



Influence of competition and age on tree growth in structurally complex old-growth forests in northern Minnesota, USA



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ARTICLE INFO

Article history:

Received 15 March 2013

Received in revised form 29 May 2013

Accepted 29 July 2013

Keywords:

Forest dynamics

Natural forest

Pinus resinosa

Pinus strobus

Mixed effects model

Multiplicatively weighted Voronoi diagram

ABSTRACT

Factors influencing tree growth in structurally complex forests remain poorly understood. Here we assessed the influence of competition on *Pinus resinosa* ($n = 224$) and *Pinus strobus* ($n = 90$) growth in four old-growth stands in Minnesota, using mixed effects models. A subset of trees, with accurate age estimates, was used to further test the influence of tree age. Our analyses included the weighted Voronoi diagram (WVD) as a novel competition index, representing a detailed description of the spatial structure of a tree's neighborhood.

Competition was variably expressed depending on stand developmental history and tree species. For *P. resinosa* in single-cohort stands, and *P. strobus* in multi-cohort stands, tree size relative to the population mean size best predicted tree growth. In contrast, for *P. resinosa* in multi-cohort stands, the spatial configuration of competitors became important, as shown by the superior performance of the WVD index. Surprisingly, while tree age had a negative influence on growth, it did not influence the intensity of competition.

Our results highlight the importance of considering stand developmental history and tree age in analyses of tree growth and competition, and the potential for improving assessments of competition in complex stands, using detailed quantification of neighborhood structure.

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1. Introduction

In natural forests, tree-to-tree variation in growth can be considerable, and it results from, as well as promotes, the structural and compositional complexity that often characterize these forests (Coomes and Allen, 2007; Parish and Antos, 2004). Understanding the factors influencing this variability is essential for predicting forest responses to environmental changes, and it also has direct application to forest management, as management strategies based on natural stand dynamics require an understanding of tree growth responses under a variety of environmental and structural conditions (Roberts and Harrington, 2008).

A number of factors interact to influence tree growth. For example, the influence of neighborhoods depends on characteristics of both the individual (focal) trees and their neighboring trees. These characteristics include species, size and location of a tree relative to its neighbors, as well as their interaction (Canham et al., 2004, 2006; Lorimer, 1983). Most studies agree that these neighborhood

effects on individual tree growth are primarily negative, owing to competition for limiting resources (Burton, 1993).

Tree age is also expected to influence growth rates (Johnson and Abrams, 2009; but see Mencuccini et al., 2005; Yoder et al., 1994). Whether these effects are due to tree size rather than age has been debated, and the exact mechanisms governing the age-related reductions in tree growth remain elusive (Li et al., 2012; Mencuccini et al., 2005; Ryan et al., 2004). Another confounding factor is that comparing growth among even-aged stands has made it difficult to disentangle age-effects from edaphic factors, as soils are undergoing concomitant changes (Martinez-Vilalta et al., 2007). In general the influence of tree age on growth, and particularly its relationship to competition, remains poorly studied.

Most studies of competition and tree growth have focused on plantations, managed forests, and even-aged, relatively young natural forests (Woodall et al., 2003; but see Contreras et al., 2011; Kubota and Hara, 1995; Hartmann et al., 2009). Because the factors influencing tree growth, such as tree sizes, ages, and neighborhood structure and composition change through stand development, it is unclear how inferences from studies of early phases of stand development apply to structurally and compositionally different stages of development, especially structurally diverse uneven-aged old-growth forests.

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Tree-tree competition is typically assessed using indices that mathematically express a focal tree's competitive status relative to neighboring trees and/or the degree of localized resource competition that a given focal tree experiences. Indices differ in the various aspects of competition they intend to express, and as such, their performance in predicting tree growth has varied among studies (e.g., D'Amato and Puettmann, 2004; Kunstler et al., 2011). Several previous studies report that indices lacking tree spatial location have performed well, at times even better than more complex spatial indices, in describing competitive interactions (e.g., Lorimer, 1983). This insignificance of tree spatial locations is attributed in part to the studies having been conducted in evenly-spaced plantations (Hartmann et al., 2009). Few studies have addressed these relationships in structurally diverse, old-growth systems that include highly variable and heterogeneous spatial arrangements and sizes of trees.

