Analysis of hierarchical structures in forest stands using detailed spatial statistics

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GENERAL INTRODUCTION

The competitive nature of forest communities leads to distinct hierarchies of horizontal and vertical structures in stands (Franklin *et al.* 2002; Schulze *et al.* 2005). Recent definitions of forest structure highlight three scale-dependent components: spatial distribution of trees, spatial mingling of different tree species, and spatial variation of tree dimensions (Pommerening 2002; Aguirre *et al.* 2003).

In a resource-limited and competition-dominated system one may generally assume two contrasting kinds of biological interaction, namely repulsion and attraction (Stoyan & Penttinen 2000). Repulsion is a "negative" ecological interaction and mainly caused by inter- and intra-specific competition. As a consequence of mortality, repulsion leads to regular (or evenly spaced, hyper-/over-dispersed, uniform) spatial distributions. The spatial scale of such negative interaction is, for example, an indication for the extent at which competition is influencing the distributional pattern of plants. Attraction is a "positive" interaction. It leads to aggregation and clumped (or under-dispersed) patterns which may be due to limitations in dispersal, vegetative reproduction, facilitation on nutrient rich spots, or safe sites from disturbance (Callaway & Walker 1997). Random patterns of uncorrelated plant distributions indicate either an absence of significant spatial interaction or a temporal transition from negative to positive interaction or *vice versa* (Wiegand *et al.* 2000). Competition or facilitation, mortality or dispersal, are thus fundamental processes that determine the structure of forests in a directed manner (Holmgren *et al.* 1997; Hille Ris Lambers & Clark 2003). One major aim of scale-dependent spatial statistics is to quantify the hierarchical structures in forests and to reconstruct the underlying processes such as competitive interaction (He & Legendre 2002). Spatial structure is also of interest in itself because it influences the dynamics, composition, and biodiversity of communities (Tilman 1994). For example, the degree of aggregation in the canopy layer may strongly regulate light in the understory and thereby determine the recruitment of different species with different functional attributes (Battaglia *et al.* 2002). Structural complexity such as the amount of various gap sizes favours floristic and faunistic biodiversity. Hence, especially tree-mortality patterns relate directly to ecosystem conservation because many organisms depend on the presence of gaps and snags. These examples illustrate why investigations, particularly on competition and self-thinning, are a central topic in the structural analysis of forests (Ferguson & Archibald 2002).

Tree-on-tree interactions occur at fine scales (up to ten meters) and are influenced by differences in shade-tolerance among species (Kobe *et al.* 1995). This functional variation may lead to the displacement of dominant but shade-intolerant pioneer species by dominant shade-tolerant colonizer species during long time scales of natural succession (Huff 1995; Schulze *et al.* 2005). Such displacement depends also on disturbance frequencies and environmental heterogeneity. However, the influences from spatial heterogeneity on species patterns and survival are still poorly understood (Chesson 2000; Gratzer *et al.* 2004). The functional differences in shade-tolerance or growth rate may also lead to the long-term suppression of minor tree species that usually occupy less than 20% in forest stands. Here, the scientific challenge is to better understand the spatial demand of suppressed tree species in order to enhance and maintain the coexistence of both weak and strong competitors and of forest biodiversity in general (Jack & Long 1991; Bengtsson *et al.* 2000; Frech *et al.* 2003).

Considering whole stands, hierarchical structures affect the functional dynamics of forest systems at large scales (tens of meters and above). For example, in their article "*Details that matter: the spatial distribution of individual trees maintains forest ecosystem function*", Pacala & Deutschman (1995) have demonstrated that a temperate mixed forest without horizontal structure (e.g. gaps in the canopy layer) would have 50% less standing biomass than a forest with spatial structures. Canopy structure and the presence of gaps depend on the interactive effects of incoming solar radiation and neighbourhood competition between trees. One of the few studies attempting to untangle these interactive effects has shown that asymmetric bending of tree crowns away from the perpendicular position may be primarily attributed to the large-scale direction of incoming sun light on slopes but only secondarily to small-scale shading effects from nearest neighbouring trees (Umeki 1995). Relating to this exemplary study and hierarchical structures at the stand level, it is still a disputed basic question whether randomly or evenly spaced tree crowns in the horizontal canopy layer would be optimal for light harvesting. More detailed investigations of current hypotheses on that issue may be particularly revealing for improving the simulation of individual tree growth and for modelling of biomass increment in forest stands.

There are still essential, unsolved topics and open questions concerning e.g. species interaction, competition and canopy architecture in forest stands (Song *et al.* 1997). One reason for that lack in understanding is the spatial scale dependency of processes that lead to forest structure (Levin 1992; Chen *et al.* 2004) in combination with the still limited application of spatial statistics to answer these questions (Stoyan & Penttinen 2000; Wiegand & Moloney 2004; Lancaster 2006). In order to better understand the mechanisms that generate diversity and patterns in ecosystems, international journals pay increasingly attention to the statistical analysis of spatial data sets, e.g. *Ecography* 2002, Vol. 25[5], special issue "Statistical analysis of spatial data in ecology".

In this Ph.D. thesis, I attempt to contribute to some selected topics in forest ecological research in order to better understand essential processes that lead to small- and large-scale forest structures. These selected topics range from detailed analyses of species patterns to broader structures at the stand level. Common themes are e.g. comparisons between the competitive performances of shade-intolerant and shade-tolerant tree species[*]. These investigated topics are also linked via the same species Douglas-fir in Canada and Germany or via the scale-dependency of spatial structures and interactions. Much emphasis will be given to demonstrate the application and benefit of innovative statistical methods to uncover scale-dependent interactions and processes. My results based on data from North America and central Germany will hopefully foster ecological research cooperation on an inter-continental scale (Acker *et al.* 1998; Koch & Skovsgaard 1999). In the next two sections, I will briefly explain the main ecological and statistical research aims of this Ph.D. thesis.

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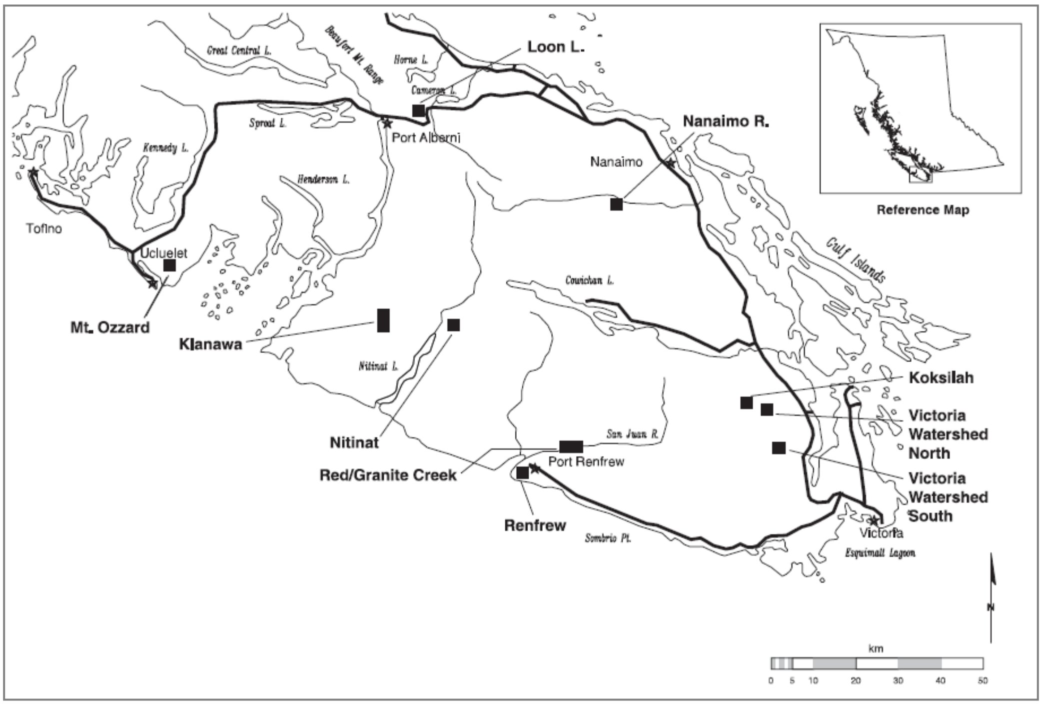
[*] Please note that the formal writing style (such as British or American English, section headings, figure or reference formatting) of the four chapters varies according to the style of the target journals.

Ecological research aims

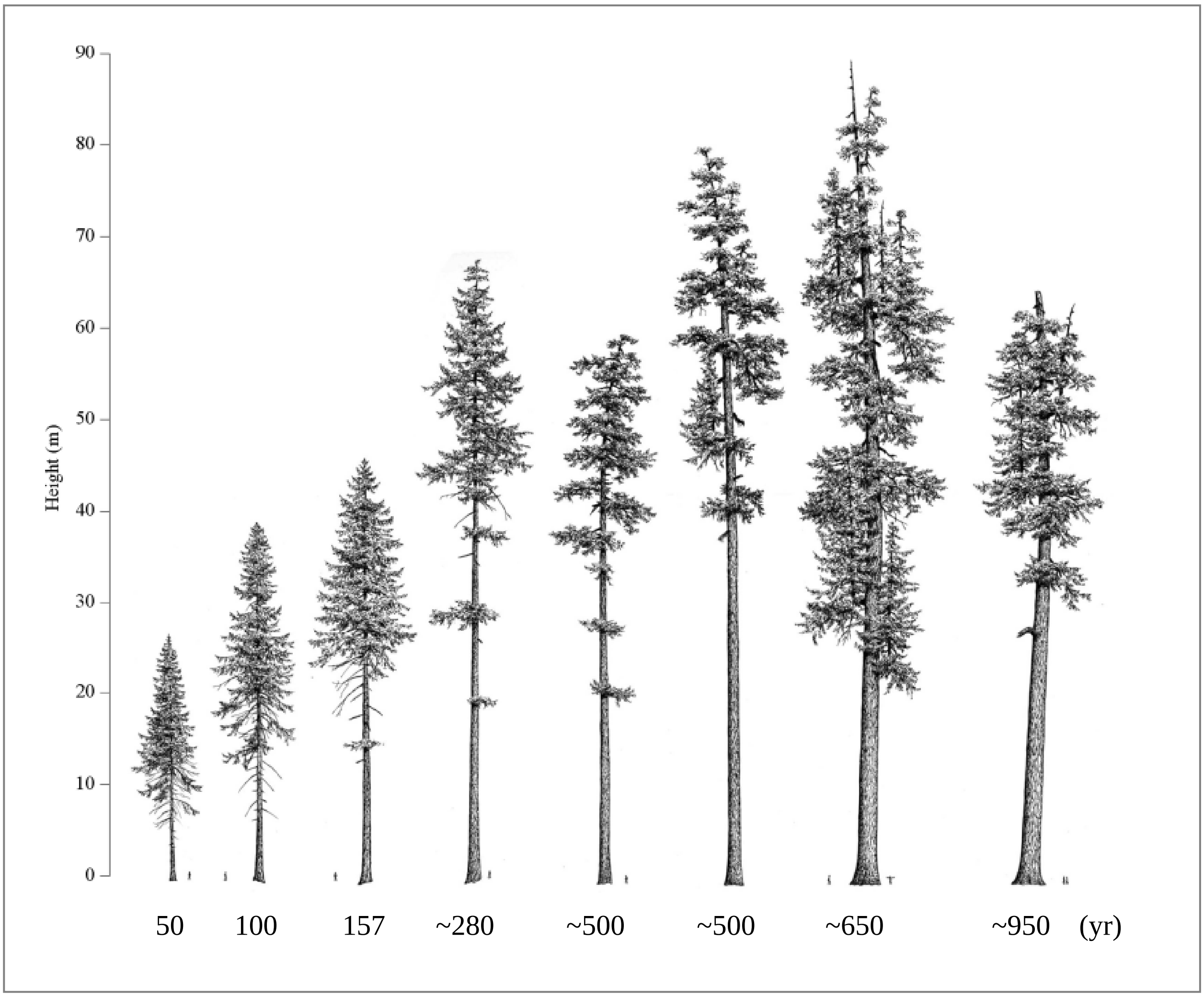
In CHAPTER 1, the most important research aim was to better understand the change in fine-scale spatial characteristics of shade-intolerant pioneer Douglas-fir and shade-tolerant colonizer species such as western hemlock and western redcedar during large time scales of natural succession. Here, the main question was how intra- and inter-specific competition would change the spatial distributions and hierarchical dominance of species in immature, mature and old-growth stands. This investigation of interaction and coexistence was made possible due to an invitation by Prof. Fangliang He from the University of Alberta/Canada to analyse his complex chronosequence data from Vancouver Island.

Subsequently, these data were used in CHAPTER 2 to study the effects of large-scale environmental heterogeneity on the dispersal patterns and demographics of western hemlock in detail, and on the intensity of ecological dynamics in general.



Vancouver Island and the chronosequences Victoria Watershed South & North (source: Frazer *et al.* 2000).

From left to right: Douglas-fir, western hemlock, western redcedar.



Douglas-fir in the Pacific Northwest: aging after fire disturbance (source: Van Pelt & Nadkarni 2004).

While fully mapped stem-base positions from chronosequences can be used to study the changing spatial structure over large time scales, additional information on the position of crown centroids and the horizontal extent of crowns may be used to analyse competition and gap-dynamics within the three-dimensional stand architecture.

In CHAPTER 3, the focus was particularly on asymmetric tree growth at the stand level to infer, from spatial characteristics of the horizontal canopy layer, possible structural modes to maximise photosynthesis. Here, the main question was whether plasticity in asymmetric growth is used to form random or more regular crown patterns in comparison to the fixed stem-base positions. Another aim of this study was to compare the strength of asymmetric growth between deciduous and coniferous trees and how these functional groups differ in their angular growth response to the direction of incoming solar radiation and slope aspect. The data for this and the fourth chapter were collected by myself in two deciduous and two coniferous forest stands in Thuringia/Germany. Plot 1 was dominated by common ash and wild cherry, while Plot 2 by durmast oak and wild service tree. Plot 3 was composed of common spruce and Douglas-fir, and Plot 4 consisted only of Douglas-fir.

Plot 1 & 2 with deciduous and Plot 3 & 4 with coniferous trees in Thuringia.

Suppressed minor tree species in Thuringia: wild cherry (left) and wild service tree.

In the first part of CHAPTER 4, the same field-measured data were taken to demonstrate how crown size can be used to quantify scale-dependent effects of competition in stands. The novel approach of this study was to detect competition based on the distance-dependent pattern of crown centroids in combination with the size attribute “crown area”. Although foliage reacts faster to competition than stem size, such an analysis has apparently never been undertaken before. The suitability of this method for the large-scale monitoring of forest stands was highlighted when the competitive dynamics were traced back between different years based on orthophotos. In the second part of CHAPTER 4, the size-dependent hierarchy in competitive response ability was compared between minor and major tree species. Aim of this investigation was to decouple different competitive abilities of different species from their size because plant size affects competitive strength.

Statistical research aims

Modern spatial statistics use correlation functions, such as the pair-correlation function *g*(*r*), Ripley's *K*-function or the mark-correlation function (MCF), instead of structural indices to quantify the scales of interaction between plants (Pommerening 2002, Gratzer *et al.* 2004). The primary advantage of correlation functions over indices is that they do not ignore spatial information beyond the nearest neighbours (Perry *et al.* 2006). This is important in natural systems because the range of influence of plants becomes greater with size and age (Callaway & Walker 1997). Therefore, larger plants beyond immediate neighbours have often the greatest influence on the growth of a focal plant.

One of the most challenging goals in the field of spatial statistics is to adapt mathematical null models to specific natural phenomena and hence to realistic biological null hypotheses (Wiegand & Moloney 2004; Lancaster 2006). In the following four chapters it was a primary goal to formulate null models that accounted for the specific biological questions under investigation. For example, in CHAPTER 1 the *heterogeneous Poisson* null model was applied to the tree positions in our plots because the investigated chronosequence was influenced by large-scale abiotic heterogeneity. Hence, the application of the classical and widely used null model *complete spatial randomness* (*CSR*) would not have been adequate since the null assumption of spatially equal establishment conditions for trees within the study plot is violated under heterogeneous site conditions. In this same chapter, the innovative null model *bivariate random labelling* was used to investigate whether large trees of the overstory would die randomly or non-randomly in space. In CHAPTER 2, special null models were applied by using the inhomogeneous *g*-function to account for underlying heterogeneity. The novel approach was to use the density distribution of mature adult trees as surrogate for habitat quality and thus to account for spatial heterogeneity. In CHAPTER 3, a rarely applied statistical sub-discipline called circular statistics was utilized. Here, the underlying basic assumption was not the conventional normal distribution but the *von Mises* distribution against which the angular directedness of asymmetric tree growth was tested. While in the first three chapters solely distances between trees were used in scale-dependent correlation functions, in CHAPTER 4, growth reduction (size) conditional on the distances between trees was integrated to detect competition in a more refined way. The mark-correlation function was applied to the continuous size attribute (mark) "crown area" to detect simultaneously competitive effects on inter-tree distances and on tree size.

An important reason for the increasing popularity of modern correlation functions is that these second-order statistics focus primarily on the variation of spatial data rather than on the mean (which is done by first-order statistics). This focus on variation receives increasing attention in ecology because essential information is often hidden by the mean. Therefore, also other statistical sub-disciplines like regression analyses attempt to pay growing attention to the variation in data. For example in CHAPTER 4, modern *quantile regression* techniques were applied to estimate size-dependent multiple rates of change for species response to neighbourhood competition. These examples are the main statistical innovations that were applied in the following four chapters.

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CHAPTER 1

Spatial patterns and competition of tree species in a Douglas-fir chronosequence on Vancouver Island

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Abstract

While the successional dynamics and large-scale structure of Douglas-fir forest in the Pacific Northwest region is well studied, the fine-scale spatial characteristics at the stand level are still poorly understood. Here we investigated the fine-scale spatial structure of forest on Vancouver Island, in order to understand how the three dominant species, Douglas-fir, western hemlock, and western redcedar, coexist and partition space along a chronosequence comprised of immature, mature, and old-growth stands. We quantified the changes in spatial distribution and association of the species along the chronosequence using the scale-dependent point pattern analyses pair-correlation function $g(r)$ and Ripley's L-function. Evidence on intra- and inter-specific competition was also inferred from correlations between nearest-neighbor distances and tree size. Our results show that (1) the aggregation of Douglas-fir in old-growth was primarily caused by variation in local site characteristics, (2) only surviving hemlock were more regular than their pre-mortality patterns, a result consistent with strong intra-specific competition, (3) inter-specific competition declined rapidly with stand age due to spatial resource partitioning, and (4) tree death was spatially randomly distributed among larger overstory trees. The study highlights the importance of spatial heterogeneity for the long-term coexistence of shade-intolerant pioneer Douglas-fir and shade-tolerant western hemlock and western redcedar.

Introduction

One challenge of plant ecology is to understand how competition contributes to the patterning of plant distributions and how the patterning changes over succession. Remarkable progress has been made in using the spatial distribution of trees to infer ecological mechanisms (Ford 1975, Kenkel 1988, Duncan 1991, He and Duncan 2000, Wiegand et al. 2000), to understand the genesis and maintenance of biodiversity patterns (Plotkin et al. 2000, He and Legendre 2002, Fang 2005), and to predict stand dynamics (Mateu et al. 1998, Stoyan and Penttinen 2000, Kokkila et al. 2002). However, the fine-scale spatial distributions of trees remain poorly understood (Condit et al. 2000). Empirical studies have repeatedly shown that spatial and size distributions of trees in a community bear the fingerprint of growth, competition, and habitat heterogeneity (Ford 1975, Harms et al. 2001, Chen et al. 2004). Spatial distribution and tree size are not independent patterns but are commonly affected by competition. If competition is an important working mechanism in structuring forest communities, two consequences should be expected: (1) there is a significantly positive correlation between tree growth (size) and nearest-neighbor distances, and (2) due to competition-induced mortality, spatial distributions of trees become more regular with time (Pielou 1962; Sterner et al. 1986, Duncan 1991, Shackleton 2002).

A simple method for detecting competition during succession is to compare the spatial patterns of a given species at subsequent stages of a chronosequence. Such a snap-shot approach using static point patterns is particularly useful in forests with slow plant growth. The pattern at late-successional series, comprising older trees that survived competition, should be more regular than that in early succession. If additional data on dead trees are available, the random mortality hypothesis can be used to detect competition. This hypothesis predicts that second-order characteristics of the spatial patterns would remain unchanged if individuals in a community are equal in death probability (Sterner et al. 1986). Opposite to this hypothesis are elevated death rates among neighboring trees due to competition. In this case, the post-mortality pattern of surviving trees becomes more regular than the pre-mortality pattern. This process is not only observed in even-aged, monoculture stands (Kenkel 1988, Newton and Jolliffe 1998) but also in uneven-aged, mixed coniferous forests (Duncan 1991, Mast and Veblen 1999, He and Duncan 2000). This method can be equally applied to infer intra-specific and inter-specific interactions. Whether the resulting spatial patterns are regular, aggregated, or random depends on the life histories of the species and on the scale at which the pattern is observed. For example, shade-intolerant and tolerant species colonize different habitats (gaps vs. shades) and form segregated distributions (North et al. 2004).

However, inconsistent results are observed in some tree species (e.g. Peterson and Squiers 1995) or in more heterogeneous and older forest stands (Dovčiak et al. 2001, McDonald et al. 2003). Environmental heterogeneity, uneven age distributions, limited dispersal of seeds or random germination may prevent a pattern from becoming more regular even though competition is present (Kenkel 1988). Moreover, sometimes competition may not be strong enough to cause substantial mortality but just cause growth reduction. In such situations where spatial patterns are ambiguous about competition, the correlation between tree size and neighborhood density provides a useful measurement (Shackleton 2002).

In this article, we use spatial pattern analysis to infer, from the fine-scale spatial distributions of trees, how the dominant tree species in a forest compete and partition space, and how their spatial interactions change during succession. More specifically, we analyze the successional dynamics of shade-intolerant pioneer Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* [Mirb.] Franco) and of two shade-tolerant late-successional species, western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) and western redcedar (*Thuja plicata* Donn ex D. Don) in a chronosequence in the Pacific Northwest region on south-eastern Vancouver Island.

To understand the change in spatial structure and species interactions in Douglas-fir forests across spatial and temporal scales, we first present the stand structural characteristics of the forests and infer intra-specific and inter-specific competition from correlations between tree size and nearest-neighbor distances before performing detailed point pattern analyses. Positive correlation between tree size and nearest-neighbor distances is expected if competition reduces growth. Evidence relating particularly to competition-induced mortality can be obtained from uni- and bivariate spatial patterns. More regular distribution in post-mortality pattern of surviving trees is expected if intra-specific competition leads to mortality. Similarly, strong inter-specific competition between shade-intolerant Douglas-fir and shade-tolerant western hemlock and western redcedar is expected to separate Douglas-fir from the two shade-tolerant species in space. Once trees have reached the upper canopy layer, their mortality should be unaffected by competition from smaller neighbors. Thus, we also test whether tree death among larger trees of the overstory is spatially correlated, or a random process.

Methods

Study sites and data collection

The chronosequence is located in the drier coastal temperate forest found on leeward side of south-eastern Vancouver Island within the Greater Victoria Watershed District (48°33′N, 123°38′W). All stands studied were within the eastern variant of the Very Dry Maritime subzone of the Coastal Western Hemlock zone (CWHxm1), which has mild and wet winters, warm and dry summers, a mean annual precipitation of 1425 mm, and a mean annual temperature of 9.4°C (Green and Klinka 1994). Pioneer Douglas-fir (Df) is the dominating tree species and western hemlock (Hw) and western redcedar (Cw) are two primary late-successional species that usually aggregate in gaps (Fig. 1). Other minor components include, e.g. western white pine (*Pinus monticola* Dougl.) or red alder (*Alnus rubra* Bong.). The chronosequence consists of an immature (IM), mature (MA) and old-growth (OG) stand with ages varying from 39 (IM), 109 (MA) to 254 years (OG) at the time of data collection in 1999 and 2000. The stands are located on gentle to moderate slopes with elevations ranging from 240 m to 390 m. Due to some rock outcrops, slight spatial heterogeneity was present in the plots. The immature stand was originally regenerated from artificial planting of Douglas-fir seedlings after harvesting and broadcast burn. However, the majority of Douglas-fir individuals in this plot are already naturally regenerated offspring from the planted trees. All other species were naturally regenerated.

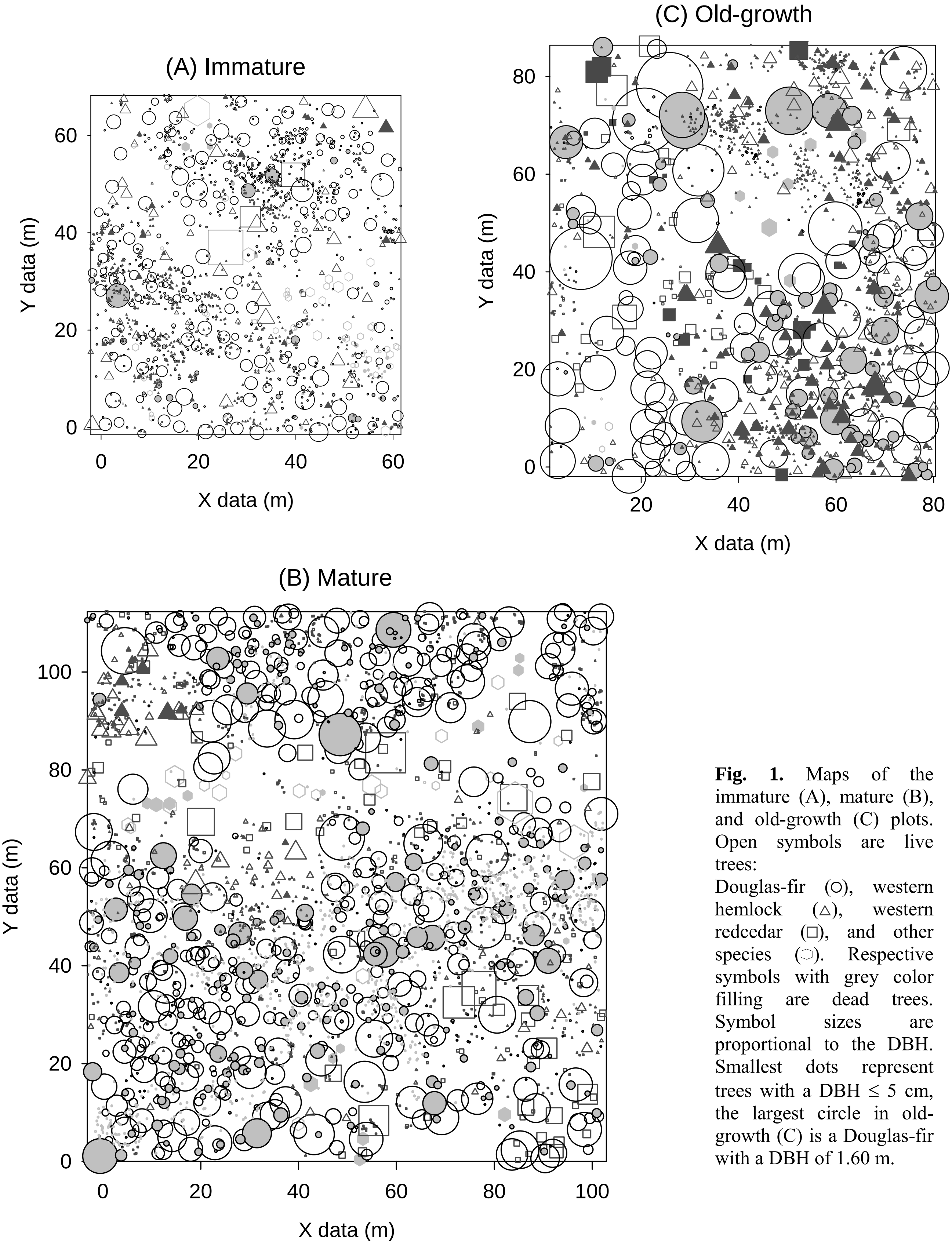

Fig. 1. Maps of the immature (A), mature (B), and old-growth (C) plots. Open symbols are live trees:
Douglas-fir (○), western hemlock (△), western redcedar (□), and other species (⬡). Respective symbols with grey color filling are dead trees. Symbol sizes are proportional to the DBH. Smallest dots represent trees with a DBH ≤ 5 cm, the largest circle in old-growth (C) is a Douglas-fir with a DBH of 1.60 m.

