A neighborhood analysis of canopy tree competition: effects of shading versus crowding

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Abstract: We have developed extensions of traditional distance-dependent, spatial competition analyses that estimate the magnitude of the competitive effects of neighboring trees on target tree growth as a function of the species, size, and distance to neighboring trees. Our analyses also estimate inter- and intra-specific competition coefficients and explicitly partition the competitive effects of neighbors into the effects of shading versus crowding. We tested the method using data from forests of northern, interior British Columbia dominated by western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and western redcedar (*Thuja plicata* Donn ex D. Don). For both species, the most parsimonious regression models included terms for the effects of tree size, crowding, and shading and separate competitive effects of four different groups of competing species. The models explained 33%–59% of the variation in radial growth of the two species. For both species, growth declined more steeply as a function of crowding than shading. There was striking asymmetry in the strength of interspecific competition between hemlock and redcedar, with crowding by hemlock having a strong per capita effect on redcedar, while crowding by redcedar had relatively little effect on the radial growth of hemlock.

Résumé : Nous avons élargi l'analyse traditionnelle de la compétition spatiale dépendante de la distance pour estimer l'ampleur des effets de la compétition des arbres voisins sur la croissance d'un arbre central, en fonction de l'espèce, de la taille et de la distance aux arbres voisins. Nos analyses estiment également les coefficients de compétition inter et intraspécifique et distinguent explicitement, parmi les effets de la compétition des voisins, les effets de l'ombrage de ceux de la densité. Nous avons testé la méthode en utilisant des données issues de forêts du nord de l'intérieur de la Colombie-Britannique dominées par la pruche de l'Ouest (*Tsuga heterophylla* (Raf.) Sarg.) et le thuya géant (*Thuja plicata* Donn ex D. Don). Pour les deux espèces, les modèles de régression les plus parcimonieux comportent des termes pour les effets de la taille des arbres, de la densité et de l'ombrage et pour les effets compétitifs distincts de quatre groupes différents d'espèces compétitrices. Les modèles expliquent de 33 à 59 % de la variabilité en croissance radiale pour les deux espèces. Pour les deux espèces, la croissance diminue plus rapidement en fonction de la densité que de l'ombrage. Il y a une asymétrie frappante dans l'intensité de la compétition interspécifique entre la pruche et le thuya; une abondance de pruches a un effet individuel marqué sur le thuya alors qu'une abondance de thuyas a relativement peu d'effet sur la croissance radiale de la pruche.

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Introduction

Forest ecologists have used a wide range of methods to study the effects of competition on the growth and survival of adult trees. The most common approach has been to use regression models to test the effects on tree growth of distance-independent or distance-dependent measures of the local abundance of competitors (e.g., Bella 1971; Hegyi 1974; Lorimer 1983; Biging and Dobbertin 1995; Wimberly and Bare 1996; Vettenranta 1999). Although it has been much less often done, the same approach can be used to analyze a categorical response variable such as survival (e.g., He and Duncan 2000). In relatively uniform even-aged stands, simple distance-independent indices are generally sufficient to predict the effects of competition (Lorimer 1983). In stands with more complex structure, distance-dependent approaches incorporate spatially explicit variation in the strength of competitive interactions within stands (Wagner and Radosevich 1998; Larocque 2002.). These models reflect the mechanistic link between the abundance, size, and spatial distribution of neighboring trees and the strength of both aboveground and belowground competition (Larocque 2002).

All-aged management now accounts for >60% of logging in the United States (USDA Forest Service 2001) and a substantial fraction of logging in Canada. Forest managers and landowners face a complex set of trade-offs in the maintenance of diverse stand composition and structure that meets ecological and social goals while providing economically viable yields. Traditional growth and yield models and the enormous body of empirical research on which they were based provided a strong, predictive foundation for even-aged management (see Vanclay (1995) and Peng (2000) for reviews). Partial harvesting and all-aged management, in contrast, require consideration of an almost infinite variety of spatial configurations of the level of removal of different

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species and tree sizes within a stand and an almost infinite variety of permutations of residual stand conditions. The predictive power of traditional growth and yield models is based on measurable past growth of similar species on sites of similar quality but assuming a relatively constant climate. Given potential changes in climate, the level of predictive power provided by these empirical models is unlikely to be matched in the future. More fundamentally, we suggest that the challenges of managing and maintaining structurally complex stands require a shift in emphasis away from empirical, nonspatial models that emphasize prediction to more mechanistic, spatially explicit models that can incorporate the consequences of changing physical and competitive environments and dynamic spatial structure within stands.

We have developed an extension of traditional distance-dependent, spatial competition analyses that allows independent estimates of (1) the potential maximum tree growth for a given set of climatic and edaphic conditions, as a function of tree species and size, and (2) the magnitude of the competitive effects of neighboring trees on target tree growth as a function of the species, size, and distance to neighboring trees. As part of 2, the analyses provide empirical estimates of competition coefficients that quantify the relative magnitude of the competitive effect of species *i* on species *j* and explicitly partition the competitive effects of neighbors into the effects of shading versus the residual effects of "crowding", which is assumed to reflect both belowground competition and physical, aboveground inhibition of crown development (Kelty 1986; Foli et al. 2003). One of our objectives was the development of methods of quantifying canopy tree competition that could be parameterized using data readily available from permanent plots in mapped forest stands and that could then be incorporated in spatially explicit models of forest dynamics, such as SORTIE (Pacala et al. 1996; Coates et al. 2004).

Materials and methods

Study area

Our research was conducted as part of the Date Creek Silvicultural Systems Study (Coates et al. 1997) located near Hazelton, British Columbia, Canada (55°22′N, 127°50′W; 370–665 m elevation). The study area occurs in the moist cold subzone of the Interior Cedar–Hemlock biogeoclimatic zone (ICHmc) (Pojar et al. 1987; Banner et al. 1993). Mature forests at Date Creek became established after a landscape-level 1855 stand-destroying fire and are dominated by western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) but have a diverse canopy with western redcedar (*Thuja plicata* Donn ex D. Don), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.), hybrid spruce (the complex of white spruce (*Picea glauca* (Moench) Voss), Sitka spruce (*Picea sitchensis* (Bong.) Carrière), and occasionally Engelmann spruce (*Picea engelmannii* Parry ex Engelm.)), paper birch (*Betula papyrifera* Marsh.), trembling aspen (*Populus tremuloides* Michx.), and black cottonwood (*Populus balsamifera* subsp. *trichocarpa* (Torr. & A. Gray) Brayshaw). Subalpine fir is typically replaced by amabilis fir (A*bies amabilis* (Dougl. ex Loud.) Dougl. ex J. Forbes) at higher elevations. Western hemlock also dominates in old-growth stands (350+ years since fire), with minor components of western redcedar, subalpine fir, and amabilis fir.