Despite the sometimes poor performance of indices incorporating tree spatial location, competition for resources affecting tree growth is generally assumed to be a spatially-explicit process. When modeled, competition for resources is typically assumed to occur within a circular neighborhood centered on the focal tree (Burton, 1993). However, the spatial variation in tree architecture (e.g., root and crown distributions) and resource availability in natural populations would suggest that the zone of perception need not be circular (Simard and Sachs, 2004). An alternative neighborhood characterization is the 'area potentially available', defined as a typically irregularly shaped polygon constructed around each focal tree such that no other trees are included within the polygon (Moore et al., 1973). We propose that such an index could better capture and explain competitive effects in structurally heterogeneous old-growth forests where trees exhibit irregular spatial patterns.

Our objective was to quantify the influence of competition on tree growth in structurally heterogeneous old-growth forests, and its relationship to tree ages. We address this objective using a novel approach to neighborhood characterization, namely the multiplicatively weighted Voronoi diagram (WVD), which represents a more detailed description of the spatial relationship of trees within stands compared to traditional indices of neighborhood conditions. We believe this approach will better capture the competitive environment in structurally heterogeneous conditions. The polygon-approach is intuitively appealing because it considers the entire neighborhood structure simultaneously and seamlessly (as opposed to tree-by-tree search radii), such that the size and location of one neighbor appropriately influences the competitive influence of other neighbors. Further, this approach allows for asymmetric partitioning of the growing space, rather than assuming isotropy and uniform shape of the focal tree's growing space. We expected that tree growth in structurally complex forests would be influenced by characteristics of a focal tree's competitive neighborhood, as well as characteristics of the focal trees themselves (including species, size and age) and their interaction. Moreover, we further hypothesized that the characteristics of competition would differ among populations according to stand developmental history, such that spatial structure is of increasing importance in uneven-aged, old-growth forests. We test these hypotheses for the dominant conifers *Pinus resinosa* (red pine) and *Pinus strobus* (white pine) in four structurally heterogeneous old-growth stands in northern Minnesota using the novel WVD approach in combination with six commonly used competition indices. Though applied here to just one forest type, we believe our approach provides an improved framework for assessing the influence of spatial structure on tree growth in other structurally heterogeneous forest systems.

2. Materials and methods

2.1. Study area, plots and field measurements

Our study builds on data from Fraver and Palik (2012), who investigated cohort age structures of four remnant old-growth *P. resinosa*-dominated forests in northern Minnesota. These sites (Itasca State Park, Scenic State Park, Sunken Lake, Pine Point) are located in the Minnesota Drift and Lake Plains (according to the national hierarchical framework of ecological units; Cleland et al., 1997). The area has typically deep soils, consisting of complex juxtapositions of ice contact, fluvio-glacial and lacustrine deposits. Fraver and Palik (2012) showed that *P. resinosa* on two of these sites (Itasca and Scenic State Parks) consists of a single cohort that likely regenerated following a stand-replacing disturbance. On the other two sites (Sunken Lake and Pine Point), *P. resinosa* has a more complex age structure, forming two or more cohorts, reflecting a more complex history of stand development. All four sites are dominated by *P. resinosa*, but *P. strobus* represents a considerable proportion of basal area in the two multi-cohort sites. Other species in these stands included *Abies balsamea*, *Picea glauca*, *Betula papyrifera*, *Acer rubrum*, *Populus* spp., and *Quercus* spp.

Each site included a square plot, which consisted of an inner core area of 70.7 × 70.7 m (0.5 ha) and a surrounding 10-m buffer area (see Fraver and Palik (2012), for further details of plot establishment). Within the entire plot, diameter at breast height (DBH, 1.37 m), species, and X and Y coordinates for all living and standing dead trees (stems ≥ 10 cm DBH) were recorded. Trees in the buffer were inventoried to provide a full set of potential competitors for focal trees located within the core area.

2.2. Tree ring data, basal-area increments and tree ages

Using cross-dated tree-ring data from Fraver and Palik (2012), we calculated annual basal-area increments for each focal tree ($n = 224$ for *P. resinosa*, $n = 90$ for *P. strobus*). By convention, these increments included bark thickness, which was estimated for each year, following Fowler and Damschroder (1988). We used the mean annual basal area increment over the most recent 20 years (see below) as our metric of growth in all subsequent analyses. Although non-pines were present at each site, we focused our analyses on the dominant conifers *P. resinosa* and *P. strobus* located within the 0.5 ha inner core area. Tree ages were also determined from these same tree-ring data, with age estimates refined following methods outlined in Fraver et al. (2011).