The mature stand originated naturally from wildfire followed by some salvage logging. The old-growth plot originated from a catastrophic wildfire. Further information on site characteristics and plot locations can be found in Trofymow et al. (1997), including the descriptions pertaining to plots 2 (IM), 5 (MA), and 6 (OG). Data were collected on 0.5 - 1.2 ha plots. All dead and live trees, including seedlings were stem-mapped. Diameter at breast height (DBH) of each live tree was measured at 1.4 m above ground, and all individuals were identified to species.

Data analysis

(1) *Stand structure and composition*

The mean nearest-neighbor distance for each species in each plot was calculated using S+SpatialStats. The number of stems (*N*) and relative proportion (%) of live and dead trees of each species were counted for the three dominant species Df, Hw, and Cw. Cw was not analyzed for the IM plot because its proportion was below 3%. We also calculated the mean DBH for each species in the plots, the species proportions within their smallest DBH class of 0.1-10 cm, and the proportion of dead trees of a species within this small diameter class.

Pielou's segregation index *S* was calculated for these species to quantify their relative spatial mixing (Pielou 1961). The index *S* was computed from the properties described in Table 1 as,

$$S = 1 - \frac{M_o}{M_E} = 1 - \frac{N(b+c)}{vn + wm}$$

where M_O is the observed number of mixed nearest neighbor pairs and M_E is the expected number under random conditions (Kint et al. 2003). Under segregation, values of *S* range between 0 and 1, with 1 indicating highest spatial separation. In communities of more than two dominant species *S* was calculated by comparing one species against all other species in the plot.

Table 1. Contingency table, defining the types of nearest-neighbor relationships between species A and B, for calculating Pielou's *S*.

	No. of nearest neighbors of		
	Species A	Species B	Species A + B
Species A	a	b	m
Species B	c	d	N
Species A + B	v	w	N

(2) *Correlations between tree size and nearest-neighbor distances*

For each of the three species and for each successional stage, we analyzed the correlation between the sum of the DBH of the four nearest neighbors plus the DBH of the focal tree and the sum of the distances of the four nearest neighbors to that focal tree (Shackleton 2002). The coefficient of determination r^2 describes the relative importance of competition as an agent in structuring the forest community (Welden and Slauson 1986). Although one cannot derive causal links from regression analyses, r^2 has been shown to be a robust index of competition, despite the complexity of biotic and abiotic factors influencing forest structure (Welden et al. 1988). In this paper, 'nearest neighbors' refers to the four nearest neighbors of a focal tree, trees with a 'conspecific neighborhood' have three or four conspecific nearest neighbors and trees with a 'heterospecific neighborhood' have none or one conspecific nearest neighbor. The size-distance correlation was conducted for inferring species, intra-specific, and inter-specific competition by including only the following subset of focal trees in the analysis: all focal trees of a given species, focal trees with a conspecific neighborhood, and focal trees with heterospecific neighborhood, respectively. We then plotted the importance of species, intra-, and inter-specific competition (measured by r^2) against stand age.

To measure how well species survive intra- and inter-specific competition during different successional stages, we compared the proportion of dead trees for each of the three species with a difference test, once between their con- and heterospecific neighborhoods and once between the species only in heterospecific neighborhoods. We also compared both, mean distance and mean DBH of the four nearest-neighbors by means of a two-sided *t*-test.

(3) *Spatial pattern analysis*

We used the pair-correlation function $g(r)$, which is a distance-dependent correlation function for completely mapped point patterns (Stoyan and Stoyan 1994, Wiegand and Moloney 2004). Based on point-to-point distances, the *g*-function describes clumping and regularity at a given radius r, using a standardized density. Consequently, $g(r) = 1$ under complete spatial randomness (CSR), $g(r) > 1$ indicates aggregation, while $g(r) < 1$ indicates regularity. The univariate pair-correlation function $g(r)$ is related to the derivative of the widely used *K*-function (Ripley 1976), i.e.

$$K(r) = 2\pi \int_0^r g(r')r'\,dr'$$

and can be interpreted as 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, Dale et al. 2002). Similar to the *K*-function, $g(r)$ can also be extended to describe point patterns with two types of points (e.g. dead and live trees): the bivariate pair-correlation function $g_{12}(r)$ is the expected density of points of pattern 2 at distance r of an arbitrary point of pattern 1, divided by the intensity λ_2 of pattern 2.

Compared with Ripley's K-function, which has a character comparable with that of a distribution function, $g(r)$ has a character comparable with that of a probability density function and is considered more powerful in detecting spatial patterns across scales (Wiegand and Moloney 2004). This is because $g(r)$ has the advantage of isolating specific distance classes and can therefore be used to precisely determine spatial scales at which a given null model is violated. In contrast, $K(r)$ is a cumulative distribution function that calculates point densities within the entire circle of a given radius (Ripley 1976). Therefore, it confounds the effect at large distances with the effect of small distances (memory effect), which can complicate its interpretation (Condit et al. 2000, Schurr et al. 2004). However, $K(r)$ or its transformation $L(r)$ is more pertinent for the confirmation of null models (Stoyan and Penttinen 2000).

In this study we used both $g(r)$ to analyze the fine-scale spatial patterns and $L(r)$ for the confirmation (not shown) of underlying null models (Table 2). These functions were computed using the grid-based software *Programita* for point pattern analysis (Wiegand and Moloney 2004). Significant departure from an underlying null model was tested by 99 Monte Carlo simulations which generates $n/(n+1) \times 100\%$, hence 99% confidence limits (Bailey and Gatrell 1998).

To investigate whether the basic pattern of all (dead and live) trees of a species would become more regularly distributed during succession, we implemented a null model based on a heterogeneous Poisson process. A heterogeneous Poisson process was chosen because our plots were partly influenced by first-order heterogeneity (Fig. 1), hence the intensity λ is not approximately constant but varies with the location (x, y). We used a circular moving window with a fixed bandwidth R to estimate $\lambda(x, y)$. Hence, patterns may be interpreted up to a radius of $R = 10$ m only (Wiegand and Moloney 2004; Hypothesis 1, Table 2).

For the random mortality hypothesis, we used univariate random labeling as null model to investigate whether the n_1 live trees of a species (post-mortality pattern) are a random subset of the pre-mortality pattern, i.e., the joined pattern of dead (n_2) and live (n_1) trees. The test was conducted by computing the function $g_{11}(r)$ from the observed data, then randomly re-sampling sets of dead trees from the joined pattern of live and dead trees to generate the confidence limits. This null model also accounts for first-order heterogeneity (Hypothesis 2, Table 2).

To investigate the interaction between shade-intolerant Df and late-successional, shade-tolerant species, we used the toroidal shift null model (independence), in which the second-order structure of both patterns is preserved but shifted relative to each other. We directly compared Df and Hw in the IM plot with each other. In other plots where more than one shade-tolerant species dominated, Df was compared against all other species. These analyses were conducted once for all (live and dead) trees and once for live trees only (Hypothesis 3, Table 2).

To investigate the mortality of larger trees, we used bivariate random labeling with $g_{21}(r) - g_{22}(r)$. Under random labeling, g-functions are invariant, hence we would expect $g_{12}(r) = g_{21}(r) = g_{11}(r) = g_{22}(r)$. Departure from random labeling is assessed using specific combinations of pairwise differences that correspond to specific biological effects. If $g_{21} - g_{22} < 0$ at radius r, then type 2 points (dead trees) are relatively more frequent around type 2 points than type 1 points (live trees) around type 2 points, hence dead trees are positively correlated at radius *r*. We included all trees with DBH > 10 cm in the IM, > 20 cm in the MA, and > 30 cm in the OG plots (Hypothesis 4, Table 2). Both bivariate null models (toroidal shift and random labeling) are very robust and produce reliable results when the heterogeneity of the plot is slight (Diggle and Chetwynd 1991, Wiegand and Moloney 2004).

Table 2. Hypotheses, applied point pattern analyses, and related figures used in this study.

Hypotheses	Point pattern analyses; null hypotheses applied	Related figures
(1) The spatial pattern of all dead and live Douglas-fir becomes regular during succession.	Pair-correlation function $g(r)$, heterogeneous Poisson null model; CSR only within moving window R = 10 m.	Fig. 3 A-H
(2) Intra-specific competition leads to a more regular post-mortality pattern of surviving trees, which is indicative of self-thinning.	Univariate random labeling with $g_{11}(r)$; live trees are a random subset of pre-mortality pattern (dead and live trees).	Fig. 4 A-H
(3) Inter-specific competition between shade-intolerant Douglas-fir and shade-tolerant species (western hemlock and western redcedar) leads to inter-specific repulsion.	Bivariate analysis with $g_{12}(r)$ and the toroidal shift null model; no spatial correlation between Douglas-fir (pattern 1) and shade-tolerant species (pattern 2).	Fig. 5 A-C
(4) Tree death of larger overstory trees is a spatial random process at each succession stage.	Bivariate random labeling with $g_{21}(r)$-$g_{22}(r)$; no spatial correlation of larger dead trees (pattern 2).	Fig. 6 A-C

Results

1) *Stand structure and composition*

Douglas-fir – The relative species frequency of Df declined during succession from 49.9% to 16.7 % (Table 3). Also, its mortality declined with increasing stand age from 56.8% in the IM plot to 36.5% in the OG plot. Its mean DBH increased with stand age from 8.2 cm to 52.2 cm. Compared to other species, Df consistently had the lowest segregation index in each plot and was thus spatially least separated (Table 3).

Western hemlock – The species proportion of Hw was intermediate in the IM plot, low in the MA plot but high in the OG plot (Table 3). Its proportion in the smallest DBH class of 0.1 - 10 cm was highest (86.6%) due to the initial colonization in the IM plot, but lowest in the OG plot. In each succession stage, Hw was spatially more separated than Df but less than Cw (Table 3).

Western redcedar – This species was virtually absent from the immature plot but started to colonize at the mature succession stage, as indicated by both its overall proportion (23.8%) and its high proportion in the smallest DBH class of 0.1 - 10 cm (80.5%) in the MA plot (Table 3). Its mortality was always lowest in this small size class. Cw had the highest segregation index within a plot, and thus was spatially more separated than other species.

2) Correlations between tree size and nearest-neighbor distances

Douglas-fir – The relative importance of competition for Df as whole group as well as intra-specific competition declined from the IM plot to the MA plot but increased strongly in the OG plot (Fig. 2A-B). Inter-specific competition of Df declined constantly with increasing stand age (Fig. 2C). There was no significant difference in mortality of Df within con- or heterospecifics, neither in the IM nor in the MA plot, but intra-specific mortality was significantly lower than inter-specific mortality in the OG plot (Table 4A).

Table 3. Stand structure and composition of the chronosequence. 〈〉 = mean, NN = nearest neighbor; *S* = Pielou's segregation index.

Plot / species	〈NN〉 distance (m) in plot	Number of stems	% stems	% mortality per species	〈DBH〉 (cm) per species	% with DBH of 0.1-10 cm	% mortality within DBH class of 0.1-10 cm	Pielou's *S*
Immature	0.63							
Douglas-fir		885	49.9	56.8	8.2	74.0	60.8	0.296
Western hemlock		750	42.3	71.7	5.4	86.6	75.6	0.318
Mature	0.82							
Douglas-fir		875	28.9	50.1	33.7	6.5	95.5	0.193
Western hemlock		381	12.6	19.7	10.0	65.7	23.9	0.398
Western redcedar		720	23.8	5.3	7.8	80.5	5.1	0.567
Old-growth	0.93							
Douglas-fir		244	16.7	36.5	52.2	15.3	44.4	0.350
Western hemlock		1061	72.6	40.3	11.0	59.0	57.3	0.485
Western redcedar		130	8.9	24.6	19.9	36.0	21.9	0.600

Western hemlock – The temporal pattern of competition of Hw is similar to Df. Competition of Hw as a whole species group and intra-specific competition within conspecifics declined from the IM plot to the MA plot but increased in the OG plot (Fig. 2A-B). Similar to Df, inter-specific competition of Hw declined with increasing stand age. Inter-specific competition was strong for hemlock in the IM plot, as indicated by the high coefficient of determination (0.59) (Fig. 2C). Unlike Df, inter-specific mortality of Hw was significantly lower than intra-specific mortality in the IM and MA plots (Table 4A). In comparison to Df, the strength of Hw as a shade-tolerant colonizer is also reflected in the four times lower inter-specific mortality of Hw in the MA plot, although Hw was surrounded by significantly larger trees than Df (Table 4B).

Western redcedar – Competition of Cw as a whole species group and intra-specific competition declined from the MA plot to the OG plot (Fig. 2A-B). Similar to Df, intra-specific and inter-specific mortality was not significantly different for Cw during its initial colonization in the MA plot. However, it had a significantly lower inter-specific mortality (3.3%) than Df and Hw, although Cw was in both cases surrounded by significantly larger trees (Table 4B).

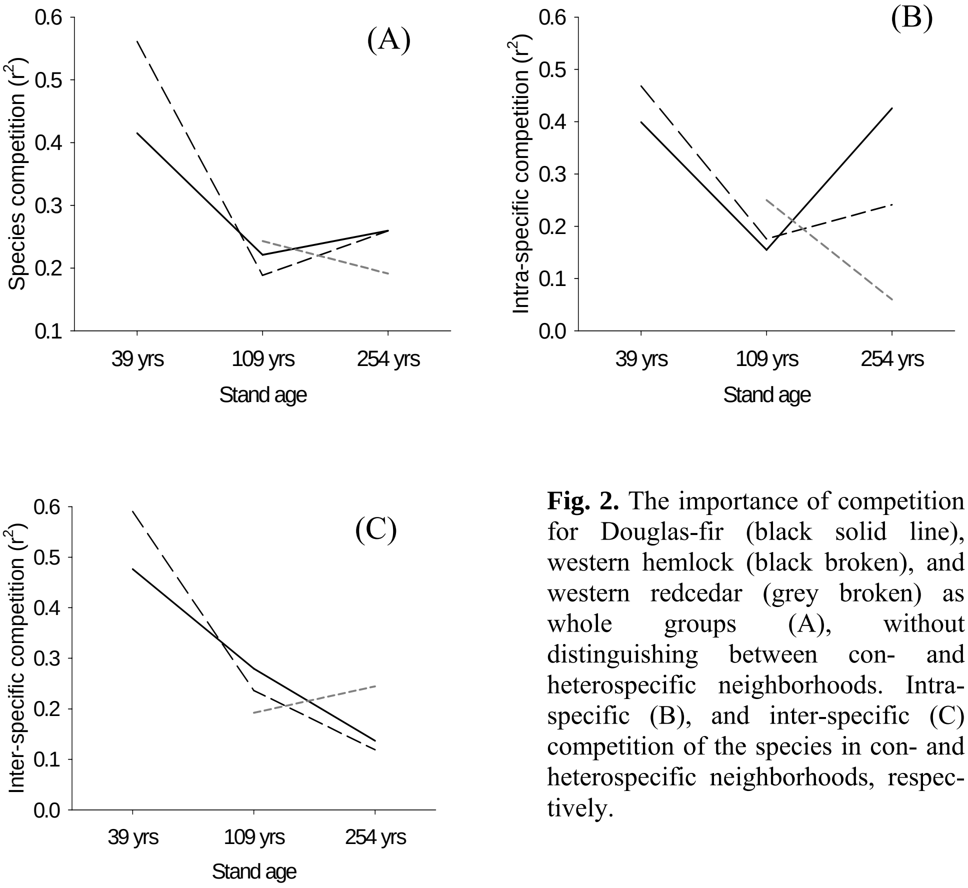

Fig. 2. The importance of competition for Douglas-fir (black solid line), western hemlock (black broken), and western redcedar (grey broken) as whole groups (A), without distinguishing between con- and heterospecific neighborhoods. Intra-specific (B), and inter-specific (C) competition of the species in con- and heterospecific neighborhoods, respectively.

3) Spatial pattern analysis

Univariate patterns

Douglas-fir – Pre-mortality Df (dead + live) aggregated up to 5.5 m in the IM plot, were randomly distributed in the MA plot, and showed a strong small-scale aggregation at scales ≤ 2 m in the OG plot (Fig. 3A-C). The random mortality hypothesis could not be rejected for Df in the IM and MA plots (Fig. 4A-B). However, the distribution of live Df in the OG plot was aggregated at scales up to 2.5 m (Fig. 4C).

Western hemlock – Pre-mortality patterns of Hw were aggregated in all plots (Fig. 3D-F), with the strongest aggregation in old-growth. In comparison to the pre-mortality patterns, surviving Hw (post-mortality) were partly regularly distributed in the IM and MA plots, showing strong evidence of self-thinning, but were more aggregated in the OG plot (Fig. 4D-F).

Western redcedar – All Cw were strongly aggregated in the MA and OG plots (Fig. 3G-H). The post-mortality pattern was random in the MA plot but aggregated in the OG plot (Fig. 4G-H).

Table 4. Pairwise comparison of mortality, nearest neighbor distances (NN), and surrounding tree size (DBH) (A) within the same species undergoing intra- and inter-specific competition and (B) between two species undergoing inter-specific competition. There were not enough data for redcedar in the immature plot.
(* = significant at $p < 0.05$; ** $p < 0.01$; ^ $p = 0.052$; ^^$p = 0.057$).

(A) Within Species

Plot / Attribute	Df intra	Df inter	Hw intra	Hw inter	Cw intra	Cw inter
Immature						
Mortality (%)	48.6	50.3	77.1	53.8**		
⟨4 NN dist.⟩ (m)	4.85	4.87	3.45	5.36**		
⟨4 DBH⟩ (cm)	24.8	24.3	18.4	30.9**		
Mature						
Mortality (%)	40.9	39.4	33.3	10.0**	4.2	3.3
⟨4 NN dist.⟩ (m)	9.44	8.25**	7.23	8.46**	5.83	8.83**
⟨4 DBH⟩ (cm)	112.7	43.9**	42.0	70.2**	39.1	89.8**
Old-growth						
Mortality (%)	24.0	51.4*	53.8	62.3	17.9	41.2^
⟨4 NN dist.⟩ (m)	11.39	9.47*	6.86	10.90**	9.23	11.21*
⟨4 DBH⟩ (cm)	166.8	65.4**	50.6	110.3**	62.3	96.4**

(B) Between Species

Plot / attribute	Df inter	Hw inter	Df inter	Cw inter	Hw inter	Cw inter
Immature						
Mortality (%)	50.3	53.8				
⟨4 NN dist.⟩ (m)	4.87	5.36				
⟨4 DBH⟩ (cm)	24.3	30.9**				
Mature						
Mortality (%)	39.4	10.0**	39.4	3.3**	10.0	3.3*
⟨4 NN dist.⟩ (m)	8.25	8.46	8.25	8.83	8.46	8.83
⟨4 DBH⟩ (cm)	43.9	70.2**	43.9	89.8**	70.2	89.8**
Old-growth						
Mortality (%)	51.4	62.3	51.4	41.2	62.3	41.2^^
⟨4 NN dist.⟩ (m)	9.47	10.90*	9.47	11.21*	10.90	11.21
⟨4 DBH⟩ (cm)	65.4	110.3**	65.4	96.4**	110.3	96.4

Bivariate patterns

Inter-specific competition between shade-intolerant Douglas-fir and shade-tolerant species was not detectable via regular distributions from point pattern analysis. Hw aggregated strongly at the smallest scale around Df in the IM plot (Fig. 5A), but with the increase in stand age, the spatial association of other species around Df disappeared (Fig. 5A-C). Analyses with only live trees revealed the same results (not shown).

Tree death was spatially randomly distributed among larger overstory trees in the IM and MA plots (Fig. 6A-B). However, there was a significant positive correlation for dead trees at distances up to 1.5 m in the OG plot (Fig. 6C). This was probably a size class effect because most dead trees had a DBH of 30 - 40 cm. To exclude such size class effect, one would have to exclusively look at DBH classes above 40 cm. But there were too few trees in this large size class in the OG plot to permit a reliable statistical analysis.

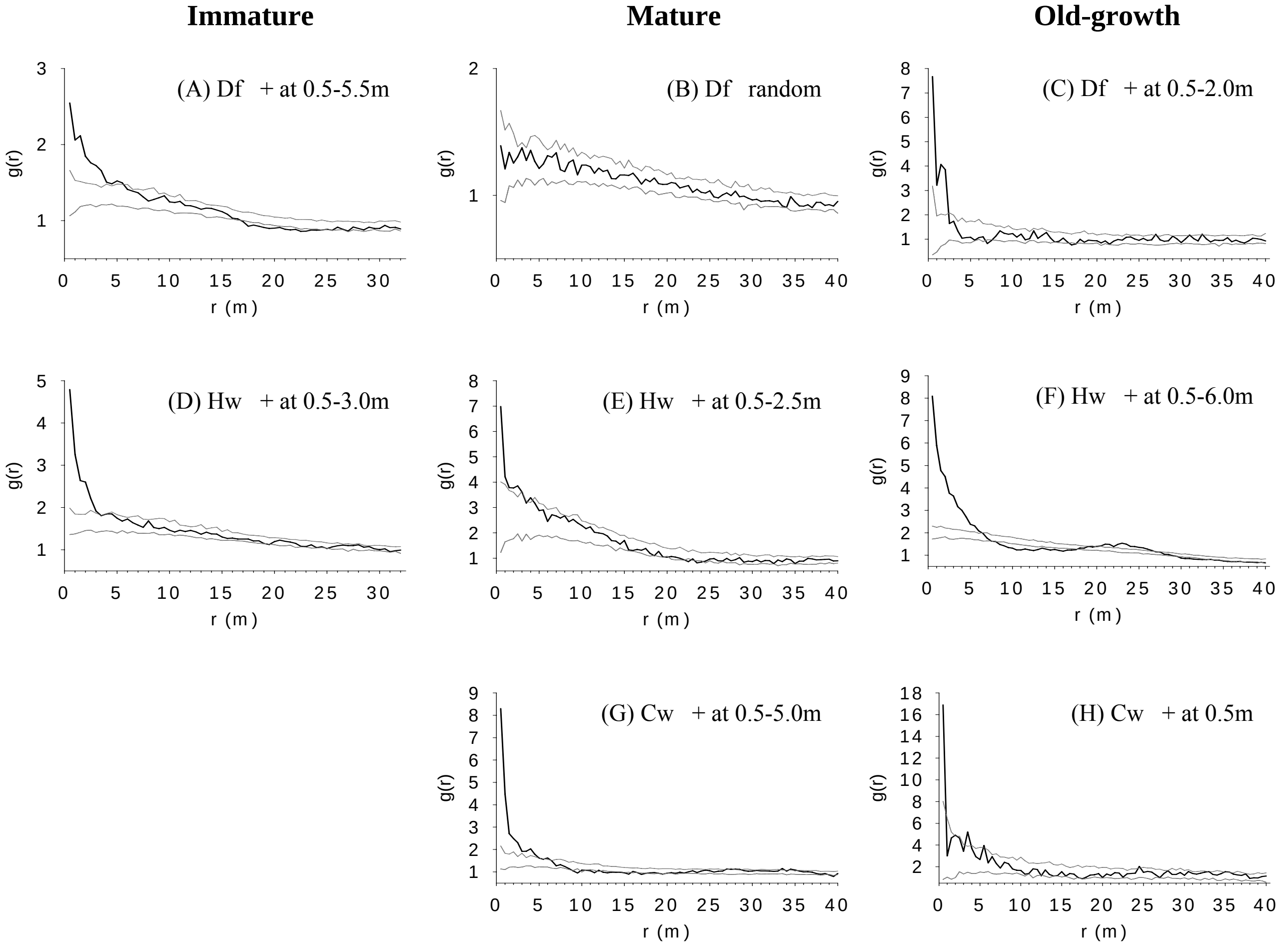

Fig. 3. Univariate analyses of the overall (pre-mortality) patterns of dead and live Douglas-fir (A, B, C), western hemlock (D, E, F) and western redcedar (G, H), using $g(r)$ and the heterogeneous Poisson null model with a moving window of $R = 10$ m. The large-scale heterogeneity was well captured by the null model at scales beyond $R = 10$ m, but deviation from CSR occurred within the moving window. Significant aggregation is indicated by a "+". ($g(r)$ = black solid line; 99% upper and lower confidence limits = grey lines).

Discussion

Spatial patterns and competition

Using scale-dependent spatial statistics, small-scale negative interactions among Douglas-fir trees have been observed on Vancouver Island (He and Duncan 2000). In contrast, our analysis of a chronosequence of Douglas-fir forest showed aggregation at distances below 6 m, which indicates a positive interaction at small spatial scales. Moreover, the degree of spatial aggregation and the importance of competition were positively linked in our study (cf. Fig. 3 vs. Fig. 2A). For Douglas-fir and hemlock, spatial aggregation and competition were highest in the immature and old-growth plots but lowest in the mature plot. Likewise, the pattern of redcedar was more aggregated and competition more important in the mature plot, as compared to old-growth. Here, we suggest that competition during the long time span of succession does not necessarily need to result in small-scale regularity of whole species patterns and propose three reasons for that observation.

Firstly, a positive link between competition and aggregation may arise when competitive thinning of large trees leads to gaps in which clustered offspring regenerate. This has been proposed by Pileou (1962) and was recently supported by a forest model (Moravie and Robert 2003). Under such circumstances, the overall pattern of a species is only indirectly influenced by mortality of large trees but directly determined by the pattern of gap recruitment of small competing trees (Simard and Sachs 2004, Wolf 2005). This did not occur with Douglas-fir in the homogeneous old-growth plot of He and Duncan (2000), because canopy gaps are usually not large enough for shade-intolerant Douglas-fir to regenerate underneath. However, with 500 mm less precipitation per year our chronosequence was much drier, and on dry sites gaps may reach sizes that lead to clustered regeneration of Douglas-fir (Spies et al. 1990).

Secondly, spatial heterogeneity induced by edaphic gaps may cause a patchy (clumped) size class distribution, thereby masking the tendency towards regular growth patterns (Sterner et al. 1986, Dovčiak et al. 2001). Such gaps often have sufficient sizes for regeneration and pioneer species like Douglas-fir may re-colonize the gap peripheries after other species have died due to wind throw (Lertzman et al. 1996). Besides temporal disturbances by fire (Franklin and DeBell 1988), spatial heterogeneity may be crucial for the long-term persistence of shade-intolerant pioneer Douglas-fir during succession. This assumption is supported by the lower mortality (36.5%) of Douglas-fir in our heterogeneous old-growth stand, as compared to its higher mortality (47.8%) in the homogeneous old-growth stand of He and Duncan (2000). Whereas the spatial pattern of western hemlock and western redcedar is typically aggregated (Keeton and Franklin 2005), the pattern of Douglas-fir seems to be largely dependent on the degree of spatial variation in local dryness and edaphic heterogeneity. In agreement with results from other forest types (McDonald et al. 2003), we highlight the importance of variation in local site characteristics and site history for the unexpected small-scale clumping of Douglas-fir in our old-growth stand.