The treatments applied at Date Creek created a wide range of overstory canopy density and structure. Specifically, two levels of partial cutting were used and compared with both undisturbed forests and clearcuts. In the light partial cutting treatments, approximately 30% of the stand volume was removed by cutting either single stems or small gaps (3–10 trees). In the heavy partial cutting treatments, approximately 60% of stand volume was removed. The cutting pattern utilized both large gaps (0.1–0.5 ha in size) evenly distributed across the treatment unit and either single-tree removal or small gaps created in the forest matrix between the openings. There were four replicates of each of the four treatments organized in a randomized block design. The treatment units were approximately 20 ha in size and logging was conducted in the fall and winter of 1992–1993 (Coates et al. 1997).

Study sites and field sampling

Our current study did not use the treatment units in a formal experimental design but instead took advantage of the spatial variation in canopy structure created by the treatments to sample the wide range of local competitive environments created by logging. Specifically, we used eight sites established at Date Creek by LePage et al. (2000) for a study of seedling recruitment. Two of the sites were in undisturbed treatment units, and the remaining six sites were located in either the light or heavy partial logging treatment units. At each site, a central transect 50–350 m long was established, and LePage et al. (2000) recorded the species, diameter at breast height (DBH), and location of each tree with a DBH ≥15 cm within 20 m of the center line of the transect and in a 20-m radius semicircle at the end of each transect. Tree locations were mapped using a Criterion Laser 400 survey transit. Western hemlocks made up 60.0% of the 3122 mapped trees in the eight sites, followed in abundance by western redcedar (21.2%), paper birch (6.0%), hybrid spruce (5.3%), amabilis fir (3.8%), trembling aspen (1.4%), black cottonwood (1.0%), lodgepole pine (1.0%), and subalpine fir (0.5%).

For the current study, all conifers within 10 m of either side of the center transect of the eight sites were cored, and radial growth rates were measured for the past 25 years. A total of 839 trees were cored, but the vast majority of the trees consisted of either hemlocks (n = 582) or redcedars (n = 194). Because of the small sample sizes for species other than hemlock and redcedar, we have limited our analyses to those two species. For the analyses described here, the average radial growth (mm/year) over the last 5 years (1995–1999) was used as the response variable (i.e., 5-year average growth after allowing 2 years for the changes in canopy structure resulting from the logging treatments to take effect). One redcedar with extremely high radial growth (3.6 mm/year) was dropped as an outlier.

A simple neighborhood model of canopy tree shading

We have developed a new, spatially explicit analysis to calculate shading of canopy trees by neighbors. The calculations are derived from the models developed by Canham et al. (1994, 1999) for the SORTIE model of forest dynamics

(Pacala et al. 1996). The basic design of the light model in SORTIE is extremely simple. The crowns of individual trees (from seedlings to adults) are represented as cylinders, with the average radius of the crown estimated as an empirical function of tree DBH. The top of the crown is set as the height of the tree (again, predicted as an empirical function of DBH), and the base of the crown is estimated as a linear function of tree height (using empirical relationships reported in Canham et al. 1999). All of the empirical functions needed to specify the dimensions of the crown can be estimated readily from field data (e.g., Canham et al. 1994, 1999). Light interception by tree boles below the live crown is ignored. The crowns of each species are assumed to have a species-specific canopy openness (i.e., fraction of sky visible through the crown), which can again be estimated readily from field data (Canham et al. 1994, 1999). For any given location in the understory, the model then divides the sky hemisphere above that specific location into regions and calculates the openness of each region of the sky as the product of the openness of each crown that blocks the sky in that direction (or =1 if no trees are present in that region of the sky). The openness of each region of the sky is then multiplied by the fraction of incident, growing season photosynthetic photon flux density (PPFD) that originates from that region of the sky and then summed across the regions of the sky to calculate the gap light index (GLI) (Canham 1988), which specifies the percentage of incident, growing season PPFD that penetrates through the canopy. For the purposes of the current study, we will equate the term "shading" to 1 – GLI (i.e., the percent of incident PPFD intercepted by neighbors). Empirical results from the original calibration of the model indicated that, for species of temperate eastern forests, openness of the crowns of individual trees was independent of the angle of view through the crown and independent of the path length through the crown (Canham et al. 1994).

The original light model was optimized for spatially explicit calculation of understory light levels, since the original version of SORTIE focused largely on the dynamics of seedling and sapling regeneration and ignored the details of competitive interactions between canopy trees. The original light model was also computationally intensive. For our current purposes, we can simplify the model because we are only dealing with canopy trees that are not overtopped by neighbors. Since our previous studies indicated that light interception per neighboring crown was not a function of the path length through the crown (Canham et al. 1994), the crowns of neighbors can be represented as two-dimensional "billboards" oriented orthogonally to the line from a focal tree to the neighbor. To simplify the calculations of the portion of the sky hemisphere blocked by a neighbor, we calculated the azimuth angles (compass directions) blocked by each neighboring crown based on the distance to the neighboring tree and average radius of the crown (i.e., angle subtended by the crown = 2.0 × arctan(radius/distance)). We also assumed that these angles did not change with angle from horizontal (i.e., as you move up the tree). In effect, this overestimates the shading by upper portions of the crowns of the neighboring trees, since the azimuth angles subtended by the cylindrical crown of a neighbor would decline slightly as the angle of perspective from horizontal increased.

To further simplify the model, and make it more usable in forests where species-specific canopy transmission coefficients are not known, we assumed that all neighboring crowns were opaque (i.e., transmission coefficient = 0). Light transmission coefficients for the nine tree species at Date Creek vary from 6% to 21% (Canham et al. 1999). The six conifer species showed much narrower variation, from 8% to 12% transmission, and the two dominant species (hemlock and redcedar, >80% of canopy density) had almost identical transmissions of ~9% (Canham et al. 1999). The analyses in Canham et al. (1999) indicated that the spatial configuration and sizes of canopy trees (and the gaps between them), rather than interspecific differences in light transmission, are the major cause of heterogeneity in understory light levels at Date Creek.

Since we assume that neighboring crowns are opaque, the calculation of shading by neighbors simplifies to the calculation of the portions of the sky hemisphere above a desired location that are blocked by at least one neighboring tree crown. As described above, we calculated the range of azimuth (horizontal) angles subtended by each neighbor as a function of the distance to the neighbor and its average crown radius. The vertical range of angles (altitude) blocked by a neighbor was then simply a function of the distance to the neighbor and the net height of the neighbor above the location for which shading was being calculated (see below). We then calculated the sky brightness distribution over the growing season at Date Creek in 1° increments of azimuth and altitude and calculated shading as the fraction of incident PPFD that was blocked by neighbors (i.e., (1 – GLI)/100; see Canham et al. (1999) for details).

