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Crown plasticity and neighborhood interactions of European beech (*Fagus sylvatica* L.) in an old-growth forest

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Abstract Competition for canopy space is a process of major importance in forest dynamics. Although virgin and old-growth European beech (*Fagus sylvatica* L.) forests in Europe have been studied for many years, there are to date no studies of individual-tree crown plasticity and the way this is influenced by local neighborhood interactions in these forests. In this study, we analyzed crown plasticity and local neighborhood interactions of individual trees in the upper canopy of the old-growth beech forests of Serrahn, northeast Germany. In a 2.8-ha sample plot, we measured crown radii of all upper canopy trees and analyzed the direction and extent of crown asymmetry. Size, relative position, and distance of neighboring trees were used to construct vectors of neighborhood asymmetry within different distances from target trees. The crowns of beech trees showed strong morphological plasticity. Mean absolute and relative displacement of crown centers from the stem base were 1.95 m and 0.37, respectively. Circular–circular rank correlation coefficients between the direction of crown displacement and the direction of neighborhood pressure showed that trees strongly positioned their crowns away from local neighbors. Highest correlation coefficients were obtained when basal area and relative position of neighboring trees within a radial distance of 12 m were considered. Clark and Evans index and Ripley's *K*-function showed that crowns were more regularly distributed than stems. Projected canopy cover was about 10% higher than canopy cover with simulated circular crowns. We conclude that the crowns of older beech trees have a high ability to plastically respond to changes in the local canopy conditions, enabling very effective exploitation of canopy space.

Keywords Canopy displacement · Competition · Crown displacement · Neighborhood asymmetry · Ripley's *K*-function

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Introduction

The size and shape of individual tree crowns is, besides a tree species' architectural model and genotype (Hallé et al. 1978), determined by competition for canopy space. In turn, crown dimensions strongly determine the individual's ability to intercept light and to shade other trees, thus defining a feedback central to the understanding of forest dynamics (Purves et al. 2007). Through phenotypic plasticity, tree crowns are highly variable in their response to changes in environmental conditions (Canham 1988; Valladares et al. 2007). Tree photomorphogenetic response has been shown to be caused by a locally enhanced growth in response to abundant light (phototrophic growth) as well as a coupling of this enhanced growth with an inhibition of the growth and survival of shoots and branches in the shaded part of a crown (correlative inhibition; Stoll and Schmid 1998; Takenaka 2000). Light-related phenotypic plasticity is caused by biotic interactions between neighboring trees (Vincent and Harja 2007), but also abiotic conditions such as latitude and topography may play an

important role (Umeki 1995b; Rouvinen and Kuuluvainen 1997; Lang et al. 2010). In addition, the direct abrasion and growth inhibition caused by wind-induced crown collisions with neighboring trees play a crucial role in limiting crown development (Takenaka 2000). The resulting crown asymmetry is a mechanism that allows for an optimal packing of the horizontal canopy (Olesen 2001). The direction or degree of crown asymmetry can be assessed by measuring the divergence of the centroid of the projected crown area from the position of the stem base (crown displacement; Rouvinen and Kuuluvainen 1997; Brisson 2001; Muth and Bazzaz 2002).

There is abundant evidence for species-specific differences in the extent of the plastic responses of tree crowns to environmental challenges (Valladares et al. 2007). It is well established that morphological plasticity is smaller in gymnosperms than in angiosperms (Umeki 1995a; Muth and Bazzaz 2002; Pretzsch and Schütze 2005; Getzin and Wiegand 2007). In addition, for a given species, phenotypic plasticity may change dramatically over the course of plant growth (ontogenetic drift; Valladares et al. 2007).

In recent years, interest in understanding the natural processes in forest ecosystems has grown considerably, and as only a few primary forests remain in many regions (e.g., Europe, Peterken 1996), forests with old-growth attributes (Bauhus et al. 2009) are important reference sites for more natural management approaches and have, thus, become important study objects involving a broad range of ecosystem functions and services (Wirth et al. 2009). In large parts of Europe, European beech (*Fagus sylvatica* L.) forests are the most important forest communities in the potential natural vegetation (Bohn et al. 2003). Stand structure, distribution of developmental phases, spatio-temporal dynamics of regeneration, dead wood, and canopy gaps in primary and old-growth beech forests have been extensively studied (e.g., Leibundgut 1978; Korpel 1995; Jaworski and Paluch 2002; Meyer et al. 2003; Christensen et al. 2005; von Oheimb et al. 2005; Westphal et al. 2006; Drössler and von Lüpke 2007; Paluch 2007; Heiri et al. 2009; Vandekerkhove et al. 2009; Kucbel et al. 2010). However, surprisingly, little is known about individual-tree crown dimensions of canopy trees and the way these are influenced by local neighborhood interactions in these forests.

Beech is known for its outstanding capacity to occupy canopy space as a result of its high crown plasticity (Roloff 2001; Pretzsch and Schütze 2005, 2009). In a large number of experimental plots in even-aged pure and mixed stands of Norway spruce (*Picea abies* [L.] Karst.) and beech in southern Germany, Pretzsch and Schütze (2009) found evidence for transgressive overyielding on stand level, a process that, however, depends on site quality (Pretzsch et al. 2010). Individual-tree level analyses revealed that

crown efficiency (i.e., the mean annual biomass growth per unit of crown projection area) of Norway spruce increased significantly in mixed forests. By contrast, the overyielding of beech was attributed to the effects of multilayering, and high efficiency and dynamics of canopy space occupation (Pretzsch and Schütze 2009). Although it is generally assumed that older trees react more slowly than younger ones (Oliver and Larson 1996), several studies indicate that even older beech trees show growth responses to density reductions (Börner 1998; Debeljak and Mlinsek 1998; Utschig and Küsters 2003). Even in the terminal and degradation phase of a beech forest, canopy trees continue to close small gaps by lateral crown expansion (Emborg et al. 2000). However, the asymmetry of crown expansion of older individual beech trees and the plastic response to local neighborhood interactions or natural disturbances have rarely been studied in detail (Haywood 2002). With an increasing focus on sustainable forest management practices, a detailed understanding of how older beech trees respond to competitive interactions in the upper canopy has gained importance in silviculture.