Thirdly, a reason for the lack of evidence of spatial regularity despite finding important competition via size correlations is that competition may not be strong enough to cause mortality but just to reduce growth. Only when competition leads to sufficient mortality within a species pattern, it will cause regular distributions (Stoll and Bergius 2005). Also, species may have differential abilities to cope with intra-and inter-specific competition. To account for such confounding effects on the spatial pattern of species, it is important to look at intra- and inter-specific competition within a succession stage.

Intra-specific competition

Previous studies have shown that post-mortality patterns of surviving trees were more regular than expected under random-thinning (Sterner et al. 1986, Kenkel 1988, Duncan 1991, He and Duncan 2000). In this case, resource depletion leds to density-dependent self-thinning and thereby to a non-random mortality of trees.

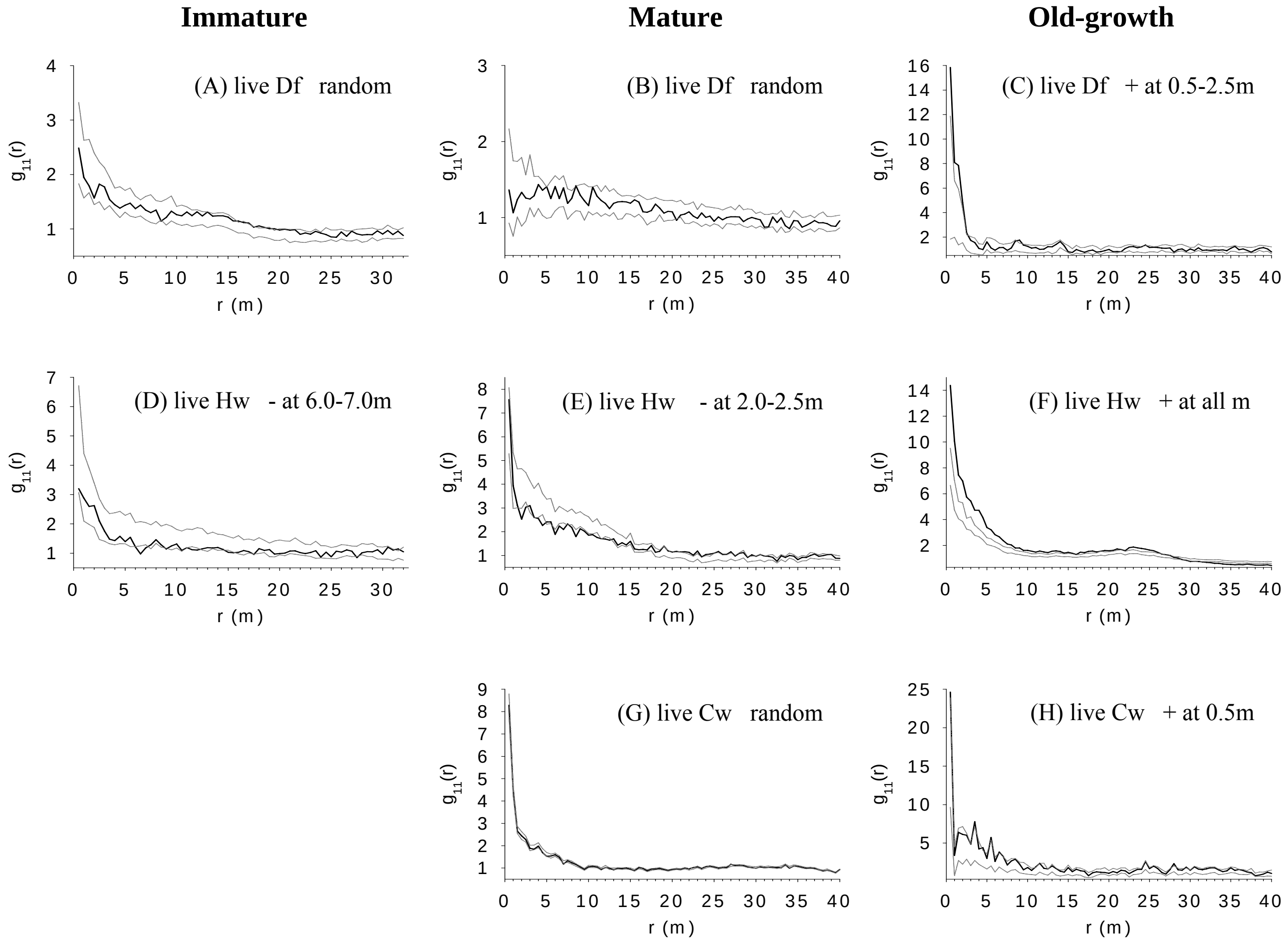

Fig. 4. Univariate analyses of the post-mortality patterns of live Douglas-fir (A, B, C), western hemlock (D, E, F), and western redcedar (G, H), using univariate random labeling (g_{11}) as null model which also accounts for the heterogeneity.

Despite the shift from aggregation to a random distribution of all (dead and live) Douglas-fir in the immature and mature plots, respectively, intra-specific mortality was not significantly different from random mortality. Of the three species, only surviving hemlock showed a more regular post- mortality pattern in the IM and MA plots. Self-thinning effects must have been strong for that species but were less important for Df and Cw in our sites. These findings were also supported by comparing the mortalities in conspecific and heterospecific neighborhoods. Of the three species, only Hw showed a significantly higher mortality rate in conspecific than in heterospecific neighborhoods (Table 4A).

Although, comparing pre- and post-mortality patterns is a strong approach in detecting competition, a single plot only represents a snap-shot analysis. Possibly, the snap-shot within the immature plot does not contain information from a sufficiently long time period to capture the signature of self-thinning. In our old-growth plot, mortality of Df was clustered, leading to an even more aggregated pattern of live trees. This deviation from random mortality is again opposite to the pattern of the old-growth forest studied by He and Duncan (2000), who found Df to shift towards a more regular distribution. It is likely that in our study sites intra-specific competition was relatively important for recruiting Df in gaps of the OG plot (Fig. 2A), but that there were also facilitating effects at the same time, leading to an increased aggregation of surviving Df. In ecological studies, the concept of facilitation has been often neglected and negative interactions have been over-emphasized but, for example, in harsh terrestrial environments high seedling densities can increase growth and survivorship (Bruno et al. 2003). A low mortality of just 24% in conspecific Df as compared to 51% within heterospecifics in the OG plot supports this assumption. For shade-intolerant pioneer Douglas-fir it is almost impossible to regenerate under the out-shading canopy of late-successional colonizers such as hemlock and redcedar (Franklin and DeBell 1988, Spies et al. 1990). Since regeneration of Df in old-growth is only sufficient under suitable gaps and under more similar and light-transmitting crowns within conspecifics, facilitation within Df could be important and may reduce this thinning process.

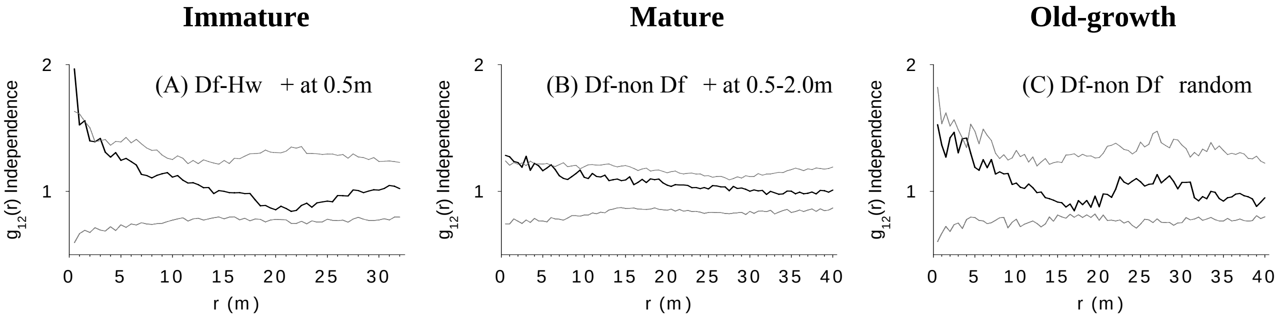

Fig. 5. Bivariate analysis of all hemlock (pattern 2) around all Douglas-fir (pattern 1) in the immature plot (A), using $g_{12}(r)$ and the toroidal shift null model. In the mature and old-growth plots (B, C) more than one shade-tolerant species was dominating. Therefore, at each time, we used all other species as pattern 2 and Douglas-fir as pattern 1.

Inter-specific competition

In temperate forests a fundamental trade-off exists for the growth rate in high light, which is correlated with good seed dispersal, *versus* the survival rate in shade (Kobe et al. 1995, Silvertown 2004). In terms of an expected negative spatial association between shade-intolerant Df and shade-tolerant species, we found that inter-specific competition was not strong enough to lead to sufficient tree death and hence being detectable via spatial pattern analysis. None of the bivariate analyses found repulsion between Df and shade-tolerant species, not even when we did these analyses just for live trees (not shown).

However, there was important inter-specific competition when hemlock initially colonized the immature plot, as can be seen from correlation between tree size and nearest-neighbor distances. But competition of Hw within heterospecifics resulted in a significantly lower mortality than within conspecifics (Table 4A). This explains, why shade-tolerant Hw aggregates around Df in the immature plot although inter-specific competition is important. As a late-successional species, hemlock survival appears highly adapted to competition within heterospecifics (but not within conspecifics), thus to replacing the pioneer Douglas-fir. In contrast, survival of Douglas-fir within hetero- and conspecifics was not significantly different, neither in the immature nor in the mature plot, pointing to its strength as a pioneer that equally withstands intra- and inter-specific competition in the first succession phases.

Direct competitive interaction between the species strongly declined with increasing stand age (Fig. 2C). Here, spatial niche separation stabilized the coexistence of species towards older succession stages as is also indicated by the increase in spatial segregation of the species (Pielou's *S* in Table 3). The spatial niche separation does not need to be a direct result of inter-specific competition, because it can also be caused by micro-habitat heterogeneity such as the variability in forest-floor micro-relief (Duncan 1991). A recent study on Vancouver Island has shown that redcedar has a greater proportion of fine roots in the lower soil horizons than hemlock and that such spatial resource partitioning may be a mode to avoid direct inter-specific

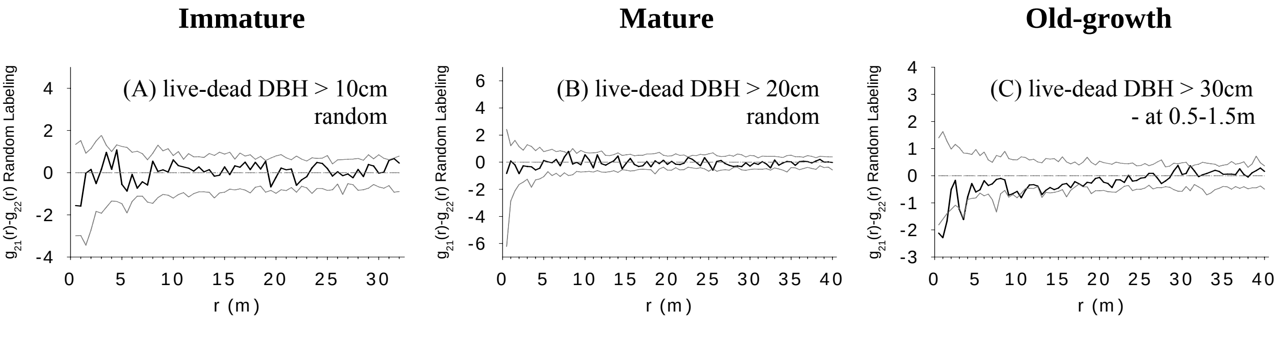

Fig. 6. Bivariate random labeling ($g_{21}(r)$-$g_{22}(r)$) to investigate whether tree death (pattern 2) was a random process among larger trees in a plot. Under the null model "random labeling", $g_{21}(r)$-$g_{22}(r) = 0$ (grey broken line). Analyses included trees with a DBH > 10 cm in the immature plot (A), > 20 cm in the mature plot (B), and > 30 cm in the old-growth plot (C).

competition (Bennett et al. 2002). Hw has usually stronger inter-specific effects on Cw than *vice versa* (Weber et al. 2003, Canham et al. 2004), but in this dry chronosequence Hw was probably physiologically disadvantaged and Cw was favored due to its better root penetration (Burns and Honkala 1990).

The different mortalities of species may also reflect different survival and dispersal strategies. Our results suggest that western hemlock seems to follow a “seed-flooding strategy” with generally high mortality during initial colonization. This initial high mortality is primarily attributed to its lower survivial within conspecifics. These findings are supported by results from interior British Columbia, where the abundance of hemlock was always highest of all species under a gradient from closed to fully open canopy although overall mortalities were relatively high, too (Coates 2002). In contrast, redcedar is spatially much more selective as indicated by the consistently highest segregation index within a plot. This favored its survival during initial colonization of the mature plot but such a spatially confined strategy would be at the cost of missing favorable gaps during critical temporal changes in the forest structure and hence at the cost of not being dominant in older succession stages. Also, the best place for early establishment is not necessarily the best place for survival and growth. Coates (2002) has shown that tree abundance and composition was rather controlled by differentiation among growth and survival niches than by regeneration niches. Hence, the strength of hemlock as a successful colonizer may be attributed to a seed-flooding strategy whereby it not only increases the risk of mortality, primarily within conspecifics, but also the chance of reaching suitable survival niches within heterospecifics.

Once the trees have reached the upper canopy layer, mortality of large trees was spatially randomly distributed. Only in old-growth there was a spatial correlation of dead trees at very small scales, but this was only observed in certain smaller size-classes. Hence, competition or other mortality inducing processes did not affect the pattern of large trees of the overstory.

In summary, our study highlights the importance of spatial resource partitioning as a mode to avoid direct competitive interaction during succession. It emphasizes that late-successional species may initially exhibit strong inter-specific competition but their strength lies in a relatively high survival rate during competition which is mediated by micro-habitat heterogeneity.

Acknowledgments

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CHAPTER 2

Environmental heterogeneity influences spatial patterns and demographics in forest stands

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Summary

1 Dispersal of tree species often results in aggregated patterns. The size of the clusters depends on intrinsic dispersal limitations of species, available resource patches for establishment, and the observed life-history stage. Demographic processes may be analysed by comparing the distribution of different size classes within the overall aggregation of the species. However, such spatial growth dynamics may be masked by large-scale heterogeneous site conditions when the restricting size of survival templates superimposes emergent patterns.

2 Here, we analysed the dispersal strategies and demographics of western hemlock in two old-growth Douglas-fir forests on Vancouver Island. We used explicit cluster processes and case-control studies to quantify the change in spatial distribution for different size classes of this late-successional species.

3 Our results emphasize that the dispersal kernel of western hemlock depends strongly on the distribution and density of prevailing canopy cover from pioneer Douglas-fir. Although dispersal kernels were smaller under heterogeneous site conditions, recruitment into the larger size classes was enhanced by these survival niches.

4 Our study supports the hypotheses that a tree species may simultaneously operate with two different dispersal modes (colonization and phalanx strategy) and that intra-specific competition and ecological dynamics are intensified in heterogeneous stands with strong spatial structures.

Keywords: Case-control, dispersal strategies, inhomogeneous *g*-function, large-scale heterogeneity, point pattern analysis, western hemlock

Introduction

Dispersal strategies of species have a profound influence on their survivorship in different environments (Dieckmann *et al.* 1999; Hovestadt *et al.* 2000; Hille Ris Lambers & Clark 2003). In variable habitats, some species may follow a generalist dispersal strategy with randomly or evenly spaced global distributions to be able to colonize new suitable sites while others may specialise in local regeneration to form distinct clusters to quickly access resources (Wiegand *et al.* 1998; He & Duncan 2000; Hovestadt *et al.* 2001). The dispersal modes parallel differential abilities of species to survive intra- and inter-specific competition during succession (Getzin *et al.* 2006). Density-dependent mortality and other demographic processes may be revealed by comparing the change in the spatial pattern of trees of distinct size classes that represent different life-history stages (Peterson & Squiers 1995; Moeur 1997; Dovčiak *et al.* 2001; Plotkin *et al.* 2002).

Spatial pattern analysis becomes more complicated when large-scale environmental heterogeneity masks the intrinsic dispersal and demographic behaviour of a given species by forcing it to aggregate in survival templates (He *et al.* 1997; Coomes *et al.* 1999; Levine & Murrell 2003). A patchy distribution of limiting resources may then influence demographics, the size and shape of emerging species patterns, and consequently population dynamics and ecological feedbacks tend to be intricate (Clark *et al.* 1998; Dieckmann *et al.* 1999; Condit *et al.* 2000; McDonald *et al.* 2003). Gaining understanding of the effects of environmental variation in space remains a major challenge in spatial ecology (Chesson 2000; Gratzer *et al.* 2004; Ronce *et al.* 2005). However, the problem at hand is to separate second-order effects of direct tree-tree interaction from first-order effects resulting from large-scale variation in habitat quality, which may both lead to similar point patterns (Coomes *et al.* 1999; Lancaster 2006). Contrasting environmental conditions in plant communities may not simply cause an ambiguity between first- and second-order effects which can now be resolved to a certain extent (i.e., using inhomogeneous *K*-functions; Baddeley *et al.* 2000; Diggle 2003), but may additionally change key-processes, such as regeneration due to different gap sizes. A rarely used but important possibility for studying such cascade effects of environmental heterogeneity is to compare plots within the same type of forest but with different variability in large-scale habitat condition (Amarasekare 2003).

To study how environmental heterogeneity influences the spatial patterns and the demographics of plant communities, we performed comparative analyses of two old-growth stands both dominated by Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* [Mirb.] Franco), western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) and western redcedar (*Thuja plicata* Donn ex D. Don) but locate in north and south environmental conditions in the Greater Victoria Watershed, on southern Vancouver Island. At large scales, the old-growth north plot showed homogeneous environmental conditions where mature adult trees were randomly distributed. Consequently, possible regeneration sites for the late-successional species western hemlock were scattered over the entire plot. In contrast, the old-growth south plot showed large-scale habitat heterogeneity, and some edaphic gaps (e.g. rock outcrops or wet drainage sites) prevented tree growth. In this plot canopy cover of mature adult trees was more clumped and possible regeneration sites for western hemlock were spatially more aggregated. Here, we used point pattern analyses to study how the spatial patterns of western hemlock changed with age under the two contrasting environmental conditions and how the proposed “seed-flooding strategy” of hemlock (Getzin *et al.* 2006) is affected by these site characteristics.

We were particularly interested in comparing the processes of self-thinning and demographics under different environmental conditions. To characterise the degree of spatial clustering of trees of different size classes, we used Thomas cluster processes (Stoyan & Stoyan 1994; Diggle 2003) as null models and homogeneous and inhomogeneous *K*- and pair-correlation functions (Baddeley *et al.* 2000; Diggle 2003) to describe the second-order characteristics of the spatial patterns. To study self-thinning (i.e., changes in the spatial structure of subsequent age classes) we used the random-labelling null model within a case-control design (Diggle & Chetwynd 1991). Based on these analyses, we investigated two general questions raised by Bolker & Pacala (1999): (1) Is there empirical evidence that a tree species may simultaneously exhibit short- and long-range seed dispersal to cope with environmental variation, and (2) are intra-specific competition and ecological dynamics more intense in spatially structured heterogeneous than in homogeneous stands?

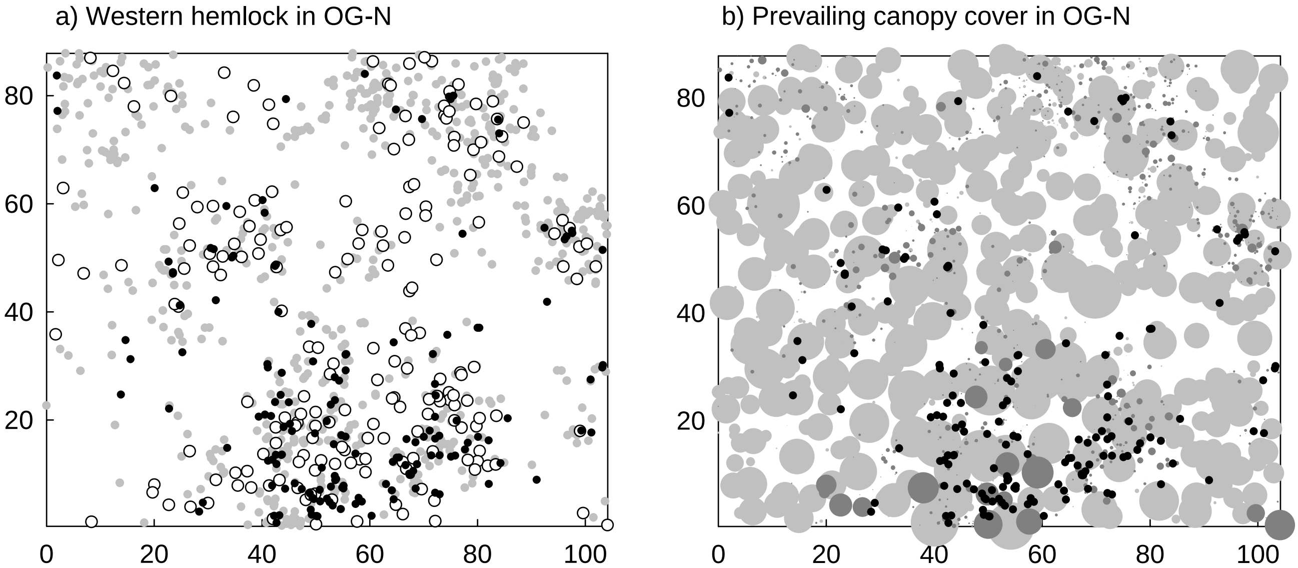
Methods

Species

The native range of western hemlock (Hw) is the Pacific coast between northern California and southern Alaska, but it also prevails in the northern Rocky Mountains. As a very shade-tolerant late-successional species, Hw colonizes the post-fire habitats after mortality of pioneer Douglas-fir (Df) opens up canopy gaps (Huff 1995). Although Hw has clustered regeneration within these gaps (He & Duncan 2000), seedlings can also grow in large numbers under partial or full canopy (LePage *et al.* 2000; Coates 2002). Western hemlock produces usually more seeds than most associated tree species, and up to 19.8 million seeds per ha have been recorded. Two years old seedlings are usually less than 20 cm tall, but once established, seedlings in full light may have an annual growth rate of 60 cm (Burns & Honkala 1990).

Study area and data collection

We studied western hemlock in two old-growth stands of Douglas-fir on south-eastern Vancouver Island. Both stands originated from catastrophic wildfires. The old-growth north (OG-N) stand (48°38’ N, 123°43’ W) had an age of 325 years and Douglas-fir a mean diameter at breast height (DBH) of 43.0 cm. This plot on a 40% WSW slope had large-scale homogeneous habitat conditions with Df being regularly spaced over the entire study region (Fig. 1). The plot is at 465 m elevation and has a straight surface profile. The soil is an Orthic Humo-Ferric Podzol with fine-silty and loamy family particle size classes (Trofymow *et al.* 1997; He & Duncan 2000).


a) Western hemlock in OG-N

b) Prevailing canopy cover in OG-N

c) All mature adult trees in OG-N

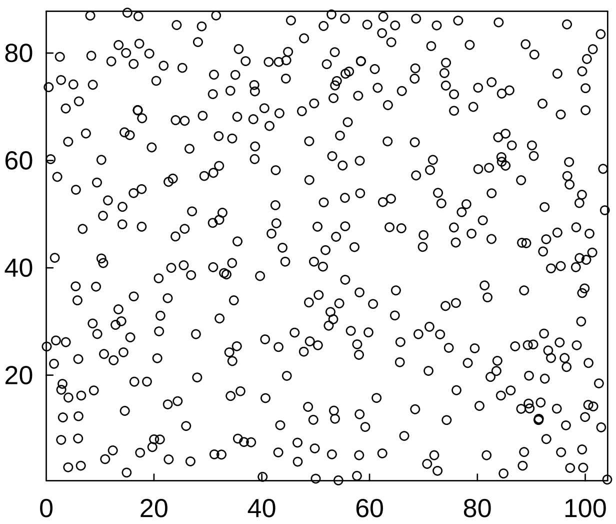


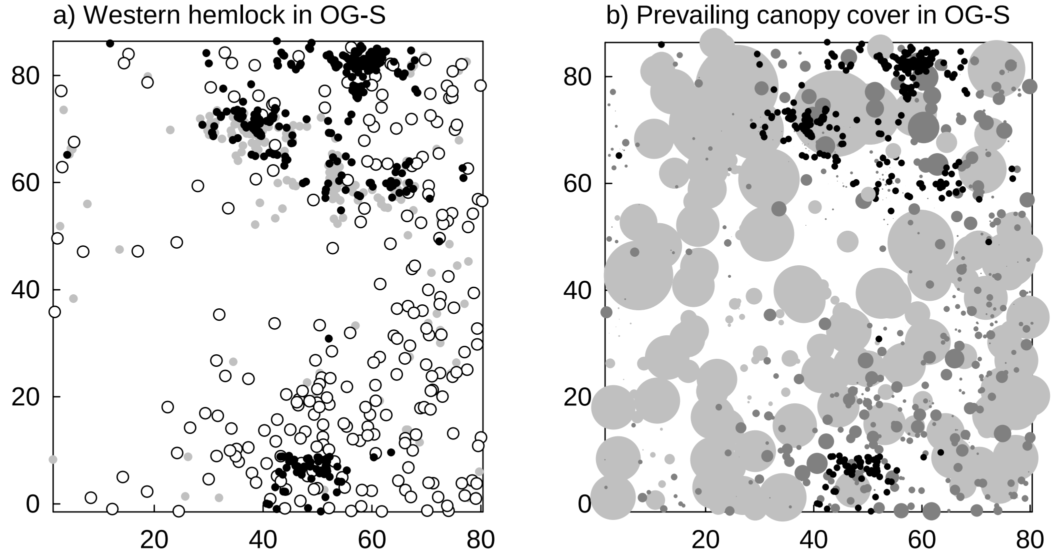
Fig. 1. Western hemlock in old-growth north (OG-N). (a) Spatial distributions of seedlings (black dots), small and large saplings (grey dots) and adult trees (open circles).

(b) Prevailing canopy cover of all other trees, being mainly Douglas-fir (light grey circles) and of western hemlock (dark grey circles), represented by circles with a radius proportionally to the DBH of the trees, shown together with western hemlock seedlings (black dots).

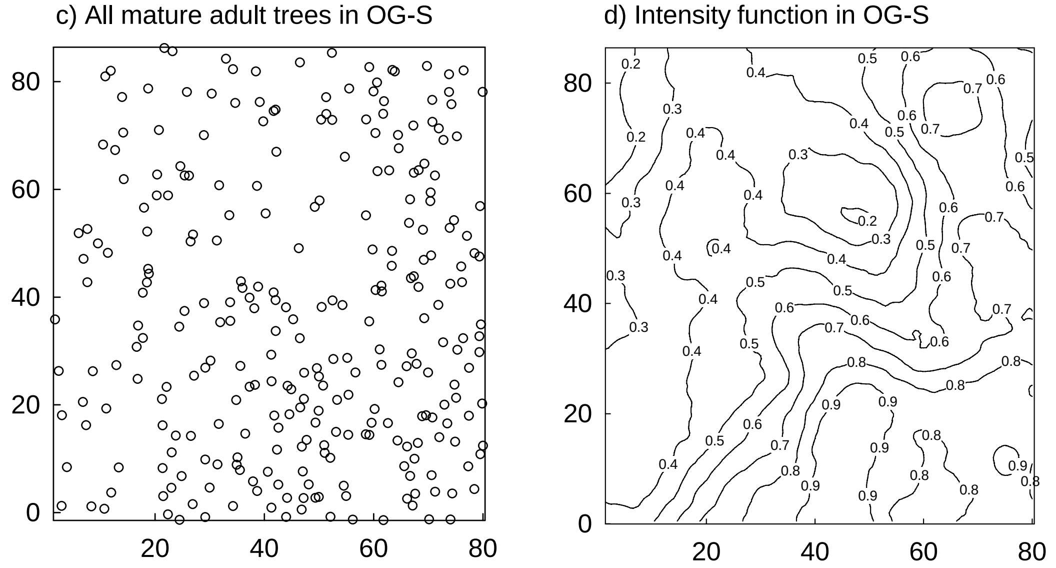
(c) Spatial distribution of stems of all mature adult trees in the plot with a DBH ≥ 15 cm. The unit of x-y-axes is meters.