The light model is spatially explicit and thus requires the specification of a set of x and y (horizontal) coordinates and a z (elevation) coordinate to define the exact location at which the shading calculation is done. The tops of trees obviously receive much less shading by neighbors than lower portions of the crowns. We initially calculated shading at the x,y location of each target tree and at three heights (z): the base of the crown, the middle of the crown, and the top of the crown. Analyses based on shading calculated at the middle of the crown gave the best fits to the data, so all analyses presented below are based on calculation of the amount of shading by neighbors at a point located in the vertical and horizontal center of the crown (and ignore self-shading by the target tree).

We tested the new light model at a set of 67 locations in stands used by Canham et al. (1999) for the development of the full SORTIE light model at Date Creek. GLI was measured at each of the locations using fisheye photographs taken at a height of 1 m above the ground (see Canham et al. (1999) for details). The new model was then used to predict GLI at those locations, based on maps of the surrounding canopy trees (stems ≥15 cm DBH), for neighborhoods of 15 and 25 m radius. Very little light reaches the ground from low incidence angles (i.e., near horizontal) (Canham et al. 1994, 1999) because of the very long path length through the canopy. Thus, we assumed that the sky hemisphere below 30° from horizontal was completely blocked by the surrounding forest, regardless of the configuration of the local neighborhood. The goodness of the fit of the model (R^2 of the relationship between observed GLI and predicted GLI) varied depending on the neighborhood radius. For the 25-m-radius neighborhoods, the R^2 of the new, simpler model was only slightly smaller than the original model (85% versus 87%), while the goodness of fit at the smaller 15-m-radius neighborhood was slightly lower (80%). For both neighborhood sizes, the simpler model tends to overestimate incident radiation slightly at low observed GLI levels (intercepts of linear regression of observed versus predicted GLI were significantly less than zero: –5.7 for the 25-m radius and –8.1 for the 15-m radius). In both cases, however, the relationship was clearly linear, indicating that the new model is an effective index of shading by neighboring canopy trees.

There is no question that the accuracy of our model could be improved by elaborate calculations using ray-tracing algorithms (e.g., Herwitz et al. 2000) and more realistic representations of crown shapes. One of the goals in the development of this very simple model was to produce an algorithm that could be implemented efficiently in the SORTIE model, where the calculations would have to be done for thousands of trees in every time step of each run of the model. The relatively high R^2 achieved with this simple model suggests that more elaborate computations are likely to add a significant computational burden without significant gain in the accuracy of model predictions. Deutschmann et al. (1999) have already shown that even the basic light model in SORTIE can be drastically simplified without significantly altering model predictions.

A distance-dependent model of canopy tree crowding

Our analysis of the effects of crowding begins with the long tradition of distance-dependent analyses of competition in which tree growth is analyzed as a function of the sizes of and distances to neighboring trees (e.g., Bella 1971; Hegyi 1974; Lorimer 1983; Biging and Dobbertin 1992, 1995; Wimberly and Bare 1996; Vettenranta 1999; Berger and Hildenbrandt 2000). The net effect of a neighboring tree on the growth of a target tree of a given species is assumed to vary as a direct function of the size of the neighbor and as an inverse function of the distance to the neighbor. Most previous studies have assumed that all species of competitors are equivalent (but see Pretzsch 1997). In our analysis, the net effect of an individual neighbor is multiplied by a species-specific competition index (λ_s) that ranges from 0 to 1 and allows for differences among species in their competitive effect on the target tree. Then, for $i = 1,..., s$ species and $j = 1,..., n$ neighbors of species s within a maximum radius (R) of the target tree, a neighborhood competition index (NCI) specifying the net competitive effect of the neighbors on the target tree is given by

$$[1a] \qquad \mathrm{NCI} = \sum_{i=1}^{s}\sum_{j=1}^{n} \lambda_i \frac{(\mathrm{DBH}_{ij})^{\alpha}}{(\mathrm{distance}_{ij})^{\beta}}$$

where α and β are estimated by the analyses (rather than set arbitrarily as in previous studies) and determine the shape of the effect of the DBH and the distance to the neighbor, respectively, on NCI. Our analysis also estimates R as a fraction of the maximum neighborhood radius of 15 m (the limit allowed by the size of our mapped transects). To keep the number of parameters in the model manageable, α, β, and R were assumed to be similar for all species of neighbors.

We also tested several alternate formulations of eq. 1. Previous distance-dependent models have typically used the ratio of the DBH of a neighbor relative to the DBH of the target tree (e.g., Hegyi 1974) instead of simply the DBH of the neighbor. In effect, this formulation assumes that larger trees are less sensitive than smaller trees to the effects of crowding by neighbors (i.e., the effects of a given level of neighbor crowding decline as an inverse function of the size (DBH) of the target tree):

$$[1b] \qquad \mathrm{NCI} = \frac{1}{\mathrm{DBH_t}}\sum_{i=1}^{s}\sum_{j=1}^{n} \lambda_i \frac{(\mathrm{DBH}_{ij})^{\alpha}}{(\mathrm{distance}_{ij})^{\beta}}$$

where $\mathrm{DBH_t}$ is the DBH of the target tree. We also generalized this to test the broader question of whether sensitivity of the target tree to competition decreased or increased with tree size using the equation

$$[1c] \qquad \mathrm{NCI} = (\mathrm{DBH_t})^{\gamma}\sum_{i=1}^{s}\sum_{j=1}^{n} \lambda_i \frac{(\mathrm{DBH}_{ij})^{\alpha}}{(\mathrm{distance}_{ij})^{\beta}}$$

where $-2 \leq \gamma \leq 2$.

We also tested a model of asymmetric competition in which neighbors only have a competitive effect if they are larger than the target tree and the magnitude of the effect is proportional to the difference in sizes of the target and neighboring tree, i.e.,

$$[1d] \qquad \mathrm{NCI} = \sum_{i=1}^{s}\sum_{j=1}^{n} \lambda_i \frac{(\mathrm{DBH}_{ij} - \mathrm{DBH_t})^{\alpha}}{(\mathrm{distance}_{ij})^{\beta}}$$

Equation 1 does not take into account the effects of the angular distribution of the neighbors around the target tree (i.e., whether neighbors are uniformly distributed around the target tree or whether they are clumped). This can be factored into the model using a clumping index (δ) developed by Zar (1996). The index is calculated as a function of the angles from the target tree to each neighbor and ranges from 0 when the neighbors are uniformly distributed around the target tree to 1 when they are tightly clumped.

$$[1e] \qquad \mathrm{NCI} = \left[\sum_{i=1}^{s}\sum_{j=1}^{n} \lambda_i \frac{(\mathrm{DBH}_{ij})^{\alpha}}{(\mathrm{distance}_{ij})^{\beta}}\right](1-\delta)$$

Both shading and crowding are assumed to reduce the potential growth of a hypothetical “free-growing” tree with no shading or crowding. Our method estimates potential radial growth as essentially the “intercept” of the function relating observed growth to variation in shading and crowding (i.e., the predicted growth rate when shading and crowding both = 0). Potential radial growth (PotRG) is assumed to vary with the DBH of the target tree. We use a lognormal function for the shape of this effect because it is flexible and supported by both empirical evidence and theory:

$$[2] \qquad \mathrm{PotRG} = \mathrm{MaxRG}\exp\left[\frac{-1}{2}\left(\frac{\ln(\mathrm{DBH}/X_0)}{X_\mathrm{b}}\right)^2\right]$$

where MaxRG is the maximum potential radial growth (mm/year) (i.e., at the peak of the lognormal shape), X_0 is

Table 1. Likelihoods and goodness of fit (R^2, in parentheses) of the alternate models for each target tree species.

