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Scale-dependent competition at the stand level assessed from crown areas

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Abstract

The detection and quantification of competition at the stand level is important in forest management because competition reduces growth and increases the risk of mortality. This is of interest for timber production where efficient tools of forest inventory are increasingly demanded. Especially modern planning of thinning based on aerial or satellite images requires a deeper and spatially explicit understanding of the growth dynamics of tree crowns relative to the dynamics of stems.

Past studies have evaluated competition in forests with scale-dependent correlation functions applied to tree-size attributes (continuous marks) such as diameter at breast height (DBH) or tree height. Despite the fast reaction of foliage to changes of neighborhood density in the canopy, horizontal crown extent has apparently not been used in such competition analyses of marked point patterns. Here we investigated in a spatially explicit approach the formation of crown-size patterns under neighborhood competition. We also compared how mutual growth reduction in reaction to competition differs between crown extent and stem diameters. This response of tree-size attributes to competition was analyzed with the scale-dependent mark-correlation function (MCF) applied to the marks 'DBH', 'crown area' of all live trees, and 'upper crown area' of overstory trees. These analyses were conducted for two deciduous and two coniferous forests in central Germany.

Unlike stem diameters, crown areas were very sensitive for the detection of competition in stands. In relation to 'crown area' of all trees in a plot, this sensitivity was greater when only the mark 'upper crown area' of overstory trees was analyzed because both the strength and the spatial range of negative size correlation increased. Upper crown areas showed a finite range of negative interaction of about 6 m.

These results demonstrate that (1) the 'functional growing space' of large and light-exposed canopy trees is highly suitable to detect competition and (2) the spatial range and strength of competition can be assessed and differentiated between stands in a spatially explicit manner. Our application may have practical value for monitoring competition based on remotely sensed forest inventory because upper crown areas as seen by the 'bird-eye's view' were most sensitive for detecting competition in stands.

Keywords: Competition; Crown area; Douglas-fir; Mark-correlation function; Remote sensing; Spatial scale

1. Introduction

There is a growing interest in the scale-dependent analysis of spatial forest dynamics and tree patterns at the stand level (Stoyan and Penttinen, 2000; Pommerening, 2002). While stem-base positions have been frequently used to study the spatial dynamics of forest stands, more recently, large-scale spatial data acquisition based on remotely sensed images has revolutionized forest inventory (Gougeon, 1995; Nelson et al., 2002; Wulder et al., 2006; Atkinson et al., 2007). Hence, there is a growing demand to understand and evaluate forest stand dynamics based on tree-crown patterns as seen by the 'real bird eye's view'. Particularly, the detection and evaluation of competition processes is of major interest to forestry researchers, and indeed the industry, because competition reduces growth or enhances the risk of mortality.

Point pattern analyses of tree positions are modern tools to quantify spatial stand dynamics. With a focus on larger scales,

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such methods may be used to study natural distribution patterns of trees and their spatial variation due to specific seed dispersal kernels or habitat associations of species (Wiegand et al., 2007). In contrast, if the focus of interest is on direct competitive effects between trees, fine-scale interaction patterns need to be studied (Getzin et al., 2006). In northern forests, such interaction patterns of trees are usually correlated up to a maximal radius of 10 m (Stoyan and Penttinen, 2000) and 6–7 m have been observed as finite range of competitive tree interaction in middle European forests (Parrott and Lange, 2004; Schlather et al., 2004).

At the stand level, competition can be detected via increased inter-tree distances due to natural thinning (Perry et al., 2006). In this case, the competitive forces must be strong enough or must have worked long enough to cause mortality and thus, more regular tree patterns than predicted by the random mortality hypothesis (Kenkel, 1988). However, distance alone is frequently not suitable to detect competition via regularization processes because changes in neighborhood densities may be compensated by variable growth rates and modular plasticity (Shi and Zhang, 2003). Furthermore, the formation of more regular tree patterns can be prevented by clonal regeneration modes (Peterson and Squiers, 1995), clumped seed dispersal (Nathan and Muller-Landau, 2000), or a spatially patchy distribution of cohorts (Dovčiak et al., 2001). In managed forests, a regular trunk pattern may also just reflect a man-made planting scheme. Even if in this case the more dynamic crown centroids instead of the regular trunk distributions are used to analyze competition via inter-tree distances, random and not regular crown patterns may dominate and thus mask competitive interaction (Koukoulas and Blackburn, 2005; Getzin and Wiegand, 2007).

A more promising approach in such competition analyses is to complement tree position by quantitative size attributes (continuous marks), i.e. to use marked point patterns (Parrott and Lange, 2004; Schlather et al., 2004). Correlation between the marks at different points conditional on the inter-point distances characterizes negative or positive relations between plants. Continuous marks such as diameter at breast height or tree height have been used successfully to quantify the range of spatial scales of competition for genuine point locations in forests, and involving methods such as the mark-correlation function, weighted Ripley's K-function, or spatial autocorrelation (e.g. Penttinen et al., 1992; Capobianco and Renshaw, 1998; Mateu et al., 1998; Wells and Getis, 1999; Pommerening, 2002; Shi and Zhang, 2003; Doležal et al., 2006). Such spatially explicit assessments of competition are particularly successful because both the strength and the spatial range of competition are highly dependent on tree size and thus change with stand maturation over time (Moravie and Robert, 2003).

Spatially explicit competition analyses should be particularly suitable for the study of forest canopies because competition for light directly affects the horizontal growing space of neighboring trees (Popescu et al., 2003; Wyckoff and Clark, 2005). Larger trees are more efficient than small trees in utilizing available space by laterally expanding their crowns over larger distances into new tree-fall gaps (Hamilton, 1969; Rouvinen and Kuuluvainen, 1997). This spatio-temporal competition process fully benefits the size increment of dominant trees with above-average crown areas because their carbon production may be as much as five times greater than that of small trees with more shaded branches (Lebaube et al., 2000). In contrast, the less efficient suppressed trees have to remain in unfavorable dense neighborhoods and eventually die.