The old-growth south (OG-S) stand (48°33’ N, 123°38’ W) had an age of 254 years and Douglas-fir a mean DBH of 52.2 cm. This plot on a 40% NNE slope was influenced by large-scale habitat heterogeneity such as edaphic gaps (e.g. rock outcrops or wet drainage sites) with Douglas-fir growing in spatially restricted aggregations (Fig. 2). The plot is at 390 m elevation and has a straight surface profile. The soil is a well-drained Orthic Dystric Brunisol overlain by a mull-like moder humus form (Trofymow *et al.* 1997; Getzin *et al.* 2006).

Data were collected on plots 0.9 ha (OG-N) and 0.7 ha (OG-S) in size. All dead and live trees and seedlings were stem-mapped. DBH was measured at 1.4 m above ground. Including live and dead trees, we classified western hemlock into four basic size classes: (1) “seedlings” below a height of 1.40 m, hence having no measured DBH, (2) “small saplings” with a DBH < 5 cm, (3) “large saplings” from DBH 5 cm to < 10 cm, and (4) “adult trees” with a DBH ≥ 10 cm. We have chosen a DBH ≥ 10 cm for adult hemlock, because regular cone production begins at a relatively young adult age of 25 to 30 years (Burns & Honkala 1990) and because only this cut-off line provided enough spatial data for adequate statistical comparisons between the largest and smaller size classes. However, for the purpose of describing large-scale variation in habitat quality (see next section for details) we defined an extra size class of "all mature adult trees" with a DBH ≥ 15 cm, consisting mainly of pioneer Douglas-fir but including also all other species.


a) Western hemlock in OG-S

b) Prevailing canopy cover in OG-S


c) All mature adult trees in OG-S

d) Intensity function in OG-S

Fig. 2. Western hemlock in old-growth south (OG-S). (a), (b), (c) as in Fig. 1. (d) The intensity function of the distribution of all mature adult trees, normalized between 0 and 1, and estimated using an Epanečnikov kernel with bandwidth 15 m. The unit of x-y-axes is meters.

Spatial pattern analysis

In this study we used the pair-correlation function and Ripley's *K*-function to analyse the spatial pattern of tree distributions (Ripley 1976; Stoyan & Stoyan 1994). Both second-order statistics are based on the distances of all pairs of points of a pattern. For approximately homogeneous patterns, the bivariate *K*-function $K_{12}(r)$ is defined as the expected number of type 2 points within distance r of an arbitrary type 1 point, divided by the intensity λ_2 of pattern 2 (Ripley 1976). The bivariate pair-correlation function $g_{12}(r)$ is related to the derivative of the *K*-function, i.e., $g_{12}(r) = K'_{12}(r)/(2\pi r)$ (Ripley 1976; Stoyan & Stoyan 1994), and due to its non-cumulative properties, $g(r)$ is more suitable for exploratory data analysis (Wiegand & Moloney 2004; Perry *et al.* 2006). However, the *K*-function (or its commonly used transformation, the *L*-function) is cumulative and thus more suitable for the confirmation of null models (Stoyan & Penttinen 2000) and for estimating model parameters when fitting specific point processes to the data, e.g., by the minimum-contrast method (Stoyan & Stoyan 1994; Diggle 2003).

To account for the spatial heterogeneity at the OG-S plot (Fig. 2), we used inhomogeneous second-order statistics recently proposed by Baddeley *et al.* (2000). For construction of inhomogeneous *K*- and *g*-functions, the assumption is made that the observed point pattern resulted from a two-step process, where an initially homogeneous pattern was independently thinned by an inhomogeneous thinning surface (Baddeley *et al.* 2000). The thinning surface $\lambda(x)$ changes with location x and describes the environmental heterogeneity. In our study, $\lambda(x)$ may be related to local habitat quality which determines the large-scale probability of occurrence of trees at specific locations x. This method is well suited for accounting for large-scale environmental trends and $\lambda(x) > 0$ is required inside the study area. If one point of the final heterogeneous pattern is located at location x, we may expect on average $1/\lambda(x)$ points for the initial, pre-thinning, homogeneous pattern at this location. Thus, the inhomogeneous *K*- and *g*-functions may be estimated analogously to homogeneous *K*- and *g*-functions, but by weighting each data point by $1/\lambda(x)$. For example, the estimator of the univariate *K*-function proposed by Ripley is:

$$\lambda \hat{K}(r) = \frac{1}{n}\sum_{i=1}^{n}\sum_{j\neq i}\frac{I_r(d_{ij})}{w_{ij}} \qquad (1)$$

where n is the number of points of the pattern, $\lambda = n/A$ is the intensity of the pattern in the study region of area A, d_{ij} is the distance between points i and j, I_r is a counter variable, $I_r(d_{ij}) = 1$ if $d_{ij} \leq r$, and $I_r(d_{ij}) = 0$ otherwise, and w_{ij} is a weighting factor to correct for edge effects (Ripley 1976, 1981). Re-weighting of the pattern with the thinning surface, by counting for each point in the estimator $1/\lambda(x)$ instead of one, yields:

$$\lambda \hat{K}_I(r) = \frac{1}{n}\sum_{i=1}^{n}\sum_{j\neq i}\left(\frac{1}{\lambda(x_i)}\frac{1}{\lambda(x_j)}\right)\frac{I_r(d_{ij})}{w_{ij}} \qquad (2)$$

where the thinning surface $\lambda(x)$ is normalized to yield $n = \sum[1/\lambda(x_i)]$. If the pattern is homogeneous $\lambda(x) = 1$ for all locations x within the study region, and the inhomogeneous estimator (eq. 2) collapses to the homogeneous estimator (eq. 1). The inhomogeneous *g*-function $g_I(r)$ is defined analogously.

Although theoretically appealing, the problem with inhomogeneous *K*- and *g*-functions is that the thinning surface is in general not known and using an estimate of the intensity of the pattern itself as thinning surface is problematic because in this case, both first- and second-order properties have to be determined from the same pattern simultaneously (Baddeley *et al.* 2000; Diggle 2003). To determine an appropriate thinning surface describing the large-scale environmental heterogeneity for our plots, we used biological arguments and additional information provided by the spatial pattern of all mature adult trees in the plots with DBH ≥ 15 cm (Figs. 1c, 2c). Our hypothesis was that the large-scale intensity of mature adult trees (i.e., above the scale of tree-tree interactions) should be a good indicator of environmentally driven habitat quality, e.g., caused by edaphic variation in soil moisture or nutrients since they have undergone excessive competition and thinning, and are expected to explore all available sites. By using all mature adult trees of all species, we will capture strong environmental habitat factors common to all species but not specific niches of individual species. This is analyzed later in the case-control study (see below section "*Case-control study"*).

Clearly, using inhomogenous *K*- and *g*- functions makes sense only if the thinning surface is inhomogeneous. This means in our case that the pattern of all mature adult trees significantly deviates from a homogeneous Poisson process (CSR). In case of large-scale heterogeneity we would expect a significant departure from this null model at large scales (Wiegand & Moloney 2004). Thus, we first tested the spatial distribution of all mature adult trees for deviation from CSR and then fitted the intensity surface $\lambda(x)$ to the spatial distribution of these trees using an Epanečnikov kernel

$$e_h(d) = \begin{cases} \frac{3}{4h}(1 - \frac{d^2}{h^2}) & -h \le d \le h \\ 0 & \text{otherwise} \end{cases} \qquad (3)$$

recommended by Stoyan & Stoyan (1994). Briefly, for a given location x, the intensity $\lambda(x)$ is constructed by using a moving window with circular shape and radius h around location x and summing up all points in the circle, but weighting them with factor $e_h(d)$ according to their distance d from the focal location x. We selected a bandwidth h larger than the scales at which we expect local point-point interactions, but smaller than the range over which the environmental gradient may vary. All point pattern analyses were done using the grid-based software *Programita* (Wiegand & Moloney 2004).

Explicit cluster processes

Western hemlock is a typically clustering species (He & Ducan 2000). Therefore, we described the distributions of different life-history stages (seedlings to adults, cf. Tables 1 & 2) by fitting a Thomas process to the point pattern. This point process assumes that (1) parent events (i.e., cluster centres) follow a homogeneous Poisson process with intensity ρ, (2) each parent independently produces a random number of offspring following a Poisson distribution and (3) locations of offspring, relative to the parents, have a two-dimensional normal distribution $h(r, \sigma)$ with variance σ^2. The pair-correlation function of the resulting offspring population yields:

$$g(r,\sigma,\rho) = 1 + \frac{1}{\rho}\frac{\exp(-r^2/4\sigma^2)}{4\pi\sigma^2} \qquad (4)$$

The unknown parameters ρ and σ can be fitted by comparing the empirical $\hat{g}(r)$ and $\hat{K}(r)$, or its L-transformation, with the theoretical functions using minimum-contrast methods (Stoyan & Stoyan 1994; Diggle 2003). The cluster size r_C approximately equals twice the standard deviation of the parent - offspring distance (i.e., $r_C \approx 2\sigma$) and includes approximately 87% of the offspring of a given parent. (Note that the 87% arises instead of the commonly known 95.5% since we used here a two-dimensional normal distribution; 95.6% corresponds to 2.5σ). To roughly assess how well the fitted process describes the data we performed 99 Monte Carlo simulations of the fitted process and used the 5th lowest and 5th highest values of $g(r)$ and of the distribution function of the nearest neighbour distances to construct approximately 90% confidence limits (Stoyan & Stoyan 1994; Diggle 2003). Note that this is not a goodness-of-fit test with exact confidence intervals (Loosmore & Ford 2006). As outlined, e.g., by Stoyan and Stoyan (1994: page 300-302), such a test is hypothesis friendly (the parameters are fitted to the data) and because of simultaneous inference the probability of a type I error is not exactly α but larger. To reduce the first problem, we used also the distribution function of the nearest neighbour distances as test statistic (Fig A1, appendix). The pair-correlation function and the nearest neighbour distances evaluate fundamentally different properties of the spatial pattern (Diggle 2003). The α-inflation caused by simultaneous inference is less a concern when using non-cumulative statistics and applies only for cases of weak significance.

In case of a heterogeneous pattern, we calculated the inhomogeneous K- and g-functions. In this case, the fitted parameters of the Thomas process reflect the properties of the pattern before heterogeneous thinning was applied. To test if this model describes the data well, we performed Monte Carlo simulations of the fitted (homogeneous) process to obtain approximately 90% confidence limits for the inhomogeneous g-function.

Seedling to adult relationship

To describe and compare the relationship between seedlings (pattern 2) and adult trees (pattern 1) between the two sites we used the bivariate distribution function of nearest neighbour distances of seedlings around adults (Fig. 6).

Case-control study

To analyse the demographics of western hemlock via direct spatial relationships between different life-history stages, we used a case-control design and random labelling. The advantage of random labelling is that it does not require assumptions about homogeneity of a pattern (Diggle *et al.* in press) and thus, direct corrections for non-homogeneous conditions (as included by our inhomogenous *K*- and *g*-functions) are not necessary. Although our data are not a strict case-control setting, a case-control methodology was, however, applicable because in our working hypothesis we assume that the small-scale pattern of adult trees can be used as a reference for having survived excessive thinning whereas the large-scale pattern reflects the underlying heterogeneity. Due to the relatively early maturation of western hemlock (Burns & Honkala 1990), we used the adult class with DBH $\geq$ 10 cm as “control” and thus, as a surrogate measure for possible variation in large-scale habitat conditions. We compared the pattern of smaller size classes (i.e., the “cases”) relative to the “control” pattern of those long-lived adults. This allowed us to estimate the relative effects of self-thinning and of short-lived regeneration sites within suitable habitat (smaller gaps in the canopy or larger tree-fall gaps) on the pattern of different size classes. Using the adult pattern as control, the clustering of different life-history stages can be compared to reveal changing patterns within the overall clustering of Hw in the homogeneous and heterogeneous old-growth stands.

Under random labelling, *g*- and *K*-functions are invariant, hence we would expect $g_{12}(r) = g_{21}(r) = g_{11}(r) = g_{22}(r)$. Departure from random labelling is assessed by using the differences $g_{12}(r) - g_{11}(r)$ and $g_{21}(r) - g_{22}(r)$, or the corresponding differences of the *L*-functions, as test statistics. With control = pattern 1 and case = pattern 2, a positive difference $g_{12}(r) - g_{11}(r)$ means that cases are (relatively) more frequently found at distance r around controls than controls around controls. Thus, if the cases do not show any pattern additional to that of the control, we would expect $g_{12}(r) - g_{11}(r) \approx 0$ (Getzin *et al.* 2006). Similarly, $g_{21}(r) - g_{22}(r)$ evaluates at different scales r if the controls are (relatively) more (or less) frequent around cases than cases around cases. If there is no different correlation, we expect again that $g_{21}(r) - g_{22}(r) \approx 0$. However, if there would be an additional clustering mechanism of the cases (e.g., regeneration sites), that is independent from the control pattern, this would not be noticed by the test statistic $g_{12}(r) - g_{11}(r)$ but we would expect $g_{21}(r) - g_{22}(r) << 0$. Thus, $g_{12}(r) - g_{11}(r)$ reveals if cases and control follow the same overall pattern, and $g_{21}(r) - g_{22}(r)$ reveals if there is an additional pattern in the cases that is independent from the control pattern of adult trees.

This analysis was done by computing the test statistics from the observed data, then randomly re-sampling sets of n_2 cases from the joined pattern of $(n_1 + n_2)$ points to generate the confidence limits. Significant departure of the test statistics from random labelling was evaluated using 99 Monte Carlo simulations to generate approximately 90% confidence limits.

Results

Environmental heterogeneity

To find out if the two plots showed large-scale heterogeneity, we compared the pattern of all mature adult trees in the plots with DBH ≥ 15 cm to a CSR null model (Fig. 3). Ripley's *L*-function showed no large-scale departure from CSR at the OG-N plot (Fig. 3a), but a clear departure at the OG-S plot (Fig. 3b), which provides first evidence that the OG-S plot exhibits large-scale heterogeneity while the OG-N plot shows large-scale homogeneity. The tendency to regularity at small scales was expected and indicates inter-tree competition. At the OG-N plot, significant regularity occurred up to scales of 1.5 m (Fig. 3a), but otherwise the pair-correlation function well approximated the value $g(r) = 1$, which is expected for a homogeneous pattern. At the OG-S plot, the tendency to regularity was not significant for small scales but significant clustering occurred at scales $r > 6$ m (Fig. 3b).

We therefore used the inhomogeneous *K*- and *g*-function for the cluster analysis with Thomas processes at the OG-S plot, but not at the OG-N plot. We used a bandwidth of $h = 15$ m for the construction of the thinning surface $\lambda(x)$ because this scale was clearly larger than competitive tree-tree interactions and captured the large-scale trend in the intensity of all mature adult trees well (Fig. 2d). However, our results were not sensitive to the selection of larger bandwidths.

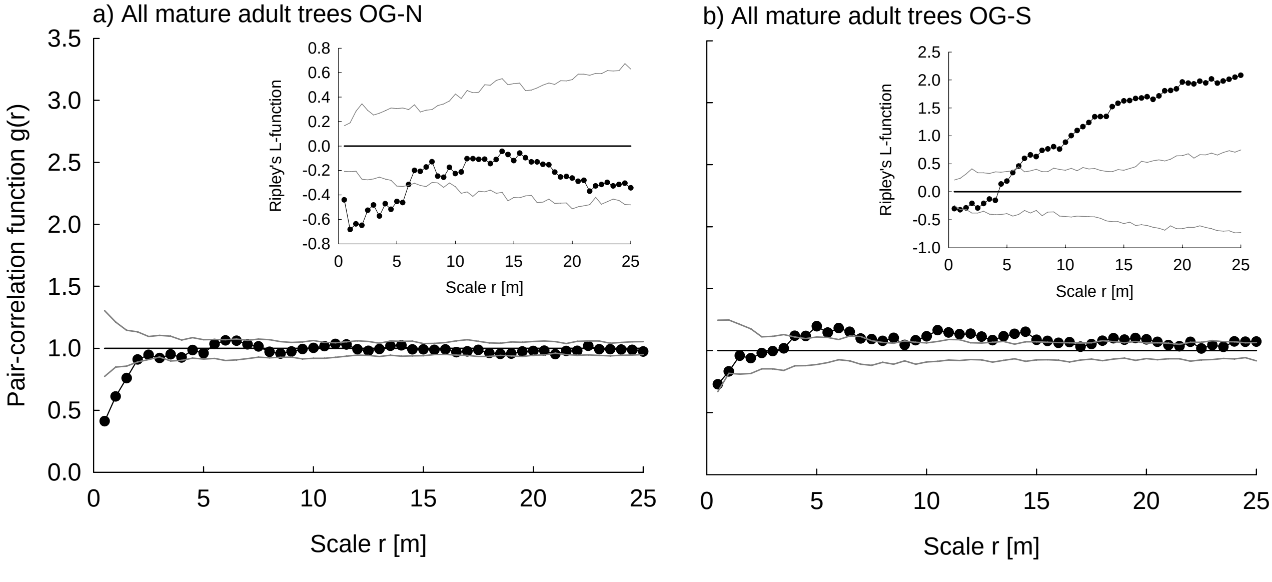


Fig. 3. The pattern of all mature adult trees in the plot with a DBH ≥ 15 cm, contrasted to the null model of complete spatial randomness (CSR). Approximately 90% confidence limits (grey solid lines) were constructed using the 5th-lowest and 5th-highest value of 99 Monte Carlo simulations of the null model. The cell size was 0.5 m × 0.5 m and the ring width for estimation of the pair-correlation function was 1.5 m.

Also the DBH distribution of all mature adult trees differed substantially between both plots (Fig. 4a). At the OG-N plot, the DBH distribution had an absolute maximum at 50 cm and a weak local maximum at small diameters of 15 cm. In contrast, at the OG-S plot, the distribution was bimodal with an absolute maximum at 15 cm and a local maximum at an intermediate size of 80 cm.

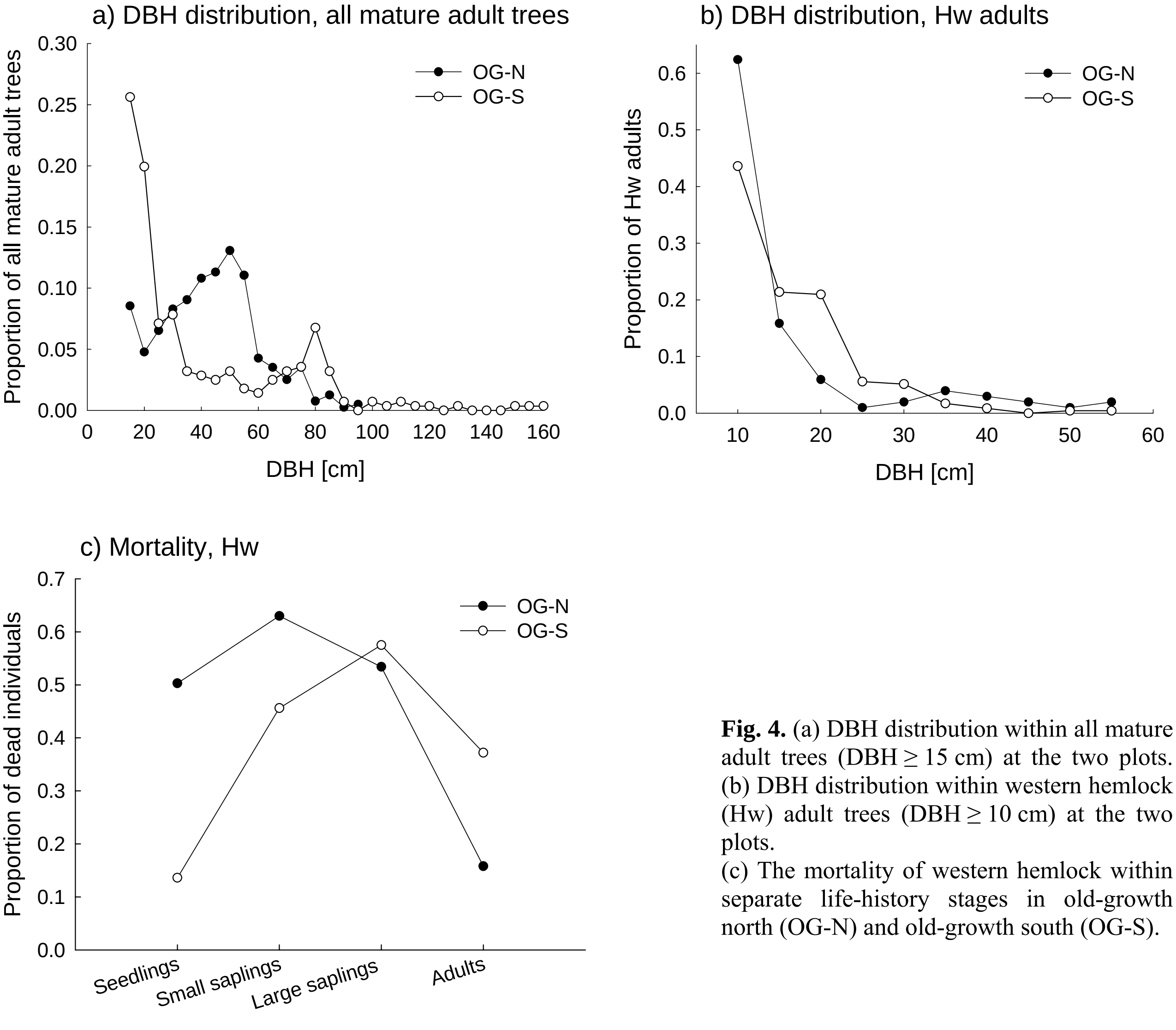


Fig. 4. (a) DBH distribution within all mature adult trees (DBH ≥ 15 cm) at the two plots. (b) DBH distribution within western hemlock (Hw) adult trees (DBH ≥ 10 cm) at the two plots.
(c) The mortality of western hemlock within separate life-history stages in old-growth north (OG-N) and old-growth south (OG-S).

Composition of life-history stages

In the homogeneous OG-N plot, seedlings were less numerous and less dense than seedlings in the heterogeneous OG-S plot (Table 1). The median nearest neighbour (NN) distance between trees in a size class increased overall 2.4-fold from seedlings to adults in OG-N and 6.7-fold in OG-S. With 234 individuals, adult trees were more numerous and denser in OG-S than the 101 adults in OG-N. The mean DBH of adult trees was 18.4 cm in OG-N and 18.1 cm in OG-S. Also, the DBH distribution of Hw adults was nearly equal in both stands, although the OG-S plot was about 70 years younger (Fig. 4b).

In both plots, mortality of Hw was highest in the sapling stages (Fig. 4c). Seedling mortality was 50.3% in OG-N but only 13.6% in OG-S. Initial mortality of seedlings and small saplings was higher in OG-N, but it was lower for large saplings and adults in OG-N, compared to OG-S. Adult mortality was 15.8% in OG-N but 37.2% in OG-S.

Table 1. Composition of different size classes of western hemlock in homogeneous (OG-N) and heterogeneous (OG-S) study regions. NN = nearest neighbour.

	Number of individuals		Mean DBH [cm]		Median NN distance [m]	
Plot	OG-N	OG-S	OG-N	OG-S	OG-N	OG-S
Seedlings	155	382	-	-	1.37	0.31
Small saplings, DBH < 5 cm	443	193	2.8	1.9	1.20	0.89
Large saplings, DBH 5 to < 10	251	120	7.0	7.1	1.92	2.42
Adults, DBH ≥ 10 cm	101	234	18.4	18.1	3.34	2.09

Pattern analysis using Thomas processes and nearest neighbours, OG-N plot

At the OG-N plot, the intensity of clustering, as indicated by the shape of the pair-correlation function, changed only slightly for the different seedling and adult size classes, but was somewhat larger for seedlings (Fig. 5a-d). This parallels the above findings where overall nearest neighbour distances increased only 2.4-fold from seedlings to adults (Table 1).

The Thomas process described the second-order properties of the data well; for OG-N, there was only weak additional small-scale aggregation or repulsion. For seedlings and small saplings, there was significant additional clustering at scales $r < 2.0$ m and $r < 1.0$ m, respectively (Fig. 5a, b), which was probably due to aggregation in small-scale regeneration sites. This aggregation disappeared for large saplings due to self-thinning (Fig. 5c). The significant regularity for adults at scale $r = 1.5$ m indicates required minimal distances for survival under the limiting light conditions of the homogeneous canopy cover (Fig. 5d). Comparing the empirical distribution of nearest neighbour distances with the Monte Carlo simulations shows basically the same results. For seedlings and saplings there was an additional significant small-scale aggregation up to 2 m and 1 m, respectively, not captured by the Thomas process, large saplings followed the Thomas process and for adults there was a significant regularity at scales $r < 2.0$ m (Fig A1, appendix).

The fitted parameters of the Thomas process revealed for OG-N that small and large saplings and adult trees were nearly identically distributed among about 23 clusters (Table 2). The cluster radius decreased with increasing size class. Seedlings showed the largest cluster radius with a size of 18 m.

Inspection of Fig. 1a, which shows that the seedlings are distributed around parent trees, reveals a clear association in the distribution of nearest neighbour distances, measured from adults to seedlings. Figure 6a shows a distinct peak in the distribution of the nearest neighbour distances from seedlings to adults, indicating that about 20% of all adults have a nearest seedling at distance 1 m, but no seedling is further away than 17 m from an adult.