2.3. Competition indices

We selected indices for initial testing based on their favorable performance in earlier studies and considering the differences in the nature of competition they represent. Seven indices from four categories were selected (Table 1): (1) relative dominance (representing focal tree's population-level competitive status), (2) distance-independent (competitive effect is strictly related to focal tree and neighbor sizes), (3) two variants of distance-dependent indices, (competitive effect is a function of size of and distance to the neighbors, or the function of focal tree size relative to competitor sizes and distances to them), and (4) the WVD growing-space polygon (resource availability is spatially restricted based on neighbor location, density and size). In addition to these, and for a more detailed assessment of the performance of the WVD, we also included the original, unweighted Voronoi diagram (alternatively known as Dirichlet tessellation or Thiessen polygons). All indices were tested by regression analysis for their influence on basal-area increment. Included in the analyses was a null model that

Table 1
Competition indices used in this study, ranked according to complexity.

Rank	Index	Type	Data	Equation	Source
1	Null	Initial size	Focal size		
2	G	Relative dominance	Tree sizes	$\frac{BA_i}{BA_{site}}$	Glover and Hool (1979)
3	L	Distance-independent	Tree sizes,	$\sum_{j=1}^n \frac{D_j}{D_i}$	Lorimer (1983)
4	NCI	Crowding index	Locations	$\sum_{j=1}^n \frac{D_j^\alpha}{Dist_{ij}^\beta}$	Canham et al. (2004)
		Distance-dependent	Competitor		
5	H	Crowding index	Size, locations	$\sum_{j=1}^n \frac{D_j}{D_i^\beta}$	Hegyí (1974)
		Distance-dependent	Tree sizes		
6	Voronoi	Crowding index	Locations	See text	Brown (1965)
7	WVD	Growing space polygons	Tree locations	See text	Mu (2004)
		Growing space	Tree sizes	See text	
		Polygons	Locations	Locations	

BA_i , basal area of the focal tree i .

BA_{site} , basal area of the tree with the mean diameter in the stand.

D_j , DBH of the competitor j .

D_i , DBH of the focal tree i .

$Dist_{ij}$, Distance between the focal tree i and competitor j .

α , β , Exponents in the NCI-index. We tested values 0, 1, and 2 for both α and β .

assumed growth as a function of tree size only (MacFarlane and Kobe, 2006).

The second distance-dependent index, the NCI (Canham et al., 2004; Table 1) contains exponents α and β , which are allowed to vary. In line with Hartmann et al. (2009), we tested a combination of these exponents, allowing both α and β to have values 0, 1, and 2. This resulted in nine variants of the NCI-index, of which the best performing variant is reported in the results.

The growing-space polygon index (often called area-potentially-available), has been employed in various forms in the past. The purpose is to partition the study area into polygons that represent each tree's available growing space (e.g., Brown, 1965; Cherubini et al., 2002; Daniels et al., 1986; Moore et al., 1973), where the area of that polygon is used as an indicator of its competitive status. Here, we introduce a modification of the traditional growing-space polygon, ours derived from a multiplicatively-weighted Voronoi diagram (WVD) as implemented by Mu (2004), using tree diameters as weights (multiplicatively weighted Voronoi diagram is alternatively known as circular Dirichlet tessellation). In the WVD-approach, a polygon is constructed around each tree stem, its size and shape determined by creating a series of Apollonius circles for all pairs of neighboring trees, calculating the intersection points of these circles and connecting these points with arcs (Mu, 2004). The calculations were done as implemented in the WVD18 software (for details on the implementation and software requests, see Mu, 2004). The approach has the intriguing property that, depending on the weights, the boundary between two trees can be either convex, concave, or a straight line (see Fig. 1 for an example of a WVD). This property allows for the possibility of the growing-space polygon for an individual tree to be completely nested within that of another individual having a greater weighting factor. Thus, a small individual (low weight) may compete with only a single large individual (high weight) located nearby. Similarly, and in contrast to earlier weighted-polygon methods (Moore et al., 1973), two large trees can influence each other's polygon area even when a small intervening tree is located between them.

All indices we examined require information on tree sizes. The ideal sizes for use in the various indices would be initial sizes, that is, from the beginning of the period under study. Tree-ring data allowed us to back-calculate initial sizes for focal *P. resinosa* and *P. strobus*; however, the lack of such data precluded back-calculations for other tree species. In all indices, we thus used current sizes for