So far, horizontal crown extent has been analyzed with competition indices in a local (e.g. Biging and Dobbertin, 1992, 1995; Rouvinen and Kuuluvainen, 1997; Ledermann and Stage, 2001) but not in a spatially explicit approach. The latter entails the quantification of competition for a continuous range of scales. Here, we propose to evaluate scale-dependent competition via correlation of horizontal crown extent. More specifically, we will apply the mark-correlation function using the attribute 'crown area' because foliage reacts faster than stem size to gap dynamics or limiting changes in the local neighborhood (Rudnicki et al., 2003; Grote and Reiter, 2004). Therefore, mutual growth reduction under competition should be easily recognizable via the spatial range and the strength of negative correlation in crown area (Wyckoff and Clark, 2005; Weiskittel et al., 2007). The proposed application of the mark-correlation function to crown areas may have considerable potential for the large-scale monitoring of forest stands using high-resolution satellite images (Gougeon, 1995; Leckie et al., 2003; Wang et al., 2004). We therefore also analyze the correlation of the mark 'upper crown area' of overstory trees.

To sum up, we introduce the use of the mark-correlation function to quantify scale-dependent competition via crown areas. The suitability of this method will be contrasted to an equivalent correlation analysis of stem-size patterns. The study is based on four forest stands in central Germany with deciduous and coniferous tree species.

2. Materials and methods

2.1. Study areas

Two of the study plots with deciduous trees are on calcareous soils and moderate slopes 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). The plot is dominated by *ca.* 50-year-old common ash (*Fraxinus excelsior* L.; 48% of live trees) and less numerous wild cherry (*Prunus avium* L.; 18%). Less common species in P1 include hornbeam (*Carpinus betulus* L.; 11%) or sycamore maple (*Acer pseudoplatanus* L.; 10%). Stand density in P1 is 815 trees/ha. All species in P1 have been naturally regenerated. Plot 2 (P2) is close to the city of Jena (50°57′N, 11°39′E). It is a coppice 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 in P2 were

European cornel (*Cornus mas* L.; 15%) and field maple (*Acer campestre* L.; 8%). Stand density in P2 is 2459 trees/ha.

The two study plots with coniferous trees, in the Thuringian Forest, were on acidic soils and moderate slopes with an annual precipitation ranging between 900 and 1100 mm. Plot 3 (P3) is located at 50°33′N, 10°45′E. It is dominated by Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* [Mirb.] Franco; 71%) and common spruce (*Picea abies* [L.] Karst.; 29%). *P. menziesii* is a fast growing timber species and was introduced to Germany in the 1870s. In Plot 3, it was planted in a regular grid some 50 years ago along with spruce in irregular groups. Stand density in P3 was 953 trees/ha. This plot had not been thinned during the last four decades. Plot 4 (P4) is located at 50°36′N, 10°32′E. It is a monoculture of *P. menziesii* planted in a regular grid around 40 years ago. Stand density in P4 is 2632 trees/ha. All four plots have not been thinned for several decades. Additional information on the plots can be found in Getzin and Wiegand (2007).

2.2. Field measurements

Field data were collected in the summer of 2004. For each plot, a rectangle was established and adjusted in dimension to include at least 100 live and dead trees with a diameter at breast height (DBH) of $\geq$4 cm at 1.4 m above ground. Since the 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 $\geq$ 4 cm were mapped using a laser-based rangefinder (Leica DISTO$^{\text{TM}}$ classic 5) and the 'Interpoint method' of Boose et al. (1998). Smaller trees or seedlings were not recorded. DBH, tree height (TH), and status (live/dead) were recorded and individuals identified to species. If trees had only very few remains of green foliage, they were considered to be dead. 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 the distance of the perpendicular of its tip to the trunk was measured with the rangefinder and the exact angle of that branch relative to north recorded. We determined the vertical projections from branch tips to the ground without technical aid. However, determination of the crown centre and of crown area (CA) 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 (CR).

2.3. Correlation between tree-size attributes and analysis of scale-dependent competition

To get more insights into mutual growth reduction in different stands and associated differences for the marks 'DBH' and 'crown area', we analyzed the correlation between these two size attributes using standard linear regression fits.

We applied the mark-correlation function (MCF) at first conventionally to the mark 'DBH' based on trunk locations, then to crown areas based on the location of crown centroids in the four plots. These interaction patterns of crown areas were studied in two separate analyses. (1) We first used all live trees in a plot and analyzed the spatial correlation of the mark 'crown area'. (2) Afterwards, we analyzed the correlation of only 'upper crown area' to separate overstory trees from the three-dimensional canopy layer. We classified all those crowns as 'upper crown area' whose height exceeded two thirds of the mean of the 10 highest trees in a plot (approach as in Getzin and Wiegand, 2007).

The MCF of a marked point process is a measure of the dependence between the marks of two points of the process a distance *r* apart. From the quantitative marks m_1 and m_2 a value is calculated from which the similarity or dissimilarity of the tree's marks is assessed. This relationship is quantified by $f(m_1,m_2)$ where f is defined as $f(m_1,m_2) = m_1 \times m_2$ for quantitative marks. The mean value in the case of f, $k_f(r)$ is often normalized by division by the squared mean mark μ^2 of the variable in the plot, which yields the mark-correlation function $\kappa_{\text{mm}}(r)$ (details in Stoyan and Stoyan, 1994). If $\kappa_{\text{mm}}(r) = 1$, marks are independent at scales *r*, if $\kappa_{\text{mm}}(r) < 1$, there is negative correlation between the marks at scale *r*. Thus, the mark-correlation function is similar to the pair-correlation function $g(r)$ but the MCF investigates the size-correlation and not solely the distance-correlation at radius *r*. Significant departure from independence of the marks was estimated based on approximately 95% confidence limits, determined using the 5th-lowest and 5th-highest value of 199 Monte Carlo simulations. Note that this is not a goodness-of-fit test with exact confidence limits but Monte Carlo tests are well suited to this purpose (Stoyan and Stoyan, 1994, pp. 300–302). All analyses were performed using *R*-software (package Spatstat; http://www.R-project.org/).