Hence, the purpose of this study was to analyze crown plasticity of individual beech trees in the upper canopy of an old-growth forest. In particular, we analyzed (1) the extent to which beech forms asymmetric crowns, (2) how precisely individuals shift their crowns away from their neighbors, and (3) whether slope had an influence on crown displacement. In order to describe the effects of crown plasticity on the stand structure, we tested (4) whether crown centers are more regularly dispersed than stem bases and analyzed (5) the effect of crown plasticity on canopy cover of the stand.

Materials and methods

Study area

The study was conducted in the Serrahn beech forests (Müritz National Park, Mecklenburg-Western Pomerania, northeast Germany, 53°20′N, 13°12′E). The soils are derived from recent moraines of the Weichsel glacial period. The surface is undulating, with areas of level ground (slope inclination < 7°) and areas with slope inclination ranging from 7 to 24°. The mean height of the study area is 100 m above sea level. It has a suboceanic–subcontinental climate, with a mean annual precipitation of 593 mm and a mean annual temperature of 7.8°C (von Oheimb et al. 2005). Soil types are predominantly dystric cambisols, podzoluvisols, and luvisols, developed on a parent material of loamy sand. The main humus type is moder. The potential natural forest vegetation can be assigned to acidophytic beech forests (*Luzulo-Fagetum*) on

dystric cambisols and podzoluvisol soils and to mesophytic beech forests (*Galio-Fagetum*) on luvisols.

The beech forests of Serrahn have been a game park with little silvicultural intervention since the beginning of the nineteenth century and have been protected as a forest reserve since 1960 (von Oheimb et al. 2005). The age of trees in the upper canopy layer ranges from 180 to 240 years. Although the consequences of human interventions are still observable in the structure of the Serrahn beech forests, they show a high degree of naturalness. Large parts of the forests are in the terminal phase, but the degradation and regeneration phases also occupy considerable proportions of the total area (von Oheimb et al. 2005). Until the 1960s, the stand structure of the old-growth forests of Serrahn was single-storied with a dense canopy (von Oheimb et al. 2005). Beginning in the late 1960s, high mortality (1.3% year^{-1}; von Oheimb et al. 2007) among the canopy trees, most of which were 200–230 years old, produced numerous canopy openings. Since then, canopy gap creation is a continuous process, mainly caused by the death of single or small groups of canopy trees. As a result, the canopy structure is very heterogeneous, and larger gaps that can be clearly delineated are an exception.

Sample plot and tree measurements

The measurements were taken in a 2.8-ha (125 m × 225 m) sample plot, which is part of an existing 8-ha permanent plot (von Oheimb et al. 2005, 2007). Selection criteria for the location of the permanent plot were a long period without management (total protection since 1960, preceding minor interventions when used as a game park; for historical use of the area see von Oheimb et al. 2005), typical soil conditions for the Serrahn beech forests, dominance of beech, and a minimum distance to forest edges of 150 m. In the permanent plot, the positions of all trees ≥7 cm diameter at breast height (DBH) were mapped, and DBH was measured in 2002 and 2009. In 2002, the mean basal area and mean volume of living trees amounted to 33 m^2 ha^{-1} and 605 m^3 ha^{-1}, respectively. The average height of the 20% largest trees in the stand (i.e., top height) was 38 m. Tree density in the upper canopy layer (i.e., trees larger than 2/3 of the top height) was 92 ha^{-1}, with the proportion of beech amounting to 96% (von Oheimb et al. 2005). Mean dead wood volume was 94 m^3 ha^{-1} (von Oheimb et al. 2007). The 2.8-ha sample plot was selected to represent areas with closed canopy as well as areas with existing canopy gaps of different age classes. The sample plot was placed within the 8-ha permanent plot with a buffer strip to the borders of at least 12.5 m in order to ensure that information on the position of neighboring trees was available.

For all trees of the upper canopy layer, crown radii were measured in September and October 2009 in eight sub-cardinal directions (N, NE, E, etc.) by means of a densiometer. The horizontal distance between stem base and crown edge was measured with the Forestor VERTEX Hypsometer (Haglöf, Sweden) to the nearest decimeter. For the analyses, the radius of the corresponding stem was added to each distance measurement. A total of 235 trees were measured in the sample plot. With the exception of two Scots pine (*Pinus sylvestris* L.) individuals and one sessile oak (*Quercus petraea* [Matt.] Liebl.) individual, all trees were beech. At the same time as these measurements were taken, the hypsometer was also used to measure local slope inclination. The polar coordinates of stem bases used in the analyses were taken from von Oheimb et al. (2005).

Data analysis

A map containing all stem bases and the corresponding crowns was drawn in ArcGIS 9.3 (Environmental Systems Research Institute (ESRI) Inc., Redlands, California). Tree crown models were created by connecting the eight canopy edge points to a polygon (Fig. 1). Crown area was calculated as the sum of the area of the eight triangles. The coordinates of the gravity center of each constructed polygon were calculated as the mean of the gravity centers of the eight triangles constituting the polygon and weighted by the respective triangle area. This analysis was performed using the ArcGIS extension ET Geo Wizards 9.9 (Tchoukanski 2009).

We used absolute displacement, defined as the distance between the stem base and the corresponding center of gravity of a crown projection (hereafter crown center), as a measure of crown displacement (Brisson and Reynolds 1994; Brisson 2001; Muth and Bazzaz 2002, 2003). In order to compare displacement across a range of crown sizes, relative displacement was defined as the ratio of absolute displacement and the mean crown radius of the respective tree (Muth and Bazzaz 2002, 2003; Longuetaud et al. 2008). With a relative displacement value close to zero, a tree crown is centered above the stem base. The larger the relative displacement, the more the tree crown is shifted away from the stem base. Absolute and relative displacement were defined as vectors indicating the magnitude of displacement (length) and the direction of the crown center relative to the stem base (direction).