Model	No. of parameters	Western hemlock	Western redcedar
Sample size		582	194
Basic model (eq. 1*a*)	12	–333.60 (0.340)[a]	–76.91 (0.596)[a]
Inverse size ratio (eq. 1*b*)	12	–339.81 (0.326)	–85.10 (0.561)
Variable ratio (eq. 1*c*)	13	–335.303 (0.336)	–78.113 (0.591)
Asymmetric competition (eq. 1*d*)	12	–343.66 (0.317)	–104.30 (0.465)
Angular dispersion (eq. 1*e*)	12	–337.48 (0.331)	–86.77 (0.553)
Equivalent competitors[b]	8	–346.43 (0.310)	–88.90 (0.543)
Crowding only	11	–342.03 (0.321)	–78.10 (0.591)[c]
Shading only	4	–356.92 (0.285)	–110.93 (0.427)

Note: See the text for a description of the models.

[a] Highest likelihood model.

[b] To test the equivalence of the four groups of competitors, the basic model was compared with a simpler model in which the four λ parameters were dropped from eq. 1*a*.

[c] Alternate or simpler model that is not a significantly worse fit.

the DBH (of the target tree) at which MaxRG occurs, and X_b determines the breadth of the function. This functional form is flexible enough that for the effective range of adult trees (i.e., >15 cm DBH), the shape can be monotonically increasing (i.e., when X_0 is very large) or decreasing (i.e., when X_0 is very small) or have a single "hump" and a skew to the left when X_0 is within the normal range of DBH.

Finally, potential growth, crowding, and shading are combined to calculate expected radial growth (RG) of the target tree.

$$[3] \quad \text{RG (mm/year)} = \text{PotRG (mm/year)} - (C \times \text{NCI}) - (S \times \text{shading})$$

where C and S are parameters estimated by the analysis. Equation 3 assumes linear reductions in growth as a function of both crowding and shading. This is the simplest assumption, requiring estimation of only two additional parameters, and was the most parsimonious fit to our data

Likelihood estimation, hypothesis testing, and comparison of alternate models

For each analysis of the growth of a target tree species, the regression model described by eq. 3 requires estimation of $n + 8$ parameters for n species of competitors. There were sufficient numbers of both hemlocks and redcedars in the mapped stands to treat those as separate species of competitors. However, because of the low densities of species other than hemlock and redcedar, we lumped the four remaining conifers into one group of competitors (other conifers) and the three deciduous species into a second group of competitors (deciduous).

We solved for the coefficients of the regression models using maximum likelihood estimation and simulated annealing (Goffe et al. 1994), a global optimization procedure. The iterative optimization procedure is necessary because the summation terms in eq. 1 make it impossible to estimate the regression coefficients using traditional software packages. The analyses were done using software written specifically for this study using Delphi for Windows (Borland Software Corp., Scotts Valley, Calif.). Residuals were assumed to be normally distributed. The fit of each alternate model was assessed using two metrics. The slope of the regression (with a zero intercept) of observed radial growth on predicted radial growth was used to measure bias, with an unbiased model having a slope of 1, and the R^2 of the regression was used as a measure of goodness of fit.

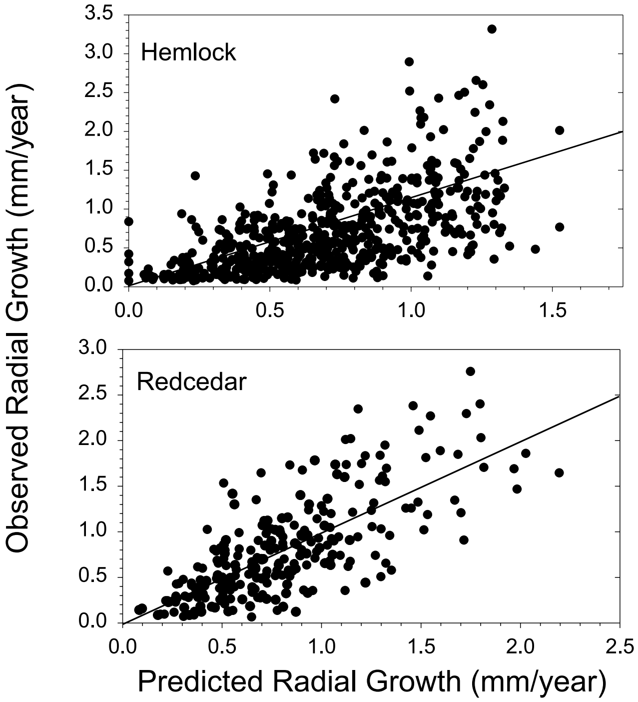
Alternate models were compared using likelihood ratio tests (Hilborn and Mangel 1997), with degrees of freedom equal to the difference in the number of parameters between the two nested models. This method tests whether the improvement (if any) in likelihood from the inclusion of additional parameters in the model results in a significant improvement in the likelihood of the resulting model. For normally distributed residuals, this is analogous to whether there is a significant improvement in goodness of fit as measured by R^2. This approach allows explicit tests of the hypotheses that are implicit in the comparison of alternate models. For example, to test whether there are significant differences among species of neighbors in their effect on a target tree species, we compared the likelihood of a model with the four species groups with that of a simpler model in which all neighboring trees were lumped into one group (i.e., a likelihood ratio test with 3 degrees of freedom).

Results

Likelihood and goodness of fit of alternate models

We estimated maximum likelihood parameter values for a series of alternate, nested models (Table 1). For both species of target trees, the most likely model included terms for effects of tree size, crowding, and shading and separate competitive effects of the four different groups of competitors (Table 1). For both species, the models produced unbiased estimates of radial growth, with a 1:1 relationship between predicted and observed and symmetrically distributed residuals (Fig. 1). The percentage of variance explained by the best models ranged from 33% in western hemlock to 59% in western redcedar. Neither the likelihood estimation methods that we used to fit the models nor the likelihood ratio statistics that we used to compare the models are particularly sensitive to heteroscedasticity, so we did not attempt to transform the growth rates to homogenize the variance before fitting the models. More generally, there is an important

Fig. 1. Goodness of fit of the maximum likelihood models (eq. 1*a*) for western hemlock and western redcedar. Lines are a 1:1 relationship between predicted and observed radial growth.