Table 1
Average values for diameter at breast height, crown radius, tree height, and percentage mortality of the most abundant tree species in the four plots

Plot	P1		P2		P3		P4
Species	*P. avium*	*F. excelsior*	*S. torminalis*	*Q. petraea*	*P. menziesii*	*P. abies*	*P. menziesii*
Attributes							
⟨DBH⟩ (cm)	19.9	25.6***	11.6	19.7***	33.9	25.1**	25.1
⟨CR⟩ (m)	1.4	2.4***	1.2	1.3	2.0	1.2***	1.1
⟨TH⟩ (m)	20.2	25.4***	7.5	10.3***	26.1	21.1**	25.7
Mortality (%)	17.4	0.0	7.5	27.5	12.9	50.0	59.0

Differences between the average ⟨ ⟩ diameter at breast height (DBH), crown radius (CR), and tree height (TH) of live trees within a plot were tested for significance using a *t*-test for independent samples. Significance levels are $^{*}p < 0.05$, $^{**}p < 0.01$ and $^{***}p < 0.001$.

3. Results

In all three plots (P1–P3) containing several species, within-plot analysis showed that the two most abundant tree species differed significantly in tree height. Both tallest and largest trees (in terms of DBH) occurred in P3. Mortality was lowest in P1 but highest in P4 (Table 1).

Correlations between crown area and DBH were low for the two deciduous stands P1 and P2. Coefficients of determination were 0.11 and 0.09, respectively (Fig. 1). Correlations between these two size attributes were higher in the mixed coniferous stand P3 ($r^2 = 0.61$) and highest in the Douglas-fir stand P4 ($r^2 = 0.77$).

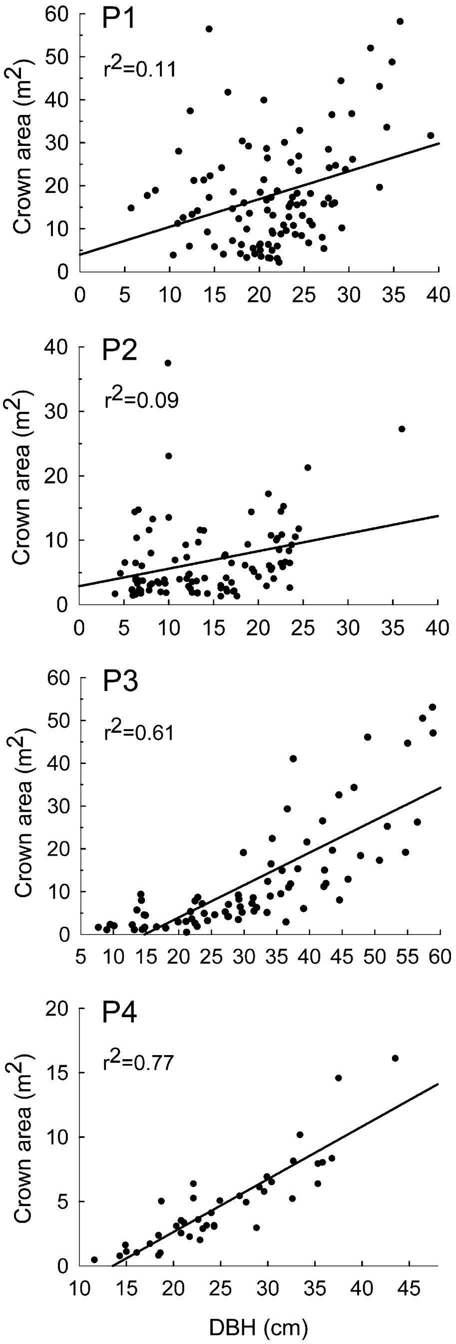

Fig. 1. Linear regressions for size attributes of stems and crowns. Correlation between 'crown area' and 'diameter at breast height' (DBH) for trees of deciduous stands (P1, P2) and coniferous stands (P3, P4). The r^2 and solid line show the standard linear regression fit based on the mean in the distribution of crown areas.

3.1. Analysis of scale-dependent competition in stands

Competition could not be detected for the stands P1, P2, and P3 when the mark-correlation function was applied to the mark 'DBH' because data of stem-size were uncorrelated at all scales (Fig. 2). However, for the high-density stand P4 the MCF detected strong inter-tree competition because DBH was significantly negatively correlated at scales up to $r = 1.8$ m (Fig. 2).