The competitive pressure of neighboring trees as a possible explanation for crown plasticity was characterized by the vector of neighborhood asymmetry (Brisson and Reynolds 1994; Brisson 2001). This vector is defined as the sum of competitive pressure vectors of all neighboring trees within a defined distance from the stem base of a target tree. Competitive pressure vectors of each

Fig. 1 Crown map of the sample plot, displaying the 235 crown projections of the trees in the upper canopy layer, positions of the respective stem bases (*dots*), and the delineation of the sample plot
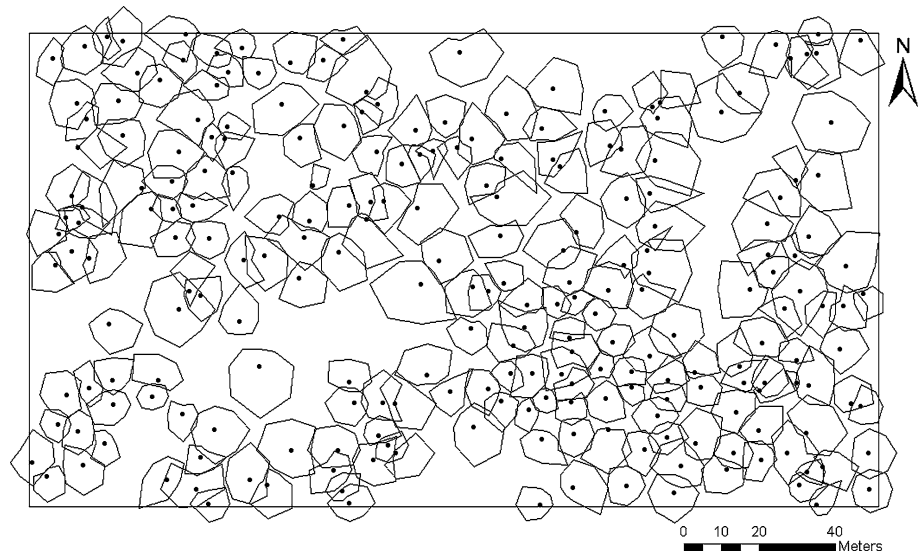
neighboring tree had the following three characteristics: (1) starting point is the stem base of the target tree, (2) direction was equal to the direction from the neighboring tree's crown center to the target tree's stem base, and (3) length was equal to an importance value (see below) indicating the intensity of competitive pressure. The summation of these vectors results in the vector of neighborhood asymmetry (Fig. 2). The perpendicular of the position of a neighboring tree's crown center, rather than stem base, was used to determine the location of a neighboring tree, as competition for light is influenced by the position of the crown rather than by the position of the stem (Umeki 1995b; Muth and Bazzaz 2003). This position is, thus, considered as the imagined center of competition effects. Four different importance values were tested: (1) importance value set at 1, (2) distance^{-1}, (3) basal area × distance^{-1}, and (4) crown area × distance^{-1}. The calculation with an importance value set at 1 for every neighboring tree only considers the position of the neighboring tree. Whereas (2) only considers position and distance of neighboring trees, (3) and (4) take into account position, tree size variables, and distance of neighbors. We tested different radial distances to select neighboring trees. All trees were considered as target trees that had at least one neighboring tree with a crown center within a radial distance of 8 m ($n = 148$), 10 m ($n = 166$), 12 m ($n = 167$), or 14 m ($n = 160$), respectively, from their stem bases. Additionally, only the nearest neighbor of the target trees was considered ($n = 221$). The number of trees included in the analysis differed for the respective radial distances, as we had to exclude trees at the edge of the sample plot for each case. With higher radial distances, the number of neighboring trees that were located outside the sample plot

increased. However, as we did not have data on crown size for these trees, the respective target tree had to be excluded from the analysis. Trees were not considered as target trees if they had a neighbor for which basal area and crown area were not measured within the respective radial distance plus 6.26 m (largest absolute displacement value observed) or where a neighboring tree outside the study site was closer than the nearest neighbor within the study site.

The vector of neighborhood asymmetry does not reflect the absolute amount of competitive pressure, but rather the position of competitors. If they are clumped around one side of the target tree (e.g., in the case of gap-edge trees), the vector of neighborhood asymmetry will be large. On the other hand, if competitors are regularly spaced around the target tree and their size (basal area, crown area) is also fairly similar, the competitive pressure vectors will cancel each other out and the vector of neighborhood asymmetry will be small (Brisson and Reynolds 1994; Brisson 2001). By comparing the direction of neighborhood asymmetry and the direction of absolute displacement, we can determine to what extent target trees grow away from the area of highest neighborhood pressure (Brisson 2001; Muth and Bazzaz 2002, 2003). Circular–circular rank correlation coefficients were calculated to determine the correlation between the angles of neighborhood asymmetry and absolute displacement (Batschelet 1981). We first converted the two pairs of angles (ϕ_i, ψ_i) into uniformly distributed angles:

$$\phi_i' = r_i \times \varepsilon \tag{1}$$

$$\psi_i' = r_i \times \varepsilon \tag{2}$$

where r_i denotes the rank of ϕ_i or ψ_i, respectively, and ε is the common arc length defined as $\varepsilon = 360°/n$. The rank
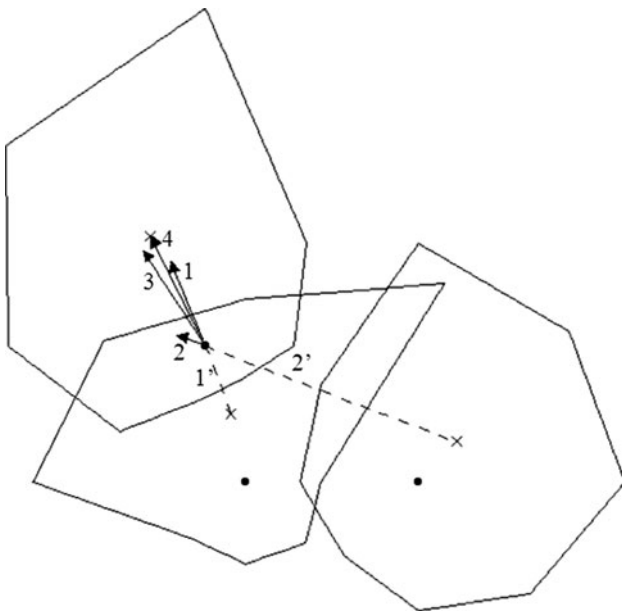
Fig. 2 Graphical representation of the derivation of the vector of neighborhood asymmetry. Two neighboring trees expose pressure on the target tree (*upper left*), stem bases are represented by *dots*, and crown centers by *crosses*. Vectors 1′ and 2′ (*dashed lines*) start at the respective neighboring tree's crown center and end at the target tree's stem base. They indicate the direction of neighborhood pressure as well as the distance of the neighboring trees to the target tree. Starting at the target tree's stem base, vectors 1 and 2 exhibit the same direction as 1′ and 2′, and their length (importance value) is, in this case, determined by the crown area of the neighboring trees divided by the length of 1′ and 2′. Vector 3 represents the summation of vectors 1 and 2. Vector 4 exhibits the direction and the length of absolute crown displacement of the target tree. In this example, neighborhood asymmetry and absolute displacement are closely correlated