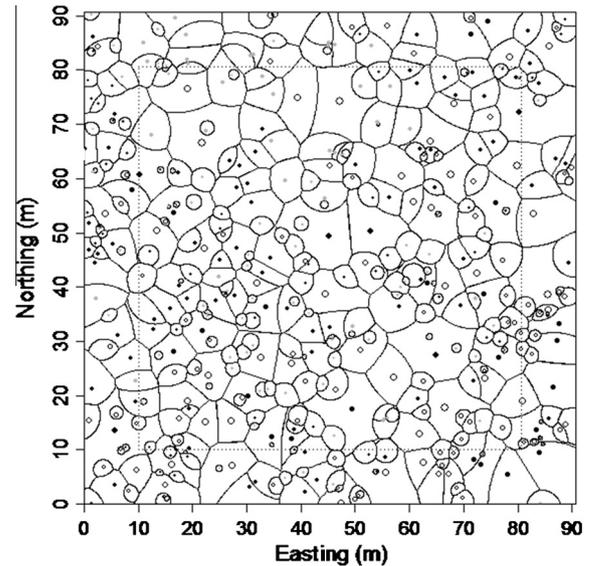


Fig. 1. An example of a weighted Voronoi diagram, from the Sunken Lake site. The irregular polygons represent a tree's available growing space, weighted by trees size. Small circles represent tree stems, with filled circles showing focal trees (black: *P. resinosa*, gray: *P. strobus*), and open circles trees of other species. The dotted line depicts the boundary of the plot core area; the area outside is the buffer from within which trees were used only as competitors, but not as focal trees (see text).

all trees, assuming relative tree sizes and their respective canopy positions remained relatively stable over the past 20 years. Given the typically shade-tolerant nature and subordinate canopy positions of the non-pine competitors, we feel this was a reasonable assumption.

The use of crowding indices (e.g., our L, H, and NCI indices in Table 1) requires tallying neighbor trees within a fixed-radius circle centered on the focal tree, with each tallied tree considered as a competitor. To evaluate the optimum search radius, we analyzed radii at every 1 m from 5 m to the 10 m maximum (the width of the buffer area around the core plot), which is a commonly assumed neighborhood size for north temperate and boreal *Pinus* species (e.g., Thorpe et al., 2010).

2.4. Statistical analyses

Using data pooled from all sites, we employed linear mixed-effects models (version 3.1 of package nlme in R; Pinheiro et al., 2011) to evaluate tree growth as function of tree size and the various competition indices (Table 1), using mean annual basal area increment over the most recent 20 years as the response variable. Growth over the 20-year period was chosen to ensure the series was sufficiently long to filter out short-term irregularities in tree growth, yet short enough to assume that competitive conditions have been relatively static. We also tested relationships using 10-years as the growth averaging period, but the model performance was generally poorer (based on the goodness-of-fit statistics; see below).

For analyses the data were divided into ecologically meaningful subsets. These subsets were based on expectations that the characteristics of competition within the entire population may differ according to *P. resinosa* age structures (i.e., single-cohort or multi-cohort), reflecting stand disturbance history. Thus these subsets consisted of *P. resinosa* in single-cohort stands (Itasca and Scenic State Parks, $n = 93$), *P. resinosa* in multi-cohort stands (Pine Point and Sunken Lake, $n = 131$ and $n = 112$ for the age model). Data subset for *P. strobus* consisted of the two multi-cohort stands ($n = 90$, and $n = 65$ for the age model). Models were fit separately for each group.

In the chosen mixed-modeling approach, site was treated as a random effect (facilitating the inclusion of within-stand spatial correlation structure), and fixed effects included initial focal tree size (i.e., the null model), with each competition index added to the null model in turn. We modeled the two species separately to allow for differences in the optimal competition index. Because growth potential varies with tree size, it is recommended that the initial size be included in regression models of tree growth (MacFarlane and Kobe, 2006). For this purpose we back-calculated focal tree diameters to the beginning of the growth increment analyzed (i.e., 20 years). In screening for the best-performing model, random effects were allowed to be intercept-only, or contain the intercept and slope for all combinations of the predictors that were included in the fixed effects. To satisfy the assumptions of linearity and homogeneity of residuals, we used natural-logarithm transformations on the response as well as the continuous predictor variables size, age and competition index. In addition, spatial autocorrelation structure was taken into account, using an exponential variogram model for autocorrelation of the residuals (Pinheiro et al., 2011). Models were fit using the restricted maximum likelihood estimation, and were validated through visual inspection of homogeneity and normality of residuals.

Owing to stem rot, accurate estimates of tree ages were available for only a sub-set of trees on each site. To test for the influence of age on tree growth and competition, we first fit the model with the best-performing index to the data subset consisting of trees with known age (but without age as a predictor), then added age as a fixed effect, and re-fit the model with the subset of trees of known ages (131 *P. resinosa* and 65 *P. strobus*) using maximum likelihood estimation. The significance of including age in the model was then tested with a likelihood ratio test. Similarly, we tested for the inclusion of age-competition index interaction term.