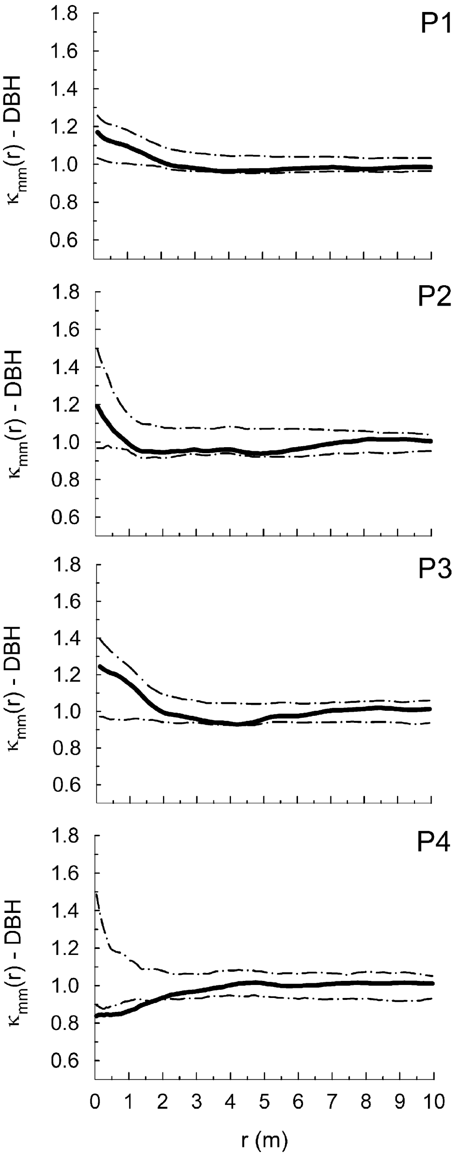

Fig. 2. The mark-correlation function applied to DBH. The mark-correlation function $\kappa_{\mathrm{mm}}(r)$ for the mark 'DBH' of deciduous stands (P1, P2) and coniferous stands (P3, P4). Values of $\kappa_{\mathrm{mm}} < 1$ indicate negative correlation between the marks at inter-tree distance r (stem-base positions). Negative correlation is significant if κ_{mm} (solid line) is below the lower 95% approximated confidence limit (broken line).

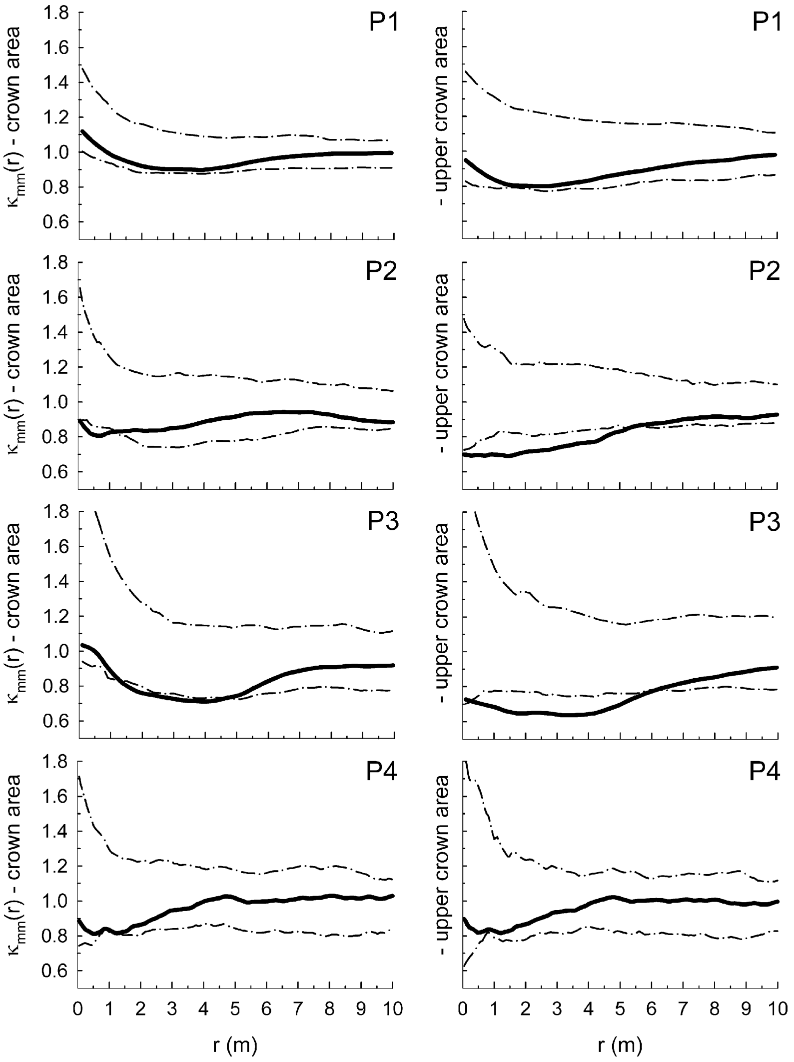

Fig. 3. The mark-correlation function applied to crown areas. The mark-correlation function $\kappa_{mm}(r)$ for the field-measured marks 'crown area' (left) and 'upper crown area' (right) of deciduous stands (P1, P2) and coniferous stands (P3, P4). Values of $\kappa_{mm} < 1$ indicate negative correlation between the marks at inter-tree distance r (crown centroids). Negative correlation is significant if κ_{mm} (solid line) is below the lower 95% approximated confidence limit (broken line).

For field-measured crown extent in the low-density deciduous stand P1, the mark-correlation function showed independence of the marks 'crown area' and 'upper crown area' at all spatial scales (Fig. 3). For the high-density deciduous stand P2, 'crown area' was significantly negatively correlated at scales between $r = 0.1$ and $r = 1.2$ m, indicating growth reduction under competition at small scales. 'Upper crown area' of overstory trees in P2 showed stronger mutual growth reduction with negatively correlated marks up to $r = 5.6$ m (Fig. 3). For the coniferous stand P3, 'crown area' of all trees was marginally negatively correlated at larger scales between $r = 1.3$ m and $r = 4.6$ m. Unlike for all tree crowns in the plot, the significant negative correlation was stronger for 'upper crown area' of overstory trees and the spatial range of this negative correlation was greater, extending from scales $r = 0.3$ m to $r = 6.1$ m (Fig. 3). In P4 comprising only Douglas-fir, 'crown area' was uncorrelated at nearly all scales. Only at scale $r = 1.2$ m was there a marginally significant negative correlation. This correlation was not significant for 'upper crown area' (Fig. 3).

4. Discussion

Forest scientists have highlighted the advantages of modern spatial correlation functions over structural indices (Stoyan and Penttinen, 2000; Pommerening, 2002). Structural indices consider influences just from nearest neighboring trees, although direct competitive effects may extend to scales far beyond the nearest neighbors (Stoyan and Penttinen, 2000; Perry et al., 2006). Even if a competition index based on crown size comprises a pre-defined search radius to determine competitors beyond the nearest neighbors, "it is difficult, if not impossible, to define an exact zone of influence" (Biging and Dobbertin, 1995). For competition indices, Biging and Dobbertin (1995) therefore concluded that expanding the neighborhood zone of influence is more important than the exact location of the nearest neighboring trees. The applied mark-correlation function takes advantage of both because it considers (a) exact locations of tree-size attributes for (b) all possible (continuous) scales of mutual growth reduction. It thereby combines properties of distance-dependent and distance-independent (stand-average) competition measures. Here, we investigated the suitability of crown areas for the spatially explicit detection of competition and how crown areas respond to neighborhood suppression in stands relative to the response of stem diameters.