correlation coefficient is defined as the length of the mean vector length r:

$$r = \frac{1}{n} \sqrt{\left(\sum_{i=1}^{n} \cos\delta_i\right)^2 + \left(\sum_{i=1}^{n} \sin\delta_i\right)^2} \tag{3}$$

where n denotes the number of pairs, and δ_i is the difference (positive correlation) or the sum (negative correlation) of ϕ_i and ψ_i, respectively. We took the larger of the resulting two correlation coefficients as the result and tested it for significant deviation from 0 (Batschelet 1981). The analyses were conducted including neighbors at different radial distances from the target tree and using different importance values in order to determine the most appropriate zone of influence of neighboring trees and the relative importance of the size of, and distance to, neighbors. Furthermore, to test whether a high asymmetric competitive pressure results in higher crown displacement, we regressed absolute values of relative displacement against absolute values of neighborhood asymmetry.

A positive relationship would indicate that a higher asymmetric pressure results in a stronger shift of the target tree's crown.

In order to determine the degree of correspondence of the direction of neighborhood asymmetry and the direction of absolute displacement, we calculated an angle δ, the "canopy deviation from optimal" (where optimal refers to light foraging; Muth and Bazzaz 2002, 2003), which ranges from 0° to 180° and is defined as the difference between these two angles:

$$\delta_i \begin{cases} \phi_i - \psi_i + 180° & \text{if } (\phi_i - \psi_i) < 0° \\ \phi_i - \psi_i - 180° & \text{if } (\phi_i - \psi_i) > 180° \end{cases} \tag{4}$$

where ϕ_i denotes the angle of NA, and ψ_i denotes the angle of absolute displacement. A value of 0° indicates that a tree crown is growing directly away from the area of highest competitive pressure and thus indicates high precision in light foraging. The higher the angle δ, the larger the deflection between the two angles and the smaller the competition avoidance. We predicted that higher asymmetry leads to lower canopy deviation from optimal (Muth and Bazzaz 2002, 2003). This relationship was tested by the regression of canopy deviation from optimal against absolute values of the vector of neighborhood asymmetry for each importance value and each zone of influence. A negative slope would support our hypothesis.

In order to approximate the main slope direction of every tree, we calculated a vector as a sum of all observed downward slope vectors (direction equal to direction of measurement, i.e., N, NE, E,…; length equal to steepness for each direction). The mean steepness of slope was then approximated by the arithmetic mean of all observed downward slopes. We calculated a circular–circular rank correlation coefficient to describe the correlation between the direction of slope and the direction of crown displacement. For those trees that were both considered as target trees and had a local slope inclination ≥7°, we calculated partial correlation coefficients, holding the influence of slope constant (Zar 1999):

$$r_{\text{NAAD.SL}} = \frac{r_{\text{NAAD}} - r_{\text{ADSL}} \times r_{\text{NASL}}}{\sqrt{(1 - r_{\text{ADSL}}^2) \times (1 - r_{\text{NASL}}^2)}} \tag{5}$$

where $r_{\text{NAAD.SL}}$ denotes the correlation coefficient between neighborhood asymmetry and absolute displacement holding constant for slope, r_{NAAD} denotes the correlation coefficient between neighborhood asymmetry and absolute displacement, r_{NASL} is the correlation coefficient between neighborhood asymmetry and slope, and r_{ADSL} is the correlation coefficient between absolute displacement and slope. Trees with local slope inclination <7° were considered to grow on level ground and were excluded from this analysis. For trees on sloping ground, we used circular–circular rank correlation coefficients (Batschelet 1981)

between each two of the three variables, direction of slope, absolute displacement, and neighborhood asymmetry as inputs. Differences between correlation coefficients $r_{NAAD.SL}$ and r_{NAAD} were tested for significance ($\alpha = 0.05$) using Fisher's z transformation in a one-sided z test (Zar 1999).

For analyzing the influence of crown plasticity on stand structure, we used the aggregation index of Clark and Evans (1954), which is commonly used in forest science (e.g., Longuetaud et al. 2008; Pretzsch 2009). The index uses the distance to the nearest neighbor as a measure of spatial structures. The mean of the distances to the nearest neighbor is set into a theoretically expected mean distance:

$$R = \frac{\bar{r}_{obs}}{\bar{r}_{exp}} \tag{6}$$

where $\bar{r}_{obs}$ is the observed mean nearest neighbor distance and $\bar{r}_{exp}$ is calculated as

$$\bar{r}_{exp} = \frac{1}{2\sqrt{\rho}} \tag{7}$$

with ρ set as the ratio of number of trees to the sample plot area. R ranges from 0 to 2.1491, R values around 1 indicate a random distribution, and $R < 1$ can be interpreted as a clumped pattern and $R > 1$ as a regular pattern (Clark and Evans 1954). Edge correction after Donnelly (1978) was chosen. Significance of departure from randomness was tested (Clark and Evans 1954). Differences between R values for crown centers and stem bases were tested using a one-sided z test. As $\bar{r}_{exp}$ was the same for crowns and stems, we tested for differences between the observed nearest neighbor distances (Longuetaud et al. 2008). Calculations were made using the ArcScript "Nearest Neighbor Analysis" (Sawada 2002) in ArcGIS.