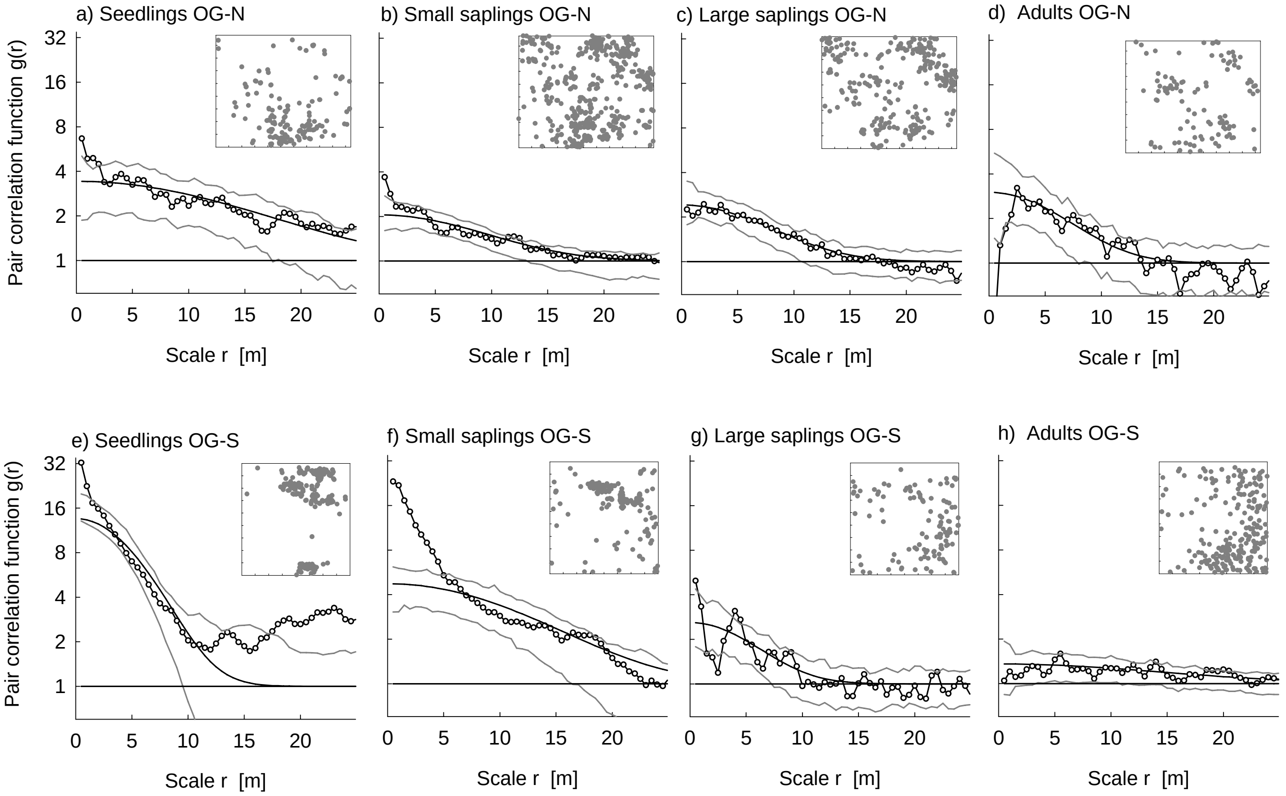


Fig. 5. Results of the univariate analyses fitting a Thomas cluster process to the data of the different size classes of western hemlock (cf. Table 2). Open circles: pair-correlation function of the data (homogeneous *g*-function in a - d and inhomogeneous *g*-function in e - h). Solid black line: best fit with Thomas process. Approximately 90% confidence limits (grey solid lines) were constructed using the 5th-lowest and 5th-highest value of 99 Monte Carlo simulations of the null model. The cell size was 0.5 m × 0.5 m and the ring width for estimation of the *g*-function was 1 m. Please note the logarithmic scaling of the y-axis.

Pattern analysis using Thomas processes and nearest neighbours, OG-S plot

Caused by the heterogeneous conditions in the OG-S plot, the intensity of clustering changed substantially for different size classes (Fig. 5e-h). This parallels the strong 6.7-fold increase in overall nearest neighbour distances from seedlings to adults.

First, there was a very strong clustering of seedlings with a cluster size of 6.6 m (Fig. 5e, Table 2) which was probably caused by the larger canopy gaps in the heterogeneous plot (cf. Fig. 2a, b). In contrast, the lower light levels at the homogenous OG-N plot did not allow for this high density of seedlings. However, similar to the OG-N plot, there was additional significant clustering at a very small scale of r = 1.0 m which may reflect locally favourable regeneration sites. The small saplings retained a very strong clustering at small scales r < 4.5 m (Fig. 5f) but showed a larger scale clustering with radius of about 15 m (Table 2). For large saplings, the strong clustering observed for smaller size classes disappeared and the inhomogeneous pair-correlation function was very similar to that of the homogeneous OG-N plot (cf. Fig. 5c, 5g). This indicates strong self-thinning during the transition from small to large saplings (cf. Fig. 4c). For the adults, no intense clustering was observed and the large cluster radius of 19 m may reflect the large-scale available habitat.

Table 2. Settings and fitted parameters of the Thomas process: $r_{\min}$ and $r_{\max}$ in meters; $2\sigma \approx$ cluster radius in meters; $100\rho \approx$ density of parents; No. parents = No. cluster centres

	OG-N				OG-S			
	Seedlings	Small saplings	Large saplings	Adults	Seedlings	Small saplings	Large saplings	Adults
$r_{\min}$	1.5	1.5	0.5	2.5	2.5	5	0.5	2.5
$r_{\max}$	25	25	25	25	12.5	25	25	35
2σ	18	11.4	9.4	8	6.6	14.9	7	19.3
100ρ	0.0101	0.058	0.0644	0.062	0.0144	0.0096	0.102	0.0615
No. parents	3.7	21.5	23.9	23	4.1	2.7	29	17.5

Comparison of the empirical distribution of nearest neighbour distances with the Monte Carlo simulations shows that the fitted process described the data reasonably well (Fig. A1, e-h; appendix). For small seedlings there was an additional clustering (already apparent from the pair-correlation function) and for distances between 3 - 7 m there were somewhat less nearest neighbours than expected by the null model. The latter appeared also for larger saplings for distances about 6 - 7 m (appendix).

The relationship between adults and seedlings was very different from that for the OG-N plot (Fig. 6). While the adults showed a similar pattern with most nearest neighbours occurring at a distance of some 2 m, the peak for the nearest seedlings at 1 m in the OG-N plot disappeared completely in the OG-S plot which showed an almost uniform distribution for distances < 20 m and a maximal adult-seedling distance at about 50 m (Fig. 6b). However, such extreme values may be an edge effect since we do not know the seedlings and adults outside the plot.

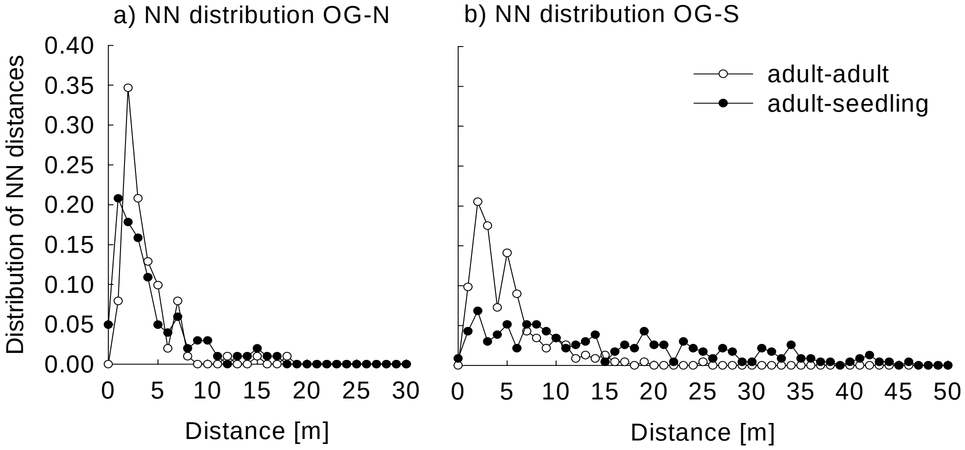


Fig. 6. Analysis of the bivariate nearest-neighbour (NN) distances of seedlings around adult (parent) trees. Filled circles show the (non-accumulated) distribution of the distances of the nearest seedlings to adults, and open circles that of adults to adults.

Pattern analysis using case-control

At the OG-N plot, the case-control analysis showed that the seedlings followed the same pattern as adult trees (Fig. 7a, small figure). Except for the significant clustering of seedlings around adults at scale $r = 0.5$ m, the test statistic $g_{12}(r)$ - $g_{11}(r)$ did not differ significantly from zero. However, the test statistic $g_{21}(r)$ - $g_{22}(r)$ was significantly smaller than zero for almost all scales (Fig. 7a, main figure) indicating an additional clustering of the seedlings independent from the adult pattern (probably some smaller gaps in the canopy). For small saplings, the additional clustering became much weaker (Fig. 7b) which indicates early effects of self-thinning (cf. Fig 4c). This clustering disappeared for large saplings (Fig. 7c).

Departures from random labelling were more obvious at the heterogeneous OG-S plot than at the homogeneous OG-N plot. The test statistic $g_{12}(r)$ - $g_{11}(r)$ did not differ significantly from zero for the smaller scales (Fig. 7d, small figure) which indicates that seedlings followed the same pattern as adults. As a consequence of spatially restricted clustering of seedlings in gaps, adults were more frequently around adults than seedlings around adults at larger scales. Due to distinct gaps in OG-S, there was a very strong clustering, independent from the adult pattern (Fig. 7d), yielding a significantly negative test statistic $g_{21}(r)$ - $g_{22}(r)$. In contrast to the OG-N plot, this strong clustering persisted into the small sapling stage (Fig. 7e) but disappeared due to strong self-thinning for the larger saplings stage (Fig. 7f).

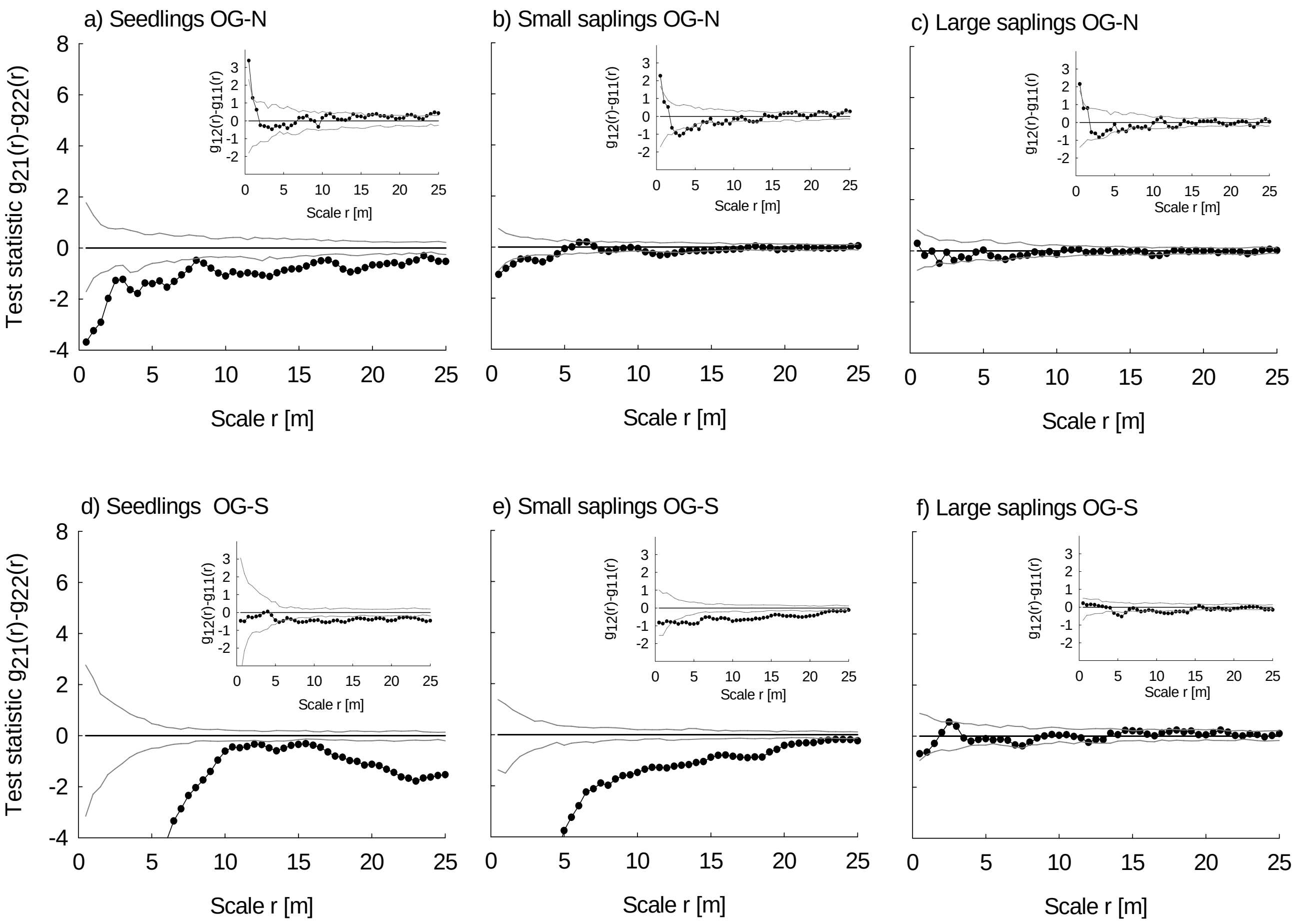


Fig. 7. Case-control study of western hemlock where the larger-scale pattern of adult trees (pattern 1) serves as control pattern which corrects for possible heterogeneity in biotic and abiotic habitat quality. The test statistic $g_{12}(r)$ - $g_{11}(r)$ evaluates if points of the case pattern follow the pattern of the control. If this is the case $g_{12}(r)$ - $g_{11}(r) \approx 0$. The test statistic $g_{21}(r)$ - $g_{22}(r)$ evaluates if there is an additional clustering in the cases (the three size classes) which is independent from the pattern of control. In this case $g_{21}(r)$ - $g_{22}(r) << 0$.

Discussion

Dispersal strategies and the seedling stage

In our two contrasting study sites we found markedly different distribution patterns of western hemlock seedlings. Under homogeneous site conditions, seedling clusters were large, seedling densities were low but mortality was high. In the heterogeneous stand the opposite occurred. Recently, Ronce *et al.* (2005) proposed that plasticity in seed dispersal would be primarily due to population age. Since their model findings of increased dispersal distances with increased age was not supported by empirical studies, they highlighted the importance to investigate the effects of environmental heterogeneity. In our study, we focused on habitat heterogeneity and its effects on species survival and patterns. Bolker & Pacala (1999) hypothesized that a species with intermediate dispersal may simultaneously operate with two different spatial strategies to exploit different aspects of the spatial community structure during succession. The "colonizing strategy" with long-range dispersal is enhanced when small gaps in the evenly spaced resident distribution (e.g. Douglas-fir in OG-N) provide space for colonization. However, in stands with strong spatial structure (e.g. Douglas-fir in OG-S), the "phalanx strategy" with short-range dispersal is greatly favoured when a shade-tolerant tree species is a superior inter-specific competitor. Then the species gains advantage through increasing its local density because heterospecific competitors will be excluded by filling its neighbourhood with its own offspring. This dual strategy combining mostly short-range dispersal with a few long-dispersing propagules would also give the largest increase in variance in the mean environment, with the smallest decrease in performance (Bolker & Pacala 1999). Although dispersal is a passive mechanism, here we found strong empirical support for this hypothesis.

In the homogeneous stand, the seedling pattern reflects more specific limitations in dispersal, independent of large-scale environmental conditions. The large dispersal kernel of around 18 m radius in OG-N agrees with similar findings from British Columbia (LePage *et al.* 2000). This wide scattering of seedlings was possible because under the even distribution of Douglas-fir, relatively small canopy openings provided weak but homogeneous light conditions (He & Duncan 2000). In contrast, the dispersal radius in OG-S was a third of that in OG-N but seedling densities within the clusters were more than double. The smaller dispersal kernel in the heterogeneous stand reflects the limiting size of survival templates in distinct tree-fall gaps. In this stand, obstacles such as rock outcrops or wet drainage sites either restricted growth of any tree or most of the available resource patches had been already covered by aggregated pioneer Douglas-fir (Getzin *et al.* 2006). Only where self-thinning provided large solitary tree-fall gaps, hemlock seedlings were able to succeed. Consequently, the spatially confined establishment niches for colonizing hemlock were the result of both, large-scale abiotic heterogeneity of the landscape and biotic feedback from the dense growth of early-successional Douglas-fir within the suitable habitat. This led to the much weaker association of seedlings around nearest neighbouring adults in OG-S and also to the strong additional spatial structure of seedlings and small saplings, as inferred from the case-control study.

Despite the wide dispersal and establishment ability under more homogeneous canopy cover in OG-N, mortality of seedlings was much lower in distinct gaps of OG-S. These findings agree with other studies (Huff 1995; Moeur 1997; LePage *et al.* 2000), suggesting that recruitment in tree-fall gaps enhances initial survival of hemlock, whereas the opposite occurs under more shady cover. For such northern temperate forests, Coates (2002) has shown that favourable locations for emergence and early establishment are less favourable for growth and survival of seedlings. This would explain the high mortality and low density of seedlings in OG-N, although wide dispersal and early establishment were principally possible. In comparison with other species and as the primary successor in Douglas-fir forest (Huff 1995), western hemlock seems to follow an intermediate dispersal strategy being spatially more segregated than the globally dispersing pioneer Douglas-fir, but less segregated than western redcedar (Getzin *et al.* 2006). This dual dispersal strategy enables hemlock to have always sufficient seedlings under a gradient from closed to fully open canopy (LePage *et al.* 2000; Coates 2002).

Demographics and intra-specific competition

Once seedlings have survived, density-dependent mortality was in both stands highest in the sapling stages. These results agree with an analysis of the entire southern chronosequence where self-thinning effects in Hw were strongest during its early colonization of immature and mature Douglas-fir stands (Getzin *et al.* 2006). However, some marked differences in the demographics occurred in both old-growth plots. Due to lower light levels under homogeneous canopy cover, density-dependent mortality peaked in OG-N at the early transition from seedlings to small saplings with overall mortalities being considerably higher than in OG-S. For increasing size-classes, this probably led to the continuous shrinking of the cluster radius around the limiting survival niches under relatively small canopy openings. In the favourable but densely packed tree-fall gaps of the heterogeneous stand, self-thinning effects were stronger and peaked later at the transition from small to large saplings (see also Moeur 1997). The price for the "phalanx strategy" with strong clustering was a higher adult mortality, although the absolute number of adult trees was more than double in OG-S than in OG-N. Surprisingly, the mean DBH and the DBH distribution of adult hemlock were nearly the same in both stands. Although the OG-S plot was about 70 years younger, largest hemlock were as large as in the older OG-N plot.

These findings support model predictions by Bolker & Pacala (1999): intra-specific competition and its outcome seems to be intensified under heterogeneous conditions with strong spatial structures. Although the cause for endogenous spatial structure was more due to biotic than to abiotic factors in their model, we agree with their general hypothesis that ecological dynamics may be faster in heterogeneous communities. This became also evident from the DBH distribution of all mature adult trees (mainly Douglas-fir) in the plots. Competitive interactions among mature adults were more balanced at the homogeneous OG-N plot, which led to regularly spaced Douglas-fir (He & Duncan 2000) and which limited maximal size of individuals to < 100 cm DBH. In contrast, at the younger OG-S plot environmental heterogeneity did not allow for equilibrated competition, leading to both more smaller and more larger trees, allowing sizes up to 160 cm DBH and a lower mortality of Douglas-fir than in OG-N (Getzin *et al.* 2006). Whereas the homogeneous site conditions led more to 'scramble' competition, edaphic gaps of the heterogeneous plot led to size-structured, asymmetric 'contest' competition (Colasanti & Hunt 1997) with stronger ecological dynamics and more tree-fall gaps.

The intensified ecological dynamics of the heterogeneous stand were also reflected by the variable number of cluster centres for different life-history stages that allow the reconstruction of previous gap dynamics. In contrast, the more stable homogeneous stand had a constant number of about 23 cluster centres for the two sapling stages and adults. The large cluster radius for adults in OG-S seems to represent the cumulative emergence of tree-fall gaps in space and likewise the successful growth of relatively many trees into the adult stage. For maturation over time, heterogeneous site conditions demanding the "phalanx strategy" appear to be more rewarding for the succession of hemlock, because heterospecific contact may be increased (Levine & Murrell 2003) and heavy seed crops are produced at short intervals of three to four years (Burns & Honkala 1990). Due to the short intervals between heavy seed crops and initial high survival in dense seedling clusters, the temporal emergence of cohorts should happen relatively synchronized in space. Although we focus here only on one particular colonizer species, these findings support the hypothesis of Chesson (2000) that the “spatial storage effect” is more important than the “temporal storage effect” (Warner & Chesson 1985). This is because the spatial storage effect is inevitable under realistic scenarios as it accounts for both concepts of spatial and spatio-temporal niches (Amarasekare 2003; Roxburgh *et al.* 2004).

Recent models have shown that coexistence in heterogeneous environments is more facilitated by short-range than by long-range seed dispersal and that species should adapt to these transient scales of favourable habitat with leptokurtic dispersal kernels (Hovestadt *et al.* 2001; Snyder & Chesson 2003). From a niche differentiation perspective, this is because short-range dispersal enhances the effects of environmental variation on scales longer than typical dispersal distances (Snyder & Chesson 2003). We propose that western hemlock is such a species with a leptokurtic dispersal kernel, being primarily adapted to gap dynamics with short-range dispersal, but to be also able to colonize new suitable sites with a few long-dispersing propagules.

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Appendix

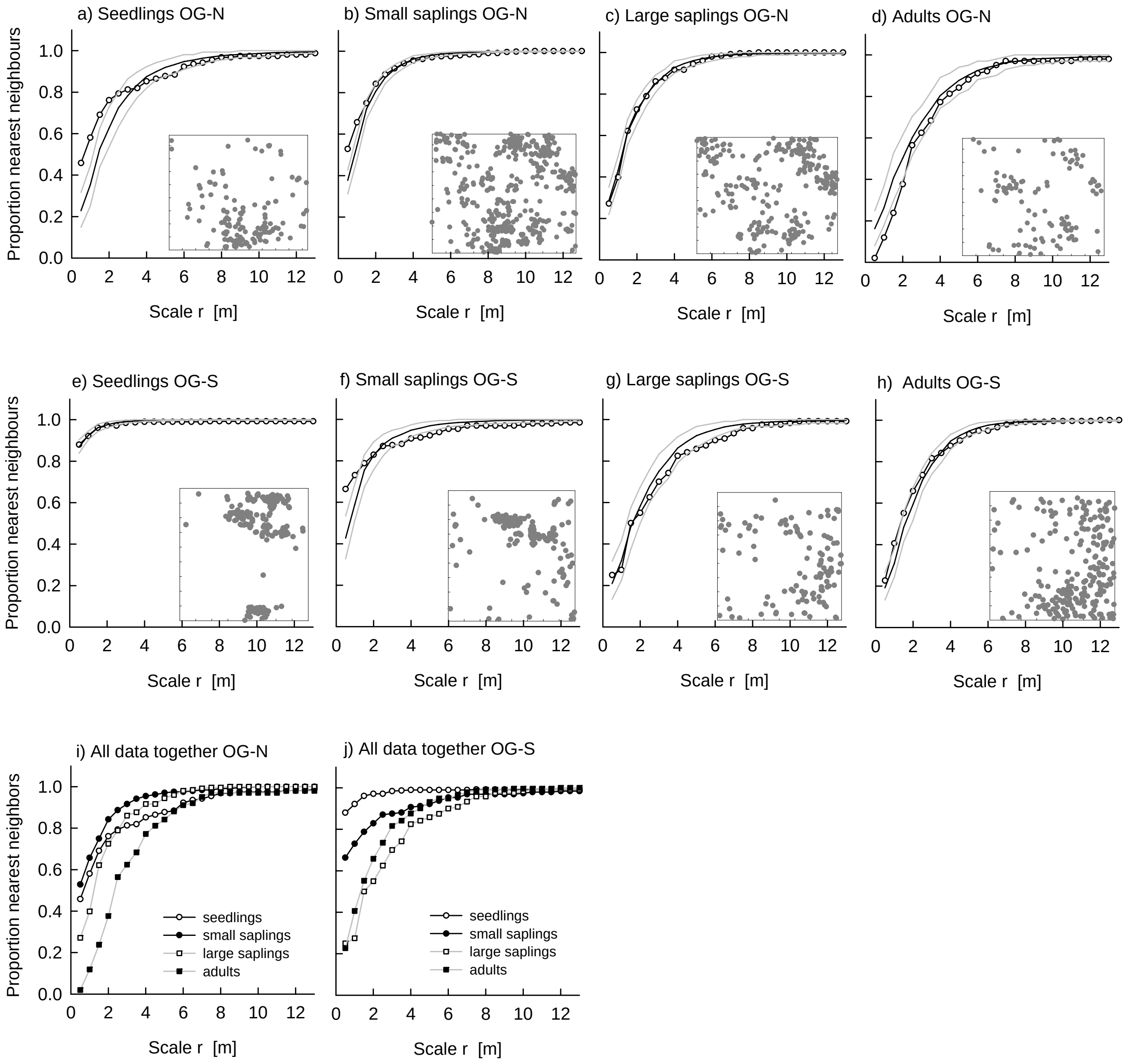

Fig. A1. The distribution function of the nearest neighbour distances (open circles) with the mean (solid black line). Approximately 90% confidence limits (grey solid lines) were constructed using the 5th-lowest and 5th-highest value of 99 Monte Carlo simulations of the null model.

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CHAPTER 3

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.

Keywords: Coniferous/deciduous stands, crown vector, Douglas-fir, g-function, light heterogeneity, slope

Introduction

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

Although second-order analyses of canopy distributions are still scarce, it is thought that regular crown patterns with even-spaced crown centres would be optimal to maximise light harvesting (Kuuluvainen and Pukkala, 1987; Umeki, 1995a, 1995c; 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 on 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.

Materials and methods

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 c. 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 c. 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 900-1100 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.

Data collection

Data were collected in summer 2004. For each plot, we established a rectangle and adjusted its dimension to record at least one hundred 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.

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*).

Results

Both in deciduous and coniferous forest, 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).

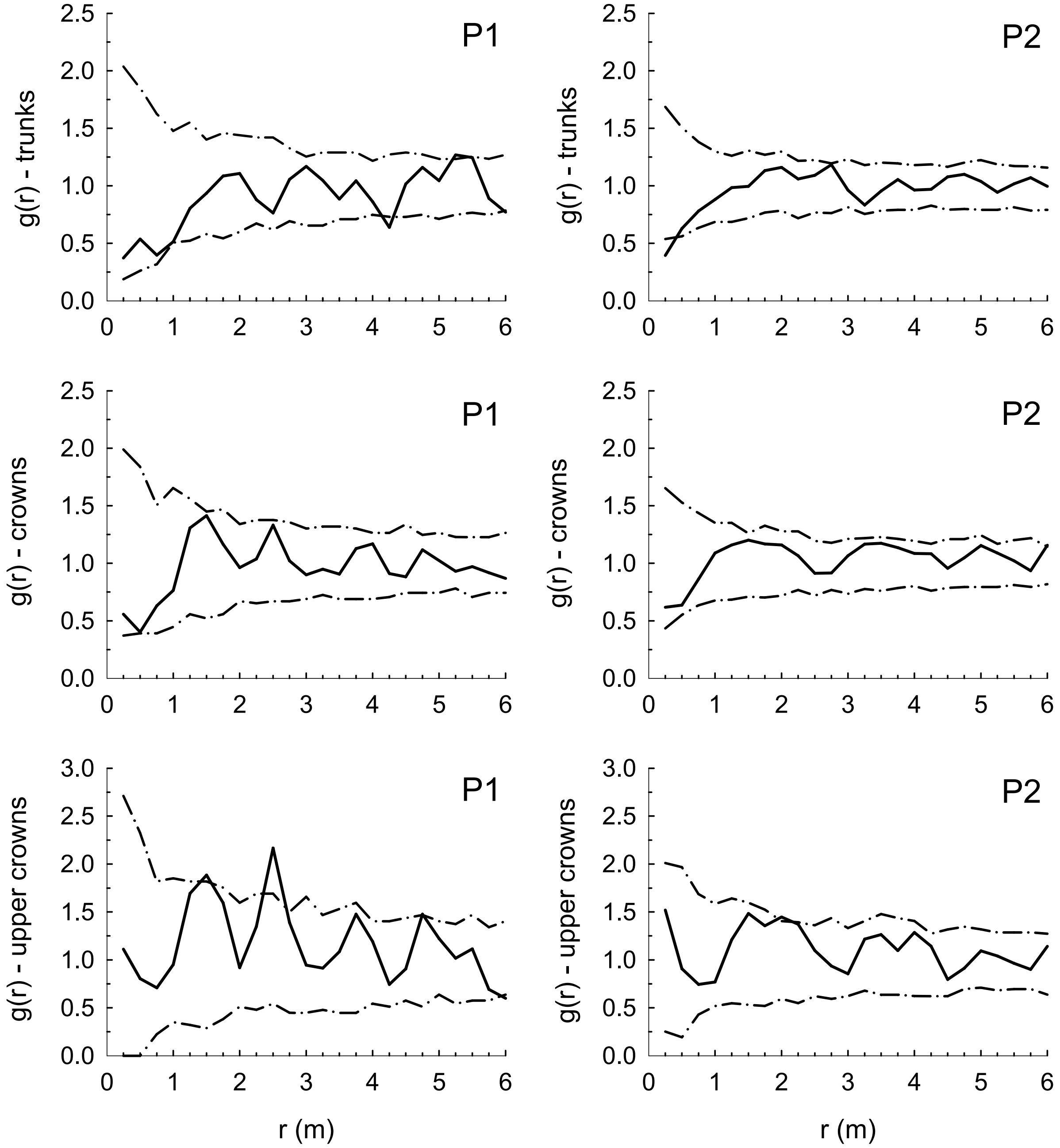
Table 1. Stand structure of the four plots. Only live trees were used to investigate crown-trunk relations and asymmetric growth. *CV* = Coefficient of variation.