For our field-measured deciduous stand P1, the MCF shows at all spatial scales no negative correlation of 'DBH', 'crown area' or 'upper crown area' of overstory trees. This independent distribution of all three size attributes in P1 was mainly due to the relatively low tree density and thus due to overall low competition in the stand. Such independence can additionally arise as a result of the distinct vertical partitioning of the canopy layer where dominating ash occupied the upper part and sub-dominant and suppressed species such as wild cherry or sycamore maple occupied the lower part of the two-tier canopy (Kerr, 2004). For similar growth conditions in central Germany, it has been shown that common ash achieves its greatest horizontal crown extent higher than other species, at more than 80% of its tree height (Frech et al., 2003). We assume that this fact and the rather low density of dominant ash accounts for the uncorrelated crown areas. Zero mortality of ash (Table 1) supports the notion that these overstory trees experienced very low competition in the canopy. The weak correlation between 'crown area' and 'DBH' in P1, as also in P2, is probably due to the greater crown plasticity of deciduous trees relative to coniferous trees (Umeki, 1995; Pretzsch and Schütze, 2005; Getzin and Wiegand, 2007) and also because of the different species involved in the stands.

Competition in the high-density stand P2 was strong, as can be seen by the MCF showing strong negative correlations of 'crown area' and also 'upper crown area'. In a previous analysis, this high-density stand P2 showed density-dependent self-thinning via small-scale regularity of tree trunks (Getzin and Wiegand, 2007). In this previous study using only the pair-correlation function, the solely distance-dependent patterns of crowns and upper crowns were random at all scales and thus did not reflect competition. In the present study, we demonstrate the sensitivity of analyzing distance-dependent crown-size patterns because crown areas conditional on the inter-tree distances were significantly negatively correlated in P2. Especially, when we analyzed 'upper crown area' separately for overstory trees, the strength and spatial range of negative correlation both became greater. For mutual growth reduction, the crown areas of overstory trees appear very useful to detect competition because the taller trees are more directly exposed to sunlight and thus they compete more directly for the same horizontal space in the canopy (Wyckoff and Clark, 2005). Thereby, the crown-size pattern of overstory trees reflects their 'functional growing space' and overall stand dynamics because most of the exchanges of mass and energy take place in the upper part of the canopy (Lebaube et al., 2000; Popescu et al., 2003).

In P2, it was mainly the larger and taller *Q. petraea* that competed with each other at greater scales in the canopy, leading to a mortality of around 28% (Table 1). For *Q. petraea* it is known that, especially under environmental stress, shoot shedding negatively affects its crown extent after this species has reached dominant size classes (Buck-Sorlin and Bell, 2000). This probably explains the stronger and more wide-ranging negative correlation for 'upper crown area' in P2. We assume that the smaller range of negative correlation of 'crown area' for all trees in the plot, including all the smaller *S. torminalis*, was mainly attributed to the shade-tolerance and extreme phototrophic crown development of this latter species. It is important to consider such species-specific crown plasticities for the interpretation of MCF results because the mark 'crown area' averages across all species within a stand.

In contrast to the crown areas, the stem diameters were not negatively correlated in P2. This is an interesting result because it shows that even in a mixed deciduous stand where size patterns are analyzed across different species, crown areas appear more sensitive to scale-dependent competition. Similar findings are also true for the mixed coniferous stand P3, where the stem-size patterns were uncorrelated but the crown areas were negatively correlated due to competition.

In the coniferous stand P3, mutual growth reduction worked up to largest scales of all four plots because this stand was mainly dominated by big trees with the largest DBH of all four plots. Hence the spatial range of horizontal and vertical influence from competitor trees was largest. As in Plot 2, overstory trees of P3 showed stronger negative correlation of 'upper crown area' than when all trees were included. Also, the spatial range of competition was greater for overstory trees, leading to negative correlation up to more than 6 m. This strong size reduction for overstory tree crowns was mainly attributed to the dominance of large Douglas-fir in the upper canopy that mutually restricted their crown areas under competition (Weiskittel et al., 2007). In contrast, the weaker negative correlation of 'crown area' for all trees in the plot, including all the smaller *Picea abies*, was likely attributed to the pillar-like crowns of spruce (Pretzsch and Schütze, 2005).

In the monoculture of P4, 'crown area' was only marginally negatively correlated at scale $r = 1.2$ m but otherwise it was uncorrelated. For 'upper crown area' it was uncorrelated. As for P2 and P3, we would have expected stronger negative correlation for 'upper crown area' of overstory trees but this Douglas-fir plantation was a special case. For this instable and dense stand with slender trees and a high mortality of almost 60%, Getzin and Wiegand (2007) found the phenomenon of mutual crown support where trees stabilized themselves (Rudnicki et al., 2003). This mechanism was observed in 2004 because after self-thinning and the extreme summer drought in 2003, large gaps emerged and the weakened trees bent with their crowns towards their neighbors. As a consequence of this relaxation in the canopy layer crown areas were predominantly uncorrelated with only marginally significant negative correlation at scale $r = 1.2$ m. Hence, at the year of census in 2004, crowns of this dense Douglas-fir plantation showed relatively unusual spatial dynamics. However, an additional analysis of this stand, using photogrammetric segmentation of crown surface areas based on orthophotos from the years 2002 and 2005 (see Supplementary data, Appendix A), has shown that competition in the Douglas-fir stand has been very intense prior to self-thinning in 2003.