Since the index of Clark and Evans only uses the distance to the nearest neighbor and is therefore density dependent, we also employed a second-order point pattern statistic. Ripley's K (Ripley 1976, 1977) is a commonly used method in point pattern analysis (Fortin and Dale 2007). Unlike the index of Clark and Evans, Ripley's K can be used to describe patterns counting neighbors within different distances, r, from a point on a continuous basis (Perry et al. 2006; Pretzsch 2009). Ripley' K is defined as

$$K(r) = \frac{\bar{n}_r}{\rho} \tag{8}$$

where $\bar{n}_r$ is the mean number of neighbors within a distance r, and ρ is the stand density defined as the ratio of number of trees to the sample plot area. A common transformation of the $K(r)$ function is the $L(r)$ function, proposed by Besag (1977):

$$L(r) = \sqrt{\frac{K(r)}{\pi}} - r \tag{9}$$

In this form, values for $L(r)$ can be plotted against r, with values for $L(r)$ around 0 indicating random distribution, positive values describing clumped patterns, and negative values indicating regular dispersion (Fortin and Dale 2007). Edge correction following Ripley (1976) was used. About 999 Monte Carlo procedures were used to calculate a 99.9% confidence envelope for the expected random distribution $L(r) = 0$ (Fortin and Dale 2007; ESRI 2009). Hence, $L(r)$ shows significant departure from 0 if values are higher (clumped distribution) or lower (regular distribution) than the confidence limits. The L-function was calculated using the ArcGIS tool "Multi-Distance Spatial Cluster Analysis (Ripley's K-function)."

To measure the effects of crown plasticity of beech on canopy cover for the entire sample plot, we compared crown cover of the polygons map with a hypothetical crown cover of circular (i.e., non-plastic) crowns that had the same crown area (Longuetaud et al. 2008). Circular crowns were constructed with a radius corresponding to a circle with the respective crown area. Canopy cover was calculated as the relation of area covered by crown projections to the area of the sample plot (2.8 ha). Calculations and constructions were done using ArcGIS 9.3. If the measured canopy cover is larger than the constructed one, this would indicate that crown plasticity reduces crown overlap, thus contributing to a more effective exploitation of light resources.

Results

DBH of the 232 beech trees in the upper canopy layer ranged from 32 to 117 cm (mean 69 cm, SD 16 cm). Mean crown radius was 5.5 m (SD 1.2 m). Crown area varied considerably between individuals and ranged from 8.6 to 258.6 m^2; the mean crown area was 93.5 m^2 (SD = 42.7 m^2). Linear regression of crown area over DBH yielded a coefficient of determination of 0.52 ($y = 0.27x + 43.56$). Large values of canopy displacement were observed with a mean absolute displacement of 1.95 m (SD = 1.12 m, range 0.14–6.26 m) and a mean relative displacement of 0.37 (SD = 0.24, range 0.03–1.65).

For all radial distances and all importance values, a highly significant, positive correlation was found between the direction of neighborhood asymmetry and the direction of crown displacement (Table 1; Fig. 3a). The correlation coefficient generally increased with radial distance and peaked at a distance of 12 m. At this radial distance, the importance value using basal area weighted by distance

Table 1 Circular–circular rank correlation coefficients r (Batschelet 1981) between direction of neighborhood asymmetry and direction of crown displacement

Importance value	Nearest neighbor ($n = 221$)	Radial distance			
		8 m ($n = 148$)	10 m ($n = 166$)	12 m ($n = 167$)	14 m ($n = 160$)
Importance value $= 1$	0.47	0.53	0.55	0.56	0.51
Distance^{-1}	0.47	0.54	0.62	0.64	0.60
Crown area $\times$ distance^{-1}	0.47	0.55	0.58	0.65	0.61
Basal area $\times$ distance^{-1}	0.47	0.58	0.61	0.69	0.65

Neighborhood asymmetry was calculated for the nearest neighbor and for all neighboring trees within different radial distances and with different importance values. For all r: $P < 0.001$

yielded the highest correlation coefficient ($r = 0.69$, Table 1). Likewise, a positive correlation between vector lengths of neighborhood asymmetry and relative displacement was found, though with much lower correlation coefficients (Table 2; Fig. 3b). The highest values occurred at radial distances of 12 and 14 m, with the importance value using crown area weighted by distance. In most cases, there was a significantly negative correlation between the vector length of neighborhood asymmetry and canopy deviation from optimal (Table 2; Fig. 3c). Again, the correlation coefficients increased with radial distance, showing maximum values at a distance of 14 m ($r = -0.43$ for the importance value crown area $\times$ distance^{-1}).

About 39% of the beech trees occurred on slopes with a local slope inclination $\geq 7°$ (maximum inclination 24°). The circular–circular rank correlation coefficient of the direction of slope and the direction of crown displacement was $r = 0.46$ ($P < 0.01$), i.e., lower than correlation coefficients for neighborhood asymmetry (Table 1). The partial correlations for each radial distance holding constant for the influence of slope showed slight, but in neither case significant differences from the circular–circular rank correlations in Table 1 (data not shown). In order to exemplify the correlation coefficients, results are given in the following for the radial distance of 12 m, importance value basal area $\times$ distance^{-1}, based on the calculation of 61 trees on sloping ground. The correlation coefficient between the direction of neighborhood asymmetry and absolute displacement was $r = 0.72$, and between the direction of absolute displacement and slope it was $r = 0.35$. The correlation coefficient between neighborhood asymmetry and absolute displacement holding constant for the influence of slope was $r = 0.74$, which was not significantly different from the uncorrected coefficient.

The index of Clark and Evans was $R = 1.335$ for crown centers and $R = 1.101$ for stem bases. Both values were significantly different from random patterns ($P < 0.01$). The difference between R values for crown centers and stem bases was also significant ($P < 0.001$), showing that crown centers were more regularly distributed than stem

bases. The $L(r)$ transformation for Ripley's K for crown centers and stem bases is depicted in Fig. 4. For distances up to 4.5 m (stems) and 9.6 m (crowns), $L(r)$-curves were significantly lower than 0, indicating regular patterns. As $L(r)$ for crowns was lower than for stem bases, crowns were more regularly distributed than stems over the observed radial distances.