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

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 to 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.



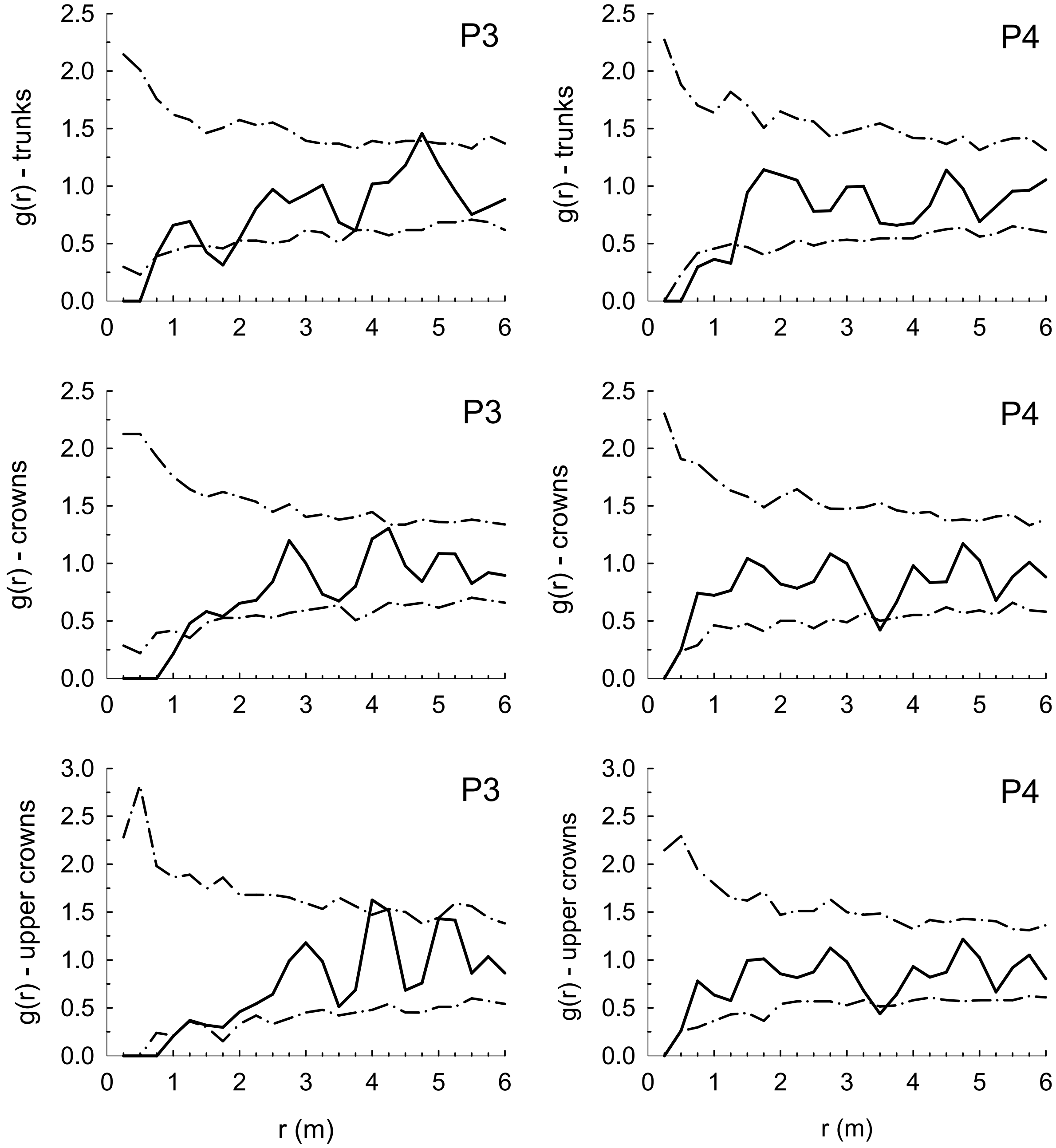


Fig. 1. Point pattern analyses of trunks, crown centres, and only upper crown centres in deciduous forest (P1, P2) and coniferous forest (P3, P4). We used the univariate *g*-function (solid line) and approximately 95% upper and lower confidence envelopes of the null model CSR (broken line) to analyse the patterns. Solid lines below the CSR null model indicate regular patterns (repulsion), *g*(*r*)-values above indicate significant clumping (attraction).

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). 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.

Table 2. The extent of asymmetric growth. *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).

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	

Table 3. The coefficients of determination (r^2) of nearest neighbour regressions. Regressions are linear regressions between dependent variables (Dbh, Crown radius, Crown vector length, Difference in growth angle α to mean angle 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 levels of correlations are **p* < 0.05, ***p* < 0.01 and ****p* < 0.001.

Linear regression	Deciduous forest		Coniferous forest	
Mean of 3 NN distances	Plot 1	Plot 2	Plot 3	Plot 4
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	Plot 1	Plot 2	Plot 3	Plot 4
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

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 $\overline{\phi}$ of the three nearest neighbours, and the variance of the angles of the neighbours. Hence, the extent and direction of asymmetric 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.

Table 4. The direction of asymmetric growth analysed with circular statistics. For Plot 3, the null hypothesis of uniformity could not be rejected, making V tests unnecessary. Significance levels are $^{**}p < 0.01$ and $^{***}p < 0.001$.

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°

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 composition, 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 to 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.

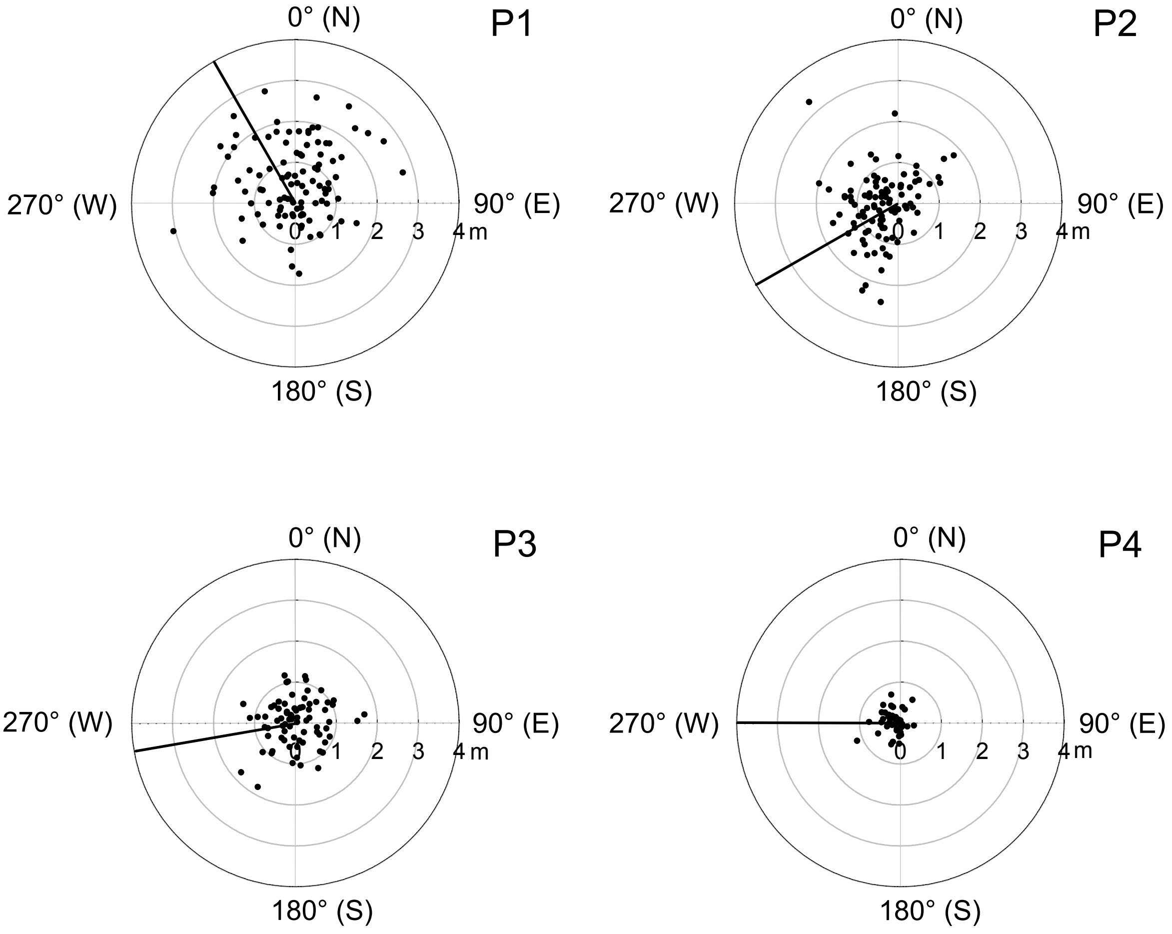


Fig. 2. Extent and direction of asymmetric growth in deciduous forest (P1, P2) and coniferous forest (P3, P4). Black dots show the individual locations of crown centres in relation to their stem-base position (centre of cross). Black lines within polar plots indicate the downward direction of slopes.

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 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.

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-scale 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?

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CHAPTER 4

Competition at stand and individual species levels assessed from field-measured and photo-derived crown extent

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Summary

1. The detection and quantification of competition is important in forest management because competition reduces growth and induces mortality. This is of interest to timber production of whole stands at larger scales, and to foster biodiversity at the individual species level.

2. At the stand level, past studies have evaluated competition with scale-dependent correlation functions, applied to tree-size attributes (continuous marks) such as diameter at breast height or tree height. Despite the fast reaction of foliage to neighborhood density, horizontal crown extent has obviously not been used in such analyses of marked point patterns. Thus, we apply the scale-dependent mark-correlation function (MCF) to field-measured horizontal crown extent. We also demonstrate how individual tree crown (ITC) delineation from aerial images can be used to monitor competitive dynamics with the MCF. At the species level, crown extent in response to neighborhood density can be used to detect competitive abilities of species. In contrast to previous, size-independent methods, we apply quantile regression to detect size-dependent competitive abilities of minor and major tree species. These analyses are conducted for four German forest stands.

3. At the stand level, the MCF was very sensitive in detecting competition via negative correlation of crown area. The temporal change in density-dependent effects was traced back and well described with the MCF when orthophotos of a Douglas-fir stand were compared between 2002 and 2005.

4. At the species level, we demonstrated the power of quantile regression to determine multiple rates of change (slopes) in the response of crown extent to neighborhood density. The major tree species were stronger competitors with more shallow slopes in most size classes.

Minor tree species showed generally steeper slopes and were most suppressed in their largest size classes.

Synthesis and applications. In this research, we demonstrate the sensitivity of modern statistical tools for the evaluation of scale- and size-dependent competition. In particular, we consider use of the MCF for remotely-sensed forest inventory as convenient to monitor competition and plan thinning activities. At the individual species level, quantile regression is shown to reveal different competitive abilities for species and with respect to tree size.

Key-words: crown area, Douglas-fir, forest monitoring, ITC, mark-correlation function, quantile regression, remote sensing, wild cherry, wild service tree

Introduction

There are two contrasting trends in the exploratory analysis of spatial forest growth, one focusing on the stand and one on the individual species level. Forest stand dynamics is generally quantified in terms of biomass, height, foliage damage, or competition and on a wide range of spatial and temporal scales. Technical advances, such as laser-based survey stations, allow to digitize large plots in the form of fully mapped stem-base positions. More recently, large-scale data acquisition based on remotely sensed images has revolutionized forest inventory (Gougeon 1995; Nelson, Niemann & Wulder 2002; Popescu, Wynne & Nelson 2003; Read *et al.* 2003; Wulder *et al.* 2004; Couteron *et al.* 2005). Likewise, the analysis of such complex data sets is now possible using advanced statistics, including scale-dependent correlation functions (Getis & Franklin 1987; Chen & Bradshaw 1999; Wiegand, Jeltsch & Ward 2000; Getzin *et al.* 2006) or geostatistical methods (Köhl & Gertner 1997; Kint *et al.* 2003). The second trend is to gain more insight into specific growth responses of individual tree species in competitive neighborhoods. Here, the application of refined regression models has greatly improved our knowledge (Biging & Dobbertin 1992; Bechtold 2003; Grote 2003; Kalliovirta & Tokola 2005). The detection and evaluation of competition processes is of major interest to forest science because competition reduces growth or induces density-dependent mortality (Weigelt & Jolliffe 2003).

At the stand level, competition can be detected via increased inter-tree distances due to natural thinning (Perry, Miller & Enright 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 (Getzin *et al.* 2006). However, distance is frequently not suitable to detect competition because changes in neighborhood densities may be compensated by variable growth rates and modular plasticity (Shi & Zhang 2003). Also, trees can have an inherent tendency to form clumps (Peterson & Squiers 1995), or a patchy size-class distribution may prevent the formation of more regular patterns (Dovčiak, Frelich & Reich 2001). In managed forests, a regular trunk pattern may just reflect a man-made planting scheme. Even if the more dynamic crown centroids instead of the trunks are used to analyze competition via inter-tree distances, random and not regular crown patterns may dominate and thus mask competitive interaction (Koukoulas & Blackburn 2005; Getzin & Wiegand in revision). A more promising approach is to complement tree position by quantitative size attributes (continuous marks), i.e. to use marked point patterns (Stoyan 1984). In such analyses, correlation between the marks at different points conditional on the inter-point distances characterizes negative or positive relations between plants. So far, continuous marks such as diameter at breast height and tree height have been successfully used to quantify spatial scales of competition for genuine point locations, using methods such as the mark-correlation function, weighted Ripley's *K*-function, or spatial autocorrelation (Penttinen, Stoyan & Henttonen 1992; Capobianco & Renshaw 1998; Mateu, Usó & Montes 1998; Wells & Getis 1999; Pommerening 2002; Shi & Zhang 2003; Doležal *et al.* 2006). However, evaluation of competition via scale-dependent correlation of horizontal crown extent is, to the knowledge of the authors, a new approach in the spatial analysis of marked point patterns.

Here, we will apply the mark-correlation function using the attribute "crown area" because foliage reacts faster to gap dynamics or limiting changes in the local neighborhood than stem size (Hamilton 1969; Rudnicki, Lieffers & Silins 2003; Grote & Reiter 2004). Therefore, mutual growth reduction under competition should be well recognizable via the spatial scale and degree of negative correlation in crown extent (Biging & Dobbertin 1995; Kalliovirta & Tokola 2005). This method should be of particular interest to large-scale monitoring of forest stands using satellite or aerial images. Recent developments in automated tree-crown delineation have considerably advanced so that precise measurement of crown surface area is possible (Gougeon 1995; Gougeon & Leckie 2003; Leckie *et al.* 2003; Wang, Gong & Biging 2004).

Besides this large-scale interest of forest inventory analysis, there is increasing research attention to growth performance and competitive ability of individual tree species. Here, the refinement of regression techniques is of particular interest to improve the predictive power for timber production (Gill, Biging & Murphy 2000; Bechtold 2003; Grote 2003) or to better understand the biomass increase and competitive ability of species for biodiversity management (Cade, Terell & Schroeder 1999; Vettenranta 1999; Fang 2005; Guisan *et al.* 2006). For biodiversity management, foresters need to know how dominant major and suppressed minor tree species respond, due to differential competitive ability, to changing neighborhood densities (Jack & Long 1991). Characterization of the competitive ability with competition indices is problematic because indices should be independent of potential growth, which is rarely met (Biging & Dobbertin 1992). For growth-competition experiments, there are new statistical methods to quantify size-dependent changes in competitive ability (Lamb, Cahill & Dale 2006). Here, we propose to use quantile regression (Cade & Noon 2003) to detect size-dependent competitive differences between tree species. Quantile regression has not often been applied by naturalists but is considered one of the most promising non-standard methods in ecology (Guisan *et al.* 2006).

Our primary goal is to suggest novel application of statistical tools for detecting competition at stand and species levels. At the stand level, we will introduce the use of the mark-correlation function to quantify scale-dependent competition via horizontal crown extent. At the species level, we will use quantile regression to differentiate between size-dependent competitive response abilities of major and minor tree species. Suitability of these methods will be shown based on examples of four German stands with deciduous and coniferous tree species.

Materials and methods

Study areas

Two 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 c. 50 year old common ash (*Fraxinus excelsior* L.; 48 % of live trees) and wild cherry (*Prunus avium* L.; 18 %). Common ash is a dominant major tree species. Wild cherry is a minor species with an average proportion of 0.01 % in Thuringian state forest (W. Arenhövel, pers. comm.). Minor tree species have usually a proportion of less than 20% in stands, but for statistical reasons of this study we have chosen plots where their proportion is relatively large. 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 copse-like low forest of c. 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. Durmast oak is a dominant major and wild service tree is a minor tree species. Unlike typical high forest, the copse-like low forest was favorable for this minor species. Less common species in P2 are European cornel (*Cornus mas* L.; 15 %) or field maple (*Acer campestre* L.; 8 %). Stand density in P2 is 2459 trees/ha.

Two plots with coniferous trees are in the Thuringian Forest on acidic soils and moderate slopes with an annual precipitation ranging between 900-1100 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%). Douglas-fir was introduced to Germany in the 1870s and has a proportion of only 0.3% in Thuringian state forest. Therefore, Douglas-fir is considered a minor tree species. Douglas-fir has been planted in a regular grid 53 years ago and spruce in irregular groups. Stand density in P3 is 953 trees/ha. This plot has 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 Douglas-fir, which have been planted in a regular grid 41 years ago. Stand density in P4 is 2632 trees/ha. All four plots have not been thinned during several decades. Additional information on the plots can be found in Getzin & Wiegand (in revision).

Field measurements and photo analysis

Field data were collected in summer 2004. For each plot, we established a rectangle and adjusted its dimension to record at least one hundred live and dead 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, Boose & Lezberg (1998). Smaller trees or seedlings were not recorded. 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 as 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 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. We determined the vertical projections from branch tips to the ground without technical aid. However, the 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).

We used two monochrome high-resolution orthophotos (20 cm/pixel) for aerial image analysis of Plot 4. For the other plots, no suitable orthophotos were available. 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 was near the centre of the image.

Automated tree crown delineation of the digitized and fully geo-referenced TIFF images was done using ITC (Individual Tree Crown) software (Gougeon 1995; Gougeon & Leckie 2003). We determined the crown centroids and crown surface area of returned shape files using ArcGIS 8.2. An exact crown-crown match with field-measured trees was not of interest because focus of this analysis was an exact comparison between photo-derived crown delineations of the years 2002 and 2005. All returned polygons with a crown area < 1 m^2 were excluded from the analysis because they were smaller than the smallest field-measured data. This inaccuracy for small crowns was mainly due to image noise or the star-like crown shape of Douglas-fir, which is tricky to delineate. Then, canopy cover was calculated as the percent forest area occupied by the vertical projection of crown surface areas (Gill, Biging & Murphy 2000).

Analysis of competition in stands

We applied the mark-correlation function (MCF) to the marked point pattern of all crown centroids and respective crown areas in a plot, as determined from field-measured and photo-derived data. The MCF (Stoyan 1984) of a marked point process X 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 which assesses the similarity or dissimilarity of the tree's marks. This relationship is quantified by $f(m_1,m_2)$ where f is defined as $f(m_1,m_2) = m_1 * m_2$ 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 $\kappa_{mm}(r)$ (details in Stoyan & Stoyan 1994). If $\kappa_{mm}(r) = 1$, marks are independent at scales r, if $\kappa_{mm}(r) < 1$, there is negative correlation between the marks at scale r. Significant departure from independence of the marks was assessed based on approximately 95% confidence limits. These confidence limits were 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 & Stoyan 1994, pp. 300-302).

Analysis of competition in individual tree species

We investigated the allometric relationship between DBH and crown radius (CR), and between DBH and TH using ordinary least squares regression for the major and minor tree species. Here, we used crown radius as measure of crown extent for better comparability with many other studies (e.g. Jack & Long 1991; Gill, Biging & Murphy 2000; Hummel 2000; Bechtold 2003; Grote 2003; Kalliovirta & Tokola 2005). After Kolmogorov-Smirnov tests that confirmed normal distributions for DBH, CR, and TH, we tested the averages of these variables for significant difference between minor and major tree species within a plot, using a *t*-test for independent samples.

Hierarchies in the response to competition entail differential abilities of species to avoid being suppressed by their neighbors (Weigelt & Jolliffe 2003). If intra-specific competition is negligible, the slope of a regression of mean individual performance of the target species on density of neighbors is a competition coefficient (Goldberg & Landa 1991). This coefficient can be interpreted as the response of the target species to one individual of the neighbor. For comparisons, target species with shallower slopes show a smaller decrease in performance (plant size) for a given increase in neighborhood density and are thus, better competitors (Goldberg & Landa 1991). Their competitive response ability to one individual of the neighbor is greater. We compared competitive response abilities for minor and major tree species using regressions between CR (dependent variable) and increasing neighborhood density. Here, we used the mean distance between the trunk of a focal tree to the three nearest neighboring (NN) trunks as measure for "neighborhood density".

We applied quantile regression as a novel approach to assess size-dependent competitive response of species. Quantile regression was considered adequate because competitive response to neighborhood density is dependent on individual tree species and on tree size, which in combination may lead to unequal variation in the response variable (Fang 2005; Meyer *et al.* 2005). Quantile regression estimates multiple rates of change (slopes) from the minimum to the maximum response to give a more complete picture of the underlying processes (Cade & Noon 2003). Such details are usually missed in standard regression because the typical focus on the mean of the response variable may be less informative than a focus on rates of change in quantiles near the maximum response (Cade, Terell & Schroeder 1999). The 0.90th quantile (also described as $\tau = 0.90$, or 90th percentile) is an estimate such that 90% of the observations are less and 10% are greater than the estimate. The 50th percentile represents the center of the distribution and is thus, an estimate of the median. We analyzed multiple rates of change for the 10th, 25th, 50th, 75th, and 90th percentile of the data. Lower quantiles represent slopes for smaller, higher quantiles represent slopes for larger individuals with larger crown radii. For hypothesis testing and judging the data basis of quantiles, we used the rank-test inversion approach (Koenker 1994) to construct approximately 90% confidence limits for estimates of the quantile slopes $b_1(\tau)$. Upper confidence limits with values smaller than zero indicate that slopes of these quantiles are significantly smaller than zero. All analyses were done using *R*-software with the packages *Spatstat* and *Quantreg*.

Results

Competition in stands

For field-measured crown extent in P1, the mark-correlation function showed at all scales independence of the marks "crown area" (Fig. 1a). For the other deciduous stand, P2, crown area was significantly negatively correlated at scales between *r* = 0.11 m to *r* = 1.15 m, indicating growth reduction under competition at small scales (Fig. 1b). For the coniferous stand P3, crown area was significantly negatively correlated at larger scales between *r* = 1.32 m to *r* = 4.57 m (Fig. 1c). In P4 with only Douglas-fir, crown area was uncorrelated at nearly all scales (Fig. 1d). Only at scale *r* = 1.20 m there was a marginally significant negative correlation.

Canopy cover as determined by automated tree crown delineation for Plot 4 was 64.9% in 2002 and 62.5% in 2005. Hence, total gap fraction (1 - canopy cover) increased only slightly, although individual gaps were larger in 2005 (Figs. 2a, c).