Overall, we have shown the usefulness of fast reacting foliage and the mark 'crown area' for the detection of competition and that lateral crown extent appears more sensitive to neighborhood suppression than the less dynamic stem diameters (see also Weiskittel et al., 2007). The advantage of the MCF applied to crown areas is that differences in competition between stands or between time intervals will be accurately assessed via both the strength and the spatial range of negative correlation of the mark. Viewed in combination, both statistical properties may allow tracing even subtleties in competitive change.

While field-measured crown projection area allows for more crown overlap, photogrammetric segmentation of crown surface area can have great potential for monitoring competition in stands based on remotely sensed images. This is because photo-derived crown extent as seen by the 'bird eye's view' better correlates with actual tree and stand volumes than field-measured crown extent, since the former is a measure of the tree's 'functional growing space' (Popescu et al., 2003; Wyckoff and Clark, 2005). However, for such future monitoring applications, we need research showing how remote sensing products can best be used to address these questions.

In conclusion, we have shown that the dynamic crown areas reflect competitive interaction better than the less flexible stem diameters. The MCF detects competition solely via mutual growth reduction relative to the mean crown area of the stand and thus even under highly symmetric competition as is often typical for plantations with even-aged trees. Since the MCF uses the average mark 'crown area' for the whole stand, it can be of particular value for monitoring plantations and well-managed/-planned forest compartments. For example, an exploratory development of a reference system to monitor competition via MCF-values for repeated snap-shot patterns of stands and between different stands would help in better planning of thinning intensity (Pommerening, 2002). A reference system for MCF-values should be ideally compared between stands of the same species or the same species mixture because crown allometries of species vary with their differential ability of space occupation versus space exploitation (Pretzsch and Schütze, 2005). Therefore, we encourage similar applications of the mark-correlation function to test more in detail its applicability to remotely sensed monitoring of competitive dynamics in stands.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2008.01.007.

References

Atkinson, P.M., Foody, G.M., Gething, P.W., Mathur, A., Kelly, C.K., 2007. Investigating spatial structure in specific tree species in ancient semi-natural woodland using remote sensing and marked point pattern analysis. Ecography 30, 88–104.

Biging, G.S., Dobbertin, M., 1992. A comparison of distance-dependent competition measures for height and basal area growth of individual conifer trees. For. Sci. 38, 695–720.

Biging, G.S., Dobbertin, M., 1995. Evaluation of competition indices in individual tree growth models. For. Sci. 41, 360–377.

Boose, E.R., Boose, E.F., Lezberg, A.L., 1998. A practical method for mapping trees using distance measurements. Ecology 79, 819–827.

Buck-Sorlin, G.H., Bell, A.D., 2000. Crown architecture in *Quercus petraea* and *Q. robur*: the fate of buds and shoots in relation to age, position and environmental perturbation. Forestry 73, 331–349.

Capobianco, R., Renshaw, E., 1998. The autocovariance function for marked point processes: a comparison between two different approaches. Biom. J. 40, 431–446.

Doležal, J., Šrutek, M., Hara, T., Sumida, A., Penttilä, T., 2006. Neighborhood interactions influencing tree population dynamics in nonpyrogenous boreal forest in northern Finland. Plant Ecol. 185, 135–150.

Dovčiak, M., Frelich, L.E., Reich, P.B., 2001. Discordance in spatial patterns of white pine (*Pinus strobus*) size-classes in a patchy near-boreal forest. J. Ecol. 89, 280–291.

Frech, A., Leuschner, C., Hagemeier, M., Hölscher, D., 2003. Neighbor-dependent canopy dimensions of ash, hornbeam, and lime in a species-rich mixed forest (Hainich National Park, Thuringia). Forstw. Cbl. 122, 22–35.

Getzin, S., Dean, C., He, F., Trofymow, J.A., Wiegand, K., Wiegand, T., 2006. Spatial patterns and competition of tree species in a Douglas-fir chronosequence on Vancouver Island. Ecography 29, 671–682.

Getzin, S., Wiegand, K., 2007. Asymmetric tree growth at the stand level: random crown patterns and the response to slope. For. Ecol. Manage. 242, 165–174.

Gougeon, F.A., 1995. A crown-following approach to the automatic delineation of individual tree crowns in high spatial resolution aerial images. Can. J. Rem. Sens. 21, 274–284.

Grote, R., Reiter, I.M., 2004. Competition-dependent modelling of foliage biomass in forest stands. Trees 18, 596–607.

Hamilton, G.J., 1969. The dependence of volume increment of individual trees on dominance, crown dimensions, and competition. Forestry 42, 133–144.

Kenkel, N.C., 1988. Patterns of self-thinning in jack pine: testing the random mortality hypothesis. Ecology 69, 1017–1024.

Kerr, G., 2004. The growth and form of ash (*Fraxinus excelsior*) in mixture with cherry (*Prunus avium*), oak (*Quercus petraea* and *Quercus robur*), and beech (*Fagus sylvatica*). Can. J. For. Res. 34, 2340–2350.

Koukoulas, S., Blackburn, G.A., 2005. Spatial relationships between tree species and gap characteristics in broad-leaved deciduous woodland. J. Veg. Sci. 16, 587–596.

Lebaube, S., Le Goff, N., Ottorini, J.-M., Granier, A., 2000. Carbon balance and tree growth in a *Fagus sylvatica* stand. Ann. For. Sci. 57, 49–61.

Leckie, D.G., Gougeon, F.A., Walsworth, N., Paradine, D., 2003. Stand delineation and composition estimation using semi-automated individual tree crown analysis. Rem. Sens. Environ. 85, 355–369.

Ledermann, T., Stage, A.R., 2001. Effects of competitor spacing in individual-tree indices of competition. Can. J. For. Res. 31, 2143–2150.

Mateu, J., Usó, J.L., Montes, F., 1998. The spatial pattern of a forest ecosystem. Ecol. Model. 108, 163–174.