Canopy cover of the projected crowns was 1.92 ha (68% of the sample plot), and cover of simulated circular crowns was 1.65 ha (59%). The difference of 0.27 ha was due to a reduction in crown overlap as a result of crown plasticity (Fig. 5).

Discussion

Crown displacement

In Serrahn, the crowns of the upper canopy beech trees showed a strong absolute displacement. The emergence of canopy gaps creates a spatially heterogeneous light environment. Because tree photomorphogenetic response due to phototrophic growth and correlative inhibition as well as wind caused crown abrasion, it is to be expected that trees in highly asymmetric neighborhoods show stronger crown displacement than trees from more symmetrical neighborhoods (Brisson 2001; Muth and Bazzaz 2003). In old-growth mixed hardwood forests in the southern Appalachians, individual American beech (*F. grandifolia* Erh.) trees extended branches into gaps by 11 cm year^{-1} over a 14-year period (and by as much as 17.4 cm year^{-1} in the first 7 years after gap creation; Runkle 1998). In a mature beech forest in southern Germany, a significant difference between the length increment of gap branches and non–gap branches (9.2 and 6.2 cm year^{-1}, respectively) was found (Haywood 2002). In addition to length increment of branches, crown expansion might also result from lowering the branch angles. In three mature beech forest reserves in central Germany, the rate of gap closure by lateral crown extension ranged from 7.4 to 14.4 cm year^{-1} (Meyer and
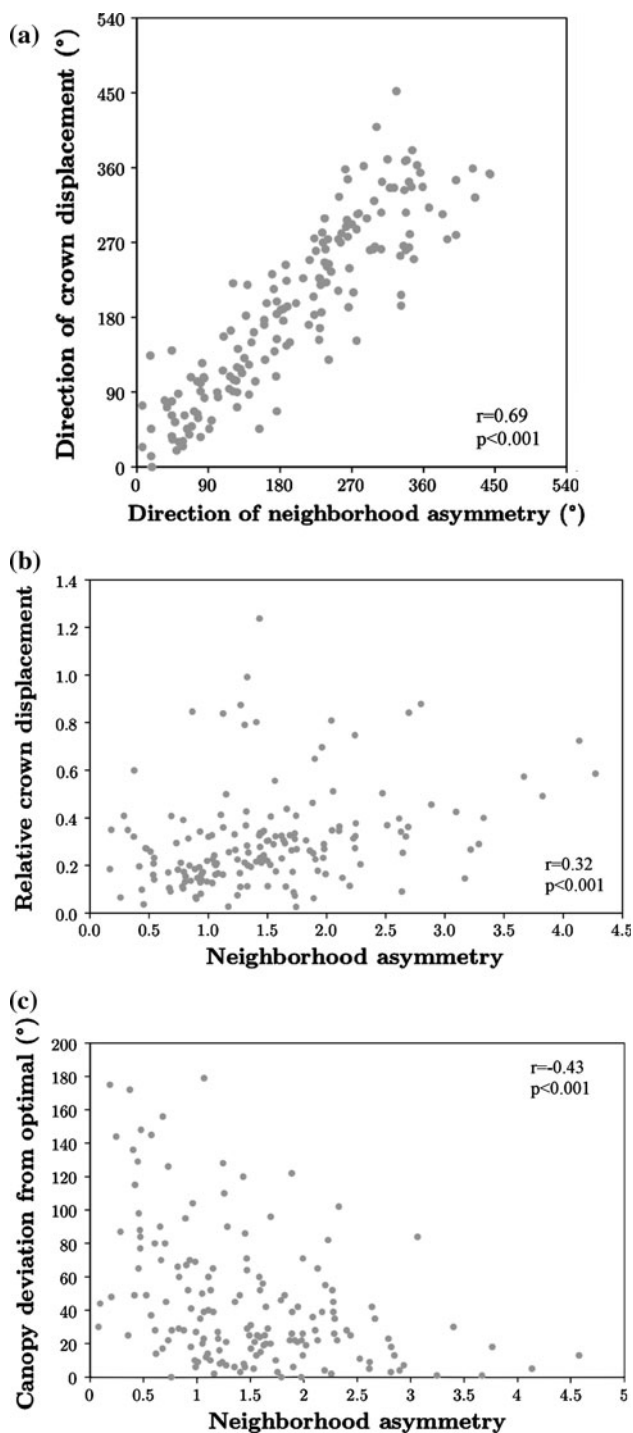
Fig. 3 a Direction of neighborhood asymmetry versus direction of crown displacement (neighborhood asymmetry calculated including all neighbors within a radial distance of 12 m and using the importance value basal area $\times$ distance^{-1}). To graphically represent this correlation, one of the angles was increased by 360° when the difference between a pair was higher than 180°. **b** Regression of relative crown displacement against neighborhood asymmetry (vector lengths) for the highest correlation (radial distance 12 m; importance value, crown area $\times$ distance^{-1}). **c** Regression of canopy deviation from optimal against vector lengths of neighborhood asymmetry (radial distance 14 m; importance value, crown area $\times$ distance^{-1})

Ackermann [2005]). Given these rates, a directional lateral crown expansion of 2 m into a gap can, thus, be achieved within 20 years, with the result that asymmetric crowns can be built.