Models with each index were first optimized for their random and fixed components, and the optimal models for each index were ranked, based on the Akaike Information Criterion corrected for small sample sizes (AICc). Further, model performance was assessed with goodness-of-fit statistic, which was calculated from the linear regression between the observed and predicted basal area increment (cf. Canham et al., 2004).

3. Results

3.1. Characteristics of competition across population structures and sites

For *P. resinosa* data subsets, the best performing competition index varied between stand developmental histories (Table 2). The model with the spatially-explicit WVD-index best predicted tree growth within the multi-cohort *P. resinosa* stands. Here, the WVD-index was clearly superior to the other indices ($\Delta\text{AICc} \geq 16.9$). In contrast, population-level competitive status, as quantified by the relative dominance G-index, best predicted growth within the single cohort *P. resinosa* stands.

For *P. resinosa* in the single cohort stands, the optimal model explained 49% of the variance in tree growth (Table 3, Fig. 2). The influence of initial tree size was non-significant, whereas increasing relative dominance as quantified by the G-index had a positive effect on tree growth (Table 3). In the multi-cohort stands, the optimal model explained 85% of the variance in tree growth. The WVD-index, as well as tree size, positively influenced tree growth, whereas their interaction was negative (Table 3). Larger sizes and WVD-index values had a positive influence on basal area increment, whereas their interaction influenced tree growth negatively, i.e., the intensity (*sensu* Weldon and Slauson, 1986) of competition decreased with increasing tree size (Fig 3). Significant random effects in the model implied that tree growth differed across sites, as did the influence of competition index and initial tree size on growth. This variation, however, was relatively minor (Table 3).

Similar to the single-cohort *P. resinosa*, the relative dominance index G was included in the top model for *P. strobus* in the multi-cohort stands ($\Delta\text{AICc} \geq 3.7$). Overall, and similar to *P. resinosa*, *P. strobus* growth was also well explained by the models: the optimal model explained 67% of variance in the growth measured.

3.2. Tree age effects on tree growth

Tree age was an important determinant of tree growth within the multi-cohort stands examined, as adding age as a predictor

Table 2

Index comparisons for each data subset. Models were ranked according to their AICc values. Degrees of freedom (Df) differ according to random components in the optimal models.

Subset	Index	AICc	Df	ΔAICc	AICc weight
<i>P. resinosa</i> Single-cohort	G	124.1	7	0.0	0.77
	H	128.3	8	4.2	0.09
	WVD	129.3	8	5.2	0.06
	L	129.7	8	5.6	0.46
	NCI* (10 m)	131.2	8	7.1	0.02
	Null	132.4	6	8.3	0.01
<i>P. resinosa</i> Multi-cohort	Voronoi	140.3	8	16.3	0.00
	WVD	167.2	10	0.0	1.00
	H	184.1	10	16.9	0.00
	G	198.2	10	31.0	0.00
	L	205.7	10	38.5	0.00
	NCI* (9 m)	220.4	10	53.2	0.00
	Voronoi	250.3	8	90.7	0.00
Null	257.8	8	90.6	0.00	
<i>P. strobus</i> Multi-cohort	G	230.5	7	0.0	0.76
	Null	234.2	6	3.7	0.12
	H	235.9	7	5.4	0.05
	L	236.8	7	6.3	0.03
	Voronoi	238.3	7	7.8	0.02
	WVD	238.6	7	8.1	0.01
NCI** (10 m)	239.0	8	8.5	0.01	

* $\alpha = 2$ and $\beta = 1$.

** $\alpha = 1$ and $\beta = 0$.

Table 3

Model parameter values, their significances and random effects (in standard deviations) for best-fitting models predicting individual growth of *Pinus resinosa* and *Pinus strobus* in northern Minnesota, USA.

Subset	Parameter	Value	Random effects (SD)
<i>P. resinosa</i> , single cohort $r^2 = 0.49$ $n = 93$	Intercept	-1.42	0.18
	Log(size)	0.19	-
	Log(G)	0.88***	-
Residual 0.45			
<i>P. resinosa</i> , multi-cohort $r^2 = 0.85$ $n = 131$	Intercept	-14.42**	3.65
	Log(size)	1.46***	0.31
	Log(WVD)	4.12***	-
	Log(size): Log(WVD)	-0.35***	-
Residual 0.40			
<i>P. strobus</i> , multi-cohort $r^2 = 0.67$ $n = 90$	Intercept	-16.11*	0.27
	Log(size)	1.76***	-
	Log(G)	-1.41*	-
Residual 0.79			

Significance values:

* <0.05.