Moravie, M.-A., Robert, A., 2003. A model to assess relationships between forest dynamics and spatial structure. J. Veg. Sci. 14, 823–834.

Nathan, R., Muller-Landau, H.C., 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends Ecol. Evol. 15, 278–285.

Nelson, T., Niemann, K.O., Wulder, M.A., 2002. Spatial statistical techniques for aggregating point objects extracted from high spatial resolution remotely sensed imagery. J. Geograph. Syst. 4, 423–433.

Parrott, L., Lange, H., 2004. Use of interactive forest growth simulation to characterise spatial stand structure. For. Ecol. Manage. 194, 29–47.

Penttinen, A., Stoyan, D., Henttonen, H.M., 1992. Marked point processes in forest statistics. For. Sci. 38, 806–824.

Perry, G.L.W., Miller, B.P., Enright, N.J., 2006. A comparison of methods for the statistical analysis of spatial point patterns in plant ecology. Plant Ecol. 187, 59–82.

Peterson, C.J., Squiers, E.R., 1995. An unexpected change in spatial pattern across 10 years in an aspen-white-pine forest. J. Ecol. 83, 847–855.

Pommerening, A., 2002. Approaches to quantifying forest structures. Forestry 75, 305–324.

Popescu, S.C., Wynne, R.H., Nelson, R.F., 2003. Measuring individual tree crown diameter with lidar and assessing its influence on estimating forest volume and biomass. Can. J. Rem. Sens. 29, 564–577.

Pretzsch, H., Schütze, G., 2005. Crown allometry and growing space efficiency of Norway spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* L.) in pure and mixed stands. Plant Biol. 7, 628–639.

Rouvinen, S., Kuuluvainen, T., 1997. Structure and asymmetry of tree crowns in relation to local competition in a natural mature Scots pine forest. Can. J. For. Res. 27, 890–902.

Rudnicki, M., Lieffers, V.J., Silins, U., 2003. Stand structure governs the crown collisions of lodgepole pine. Can. J. For. Res. 33, 1238–1244.

Schlather, M., Ribeiro Jr., P.J., Diggle, P.J., 2004. Detecting dependence between marks and locations of marked point processes. J. R. Stat. Soc. B 66, 79–93.

Shi, H., Zhang, L., 2003. Local analysis of tree competition and growth. For. Sci. 49, 938–955.

Stoyan, D., Stoyan, H., 1994. Fractals, Random Shapes and Point Fields. Methods of Geometrical Statistics. Wiley, Chichester.

Stoyan, D., Penttinen, A., 2000. Recent applications of point process methods in forestry statistics. Stat. Sci. 15, 61–78.

Umeki, K., 1995. A comparison of crown asymmetry between *Picea abies* and *Betula maximowicziana*. Can. J. For. Res. 25, 1876–1880.

Wang, L., Gong, P., Biging, G.S., 2004. Individual tree-crown delineation and treetop detection in high-spatial-resolution aerial imagery. Photogramm. Eng. Rem. Sens. 70, 351–357.

Weiskittel, A.R., Maguire, D.A., Monserud, R.A., 2007. Modeling crown structural responses to competing vegetation control, thinning, fertilization, and Swiss needle cast in coastal Douglas-fir of the Pacific Northwest, USA. For. Ecol. Manage. 245, 96–109.

Wells, M.L., Getis, A., 1999. The spatial characteristics of stand structure in *Pinus torreyana*. Plant Ecol. 143, 153–170.

Wiegand, T., Gunatilleke, C.V.S., Gunatilleke, I.A.U.N., 2007. Species associations in a heterogeneous Sri Lankan dipterocarp forest. Am. Nat. 170, 77–95.

Wulder, M.A., Dymond, C.C., White, J.C., Leckie, D.G., Carroll, A.L., 2006. Surveying mountain pine beetle damage of forests: a review of remote sensing opportunities. For. Ecol. Manage. 221, 27–41.

Wyckoff, P.H., Clark, J.S., 2005. Tree growth prediction using size and exposed crown area. Can. J. For. Res. 35, 13–20.

Appendix A. *The mark-correlation function (MCF) applied to photo-derived crown areas*

Materials and methods

In order to get deeper insights into the formation of crown patterns in Plot 4, two monochrome high-resolution orthophotos (20 cm/pixel, covering 2 km × 2 km) from different years were used for aerial image analysis of this stand. This additional spatio-temporal analysis was done because after the summer drought of 2003, field-measured trees of Plot 4 showed, unexpected for competition, the phenomenon of mutual crown support where crowns leaned towards each other. The Thuringian state surveying and geo-information office took the photos on June 3, 2002 and on May 13, 2005 from the same position and under comparable weather conditions (weak cirrus cloud cover). Perspective distortion was very low because Plot 4 is near the centre of the image.

For this study, we applied visual crown delineation of the digitized and fully geo-referenced TIFF images whilst the crown centroids and crown surface areas of the shape files were determined using ArcGIS 8.2. Our primary aim of this aerial image analysis was a temporal comparison between photo-derived crown delineations of the years 2002 and 2005 which does not require an exact crown-crown match with field-measured trees of the year 2004. Canopy cover was calculated as the percent forest area occupied by the vertical projection of crown surface areas.

Results

Canopy cover as determined by visual crown delineation for Plot 4 was around 67% in 2002 and 62% in 2005. Hence, total gap fraction (1 - canopy cover) increased only slightly, although individual gaps were larger in 2005 (Fig. A1, inset figures).

For the photo-derived crown extent of Plot 4 in 2002, the MCF revealed strong negative correlation of ‘crown area’ with significance at scales up to $r = 3.3$ m (Fig. A1). This strong evidence of inter-tree competition vanished three years later because in 2005 ‘crown area’ was uncorrelated at small scales up to $r = 1.8$ m (Fig. A1). Negative correlation of ‘crown area’ was then only marginally significant at scales between $r = 1.9$ m to $r = 3.5$ m. Thus, strong competition and its release through self-thinning were clearly detectable with the mark-correlation function for the inter-photo period.