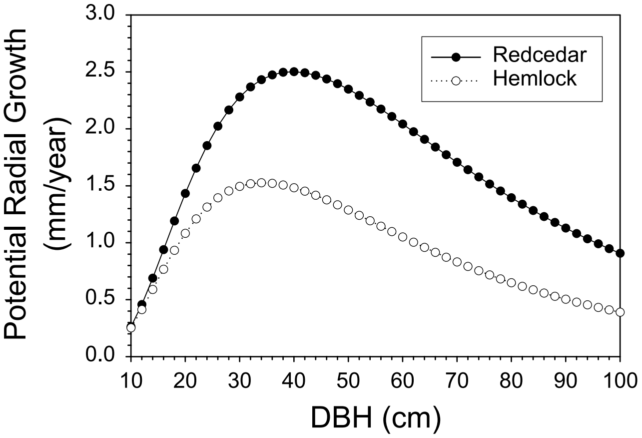
underlying message to the pattern of variation shown in Fig. 1, namely that our predictions of the average responses of the three species to crowding and shading are only reliable as estimates of the behavior of populations of trees and that individual trees may deviate significantly from those predictions, particularly under conditions favorable for growth.

Effects of DBH on potential radial growth and sensitivity to crowding

Our analyses allowed us to estimate the average potential radial growth of hemlock and redcedar (i.e., in the absence of any crowding or shading) as a function of variation in DBH (Fig. 2). In effect, the predicted average radial growth rates in Fig. 2 are the expected radial growth rates for a tree completely released from competition with neighboring trees. Note that while our data set includes trees with relatively little shading or crowding, the predicted potential radial growth rates are simply the intercepts of the linear function given by eq. 3 (i.e., the predicted radial growth when crowding and shading = 0) and represent an extrapolation from our data. Redcedar was predicted to have the highest average potential radial growth (MaxRG = 2.50 mm/year) (Table 2) and the largest tree size at which maximum radial growth occurred (X_0 = 39.68 cm DBH) (Table 2). The function for hemlock was similar in shape (X_b parameters for both species = 0.65) (Table 2) but with a lower maximum radial growth rate (1.53 mm/year) occurring at a slightly smaller DBH (34.3 cm).

There was no evidence that sensitivity to crowding varied as a function of the size of the target tree for either hemlock or redcedar (Table 1). Models based on eqs. 1*b* and 1*c* did not result in a significant increase in likelihood over the basic model (eq. 1*a*) (Table 1). In fact, the estimated γ exponent in eq. 1*c* for both species was slightly positive (0.26 for redcedar, 0.53 for hemlock), suggesting that, if anything, sensitivity to crowding increased rather than decreased with size of the target tree.

Fig. 2. Estimated average potential radial growth rates for western hemlock and western redcedar as a function of stem diameter (DBH).



Effects of neighboring tree location and size on degree of crowding

The neighborhood crowding index (NCI) sums the effects of all neighboring trees within a fraction *R* of the maximum neighborhood radius of 15 m. For both species, the *R* parameters were less than 1.0 (hemlock = 0.54, redcedar = 0.86) (Table 2), indicating that the search radius was sufficient to capture the effective range of competitive interactions between neighboring trees. Our analysis indicates that hemlock and redcedar responded to neighbors within a maximum distance of 8 and 13 m, respectively. Within those distances, for both species of target trees, the competitive effects of neighbors declined steeply with increasing distance (Fig. 3). Hemlock had both the smallest effective neighborhood size and the steepest decline in effects of competitors with distance (β = 0.7 for hemlock versus 0.47 for redcedar) (Table 2; Fig. 3).

The effect of the angular distribution of neighbors on shading of a target tree is explicitly factored into our analyses through the calculation of shading. The model (eq. 1*e*) used to incorporate the effects of the angular distribution of neighboring trees in our crowding index (NCI) did not improve the fit of the model (Table 1) and, in fact, resulted in a worse fit (lower likelihood) than the simple NCI, which ignored the angular distribution of neighbors (Table 1).

The exponent α in NCI controls the scaling of the effects of neighbor tree size on NCI (and hence on target tree radial growth). For both species, the estimated exponent was very close to 2 (Table 2), indicating that the competitive effects of neighbors were scaled to their basal area (i.e., DBH^2) and hence roughly proportional to the biomass of the neighboring tree.

Interspecific versus intraspecific crowding

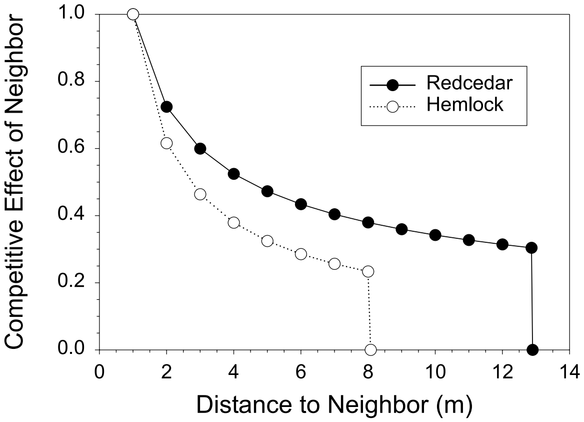
Our analyses indicate striking variation in the effects of intra- versus inter-specific crowding among adult trees (as

Table 2. Maximum likelihood parameter estimates and 95% asymptotic support intervals (in parentheses) for the best-fitting models (eq. 1*a*) for western hemlock and western redcedar target trees.

Parameter	Western hemlock	Western redcedar
MaxRG (mm/year)	1.526 (1.48–1.57)	2.502 (2.42–2.58)
X_0 (DBH)	34.246 (32.02–36.47)	39.683 (37.10–42.06)
X_b	0.649 (0.57–0.74)	0.649 (0.59–0.72)
C	1.931 (1.75–2.12)	2.221 (2.09–2.34)
S	0.789 (0.68–0.90)	0.312 (0.15–0.46)
R	0.539 (0.53–0.54)	0.858 (0.84–0.88)
α	2.170 (2.06–2.28)	1.866 (1.82–1.92)
β	0.700 (0.63–0.77)	0.466 (0.44–0.50)
λ deciduous	0.380 (0.00–1.0)	0.606 (0.43–0.78)
λ other conifers	0.418 (0.02–0.76)	0.001 (0.00–0.09)
λ western redcedar	0.004 (0.00–0.18)	0.495 (0.43–0.56)
λ western hemlock	0.664 (0.60–0.74)	0.372 (0.33–0.41)