** <0.01.

*** <0.001.

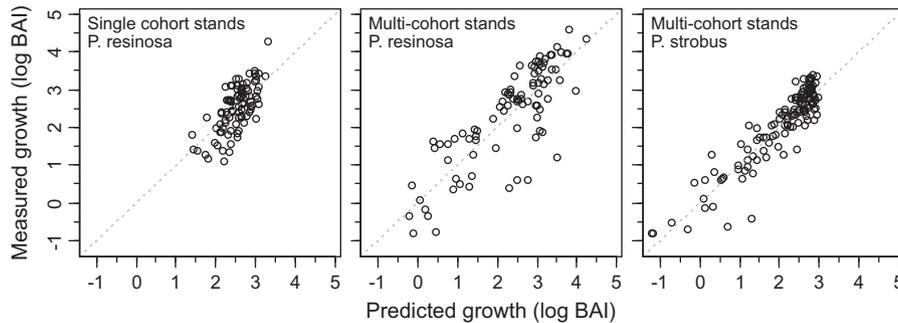


Fig. 2. Scatter plots of predicted vs. measured basal area increments (log-transformed), for models without age, and based on the best-fit model for each of the data subsets. The dotted 1:1 line is included to illustrate prediction errors.

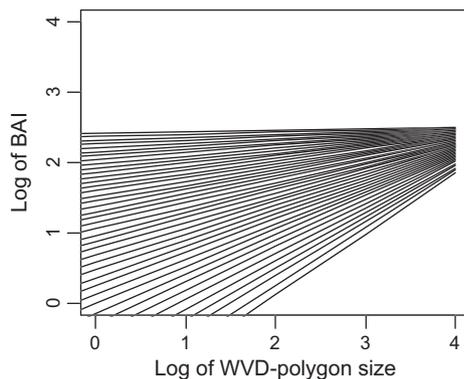


Fig. 3. Tree growth (basal area increment, BAI) predictions in the optimal model varied by *P. resinosa* diameter across a range of competitive states (as quantified by WVD polygon size) in the multi-cohort stands. Each line represents a tree with DBH between 10 (lowest line) and 50 (uppermost line) cm, shown with 1 cm increments in DBH, demonstrating that the intensity of competition (i.e. slope) decreased with increasing tree size.

significantly improved the models ($p < 0.05$ in the likelihood ratio tests, Table 4, Fig. 4). However, age as a predictor was not included in the single-cohort subset, because of the narrow age range in those stands. When age was significant, growth decreased with increasing age. Importantly, age did not influence the intensity of competition, as in all models the interaction between competition

index and age was non-significant. For *P. resinosa*, the model including age increased the variance explained only slightly, to 86% (from 85%). For *P. strobus*, the model including tree ages increased the variance explained to 76% (from 67%). Tree age and size showed little to no relationship in the data subsets ($r^2 = 0.05$ and 0.01 for *P. resinosa*, and *P. strobus*, respectively).

4. Discussion

Our results showed that in structurally diverse old-growth forests, competition can be both intense and important (*sensu* Weldon and Slauson, 1986), but that this importance varies according to stand developmental history and individual tree attributes, including species, size, and age. Results suggest that accounting for these complexities is useful for generating accurate portrayals of tree growth dynamics, particularly when using spatially-explicit simulation models. Our findings are restricted to two dominant species in north temperate forest ecosystems; however, our approach provides a framework for examining the differential and interactive importance of forest spatial structure and tree characteristics in driving individual tree growth patterns in other structurally complex forest systems.

For *P. resinosa*, our results supported the hypothesis that the influence of stand structure on tree-tree interactions varies markedly according to stand developmental history, as evidenced by contrasting findings between the single- and multi-cohort *P. resinosa* populations. In single cohort *P. resinosa* stands, competitive

Table 4

Parameters for best-fitting models including age as a predictor of *P. resinosa* and *P. strobus* tree growth. Random effects are expressed in standard deviations. The significance of including age was tested with likelihood ratio tests.

Subset	Parameter	Value	Random effects (SD)
<i>P. resinosa</i> , multi-cohort	Intercept	−9.54**	3.59
	Log(size)	1.24***	0.31
	Log(WVD)	3.71***	–
	Log(age)	−0.59	–
	Log(size): Log(WVD)	−0.30***	–
$r^2 = 0.86$			Residual 0.40
$n = 112$			
Likelihood ratio = 6.62**			
<i>P. strobus</i> , multi-cohort	Intercept	−3.93 ^{n.s.}	0.20
	Log(size)	1.27***	–
	Log(G)	−0.29 ^{n.s.}	–
	Log(age)	−1.64*	–
			–
$r^2 = 0.76$			Residual 0.63
$n = 65$			
Likelihood ratio = 8.26**			

Significance values:

* <0.05.