Discussion

Photo-derived analysis of the Douglas-fir stand P4 allows tracing back the competitive dynamics over the years 2002 - 2005. In 2002, tree crowns were densely packed (Fig. A1, inset figure). Inter-tree competition was very strong because this dense stand had not been thinned since its establishment four decades ago. The strong competition is shown by the strong negative correlation of ‘crown area’ for the first few meters. At these spatial scales, space was a severely limiting factor leading to reduced growth and thus to below average crown areas of neighboring tree crowns. Under optimal forest management, this stand should have been thinned prior to 2002 in order to avoid the high mortality (~ 60%) as recorded in 2004. Yet this stand was forced to regulate its density through natural self-thinning, an inherent process that was accelerated by the extreme summer drought of 2003. Because of this, large gaps are visible in the 2005 orthophoto and the new gain in growing space lowered direct competition between trees in their immediate neighborhoods. Such a reduction in competition is clearly indicated by the MCF because the small-scale negative correlation of ‘crown area’ in 2002 vanished in 2005. However, the presence of competition in this unthinned high-density plantation is still evident from the negative correlation of ‘crown area’ at larger scales between $r = 1.9$ to 3.5 m. Over time, this cyclical process of growth, enlarged crown areas, spatial tree suppression, and subsequent self-thinning will repeat itself and change the scale-dependent interaction patterns in forest stands. Evidently, competition is a spatio-temporal process that works on a continuous range of spatial scales.

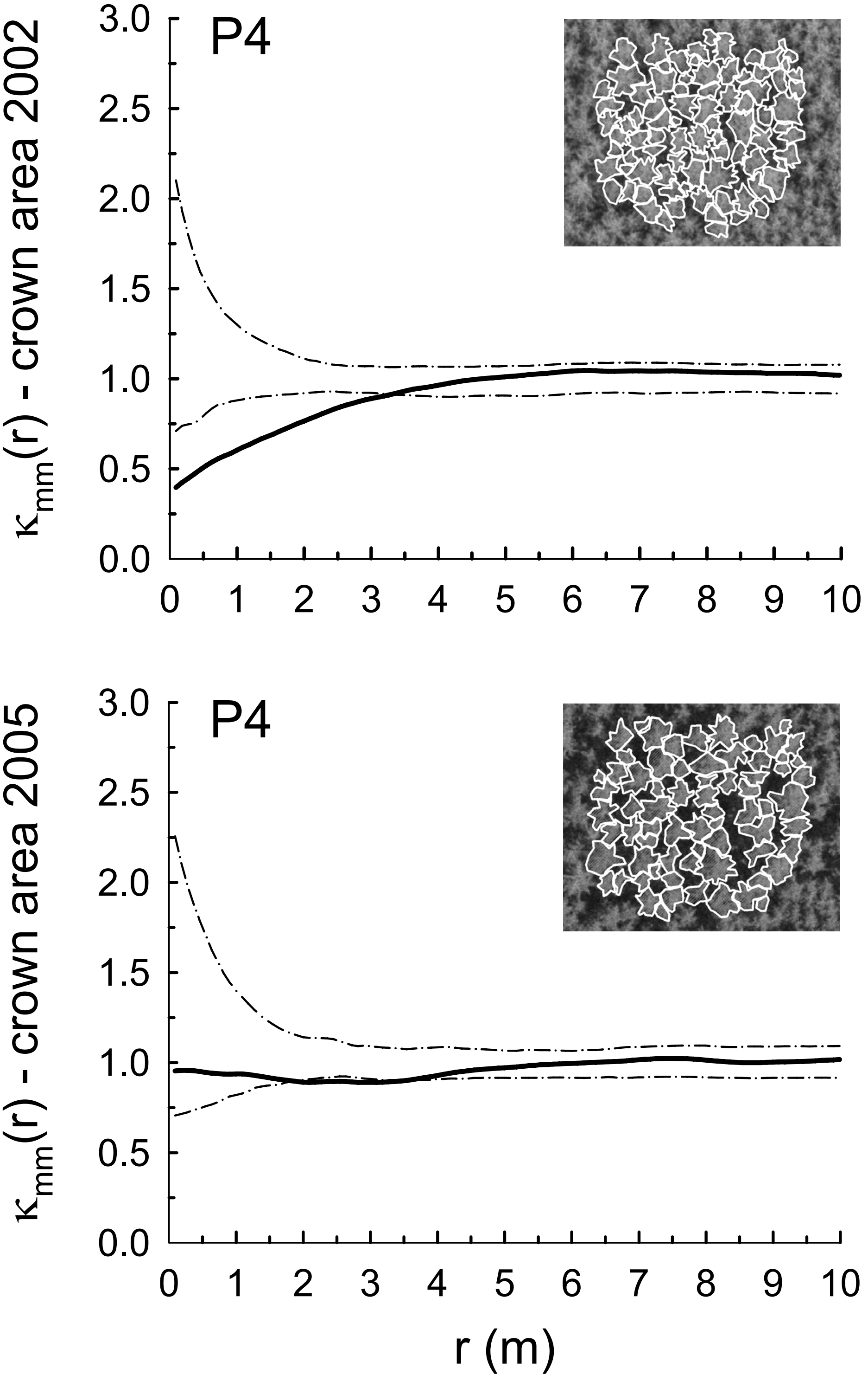

Fig. A1. *The mark-correlation function applied to photo-derived crown areas.*

The mark-correlation function $\kappa_{mm}(r)$ for photo-derived ‘crown area’ of Plot 4 in the years 2002 (top) and 2005 (bottom). Note the increase in gap size as a consequence of competitive thinning and summer drought in 2003 (inset figures). Negative correlation of crown area at inter-tree distance r is significant if κ_{mm} (solid line) is below the lower 95% approximated confidence limit (broken line).