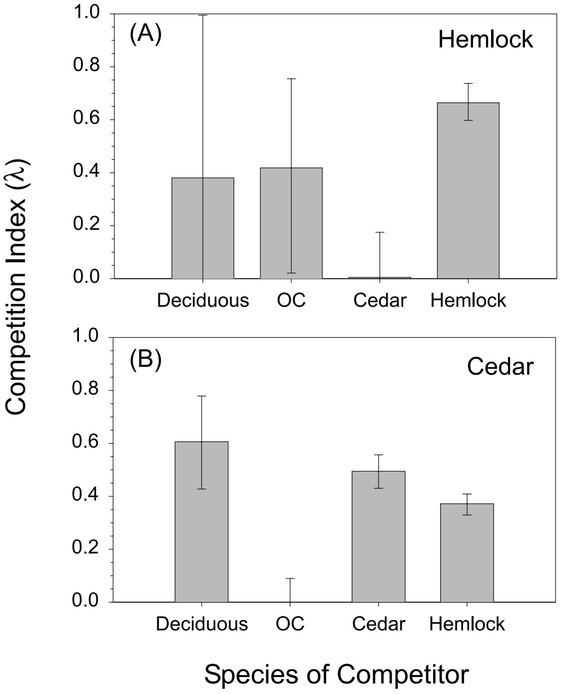
Note: See the text for descriptions of the parameters.

Fig. 3. Estimated decline in the competitive effect of a neighboring tree as a function of distance from target trees of western hemlock and western redcedar. The shapes of the curves are determined by the estimated parameter β (Table 2) and are truncated at the distance (estimated by the parameter R) beyond which the analyses indicate that target trees are no longer influenced by crowding by neighbors.



measured by λ_s, our species-specific competition indices), depending on the identity of the target tree and neighbors (Fig. 4). A simplified model that ignored differences in the identities of neighboring species (i.e., estimated a single λ regardless of species of neighbor) had a significantly lower likelihood than the model that estimated separate λ values for each species of neighbor ("equivalent competitors" model in Table 1). In general, there was strong intraspecific competition within both conifer species. In contrast, hemlock had consistently strong interspecific competitive effects on redcedar (Fig. 4B), while redcedar had very weak interspecific competitive effects on hemlock (Fig. 4A). Small sample sizes resulted in very large confidence intervals on the estimates of λ for the deciduous species group and the group of other conifers, particularly for their effects on hemlock. Our analyses, however, clearly suggest that the deciduous species had a greater competitive effect on redcedar trees than did the group of other conifer species.

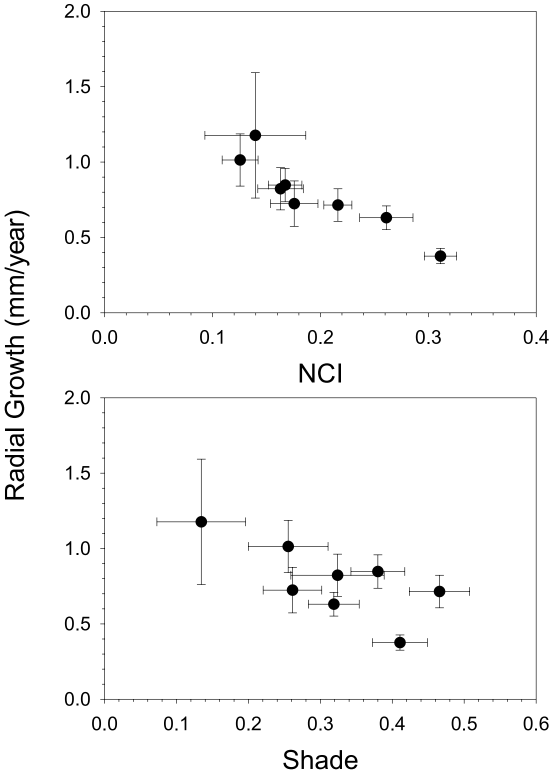
Fig. 4. Estimated competition indices (λ) and 95% support intervals for the per capita effect of each of the four species or groups of competitors on target trees of (A) western hemlock and (B) western redcedar. Deciduous = trembling aspen, paper birch, and black cottonwood; OC = other conifer species (primarily hybrid spruce, amabilis fir, and lodgepole pine).



Relative effects of shading versus crowding on adult tree growth

The target trees experienced a wide range of both crowding and shading (Fig. 5). While there was a weak correlation between levels of crowding (as measured by NCI) and levels of shading (as measured by the fraction of incident radiation blocked by neighbors), there was considerable scatter in the relationship, resulting in a wide range of shading at any

Fig. 5. Stand-level mean radial growth of western hemlock trees for the eight stands in which hemlocks were sampled,as a function of NCI, the average neighbor crowding index, and shading (the fraction of incident PPFD intercepted by neighbors). Error bars are 95% confidence intervals. Stand-level patterns for western redcedar are not shown because there were only four stands in which the species was sampled in sufficient density.



given level of crowding. The observed ranges of both NCI and shading were very similar within each species (ranging from 0 to 1). Thus, the magnitudes of the *C* and *S* parameters (Table 2) provide an approximate measure of the amount of reduction in radial growth resulting from an incremental increase in crowding or shading, respectively. The crowding parameter (C) was much larger than the shading parameter (*S*) for both species and dramatically larger for redcedar (Table 2). Of the two species, hemlock showed a much stronger reduction in target tree growth when shaded than did redcedar (hemlock S = 0.79, redcedar S = 0.32) (Table 2; Fig. 5). In fact, for redcedar, a model that ignored the effects of shading did not have a significantly lower likelihood than the full model (Table 1)

Discussion

One of the principal strengths of our iterative method of solving for maximum likelihood parameter values is the flexibility that this provides in finding the most parsimonious model of the effects of neighbors on target tree radial growth. In the past, the need to simplify the competition index into a form amenable to analysis using traditional regression methods required that investigators make a number of ad hoc assumptions about the nature of competitive interactions. For example, our approach allows estimation of α, the parameter relating neighbor DBH to its competitive effect, and β, the parameter controlling the decline in neighbor effect with distance from the target tree, rather than requiring that they be set arbitrarily as in most previous studies. Our estimates of α are very close to 2, indicating that the competitive effect of a neighbor scales to the basal area of the neighbor, in contrast with many previous studies that assume that competitive effect scales linearly with DBH (i.e., that α = 1) (e.g., Bella 1971; Hegyi 1974; see Biging and Dobbertin (1995) for a review of competition indices). Similarly, many previous studies using distance-dependent competition indices assume that β = 1 (i.e., that competitive effect declines as the inverse of the distance to the neighbor) (e.g., Hegyi 1974; Stoll et al. 1994), while our estimates of β for both target tree species are significantly less than 1 (Table 2), indicating that the decline in the effect of a neighbor with distance is less than often assumed. Another example of the flexibility allowed by our approach is the ability to estimate the effective neighborhood size (*R*, as a fraction of the maximum neighborhood radius allowed by the data). In all three cases, the ability to estimate the parameter (and associated uncertainty using support limits) from the data allows us to test hypotheses about the nature of the competitive interactions (e.g., is the competitive effect proportional to basal area and therefore proportional to the biomass of neighbors?).