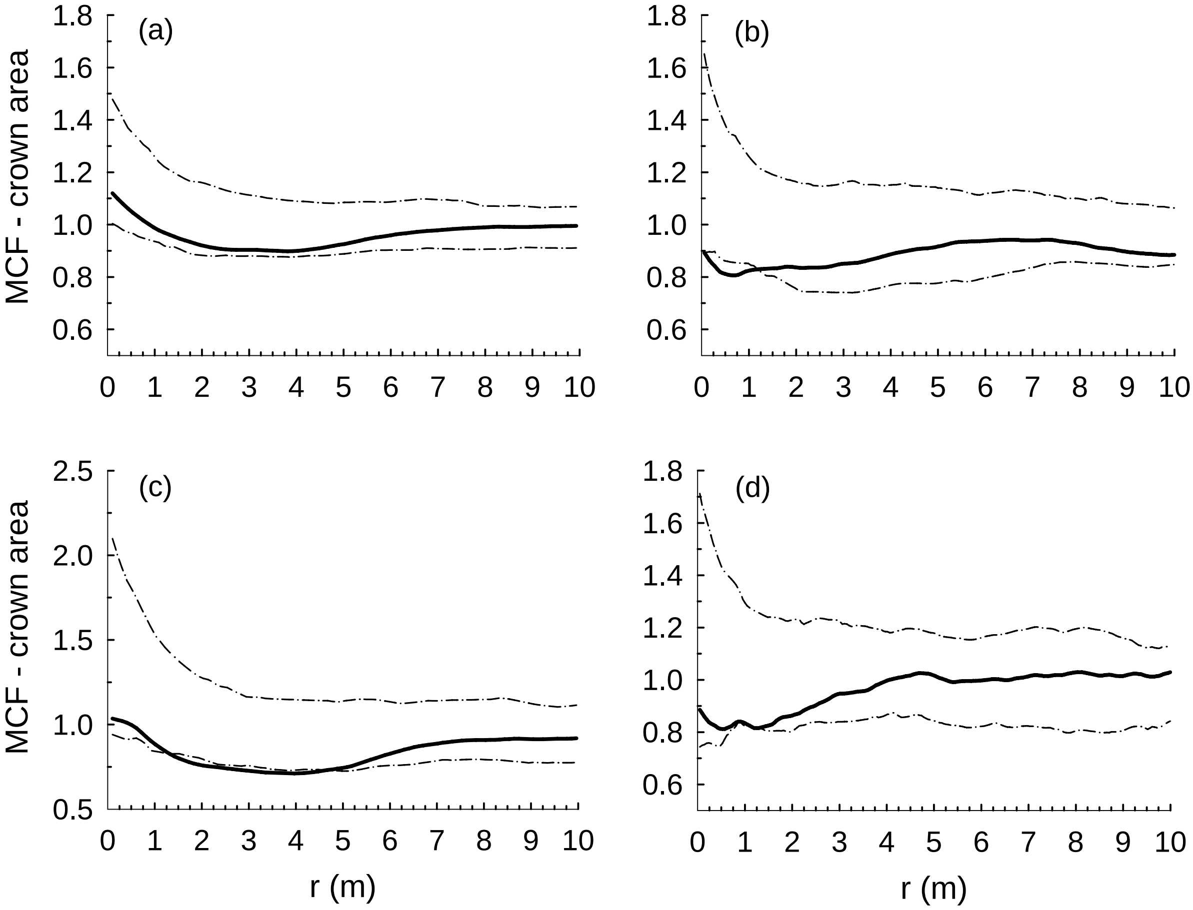
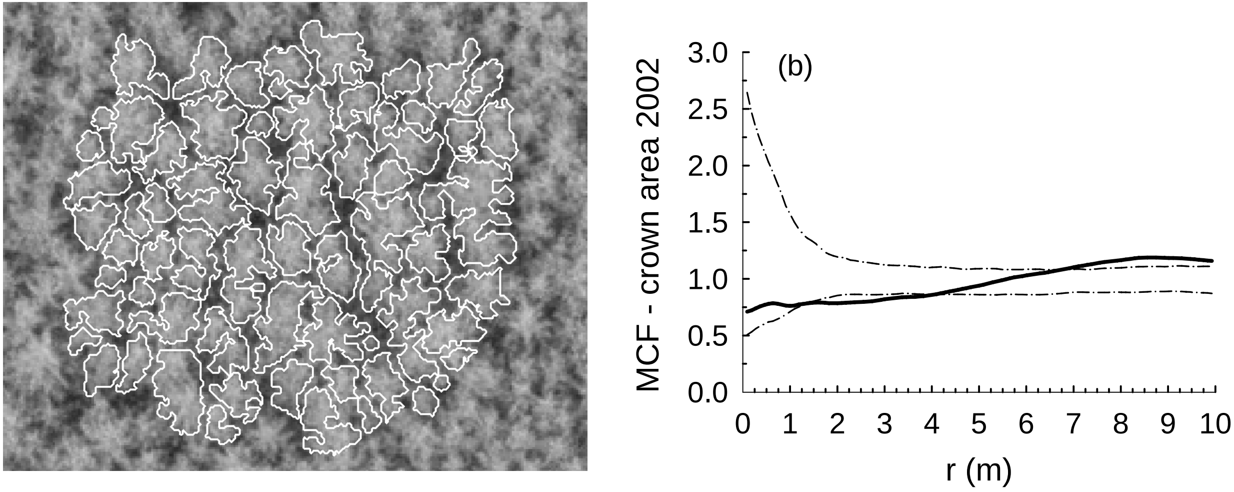


Fig. 1. The mark-correlation function (MCF) for field-measured "crown area" of deciduous P1 (a) and P2 (b), and coniferous stands P3 (c) and P4 (d). MCF values < 1 indicate negative correlation between the marks (crown area) at inter-tree distance *r* (crown centroids). Negative correlation is significant if the solid line (MCF) is below the lower 95% approximated confidence limit (broken line).

For the photo-derived crown extent of Plot 4 and 2002, the MCF revealed no correlation of crown area at small scales up to *r* = 1.28 m, but significant negative correlation at larger scales between *r* = 1.37 m to *r* = 4.01 m (Fig. 2b). After competitive thinning and the emergence of large individual gaps in 2005, crown area was significantly negatively correlated at both small and larger scales up to *r* = 4.35 m (Fig. 2d). Thus, competition over time was quantified by an increased negative correlation in spatial scale and degree with the MCF being far below the lower confidence limit.

(a) Plot 4, 2002



(c) Plot 4, 2005

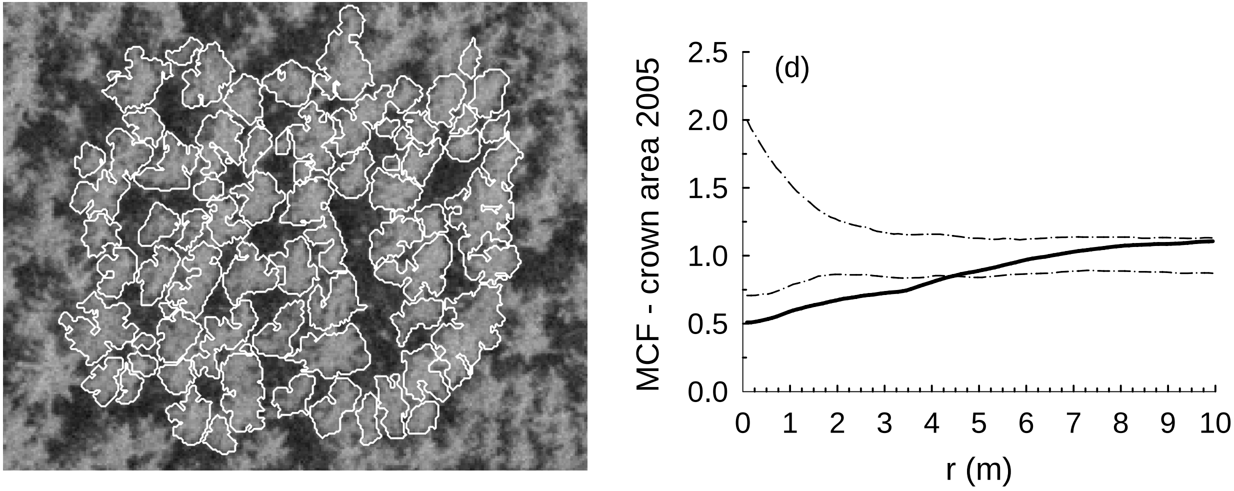


Fig. 2. Photo-derived "crown area" of Plot 4 using ITC-software for images of 2002 (a) and 2005 (c)[1]. Note the increase in gap size as a consequence of competitive thinning and summer drought in 2003. The mark-correlation function (MCF) for ITC-extracted crown area of 2002 (b) and 2005 (d). Negative correlation of crown area at inter-tree distance *r* is significant if the MCF (solid line) is below the lower 95% approximated confidence limit (broken line).

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[1] Misclassified "multiple crowns" are still unavoidable using present state-of-the-art software for automated crown delineation because grey-scale edges recorded in digital images may be inconsistent with real tree-crown boundaries (Wang, Gong & Biging 2004). However, this technical error is negligible for monitoring stands and competition because it affects the segmentation of tree crowns consistently for all analyzed images.

Competition in individual tree species

In P1, the minor tree species *P. avium* had a weaker correlation between CR or TH and DBH than the major species *F. excelsior* (Figs. 3a, b). [Regression equations and *P*-values of these allometric relationships for major and minor tree species of all four plots are supplied in the appendix, Table A.] Mean DBH, CR, and TH were significantly smaller and mortality was higher in *P. avium* than in *F. excelsior* (Table 1). The correlation between CR and decreasing NN distance was stronger in the minor ($r^2 = 0.27$) than in the major species ($r^2 = 0.02$; Figs. 3c, d). Slope steepness increased with upper quantiles in *P. avium* and thus, with increasing crown radius of larger trees (Figs. 3c, e). The major tree species did not show such an increase in slope steepness, and none of the slopes were significantly smaller than zero (Table 2; Figs. 3d, f). Also, the slope of the standard regression between CR and NN distance was more shallow in the major species (Table 2).

Table 1. Structural attributes of minor and major tree species in the plots. Differences between the average ⟨⟩ diameter at breast height (DBH), crown radius (CR), and tree height (TH) of live trees of minor and major tree species within a plot were tested for significance using a *t*-test for independent samples. Significance levels are $*p < 0.05$, $**p < 0.01$ and $***p < 0.001$.

	Plot1		Plot 2		Plot 3		Plot 4
Species (social status)	*P. avium* (minor)	*F. excelsior* (major)	*S. torminalis* (minor)	*Q. petraea* (major)	*P. menziesii* (minor)	*P. abies* (major)	*P. menziesii* (minor)
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

In P2, correlation between CR and DBH was similarly strong in the minor tree species *S. torminalis* and the major *Q. petraea* (Fig. 4a). The mean CR was not significantly different between both species, but mortality of *Q. petraea* was higher (Table 1). The r^2-value for correlation between TH and DBH was three times as high for *S. torminalis*, although its mean DBH and TH were significantly smaller than for *Q. petraea* (Table 1; Fig. 4b). The r^2-value was also higher for correlation between CR and NN distance for *S. torminalis* (Fig. 4c) as compared to *Q. petraea* (Fig. 4d). Slope steepness increased with upper quantiles in *S. torminalis* and thus, with increasing CR. Except for $\tau = 0.70$, slopes for quantiles $\tau \geq 0.40$ were significantly smaller than zero (Fig. 4e). The major tree species did not show such a distinct increase in slope steepness (Fig. 4f). Also its mean slope from standard regression between CR and NN distance was more shallow (Table 2).

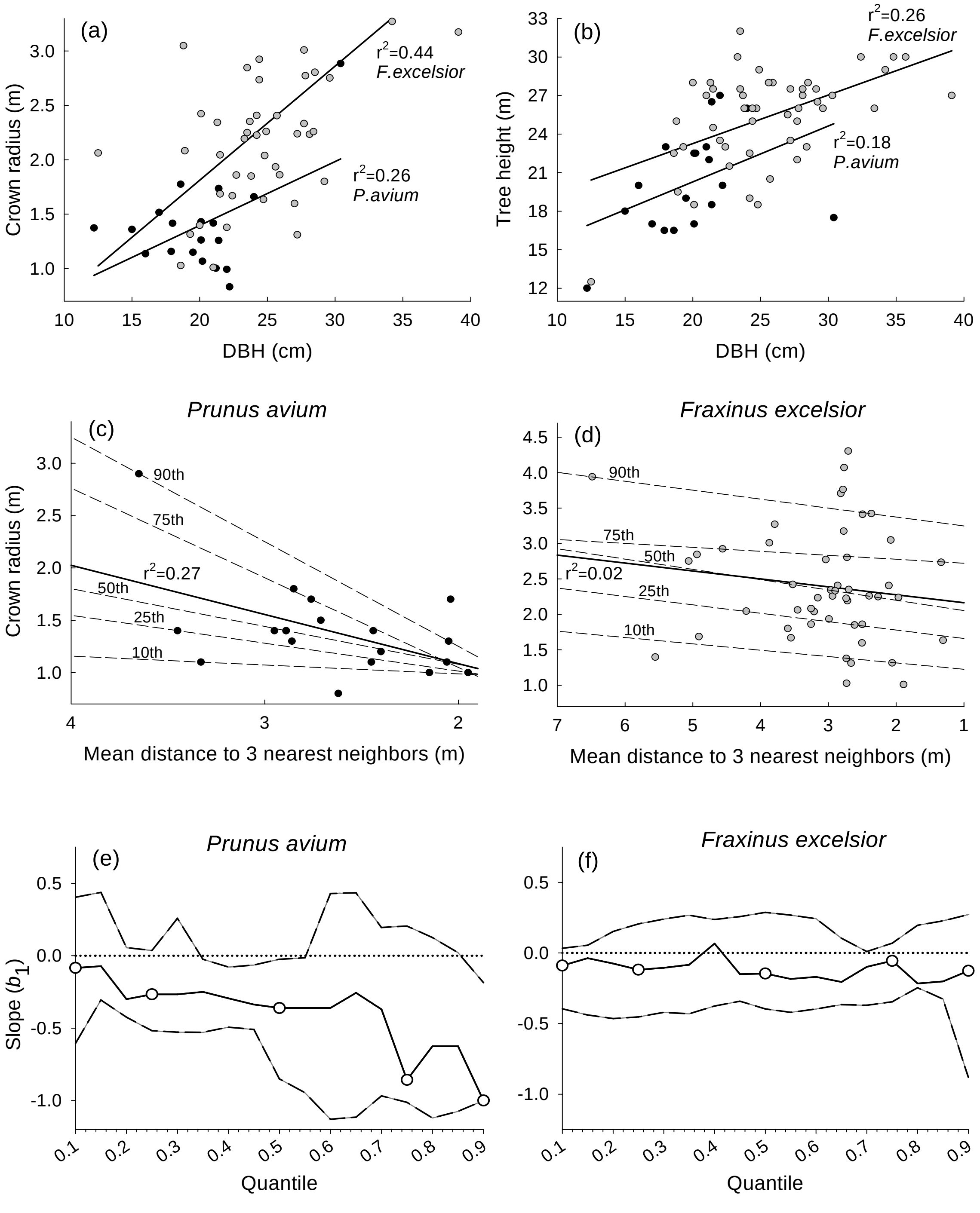

Fig. 3. Comparison of growth performance between *Prunus avium* (●) and *Fraxinus excelsior* (◍) in Plot 1 using standard linear regression (a, b). Quantile regression for the 10th, 25th, 50th (median), 75th, and 90th percentile of "crown radius" in response to the decreasing "mean distance to the three nearest neighbors" for both species (c, d). Note that the x-axis has been reversed to represent increasing densities as nearest-neighbor distances. The r^2 and solid line show the standard linear regression fit based on the mean in the distribution of crown radius. Slopes of the five quantile regression fits (○) with approximately 90% upper and lower confidence limits (e, f).

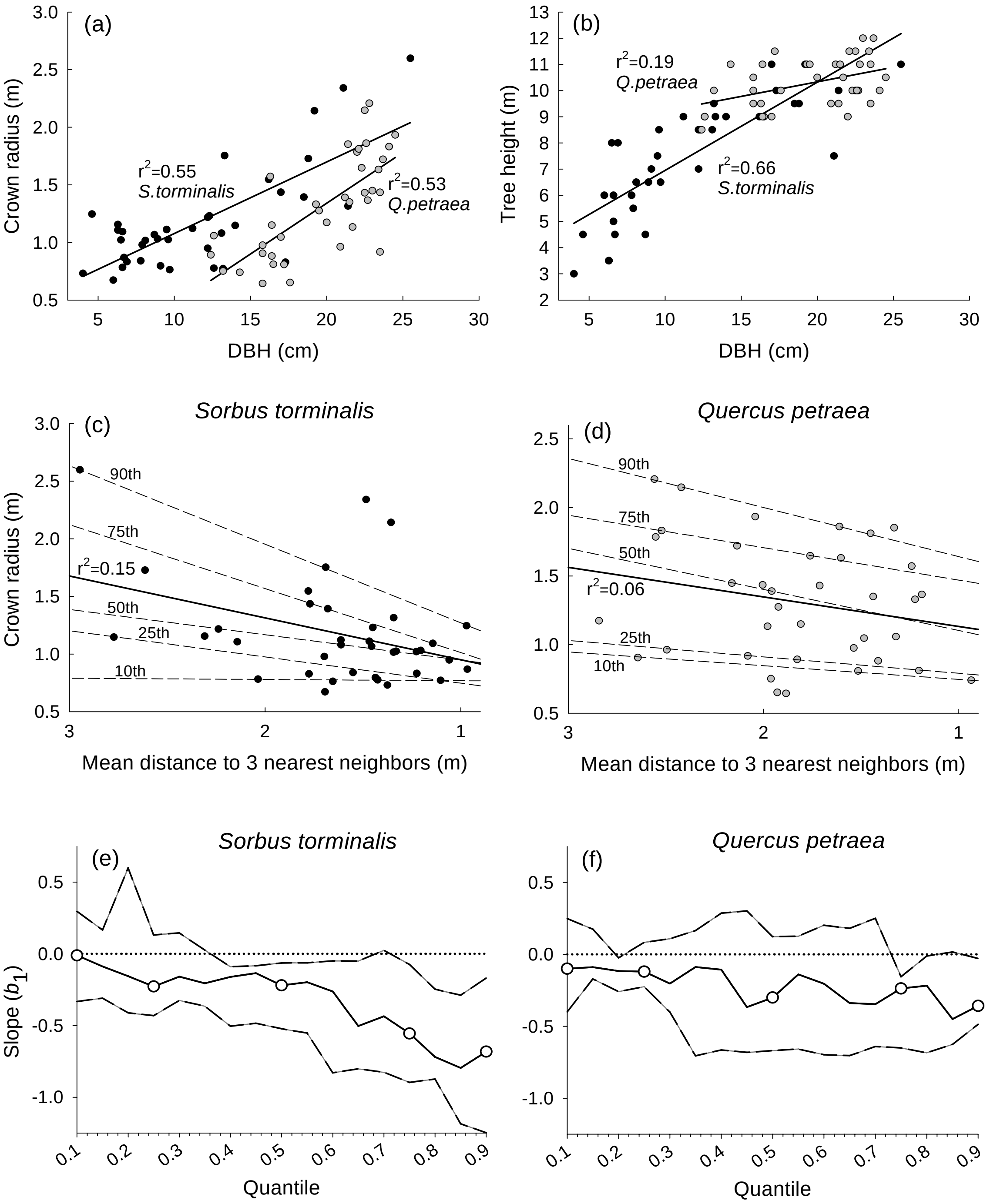

Fig. 4. As Fig. 3 but for *Sorbus torminalis* (●) and *Quercus petraea* (◉) in Plot 2.

In P3, the minor tree species *P. menziesii* and the major species *P. abies* had similarly high r^2-values for correlation between CR or TH and DBH (Figs. 5a, b). The mean DBH, CR, and TH were significantly smaller in P. *abies* and its mortality was much higher than in *P. menziesii* (Table 1). The correlation between CR and NN distance was weaker in the minor ($r^2 = 0.12$) than in the major ($r^2 = 0.26$) species (Figs. 5c, d). Slope steepness increased particularly for the upper quantiles in both species (Figs. 5e, f). Slopes of these upper quantiles were significantly smaller than zero, except for $\tau = 0.90$ in *P. abies*, where too few large trees led to very wide confidence limits (Figs. 5e, f). The mean slope from standard regression between CR and NN distance was nearly equal in both species (Table 2).

In the monospecific stand P4, r^2-values for correlation between CR or TH and DBH were very high for *P. menziesii* (Figs. 6a, b). The mean CR was small and mortality was very high in this stand (Table 1). Correlation between CR and NN distance was stronger for *P. menziesii* in Plot 4 (Fig. 6c) than in Plot 3 (Fig. 5c). Slope steepness increased for upper quantiles, however, it was only significantly smaller than zero for the lower quantiles $\tau \leq 0.70$ (Table 2; Fig. 6d).

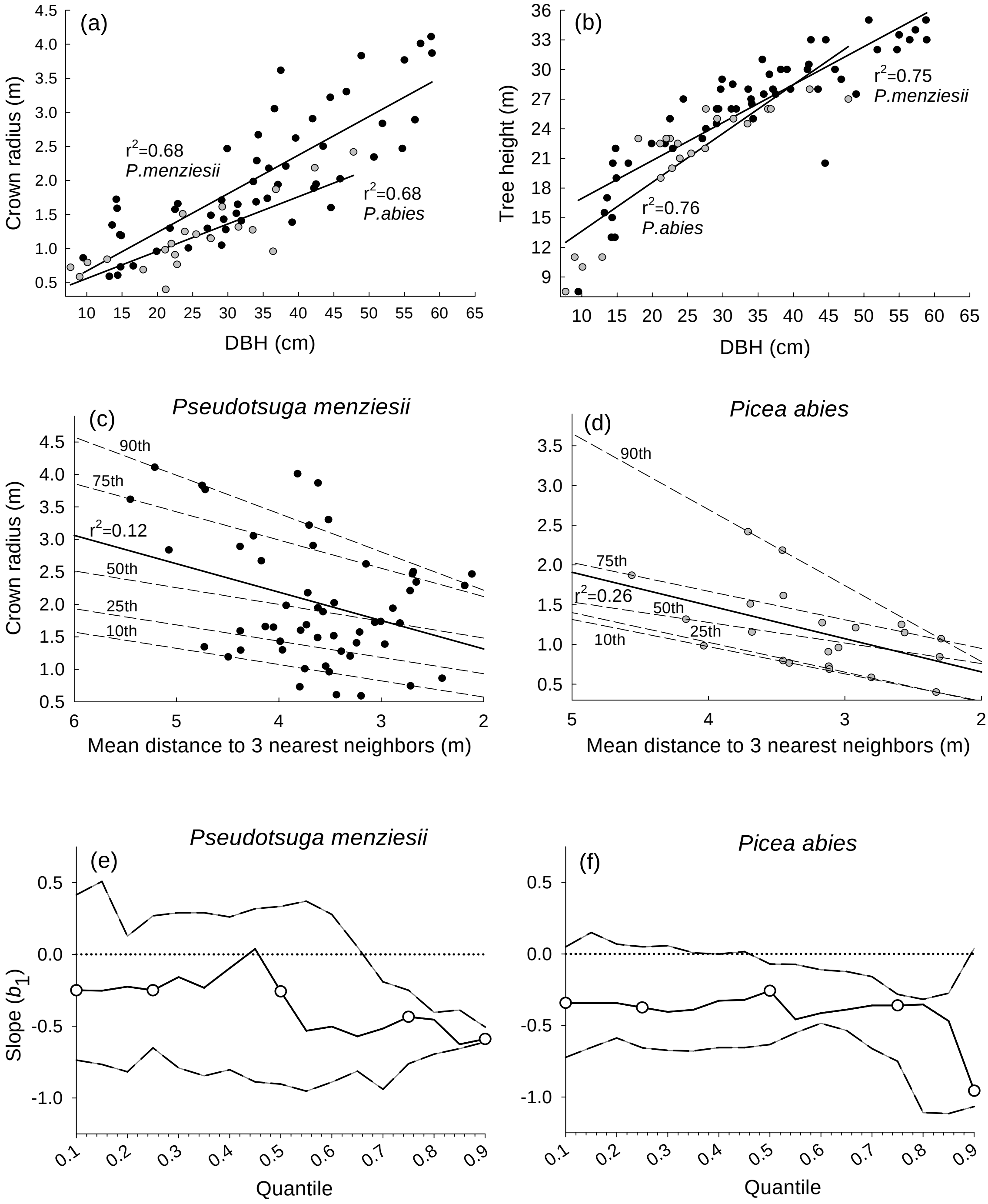

Fig. 5. As Fig. 3 but for *Pseudotsuga menziesii* (●) and *Picea abies* (◎) in Plot 3.

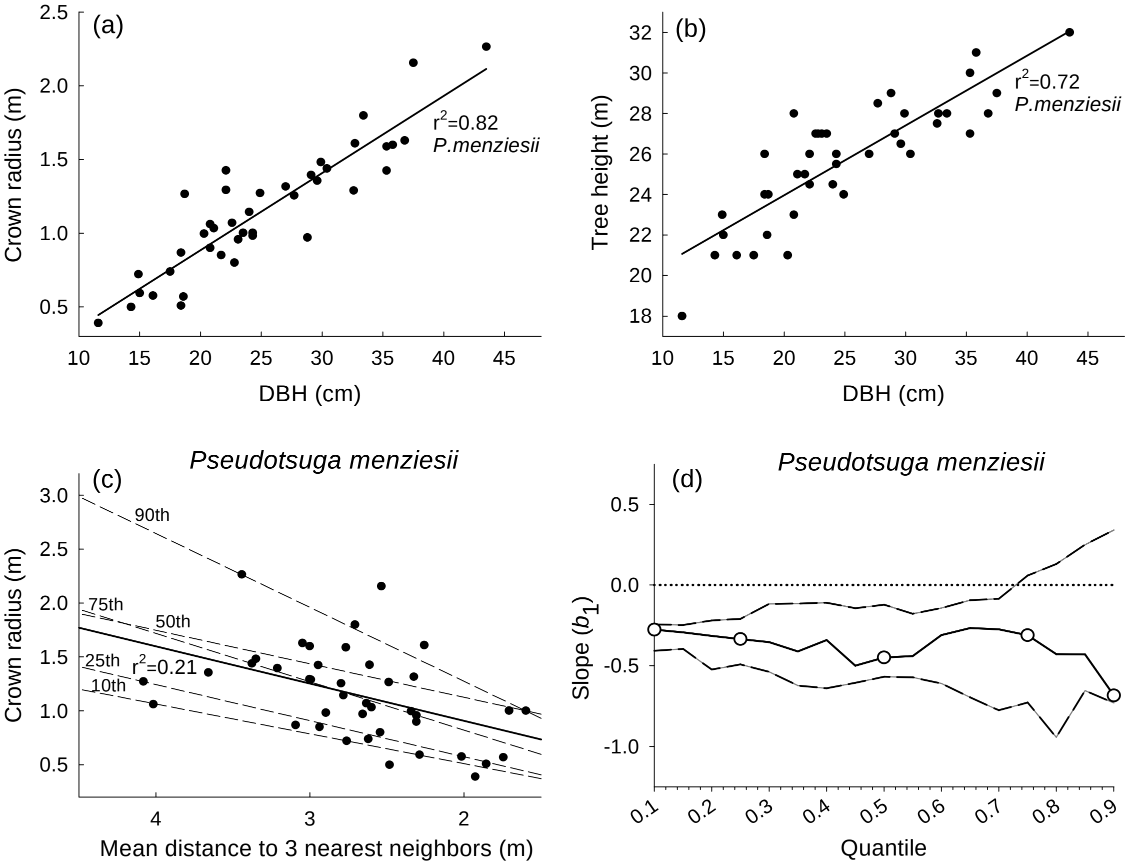

Fig. 6. As Fig. 3 but for *Pseudotsuga menziesii* (●) in the monospecific stand of Plot 4.

Table 2. Slopes for different percentiles of quantile regression and for the mean of standard linear regression, using "crown radius" as response variable to increasing neighborhood density. Asterisks * indicate that quantile slopes $b_1(\tau)$ were at approximately 90% confidence significantly different from zero.

	Plot1		Plot 2		Plot 3		Plot 4
Species (social status)	*P. avium* (minor)	*F. excelsior* (major)	*S. torminalis* (minor)	*Q. petraea* (major)	*P. menziesii* (minor)	*P. abies* (major)	*P. menziesii* (minor)
Percentiles							
10th	-0.08	-0.09	-0.01	-0.10	-0.25	-0.34	-0.28*
25th	-0.27	-0.12	-0.23	-0.12	-0.25	-0.38	-0.33*
50th	-0.36*	-0.15	-0.22*	-0.30	-0.26	-0.26*	-0.45*
75th	-0.86	-0.06	-0.56*	-0.24*	-0.43*	-0.36*	-0.31
90th	-1.0*	-0.13	-0.68*	-0.36*	-0.59*	-0.96	-0.68
Mean	-0.47	-0.11	-0.36	-0.22	-0.44	-0.42	-0.35

Discussion

Competition in stands

Many studies have used competition indices based on crown size (Biging & Dobbertin 1992, 1995; Rouvinen & Kuuluvainen 1997; Vettenranta 1999; Ledermann & Stage 2001). Novel in our approach is the application of correlation functions to horizontal crown extent in order to quantify competition for a whole range of scales. Forest scientists have highlighted the advantages of modern spatial correlation functions over structural indices (Pommerening 2002; Stoyan & Penttinen 2000). Structural indices consider influences just from nearest neighboring trees, although direct competitive effects may extend to scales far beyond the nearest neighbors (Stoyan & Penttinen 2000; Perry, Miller & Enright 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 & Dobbertin 1995). For competition indices, Biging & Dobbertin (1995) therefore conclude that expanding the neighborhood zone of influence is more important than the exact location of the nearest neighboring trees. Our applied mark-correlation function takes advantage of both because it considers a) exact locations of tree-size attributes for b) all possible scales of mutual growth reduction. It thereby combines properties of distance-dependent and distance-independent (stand-average) competition measures. Although crown area is a horizontal size attribute, the MCF incorporates indirectly also vertical influences from variation in tree height that may affect the crown size of individual trees (Biging & Dobbertin 1992; Ledermann & Stage 2001). Horizontal shading effects from very tall competitor trees may negatively affect crown areas of subject trees from distances far beyond of typical nearest neighbor distances. This ecological scale is considered by the MCF because it has no arbitrary cut-off radius beyond which spatial information would be ignored (Penttinen, Stoyan & Henttonen 1992).