Absolute and relative displacement have not yet been determined for European beech in other studies. However, the mean relative displacement value found in our study (0.37) is generally within the range of values observed in other forest types. In two thinned stands of 118-year-old sessile oak (*Quercus petraea*) in southwest Germany, relative displacement values were 0.26 and 0.30, respectively (Longuetaud et al. [2008]). However, in a third stand that had not been thinned for about 50 years, the mean relative displacement value was considerably higher (0.49). Following the changes in relative displacement over a time period of 27 years in this stand, a strong decrease was found (from 0.78 to 0.49), indicating a trend toward more symmetrical crowns over time (Longuetaud et al. [2008]). In a sugar maple (*Acer saccharum* Marsh.)-dominated temperate hardwood forest, the relative displacement with respect to four different neighborhood contexts was evaluated (Brisson [2001]). Values obtained for trees surrounded by neighbors as well as for trees at the edge of recently created gaps were 0.28 and 0.29, respectively. By contrast, isolated trees growing in the open had very low relative displacement values (0.18), and trees growing at the forest edge had high values (0.62). In a mature hemlock-white pine-northern hardwood forest, relative displacement values were 0.35 and 0.36 for the whole stand and for gap-edge trees, respectively (Muth and Bazzaz [2002], [2003]). In the eastern part of our sample plot, there is a relatively large gap created by a windthrow event in the late 1960s or early 1970s. Along the gap edge, it is possible to identify several gap-edge trees, the vast majority of which show strong relative displacement. However, in the northern part of this gap as well as in most other parts of the sample plot, it was not possible to clearly define gap-edge trees because either the tree crowns were directly adjacent to more than one gap or it was not possible to delineate the canopy gaps due to their complex structure. Hence, it was not meaningful to differentiate between gap-edge trees and non-gap-edge trees in the present study. Our comparison with relative displacement values of other studies showed that crown plasticity of beech measured in this way was on average (gap-edge and non-gap-edge trees) not exceptionally large.
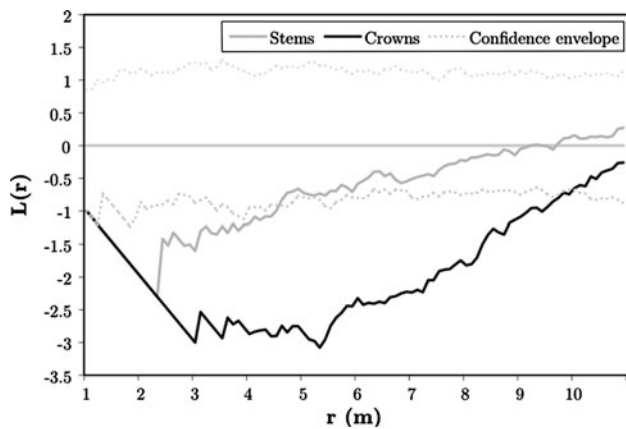
Plastic response to neighborhood asymmetry

In Serrahn, we found a high positive correlation between the direction of neighborhood asymmetry and the direction of crown displacement, indicating that beech crowns were displaced away from their neighbors and that they, thus,

Table 2 Pearson's correlation coefficient between vector lengths of neighborhood asymmetry and (a) relative canopy displacement and (b) canopy deviation from optimal
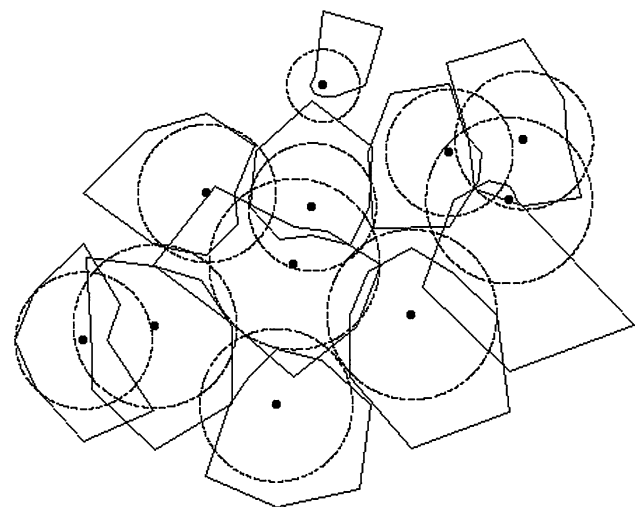
Importance value	Nearest neighbor	Radial distance			
		8 m	10 m	12 m	14 m
(a)					
Importance value = 1	0.00 ns	0.12ns	0.13ns	0.09ns	0.11ns
Distance^{-1}	0.30***	0.21*	0.26***	0.28***	0.29***
Crown area × distance^{-1}	0.28***	0.26**	0.27***	0.32***	0.32***
Basal area × distance^{-1}	0.20**	0.18*	0.17*	0.22**	0.24**
(b)					
Importance value = 1	0.00ns	−0.27***	−0.21**	−0.29***	−0.33***
Distance^{-1}	−0.05ns	−0.25**	−0.16*	−0.31***	−0.34***
Crown area × distance^{-1}	−0.16*	−0.21*	−0.32***	−0.37***	−0.43***
Basal area × distance^{-1}	−0.21**	−0.21*	−0.33***	−0.35***	−0.37***

Neighborhood asymmetry was calculated for the nearest neighbor and for all neighboring trees within different radial distances and with different importance values. *ns* not significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Fig. 4 $L(r)$-function over r (distance) for stems and crowns with a confidence envelope of 99.9%

Fig. 5 Simulated circular crowns (*dashed lines*), projected crowns (*continuous lines*), and corresponding stem bases (*dots*) of an exemplary group of beech trees. Canopy cover of projected crowns is higher due to a reduction in crown overlap

actively forage for light and avoid crown competition. However, from our analyses, it becomes obvious that the approach to identifying potential competitors as well as the selection of the importance value is of great importance. The nearest neighbor approach always yielded the lowest correlation coefficients. The highest correlation coefficients were obtained within a radial distance of 12 m if size variables (basal area, crown area) and distances to neighboring trees were considered as importance values. However, including solely the distance yielded only slightly lower correlation coefficients. Finally, when setting the importance value to 1, i.e., only the position of the neighboring trees is included, we still obtained high correlation coefficients. This indicates that the direction of crown displacement of the target tree is explained in particular by the position of neighboring trees; distance is the next most important factor, whereas neighbor tree size is of minor importance.