The heteroscedasticity shown by the western hemlock data in Fig. 1 has implications for both the community-level consequences of competitive interactions and the management implications of different levels of canopy tree retention. As with most studies of tree competition, we have assumed that there is a maximum potential growth rate (presumably determined by a combination of the genetics of the population and site-level environmental factors) that is reduced by the effects of shading and crowding by neighboring trees. But competition is clearly only one of the factors that can reduce growth below that expected for a hypothetical, healthy, free-growing tree. Other factors include pests, pathogens, and physical damage to the canopy. Any one of these can significantly reduce actual growth of a tree. As a result, the pattern of scatter of “predicted” radial growth shown in Fig. 1 is essentially a gradient from conditions where competition is predicted to control observed growth (i.e., low predicted radial growth) to conditions where tree growth could be much higher if other factors unaccounted for in the model (pests, pathogens, etc.) do not intervene. Our methods obviously do not perfectly capture the effects of competition, and, as in any study, measurement error undoubtedly also contributes to the scatter in Fig. 1. However, it would be prudent to assume that the benefits of manipulating stand structure to release residual trees from competition are potential benefits and may not be realized because of factors other than competition. Our results suggest that the benefits of release from competition are more predictable for western redcedar than they are for western hemlock (Fig. 1).

Effects of target tree size on potential growth and sensitivity to competition

There is very little consensus on the theoretical expectations for the shapes of the functions in Fig. 2. We selected the lognormal function as the shape for the relationship in part because of empirical support for that particular form (e.g., Stoll et al. 1994) but more generally because the function is flexible enough that, over the range of observed diameters, it could take a very wide range of shapes, depending on the estimated parameters X_0 and X_b. In our study, the rapid decline in potential radial growth of subcanopy stems (below 30 cm DBH) was a surprise to us. We believe that the predicted relationships may be strongly influenced by the successional status of our study sites. The vast majority (~85%) of current stems in the mature stands became established in the first 30 years following a stand-replacing fire in 1855 (LePage 1995). In these stratified, single-cohort stands, all of the smaller subcanopy hemlock and redcedar trees have been suppressed by taller, dominant stems for many decades. Moreover, our sample of subcanopy trees was dominated by individuals in undisturbed stands and from partially cut stands with still fairly continuous canopy cover of larger trees — only a small number of subcanopy individuals were sampled on gap edges where canopy release was substantial. An earlier study of the effects of suppression on juvenile tree growth demonstrated that saplings of hemlock and redcedar did not show effects of the length of past suppression on growth once they were released in canopy gaps (Wright et al. 2000). In addition, we do not believe that our subcanopy tree results apply to younger, small-diameter stems growing in open conditions that have not been subjected to prolonged suppression. We think that suppressed subcanopy redcedar and hemlock can respond if given adequate space and we are currently testing this hypothesis with additional data collected from a wider range of stand ages and disturbance histories.

Contrary to an implicit assumption in many previous studies of tree competition (e.g., Hegyi 1974) (and see discussion of eq. 1*b* in the Materials and methods), we did not find any support for the hypothesis that target trees are more sensitive to crowding when they are small than when they are larger (as implied by the inverse size ratio model (eq. 1*b*) in Table 1). One possibility is that by explicitly factoring the effects of shading into our model, we have accounted for the effects of tree size that would otherwise be attributed to crowding. In effect, smaller trees are more likely to be shaded by neighbors than larger trees given any particular configuration of neighbors. By factoring this into our analysis explicitly, we can more rigorously test for an effect of target tree size on sensitivity to crowding.

Management implications of variation in the strength of intra- and inter-specific competition

Our analyses show striking variation in the strength of the competitive effects of crowding by different species of neighbors on the two target tree species (Fig. 4). The effects of intraspecific crowding were strong for both hemlock and redcedar, but there was a dramatic asymmetry in the strength of interspecific competition between the two species. Other than through a direct, aboveground competitive effect of shading, our analyses indicate that there is very little additional effect of crowding by redcedars on the radial growth of hemlock trees. In contrast, crowding by hemlocks has a strong per capita effect on redcedars. Crowding by the other conifers as a group had very little effect on redcedar radial growth, while crowding by the deciduous species had a relatively large per capita effect on redcedar (Fig. 4). An analysis with similar methods in a species-rich tropical forest revealed equally striking variation in the strength of interspecific competition (Uriarte et al. 2004). Analyses such as these will be a crucial component of the development of silvicultural systems that optimize yield by managing for specific mixtures and spatial configurations of species (Coates et al. 2004).

Competitive hierarchies and strong asymmetries in species interactions are implicit in most competition theory (e.g., Puettmann and Reich 1995). The specific mechanisms that give rise to the variation in the strength of interspecific competition are often not clear. From a management perspective, however, this may be less important than quantifying the strength of the interaction. In mixed redcedar–hemlock forests, it has been shown that forest floor decomposition and nutrient availability decrease with increasing presence of hemlock (Prescott 2000; Collins et al. 2001). Density of roots in single-species stands of redcedar or hemlock is lower than in mixed-species stands, and in mixed stands, roots are overlapping and intermingled, suggesting intense competition for available soil resources (Wang et al. 2002). The strong competitive effects of hemlock on redcedar growth reported in our study may well be a combination of this belowground competition and hemlock's negative influence on forest floor nutrient dynamics as its abundance increases in mixed stands.

Competitive interactions between canopy trees are obviously just one component of ecologically based silviculture using partial harvesting. The spatial distribution of logging will have significant effects on both the degree of release of residual trees and the availability and spatial distribution of light for tree regeneration (Coates et al. 2004). While uniformly distributed partial harvesting may maximize the competitive release of residual canopy trees, it may not create high enough light levels in the understory for release of saplings of less shade-tolerant tree species (Coates et al. 2004). Forests often exhibit patchiness in species composition because of a combination of dynamic processes (e.g., limited dispersal, local competitive interactions; Pacala et al. 1996) and niche differentiation of tree species along soil nutrient gradients (e.g., Bigelow and Canham 2002). There are many factors to consider in the analysis of the benefits of managing for patchiness versus well-mixed distributions of species within stands, but our analyses suggest that there may be options to maximize yield through judicious management of the mixtures of species within stands. Our results also have implications for the design of silvicultural strategies that will optimize yield during the transition from the dominance of even-aged management during the late nineteeth century and most of the twentieth century to strategies that result in more structurally complex and diverse stands.

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References

Banner, A., MacKenzie, W., Haeussler, S., Thomson, S., Pojar, J., and Trowbridge, R. 1993. A field guide to site identification and interpretation for the Prince Rupert Forest Region. British Columbia Ministry of Forests, Victoria, B.C. Land Manage. Handb. 26.