For our field-measured deciduous stand P1, the MCF shows no negative correlation of crown area at all scales. This independent distribution of the mark “crown area” could be due to the relatively low tree density in P1. It could also be due to 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). Zero mortality of ash (Table 1) supports the notion that the dominant species experiences very low competition. Competition in the high-density stand P2 was stronger, especially at small scales with a high degree of negative correlation of crown area. In terms of relative frequency and mean crown extent, the two most common species, wild service tree and durmast oak, were nearly equal in P2. This could have led to intensified growth reduction and the observed higher mortality within the whole stand. Also, a previous analysis of these stands based on inter-tree distances only (Getzin & Wiegand in revision) revealed small-scale regularity of tree trunks in P2 but random patterns in P1, supporting the assumption of density-dependent mortality in P2.

In the coniferous stand P3, competition worked at larger scales. Of all four plots, this was the stand with biggest trees and thus, the zone of horizontal and vertical influence from competitor trees was largest. Possibly, the relatively low density and man-made planting scheme of Douglas-fir and common spruce allowed for greater inter-tree spacing and hence, led to independent marks at small scales and only weak negative correlation at larger scales. In the monoculture of P4, crown area was only marginally negatively correlated at scale r = 1.20 m but otherwise it was uncorrelated. For this stand, Getzin & Wiegand (in revision) found the phenomenon of mutual crown support where trees stabilized themselves (Rudnicki, Lieffers & Silins 2003). This mechanism occurred in 2004 because density, slenderness, and mortality (59%) of trees were very high. After competitive thinning and an extreme summer drought in 2003, large gaps emerged and tree crowns bended towards their neighbors. Consequently, for this particular year 2004, competition in P4 was not well detectable via negative correlation of crown area.

However, photo-derived analysis of P4 allows to trace back competitive changes from the year 2002 until 2005. Due to overall smaller crown areas in 2002, distances between crown edges of direct neighbors were greater than after size increment in 2005 (Figs. 2a, c). The size increment led to competitive thinning and the emergence of distinct gaps. This process was probably accelerated by the summer drought in 2003. Although single gaps were much larger in 2005, the growing crown areas caused the total canopy cover to decrease only slightly from 64,9% in 2002 to 62,5% in 2005. As is known from other studies (Hamilton 1969; Rouvinen & Kuuluvainen 1997), larger trees are more efficient than small trees in utilizing available scales of space by laterally expanding their crowns into new gaps. This competitive process shifts the crown centroids of codominant and dominant trees with average or above-average crown areas away from each other. However, the suppressed Douglas-fir with below-average crown areas are less efficient and have to remain in unfavorable dense neighborhoods with small distances r between their crown centroids.

These competitive dynamics at the stand level are well detected with the MCF. In 2005, the mark “crown area” was negatively correlated also at scales $r < 1.37$ m, because only suppressed trees with below average crown areas were numerous in neighborhoods with small inter-tree distances. However, in 2002, crown area was uncorrelated at these small scales because the spatially restricting consequences of competition were not yet severe enough for small trees than after overall size increment of the stand in 2005. The fact that crown area was in both years negatively correlated at larger scales may be ascribed to the intense competition of larger trees. Evidently, competition is a scale-dependent spatial process.

For the Douglas-fir stand, we have shown that the MCF was very sensitive to short-term changes in the canopy structure between 2002 and 2005. Our image analysis with ITC could have been slightly affected by differences in sun elevations (May *vs* June) or film development processes. But for the demonstration of the method we could show the usefulness of fast reacting foliage and the mark “crown area” whereas e.g. the mark “tree height” is less sensitive in similar correlation analyses (Kint *et al.* 2003). There are two reasons that may explain the spatially uncorrelated distribution of field-measured crown area in 2004. Possibly, mutual crown support of randomly leaning trees vanished after the summer drought only by the year 2005 because trees had time enough to recover and were thus able to bend upright and towards gaps. Otherwise, field-measured crown projection area allows also for more crown overlap and thereby for closer crown centroids between trees than the photogrammetric segmentation of crown surface area.

However, the latter technique is advantageous. Using photo-derived crown extent better correlates with actual tree and stand volume than field-measured crown extent because it is a measure of the tree's "functional growing space" (Popescu, Wynne & Nelson 2003).

In summary, the advantage of the MCF is that there is no need to define a zone of influence around subject trees (Ledermann & Stage 2001) because all inter-tree distances are analyzed at all spatial scales. This is also an advantage over local spatial autocorrelation (Shi & Zhang 2003). Since the MCF uses the average mark "crown area" for the whole stand, it could be of particular value for monitoring plantations and well-managed/-planned forest compartments. Development of a reference system to compare MCF-values between repeated measurements and between different stands would help in better planning of thinning intensity (Pommerening 2002). The shift from uncorrelated crown areas of young stands to negatively correlated crown areas at specific scales *r* of older stands would indicate increased competition, self-thinning and resulting changes in the canopy structure. This method is also applicable to stands with habitat variation because methodological refinements of the MCF allow for analysis of spatially heterogeneous plots (Capobianco & Renshaw 1998; Lancaster 2006). Therefore, we advocate use of the MCF (or related spatial techniques) for remotely-sensed canopy analysis because it allows for quick, inexpensive, and precise monitoring of competitive dynamics in forest inventory.

So far, we have demonstrated the appropriateness of using crown extent in the assessment of competition at the stand level. Horizontal crown extent is a useful variable for remotely-sensed forest inventory because the predictive ability of regression between DBH and crown extent is generally high and this ratio appears to be relatively unaffected by stand density (Gill, Biging & Murphy 2000; Hummel 2000; Bechtold 2003; Read *et al.* 2003). Correlations between DBH and crown extent are particularly strong for coniferous trees (Chen & Bradshaw 1999; Gill, Biging & Murphy 2000; present study: r^2 from 0.68 to 0.82 for coniferous and only 0.26 to 0.55 for deciduous species) because deciduous trees exhibit higher plasticity in asymmetric crown development (Umeki 1995; Getzin & Wiegand in revision).

Competition in individual tree species

Describing competition in mixed forests requires also analysis at the level of individual tree species with focus on smaller scales (Grote & Reiter 2004). Species may respond differently to changing neighborhood densities due to inherent differences in shade tolerance or mechanical robustness (Jack & Long 1991). Moreover, within a species the competitive response ability is directly size-dependent and needs to be decoupled from plant size in competition analyses (Lamb, Cahill & Dale 2006). Here, we applied quantile regression (Cade & Noon 2003) to detect size-dependent competition in minor and major tree species.

Competitive hierarchies were most pronounced in the deciduous stand P1. The minor tree species *P. avium* with its significantly lower mean DBH, CR, TH, its weaker correlation between DBH and TH, and 17% mortality was strongly suppressed by the major species *F. excelsior*. Both species grow rapidly during their first years and wild cherry may even grow faster in neighborhoods of common ash (Kerr 2004). However, at an age of 40 years the growth rate of *P.*

avium declines rapidly and most major tree species will suppress wild cherry (Schrötter 2001). In contrast, common ash reacts to inter-specific competition by sacrificing increment of DBH and crown radius to maintain height growth (Frech *et al.* 2003; Kerr 2004). It achieves its average dominant height of 25 m at about 50 years and eliminates competitors for light despite its slender crown (Marigo *et al.* 2000). The limited crown extent of ash in the upper canopy is probably compensated by higher photosynthetic rates (Frech *et al.* 2003). Our analysis with quantile regression reflects these known size- and age-dependent hierarchies. Slopes of *F. excelsior* were not significantly different from zero for all quantiles. But for *P. avium*, slope steepness increased for higher percentiles, being strong evidence that especially the largest cherry trees, with an age presumably above 40 years, were most suppressed. These oldest cherry trees with largest crown radii were those which had to compete with the oldest and most dominant ash. Consequently, the competitive response ability of older cherry trees was weakest within all size classes of *P. avium*. If slopes of upper and lower quantiles are interpreted as size-dependent competition coefficients (Goldberg & Landa 1991) we can quantify the relative decline in competitive ability of *P. avium* with increasing size and inferred age. Both species have equal competitive response abilities to one individual of the neighborhood during their initial rapid growth phase, as indicated by equal slopes (-0.08 *vs* -0.09) for the 10th percentile (Table 2). However, for the 90th percentile of largest and probably oldest trees, the competitive response ability of wild cherry is much smaller (-1.0) than that of dominant ash (-0.13). Largest wild cherry trees are about 40-50 years old and are strongly suppressed by common ash of similar age, leading to comparatively high mortality in wild cherry. For species coexistence, we suggest to plant wild cherry only in mixture with slower growing species such as oak and we confirm recommendations by Schrötter (2001) that wild cherry should not be mixed with common ash.

Findings for competitive hierarchies are similar for minor and major tree species in Plot 2, although differences are less distinct. *Sorbus torminalis* is a rare species in European timber forests and it survives due to its relative shade tolerance and strong phototropism (Schrötter 2001). In our study site, mean DBH and tree height of *S. torminalis* were significantly smaller than in *Q. petraea*, indicating a sub-dominant to suppressed status. Competitive effects of dominant oak (and other species) on *S. torminalis* were strongest in largest size classes because steepest slopes occurred in upper quantiles of *S. torminalis*.

The mixed stand P3 revealed very similar allometric relationships for Douglas-fir and common spruce (Figs. 5a, b). This illustrates that even though the "introduced" Douglas-fir is only a minor tree species in terms of its low proportion in German forests, it is a superior competitor which often outgrows local major tree species (Knoerzer 2002). The lower mean DBH, CR, and TH and 50% mortality of common spruce all point to the potential danger for local tree species diversity in future, if uncontrolled naturalization of Douglas-fir would happen. Compared to Douglas-fir, slopes of quantile regression were steeper in spruce for smaller trees up to the 50th percentile and also for the largest trees of the 90th percentile. This lower competitive response ability of spruce was only detectable via quantile regression because the slope of standard linear regression based on the mean was even slightly higher for Douglas-fir (Table 2). Here we highlight the power of quantile regression because it allows not only for a size-dependent analysis of competition (Lamb, Cahill & Dale 2006) but also for a more differentiated view of underlying processes that is often hidden by the mean (Cade & Noon 2003).

In the monospecific, even-aged stand P4, the strong correlations of crown radius and tree height with DBH were partly attributed to the regular planting scheme of Douglas-fir which also led to high tree slenderness (Getzin & Wiegand in revision). Interestingly, slopes for all smaller trees with quantiles $\tau \leq 0.70$ were significantly different from zero, indicating intra-specific competition and strong density-dependent suppression of weaker individuals in the stand.

In summary, we have shown that quantile regression is a sensitive technique to detect size-dependent competition in individual tree species. The slopes can be used as competition coefficients to compare general trends between species (Goldberg & Landa 1991). In our study, it was mainly the largest individuals of minor tree species that were most suppressed by dominant competitors. In order to sustain the long-term success of minor tree species in mixed forest, management should particularly consider the future spatial requirements of such rare species.

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Appendix

Table A. Equations and *P*-values of ordinary least squares regressions for allometric relationships between crown radius (CR) and DBH (independent variable), and tree height (TH) and DBH.

Figure	Species	Variables	Linear regression equation	*P*-value
3a	*P. avium*	CR - DBH	y = 0.2186 + 0.0589*x	0.0272
	F. excelsior	CR - DBH	y = -0.2899 + 0.1051*x	0.0000
3b	*P. avium*	TH - DBH	y = 11.5767 + 0.4351*x	0.0739
	F. excelsior	TH - DBH	y = 15.708 + 0.3778*x	0.0002
4a	*S. torminalis*	CR - DBH	y = 0.4561 + 0.0621*x	0.0000
	Q. petraea	CR - DBH	y = -0.4219 + 0.0881*x	0.0000
4b	*S. torminalis*	TH - DBH	y = 3.5812 + 0.3369*x	0.0000
	Q. petraea	TH - DBH	y = 8.1054 + 0.1114*x	0.0076
5a	*P. menziesii*	CR - DBH	y = 0.1027 + 0.0567*x	0.0000
	P. abies	CR - DBH	y = 0.1611 + 0.04*x	0.0000
5b	*P. menziesii*	TH - DBH	y = 13.1031 + 0.3842*x	0.0000
	P. abies	TH - DBH	y = 8.6847 + 0.4945*x	0.0000
6a	*P. menziesii*	CR - DBH	y = -0.1629 + 0.0524*x	0.0000
6b	*P. menziesii*	TH - DBH	y = 17.0774 + 0.3444*x	0.0000

GENERAL DISCUSSION

The intention of this Ph.D. thesis was to contribute to some selected topics in forest research to better understand essential processes and interactions that lead to small- and large-scale hierarchical structures. This contribution benefits ecological scientists and forest managers alike because *"spatial patterns of structures (horizontal and vertical) are significant aspects of forest stands that have not been fully appreciated"* (Franklin *et al.* 2002). In this discussion I will only briefly highlight and summarize some major aspects of this doctoral research project because each single chapter on its own has been already evaluated in its specific context. Generally, plots with completely mapped x-y-positions of tree trunks or crown centroids are ideal to study horizontal forest structure because such snap-shot patterns (time windows) bear the fingerprint of spatial growth and mortality. Especially in slowly growing forest communities with trees greatly exceeding the lifespan of humans, e.g. Douglas-fir lives up to 1400 years (Burns & Honkala 1990), snap-shot tree patterns are useful to reconstruct processes acting over such long time scales (CHAPTER 1, Fig. 1; CHAPTER 2, Figs. 1 & 2; CHAPTER 4, Figs. 2a & c).

However, such spatial investigations require caution because often competitive forces may not be strong enough or may not have worked long enough to cause mortality and thereby to change patterns (CHAPTERS 1 & 4). Additionally, environmental heterogeneity may influence inter-tree distances and mask the processes that led to the observed patterns (CHAPTERS 1 & 2). It was also demonstrated in this thesis that the spatial segregation of species may increase with age due to increased resource partitioning (CHAPTER 1). Failure to account for such processes may bias interpretation of snap-shot patterns. For example, for our southern chronosequence, influences from habitat heterogeneity were highly important in our spatial data analysis. For nearby study sites on south-eastern Vancouver Island, Nelson *et al.* (2002) used satellite images as basis for a point pattern analysis. As shown in their research, this approach may greatly simplify the monitoring of forest stands. However, the approach will fail whenever the above mentioned factors influence inter-tree distances at a particular site. To account for environmental heterogeneity or masking biological effects in pattern analysis, specific adaptation of null models is necessary (Goreaud & Pélissier 2003; Wiegand & Moloney 2004; this thesis).

The cumulative method Ripley's K-function and its L-transformation are common methods in point pattern analyses. However, for exploratory spatial data analysis, non-cumulative methods such as the pair-correlation function $g(r)$ or the O-ring statistic are more appropriate (Stoyan & Penttinen 2000, Perry *et al.* 2006). Non-cumulative methods do not have a memory effect because the second-order properties are isolated at specific radii r. This allows more detailed interpretations at what scales a null model is violated (Schurr *et al.* 2004; Wiegand & Moloney 2004). The statistical evaluation of both cumulative and non-cumulative methods commonly (including this thesis) relies on Monte Carlo simulations to construct 90%, 95%, or 99% confidence limits. This approach has been recently criticized because these Monte Carlo methods result in non-exact type I error rate performance (Loosmore & Ford 2006) and are thus approximate confidence limits (Wiegand & Moloney 2004). Therefore, it is important to interpret significant deviations from an underlying null model carefully. It can be adequate to additionally apply an independent inference method, as was done with the nearest neighbour distribution in CHAPTER 2. However, the recent criticism is indeed nothing new. In their standard book, Stoyan and Stoyan (1994: page 300-302) describe in detail that *"the probability of an error of type I is not exactly α"*. However, they also write that "*Monte Carlo tests are well suited"* and "*the most appropriate method"*. Also e.g. Dale *et al.* (2002, page 575) write in their summary on spatial methods that *"Monte Carlo techniques can be used to assess whether the spatial pattern is significantly different from random"*.

Coming back to the ecological importance of hierarchical structures, it was shown in this thesis that abiotic habitat variation may influence demographics of species and ecological dynamics in forest stands (CHAPTER 2). Also, topography may have an overriding effect on tree growth, i.e. when slope direction and thus large-scale heterogeneity in available light is more decisive for the direction of tree bending than small-scale competition from nearest neighbouring trees (Umeki 1995; CHAPTER 3). However, deciduous trees with their greater plasticity in asymmetric growth appear to better compensate competition from close neighbours than coniferous trees. This may then lead to overall lower mortalities and more random crown patterns as compared to coniferous trees. In contrast, mortality and gap formation may be particularly strong in regularly planted, dense coniferous stands (CHAPTERS 3 & 4). These findings demonstrate that functional differences between deciduous and coniferous trees can be used to relax competitive hierarchies in mixed stands due to different spatial resource partitioning (Ishizuka 1984). Retaining selected forest structures under given habitat conditions is a key task in modern forest management and may help to sustain timber production (Acker *et al.* 1998; Busing & Garman 2002; Mason 2002) or biodiversity by e.g. promoting spatial recruitment opportunities for shade-intolerant minor tree species (Lindenmayer 1999; Drever & Lertzman 2003).

The scale-dependent effects of competitive dominance were highlighted in CHAPTER 4 when orthophotos were compared between 2002 and 2005. Only trees with smaller crown areas were able to survive at small inter-tree distances in 2005 whereas large trees with large crown areas were superior in expanding into new gaps. This type of scale-dependent information on horizontal canopy structure will become of great importance in the near future when remotely sensed canopy data will be increasingly used to monitor forest stands (Read *et al.* 2003). The novel approach of using the mark-correlation function for such remotely sensed canopy data is in my view a major contribution of this Ph.D. thesis.

Hierarchical effects on size structure work both in monocultures (cf. Douglas-fir in Plot 4) and mixed stands. However, in mixed stands, the size-dependent competitive ability differs also with species identity. Here, it was shown that the largest major tree species were most dominant but the largest minor tree species were most suppressed. Thus, the spatial requirements of suppressed minor tree species are greatest at their older life-history stages. This explains a problem of modern forestry in promoting vertical stratification in stands: the future space requirements must be considered in time but this knowledge is often lacking.

Besides recommendations given for the sustainable growth of suppressed minor tree species, it was also stressed in this thesis that an uncontrolled naturalization of Douglas-fir may have negative effects on the growth of local major tree species such as common spruce (Knoerzer

2002; Broncano *et al.* 2005). Here, new insights into the spatial patterns and global dispersal modes of Douglas-fir in its native North American range, given in CHPATERS 1 and 2, may be used to better understand its behaviour as a potential invader in German forest stands.

The findings presented in this thesis and the discussions on forest structure of the individual chapters may also have broader implications for a wide readership and scientists with their own special fields of research. Some of the newly generated knowledge may also be viewed under quite different considerations that could not be accommodated here and may thus benefit and back up statisticians, ecologists, or forest scientists from other research areas. For example, the investigated dynamics of old-growth forests may also be viewed as 'inertia' and hence, may be differently stressed as a significant mechanism for ecological resistance in the face of climate change and global warming (Noss 2001).

In summary, the four chapters presented in this Ph.D. thesis show the tremendous variety of forest structures and some innovative methods to analyse this complexity. Spatial statistical methods are particularly important in this analysis (Kint *et al.* 2003) because the processes that lead to hierarchical forest structures are scale- and size-dependent. I hope that this Ph.D. thesis will help to motivate some future research in that direction.

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ZUSAMMENFASSUNG

Die Struktur eines Waldes wird von drei wesentlichen Komponenten bestimmt: der räumlichen Verteilung von Bäumen, der räumlichen Vermischung von Baumarten und der räumlichen Variation von Baumgrößen. Da der Wald ein von Ressourcen (Licht, Bodenwasser, Nährstoffe, etc.) limitiertes und somit von Konkurrenz geprägtes System ist, resultieren die Komponenten der Waldstruktur in eine Hierarchie. Diese Hierarchie ist skalenabhängig, denn sie wird auf kleinen Skalen (bis ca. 10 Meter) von den direkten Wechselwirkungen zwischen den Bäumen beeinflusst, wobei der Einfluss der Konkurrenzstärke mit dem Baumalter und somit der Größe variiert. In der vorliegenden Dissertation *„Analyse hierarchischer Strukturen in Waldbeständen mittels detaillierter räumlicher Statistik"* wird deshalb besonderer Wert auf die räumliche Quantifizierung von skalenabhängigen Einflüssen gelegt. Dies geschieht mittels moderner Korrelationsfunktionen wie der Paarkorrelationsfunktion $g(r)$ oder Ripley's K-funktion. Diese Funktionen haben gegenüber konventionellen Strukturindizes den großen Vorteil, dass sie räumliche Konkurrenzeinflüsse über den nächsten Nachbarbaum hinaus quantifizieren, was dem überproportionalen Einfluss von weiter entfernt stehenden großen Bäumen gerecht wird. Dabei werden „negative" oder „positive" Interaktionen zwischen artgleichen oder artungleichen Bäumen durch Punktmusteranalysen beschrieben. Konkurrenz und negative Wechselwirkungen führen häufig zu größer werdenden Zwischenbaumabständen und somit zu regelmäßigen Mustern. Samenverbreitung, gegenseitige Förderung und positive Wechselwirkungen führen im Gegensatz dazu zu kleineren Abständen zwischen den Individuen und somit zu geklumpten Mustern. Zufallsverteilungen sind entweder ein Indiz für keine signifikante Wechselwirkung oder den Übergang von einem Mustertyp zum anderen, zum Beispiel als Folge von sich positiv oder negativ verändernden Umweltbedingungen. Die hierarchische Struktur eines Waldbestandes kann andererseits auch von großskaligen (dutzende Meter) Faktoren wie Heterogenität in der Bodenqualität oder durch die Hangneigung (Lichteinfallswinkel) bestimmt werden. Dies hat Einfluss auf das dynamische Wachstumsverhalten des gesamten Baumbestandes. Auch können kleinskalige Wechselwirkungen zwischen den Bäumen von den großskaligen Einflüssen hierarchisch bestimmt werden.

Die vorliegende Dissertation zielt darauf, ein besseres Grundverständnis dieser komplexen Wechselwirkungen zu gewinnen, denn die Erhöhung von sowohl vertikaler als auch horizontaler Bestandesstruktur ist ein forstwirtschaftliches Hauptziel des gegenwärtig durchgeführten Waldumbaus. Zwei Untersuchungsgebiete stehen im Mittelpunkt. Zum einen wurden natürliche Chronosequenzen mit vollständig kartierten Stammfußkoordinaten auf Vancouver Island in Kanada untersucht, um die langzeitlichen Koexistenzmechanismen von schattenintoleranten Douglasien und schattentoleranten Baumarten wie der Westlichen Hemlock zu analysieren (Kapitel 1). Der Einfluss von großskaliger Habitatheterogenität auf die Ausbreitung der Nadelbäume wurde ebenso untersucht (Kapitel 1 & 2). Zum anderen wurden in Thüringer Laub- und Nadelwäldern zusätzlich zu den Stammfußkoordinaten die Baumkronen vermessen und das asymmetrische Wachstum der Bäume untersucht (Kapitel 3). Abschließend wurden die räumlichen Beziehungen zwischen konkurrenzstarken Hauptbaumarten und

konkurrenzschwachen Nebenbaumarten wie der Vogelkirsche oder Elsbeere analysiert. Hierfür wurde die zeitliche Veränderung der Konkurrenz zwischen Douglasien auch über Luftbildauswertungen von Baumkronenflächen rekonstruiert (Kapitel 4). Im Folgenden möchte ich stichpunktartig die zehn wichtigsten Ergebnisse meiner Dissertation benennen. Genaue Informationen können in den jeweils ausgewiesenen Kapiteln (K) nachgelesen werden.

1.) Räumliche Bodenheterogenität und folglich große Lichtlücken begünstigen die langzeitliche Koexistenz von schattenintoleranten Douglasien und spätsukzessionalen Baumarten. (K1)

2.) Räumliche Nischenpartitionierung kann im Laufe der Sukzession zunehmen und die direkte inter-spezifische Konkurrenz verringern. (K1)

3.) Konkurrenz muss nicht zu regelmäßigen Mustern führen. Es können sich auch geklumpte Muster bilden, wenn die Selbstausdünnung der Elternbäume zu Baumlücken führt, in denen die geklumpt nachwachsenden Jungbäume das Gesamtmuster der Baumart dominieren. (K1)

4.) Eine Baumart (Westliche Hemlock) kann sich mit zwei verschiedenen Ausbreitungsstrategien („colonization“ & „phalanx“) in homogenen bzw. heterogenen Habitaten behaupten. (K2)

5.) Entgegen verbreiteter Annahmen können auch zufällige horizontale Baumkronenverteilungen in Laub- und Nadelwäldern dominieren. (K3)

6.) Bäume in Mitteleuropa neigen sich nicht signifikant zur Hauptrichtung der Sonne (Süden), sondern den Hang abwärts, selbst wenn die Exposition nach Norden gerichtet ist. Die Exposition kann dabei auch wichtiger für das asymmetrische Wachstum sein als der Einfluss von direkten Nachbarbäumen. (K3)

7.) Asymmetrisches Wachstum ist stärker bei Laub- als bei Nadelbäumen ausgeprägt. (K3)

8.) Regelmäßige Pflanzmuster von Douglasienbeständen können zu instabilen Beständen und starken Kronenkollisionen führen. (K3)

9.) Die Auswertung des Punktmusters von Kronenflächen mit der Markenkorrelationsfunktion eignet sich zum präzisen Überwachen von Konkurrenzverhältnissen. Die automatisierte Segmentierung von Kronenschirmflächen mittels digitaler Luftbilder ermöglicht diesbezüglich eine fernerkundliche Inventur von Waldbeständen. (K4)

10.) Konkurrenzschwache Nebenbaumarten wie die Vogelkirsche oder Elsbeere werden am stärksten in ihren größten Größenklassen von den dominanten Hauptbaumarten unterdrückt. Dies erfordert frühzeitig optimale Pflanzabstände, um ihre langfristige Koexistenz in artenreichen Mischwäldern zu ermöglichen. (K4)

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EHRENWÖRTLICHE ERKLÄRUNG
(DECLARATION)

Die geltende Promotionsordnung der Biologisch-Pharmazeutischen Fakultät der Friedrich-Schiller-Universität Jena ist mir bekannt.

Die Dissertation habe ich selbst angefertigt. Sämtliche von mir benutzten Hilfsmittel, persönliche Mitteilungen oder Quellen sind in der vorliegenden Arbeit angegeben.

Personen, die mich bei der Auswahl und Auswertung des Materials und bei der Herstellung der Manuskripte unterstützt haben, sind in der Danksagung (Acknowledgements) genannt.

Als Erstautor (corresponding author) habe ich alle vier Manuskriptinhalte selbstständig konzipiert und bearbeitet. Dabei habe ich vom unterstützenden Expertenwissen von Co-Autoren wie Dr. Kerstin Wiegand, Dr. Thorsten Wiegand, Dr. Fangliang He, Dr. Jens Schumacher und Dr. François Gougeon profitiert.

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Die vorliegende Dissertation habe ich noch nicht als Prüfungsarbeit für eine staatliche oder andere wissenschaftliche Prüfung eingereicht. Ebenso habe ich auch nicht die gleiche, eine in wesentlichen Teilen ähnliche oder eine andere Abhandlung bei einer anderen Hochschule als Dissertation eingereicht.

Jena, den 07. November 2006
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Others

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