** <0.01.

*** <0.001

^{n.s.} For non-significant.

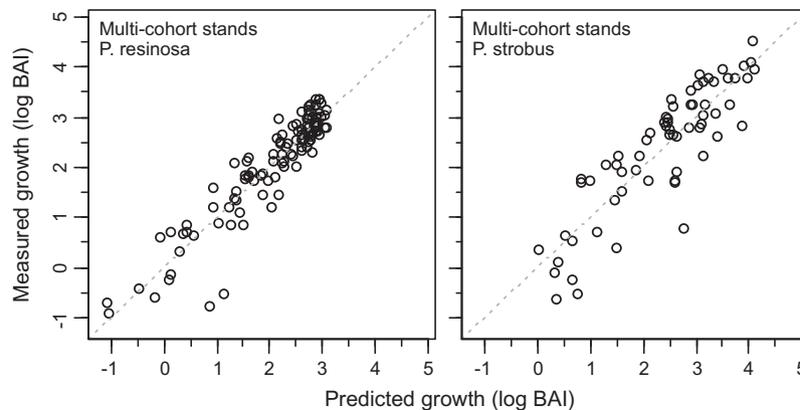


Fig. 4. Scatter plots of predicted vs. measured basal area increments (log-transformed), for models with age, and based on the best-fit model for each of the two data subsets. Note the improved fit, when compared to Fig. 2. The dotted 1:1 line is included to illustrate prediction errors. Age was not a meaningful predictor in the single-cohort stands, because the trees are of similar age.

effects were best approximated using information on tree sizes alone, similar to earlier studies from managed and younger natural even-aged stands (D'Amato and Puettmann, 2004; Lorimer, 1983). In multiple cohort *P. resinosa* stands, the inclusion of spatial information led to clearly superior model performance, an effect that has been hypothesized, but only variably supported in earlier studies (Hartmann et al., 2009; Stadt et al., 2007). A potential explanation for the difference in how competition is expressed in single and multiple cohort stands relates to differences in disturbance patterns and processes. Patterns in single cohort stands reflect a long period of orderly size-hierarchy development, where dynamics are primarily driven by endogenous processes, and the initial differences in the individuals and their growing conditions (i.e., their microsite and genetic potential) have strengthened over time through natural self-thinning processes (Ford, 1975). Following this reasoning, trees initially established as stronger competitors simply maintained or enhanced that status through stand development, with competitive effects best approximated by competitive status relative to the entire population. In contrast, for the multiple cohort forests we examined, development has been influenced periodically by stochastic disturbance events that removed competing trees and resulted in subsequent regeneration of *P. resinosa*. These events simultaneously disrupted pre-existing competitive hierarchies and increased stand structural heterogeneity, changes that were likely reflected in the superior performance of the

spatially explicit competition models, which was best conveyed by the WVD-index.

The fact that the best characterization of neighborhood conditions in multi-cohort *P. resinosa* stands was based on the WVD approach also suggests that simultaneously evaluating the entire neighborhood spatial structure represents an improvement over the tree-by-tree assessment used in crowding indices. The favorable performance of the WVD-index also implies that small trees exert their competitive effects over a very limited area when growing in crowded conditions, and their effect on large trees is negligible, as was exemplified by their small polygon areas nested within the polygon area of larger trees (Fig. 1).

For the *P. resinosa* in multi-cohort stands, both tree size and the WVD-index were important predictors of tree growth. This finding was somewhat expected, as size alone can be regarded as a metric of the resource-capturing capacity of a tree, especially when competition is asymmetric (such as competition for light; Ford and Diggle, 1981). Large trees have also been found to use light more efficiently than smaller trees in the same stands (Gspaltl et al., 2013). In our study, tree size also influenced the intensity of competition experienced by a given tree (Table 2, Fig 3). That is, our findings show that the growth of large trees was less influenced by neighborhood interactions than was growth of smaller trees (i.e., the negative interaction between WVD and initial size). Further, these findings support the relative dominance hypothesis

put forth by D'Amato and Puettmann (2004), which suggests that neighborhood competition is important for smaller trees, whereas relative size is more important in determining growth rates of larger trees. The decrease in competition intensity with increasing tree size may be attributed to the asymmetric competition for light, and it seems plausible that the remaining (minor) influence small trees exert on larger trees in these populations may be related to belowground competition, which is often considered symmetric (Canham et al., 2004; Coomes and Allen, 2007).