Bella, I.E. 1971. A new competition model for individual trees. For. Sci. **17**: 364–372.

Berger, U., and Hildenbrandt, H. 2000. A new approach to spatially explicit modelling of forest dynamics: spacing, ageing and neighbourhood competition in mangrove trees. Ecol. Model. **132**: 287–302.

Bigelow, S.W., and Canham, C.D. 2002. Edaphic effects on growth and distribution of juvenile canopy trees in northeastern USA. J. Ecol. **90**: 188–200.

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

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

Canham, C.D. 1988. An index for understory light levels in and around canopy gaps. Ecology, **69**: 1634–1638.

Canham, C.D., Finzi, A.C., Pacala, S.W., and Burbank, D.H. 1994. Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. Can. J. For. Res. **24**: 337–349.

Canham, C.D., Coates, K.D., Bartemucci, P., and Quaglia, S. 1999. Measurement and modeling of spatially-explicit variation in light transmission through interior cedar–hemlock forests of British Columbia. Can. J. For. Res. **29**: 1775–1783.

Coates, K.D., Banner, A., Steventon, J.D., LePage, P., and Bartemucci, P. 1997. The Date Creek silvicultural systems study in the interior cedar–hemlock forests of northwestern British Columbia: overview and treatment summaries. British Columbia Ministry of Forests, Victoria, B.C. For. Land Manage. Handb. 38.

Coates, K.D., Canham, C.D., Beaudet, M., Sachs, D.L., and Messier, C. 2004. Use of a spatially explicit individual-tree model (SORTIE-BC) to explore the implications of patchiness in structurally complex forests. For. Ecol. Manage. **186**: 297–310.

Collins, D.B., Feller, M.C., Klinka, K., de Montigny, L. 2001. Forest floor nutrient properties in single- and mixed-species, second growth stands of western hemlock and western redcedar. Northwest Sci. **75**: 407–416.

Deutschman, D.H., Levin, S.A., and Pacala, S.W. 1999. Error propagation in a forest succession model: the role of fine-scale heterogeneity in light. Ecology, **80**: 1927–1943.

Foli, E.G., Alder, D., Miller, H.G., and Swaine, M.D. 2003. Modelling growing space requirements for some tropical forest tree species. For. Ecol. Manage. **173**: 79–88.

Goffe, W.L., Ferrier, G.D., and Rogers, J. 1994. Global optimization of statistical functions with simulated annealing. J. Econometrics, **60**: 65–99.

He, F., and Duncan, R.P. 2000. Density-dependent effects on tree survival in an old-growth Douglas fir forest. J. Ecol. **88**: 676–688.

Hegyi, F. 1974. A simulation model for managing jack-pine stands. *In* Growth models for tree and stand simulation. *Edited by* J. Fries. Royal College of Forestry, Stockholm, Sweden. pp. 74–90.

Herwitz, S.R., Slye, R.E., and Turton, S.M. 2000. Long-term survivorship and crown area dynamics of tropical rainforest canopy trees: effects of lateral shading. Ecology, **81**: 585–597.

Hilborn, R., and Mangel, M. 1997. The ecological detective: confronting models with data. Princeton University Press, Princeton, N.J.

Kelty, M.J. 1986. Development patterns in 2 hemlock hardwood stands in southern New England. Can. J. For. Res. **16**: 885–891.

Larocque, G.R. 2002. Examining different concepts for the development of a distance-dependent competition model for red pine diameter growth using long-term stand data differing in initial stand density. For. Sci. **48**: 24–34.

LePage, P. 1995. The structure and development pattern of mixed-species forest stands in the Interior Cedar–Hemlock zone: Moist Cold subzone of northwestern British Columbia. M.Sc. thesis, Oregon State University, Corvallis, Ore.

LePage, P.T., Canham, C.D., Coates, K.D., and Bartemucci, P. 2000. Seed source versus substrate limitation of seedling recruitment in northern temperate forests of British Columbia. Can. J. For. Res. **30**: 415–427.

Lorimer, C.G. 1983. Test of age-independent competition indices for individual trees in natural hardwood stands. For. Ecol. Manage. **6**: 343–360.

Pacala, S.W., Canham, C.D., Saponara, J., Silander, J.A., Jr., Kobe, R.K., and Ribbens, E. 1996. Forest models defined by field measurements: estimation, error analysis and dynamics. Ecol. Monogr. **66**: 1–43.

Peng, C. 2000. Growth and yield models for uneven-aged stands: past, present and future. For. Ecol. Manage. **132**: 259–279.

Pojar, J., Klinka, K., and Meidinger, D.V. 1987. Biogeoclimatic ecosystem classification in British Columbia. For. Ecol. Manage. **22**: 119–154.

Prescott, C.E. 2000. The influence of the forest canopy on nutrient cycling. Tree Physiol. **22**: 1193–1200.

Pretzsch, H. 1997. Analysis and modeling of spatial stand structures. Methodological considerations based on mixed beech–larch stands in Lower Saxony. For. Ecol. Manage. **97**: 237–253.

Puettmann, K.J., and Reich, P.B. 1995. The differential sensitivity of red pine and quaking aspen to competition. Can. J. For. Res. **25**: 1731–1737.

Stoll, P., Weiner, J., and Schmid, B. 1994. Growth variation in a naturally established population of *Pinus sylvestris*. Ecology, **75**: 660–670.

Uriarte, M., Canham, C.D., Thompson, J., and Zimmerman, J.K. 2004. A maximum-likelihood, spatially-explicit analysis of tree growth and survival in a tropical forest. Ecology. In press.

USDA Forest Service. 2001. 2000 RPA assessment of forest and range lands. FS687. USDA Forest Service, Washington, D.C.

Vanclay, J.K. 1995. Growth models for tropical forests: a synthesis of models and methods. For. Sci. **41**: 7–42.

Vettenranta, J. 1999. Distance-dependent models for predicting the development of mixed coniferous forests in Finland. Silva Fenn. **33**: 51–72.

Wagner, R.G., and Radosevich, S.R. 1998. Neighborhood approach for quantifying interspecific competition in coastal Oregon forests. Ecol. Appl. **8**: 779–794.

Wang, X.L., Klinka, K., Chen, H.Y.H., and de Montigny, L. 2002. Root structure of western hemlock and western redcedar in single- and mixed-species stands. Can. J. For. Res. **32**: 997–1004.

Wimberly, M.C., and Bare, B.B. 1996. Distance-dependent and distance independent models of Douglas-fir and western hemlock basal area growth following silvicultural treatment. For. Ecol. Manage. **89**: 1–11.

Wright, E.F., Canham, C.D., and Coates, K.D. 2000. Effects of suppression and release on sapling growth for 11 tree species of northern, interior British Columbia. Can. J. For. Res. **30**: 1571–1580.

Zar, J.H. 1996. Biostatistical analysis. 3rd ed. Prentice Hall, Upper Saddle River, N.J.