Generally, the correlation coefficients obtained in our study were well above those found in other studies using a similar approach of neighborhood asymmetry analysis. Brisson (2001) considered only those canopy trees as neighbors whose crowns were immediately adjacent to the crown of the target tree and found significant circular–circular correlation coefficients ranging from 0.19 to 0.47. In a mature mixed hardwood stand at Harvard Forest, Muth and Bazzaz (2003) found significant correlation coefficients ranging from 0.19 to 0.33. The authors identified all neighbors within an 8-m radial distance and used six different importance values. Correlations were maximal when using basal area and crown area as importance values. In a natural mature *Pinus sylvestris* forest, Rouvinen and

Kuuluvainen ([1997](#)) observed correlation coefficients ranging between 0.28 and 0.47, using a radial distance of 5 m for the selection of neighbors. Correlation coefficients were lowest when only tree positions were considered, while r was maximal when using DBH weighted by distance as the importance value. In the Serrahn beech forests, correlation coefficients between vector lengths of neighborhood asymmetry and relative displacement as well as between vector lengths of neighborhood asymmetry and canopy deviation from optimal were also higher than for other tree species observed by similar studies (cf. Brisson [2001](#); Muth and Bazzaz [2003](#)). We suggest two possible explanations for these findings. First, beech trees may be characterized by considerably higher crown plasticity than other tree species, and, therefore, the response to neighborhood asymmetry may be stronger and more precise. This supports other observations of high phenotypic plasticity of European beech (Roloff [2001](#); Pretzsch and Schütze [2005](#), [2009](#)). Second, approaches to identifying potential competitors were different between studies. Brisson ([2001](#)) defined neighbors by means of immediate adjacency to target tree crowns, and Muth and Bazzaz ([2003](#)) and Rouvinen and Kuuluvainen ([1997](#)) took fixed radial distances of 8 and 5 m, respectively, whereas we tested a range of different radial distances. The correlation coefficients generally increased with radial distance, and maximum values were found at a radial distance of 12 to 14 m, which is considerably more than those distances used in the other studies. However, relevant scales at which neighborhood interactions may have an impact on tree growth increase with tree size, corresponding to the lateral extension of crowns and root systems (Puettmann et al. [2009](#)). The mean crown radii were about 4 and 1.4 m in the studies by Brisson ([2001](#)) and Rouvinen and Kuuluvainen ([1997](#)), respectively, which is considerably lower than the mean value observed in Serrahn (5.5 m). Thus, the large crown sizes of trees in our study justify the choice of larger radial distances, and a radial distance of 12 m (i.e., about 2.2 times the mean crown radius) seems to be appropriate to select competitors for light in the canopy in old-growth European beech forests. We conclude that the use of relatively low radial distances to select neighbors in the cited studies is not the primary cause of the observed differences in the correlation coefficients.

The impact of other factors on crown development

Although correlation coefficients were higher than those found in the previous studies, there was still a quite high unexplained variation in our results. This may be related to several factors, which can generally be internal, as, e.g., genetic costs or developmental constraints, or external, i.e., ecological costs and limits (Valladares et al. [2007](#)).

Concerning the specific design of our study, the three dimensional structure of tree crowns was not taken into account. However, this might be of minor importance in Serrahn, since the neighborhood asymmetry analyses demonstrated that position and distance of neighboring trees were more important than neighboring tree size. More importantly, current tree crowns are also a result of past interactions and thus mirror a tree's long-term response to neighbor competition (Oliver and Larson [1996](#); Pretzsch [2009](#)). As a consequence, current crown dimensions not always reflect tree interactions of the recent past. The effect of crown abrasion, which might also influence crown form, was not studied here. Finally, we tested for the influence of local slope inclination on crown displacement, because the shape of tree crowns has often been found to expand in a downhill direction (Umeki [1995a](#); Getzin and Wiegand [2007](#); Lang et al. [2010](#)). For example, in a warm temperate mixed slope forest in Japan, the crown vector was a function of both the position and size of neighbors as well as of slope inclination (Umeki [1995a](#)). In Serrahn, slope only had a marginal effect on crown displacement when compared to neighborhood interaction. This is because the majority of trees are located on level ground, and the slope inclination is low to moderate.

Spatial patterns and canopy cover

The spatial pattern of beech stems in our sample plot was regular. An increasing regularity over time has been observed in other forest stands (Gavrikov et al. [1993](#); Oliver and Larson [1996](#); Longuetaud et al. [2008](#)). We also found that crowns were more regularly distributed than stems as a result of the high crown plasticity. We conclude that crown displacement led to regular patterns of crowns up to a distance of 9.6 m from a crown center. Crown plasticity thus allows for more efficient use of growing space. This process has also been observed by Ishizuka ([1984](#)), Gavrikov et al. ([1993](#)), and Longuetaud et al. ([2008](#)).

More effective exploitation of growing space due to crown plasticity was also shown by a comparison between measured crown projections and simulated circular areas. Canopy cover of the projected polygons was almost 10% higher than the cover of simulated circular crowns. Longuetaud et al. ([2008](#)), applying the same approach, found an increase over time in the difference between actual measurements and simulated circular crowns for two thinned sessile oak stands. In the two 91-year old stands, actual crown projections were 1.7 and 1.6% higher than simulated projections, and 27 years later differences increased to 5.2 and 3.1%, respectively. The difference in canopy cover in the old-growth Serrahn beech forests was notably higher. There may be several reasons for this: First,

beech has higher crown plasticity than sessile oak and is, thus, able to avoid crown overlap more effectively. Second, since differences are age-related, the pattern can be partly explained by the age difference between the oak stands studied by Longuetaud et al. (2008) and the old-growth beech forest of our study, under the assumption that the differences continue to increase with age over a longer time period. Third, differences between measured and simulated circular crown areas may be density dependent, with higher densities resulting in higher canopy cover along with higher crown plasticity. Because the plots studied by Longuetaud et al. (2008) had higher stem density, but similar canopy cover compared to our sample plot (138 and 200 stems ha^{-1} and canopy cover of 69 and 64% in the two oak stands, 84 stems ha^{-1} and 68% in Serrahn), we conclude that the density effect does not explain why the present crown cover in Serrahn is notably higher than the simulated crown projection. Instead, it can be considered a further indication of the high crown plasticity of European beech.

In summary, we observed a high morphological plasticity of beech trees even at older ages. This plasticity allows for a reduction in intraspecific competition, an optimal resource exploitation as regards light, and a minimization of crown abrasion and thus gives the potential to maintain high stand productivity. Whether increased crown asymmetry may also come at a cost because it reduces individual-tree stability (according to Young and Perkocha (1994), more asymmetrical trees are more likely to fall than less asymmetrical trees in a tropical broad-leaved forest), remains to be studied in old-growth beech forests. Furthermore, it should be tested to what extent the methods used here are applicable to multilayered stands or mixed forests.

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