While spatial information was necessary to predict the growth of *P. resinosa* in the multi-cohort stands, it did not improve predictions of growth for *P. strobus* in those same stands, in which the relative dominance index was included in the top model. The size distributions between the two species were similar, i.e., they occupied similar canopy positions, and were larger than the non-pine species. The two species, however, differ in shade tolerance, with *P. strobus* being considerably more shade-tolerant. Other studies in mixed-species conifer forests have noted a lower sensitivity to competition within more shade-tolerant species (Contreras et al., 2011; Das, 2012), and these relationships may also explain the relatively poor performance of indices approximating competitive conditions for predicting *P. strobus* growth. Overall, tree size was sufficient for describing the competitive status of *P. strobus*, and there was no support for an interaction between size and competition intensity, as was observed for shade-intolerant *P. resinosa*. Given that the intensity of competition decreased with increasing tree size for *P. resinosa*, the response of *P. strobus* appears to be similar throughout its analyzed size range to that of large canopy-dominant *P. resinosa*.

4.1. Age effects on tree growth and competition effects

Our results showed that older trees grew more slowly than younger trees (all else being equal), which is consistent with earlier studies (Ryan et al., 2004), but contrary to recent work examining patterns of basal area increment in the eastern United States (Johnson and Abrams, 2009). In our work, the age effect on tree growth was negative, contrary to the positive influence of tree size. To the best of our knowledge, Stoll et al. (1994) is the only previous study to simultaneously evaluate competitive effects and tree age in uneven-aged stands, suggesting an ontogenetic reduction in tree growth with age. Also, Das (2012) reported that the relationship between tree size and growth is more complex than usually considered, and our findings that the potential growth of a young tree is greater than that of an older tree of the same size, corroborates this notion. However, tree age did not influence the trees' response to changes in the competitive environment, as deduced from the lack of interaction between age and competition index reported here. Importantly, this finding suggests that older pines retain the ability to respond to changes in their competitive environments, such as those caused by natural disturbances, or forest management, a result noted in thinning studies of old *P. resinosa* stands (D'Amato et al., 2010).

5. Conclusions

Our results demonstrate that tree–tree competition can be variably expressed in natural old-growth forests, depending on stand developmental history and tree species. For *P. resinosa* in single-cohort stands, competitive dynamics were similar to those documented for even-aged managed forests, namely that competition influences tree growth, and this influence was best predicted by relative tree sizes alone, and the inclusion of spatial structure failed to improve the models. In contrast, detailed spatial structure (best quantified here by the multiplicatively weighted Voronoi

diagrams, WVD) becomes an important factor for characterizing neighborhood conditions and predicting tree growth for structurally heterogeneous stands with complex developmental history, as shown in the multi-cohort stands. Moreover, the superior performance of the weighted Voronoi diagrams in these stands, compared to traditional competition indices, also suggests complex competitive relationships among trees, including irregularly shaped resource acquisition areas whose size and shape depends on the size and configuration of all neighboring trees.

In these same multi-cohort stands, the more shade-tolerant *P. strobus*, occupying similar canopy positions to those of *P. resinosa*, responded differently to competition. For this species, relative size was sufficient for capturing competitive effects, possibly reflecting its greater shade tolerance and lower sensitivity to competition relative to the more intolerant *P. resinosa*.

The relationship with tree growth and age was clear: tree growth declined with increasing age in the multi-cohort stands, a setting in which age and size were not positively correlated. However, age did not influence the intensity of competition, that is, all else being equal, young and old trees responded similarly to competition. This interaction of competition and tree size, and the lack of interaction between competition and tree age have important implications because the intensity of competition is a measure of potential growth response, following a change in a tree's competitive environment. This finding suggests that a tree's growth response to a disturbance (whether natural or anthropogenic) lessens with increasing tree size, but is independent of age.

Acknowledgments

We thank B. Anderson, J. Bradford, M. Curzon, S. Erlandson, J. Foster, C. Kerns, S. Jones, A. Milo, L. Patty, C. Peterson, D. Shinneman, K. Sweeney, M. Thompson, H. Telschow, D. Wenker, and J. Zasoski for assistance in the field and/or laboratory. D. Coomes and an anonymous reviewer are thanked for their comments on an earlier version of the manuscript, and L. Mu for sharing the multiplicatively weighted Voronoi diagram computer program. Support was provided by the Finnish Cultural Foundation, the Academy of Finland, (US) National Fire Plan and US Forest Service, Northern Research Station.

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