support, but would suffer frequent crown collisions in wind. Consequently, abrasion damage inhibits lateral growth and these effects combined may lead to even clumped canopy structures in boreal forests (Kucharik et al., 1999; Rudnicki et al., 2003). The fact that we found random crown patterns in P4 at scales where trunks were regular is probably ascribed to these combined effects of crown support and abrasion. Our findings support also model predictions by Song et al. (1997), where tree density was the main factor affecting crown areas and the number of canopy patches. When densities were the same or similar in this model, canopy structure was influenced by the spatial pattern of tree trunks and by species composition.

Concerning management, regularly planted trunk patterns may optimise reducing competition, because under a given density, an even spacing of trees will maximise nearest neighbour-tree distances. This may lead to larger crown diameters for a given dbh than compared to crown sizes for random or aggregated trunk patterns (Paulo et al., 2002). But if trees of a planted forest stand are all of the same age, inter-crown contact already during early growth phases may lower the initial wind loading on individual trees. This will reduce investment into stability properties and finally, resulting height/dbh ratios will be high. The slender trees of such stands are then particularly prone to damage by wind (Mason, 2002) and may be forced to rely on a strategy of mutual crown support (Rudnicki et al., 2003). For fast growing species such as Douglas-fir, avoidance of crown abrasion and high mortality rates may be achieved by fostering silviculture with uneven-aged mixed stands, preferably giving

local species like Norway spruce a competitive edge. The more stout trees and lower mortality in P3 is an example for more advantageous silviculture with mixed coniferous trees.

5. Conclusion

We have shown that random patterns may be found in crowns and upper crowns. The spatial relationship between crown–trunk locations is complex and may be determined by small- and large-scale heterogeneity in light, and even by mechanical constraints. Our results suggest that, in latitudes around 50°N, the growth response to large-scale heterogeneity in light is solely determined by slope while trees do not bent significantly towards incoming solar radiation. Where dense regular planting schemes result in very slender trees and mutual crown support, mechanical constraints may be more decisive for the crown pattern than heterogeneity in light. These considerations of asymmetric growth are essential in practical management for improving timber quality (Rock et al., 2004) and stand leaf area index (Rudnicki et al., 2001, 2003) or wind resistance of stands (Mason, 2002).

With this study we intend to motivate further research on crown patterns using scale-dependent spatial statistics. More refined analyses may be achieved with three-dimensional models by slicing the canopy into many vertical height layers (Song et al., 2004). One of the main challenging questions is to investigate the relative effects of large- and small-scale heterogeneity in light on asymmetric growth. For example, how does the presence or absence of slope affect the crown pattern, directed bending at the stand level and the crown vector length in dependence on local neighbourhood density? And how do these relative effects differ for aggregated, random and regular trunk patterns, and between deciduous, coniferous and mixed stands?

Acknowledgements

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