Above- versus below-ground competitive effects and responses of a guild of temperate tree species

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Summary

1. The neutral theory debate has highlighted the scarcity of robust empirical estimates of the magnitude of competitive effects and responses within guilds of co-occurring tree species. Our analysis quantifies the relative magnitude of all possible pairwise competitive interactions within a guild of nine co-occurring tree species in temperate forests of northern, interior British Columbia, and explicitly partitions the competitive effects of neighbours into the effects of shading versus the residual effects of 'crowding', assumed to reflect below-ground competition.

2. Models that treated neighbours as equivalent in their competitive effects were the most parsimonious for the five species with the smallest sample sizes. For the remaining species (samples sizes of ≥ 150 individuals), the best models estimated separate competition coefficients for all nine species of neighbours. We take this as evidence that species do indeed differ in their competitive effects, but that there can be a minimum sample size required to discriminate between them.

3. There was a strong size-dependency in potential growth. Six species showed an optimal growth at a size between 5 and 20 cm diameter. Potential growth declined moderately to strongly as diameter increased. Sensitivity to crowding varied as a function of tree size for five of the nine species; however, this response was not consistent by tree species.

4. The magnitude of reduction in growth due to crowding was greater on average than the reduction in growth due to shading, except for the two least shade tolerant conifers. Sensitivity to shading among the conifer species was correlated with their shade tolerance.

5. The per capita effects of crowding by different species of neighbours varied widely. A large number of the estimated pairwise per capita competition coefficients were very low. The relative magnitude of the strength of intra- versus interspecific competition also varied widely among the tree species.

6. *Synthesis.* Model selection techniques effectively separated above- and below-ground competition in complex forests, and allowed us to assess differences among species in competitive effects and responses. While below-ground effects were strong, they were due to proximity of neighbours from a very specific (and small) subset of strong competitors within the guild. Response to crowding varied with tree size but the nature of the relationship varied widely among the species.

Key-words: competition coefficients, competitive interactions, complex forests, complex stands, crowding, interspecific competition, intraspecific competition, neighbourhood models, shading, size-dependency of growth

Introduction

While plant ecologists increasingly recognize the importance of a broad range of positive and negative interactions among co-occurring species within a community, including facilitation (e.g. Baumeister & Callaway 2006; Brooker *et al.* 2008), allelopathy (e.g. Perry *et al.* 2007; Gómez-Aparicio & Canham 2007), and microbial and pathogen-mediated interactions (e.g. Packer & Clay 2004; Mangla *et al.* 2008), understanding the nature of competitive interactions among species within a guild remains central to our understanding of community organization and dynamics. This knowledge is also critical to the development of sustainable management of both forest and grassland ecosystems (e.g. Burton *et al.* 2003). Many North American forests are now routinely managed for complex residual structure following harvests, and this presents a

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host of new scientific challenges (Puettmann *et al.* 2008). The spatial pattern of a partial harvest will have important implications for understorey light levels for regeneration (e.g. Canham *et al.* 1999; Beaudet *et al.* 2002). Given the relatively limited dispersal distances of most tree species (Ribbens *et al.* 1994; Clark *et al.* 1999; LePage *et al.* 2000; Greene *et al.* 2004), the spatial distribution of seed trees will have strong effects on the distribution and abundance of regeneration. Perhaps most important from an economic standpoint, the spatial pattern of a harvest determines the degree of release from competition among residual trees, with potentially dramatic effects on growth and survival of residual trees (e.g. Wimberly & Bare 1996; Berger & Hildenbrandt 2000; He & Duncan 2000; Coates *et al.* 2003; Canham *et al.* 2004).

The long life spans and large adult sizes of forest trees have usually precluded experimental approaches to the study of tree competition except among juveniles (seedlings and saplings). Forest ecologists have typically approached the study of the competitive effects of adult trees through one of two alternate approaches. The more mechanistic of the alternatives has been to focus on competition for a particular resource and to decompose the analysis into separate studies of (i) the effects of trees on the availability of the resource (i.e. light extinction by tree canopies, e.g. Canham *et al.* 1999); and (ii) the responses of individuals to the altered availability of a resource (i.e. Wright *et al.* 1998a; Kranabetter & Coates 2004). A more phenomenological and widely applicable approach has been to use regression analyses of the growth and survival of individuals as a function of the distribution and abundance of neighbours (e.g. Bella 1971; Lorimer 1983; Biging & Dobbertin 1992, 1995, He & Duncan 2000; Canham *et al.* 2004; Uriarte *et al.* 2004a,b). This latter approach reflects the mechanistic link between the abundance, size and spatial distribution of neighbouring trees and the strength of competition (Larocque 2002; Canham *et al.* 2004).

It is often assumed that differences in relative abundance of species are, at least partly, a reflection of competitive hierarchies (e.g. Howard & Goldberg 2001) with the dominant competitor defined either in terms of the strongest competitive effects on neighbours or the least competitive response to neighbours (Goldberg 1990; Goldberg & Landa 1991). Hubbell (2001) has challenged this notion, and has argued that interspecific differences in the competitive effects are relatively unimportant in explaining patterns of diversity and relative abundance in forests. This debate has highlighted the scarcity of robust empirical estimates of interspecific competition coefficients (i.e. the per capita effect of one species on another) (Freckleton & Watkinson 2001a,b).

As part of the Date Creek Silvicultural Systems study (Coates *et al.* 1997), we developed an extension of traditional distance-dependent, spatial competition models for mature and old-growth forest types in the interior cedar-hemlock forests of Northwestern British Columbia (Canham *et al.* 2004). Sample sizes at the Date Creek study sites were sufficient to parameterize models only for the two dominant tree species in the system. That study, however, indicated that there were striking differences between the two species in the strength of per capita competitive effects of different species of neighbours. In addition, when we tested the growth models from Canham *et al.* (2004) in the stand dynamics simulator SORTIE/BC (Coates *et al.* 2003), it become clear that models parameterized with data from a narrow range of successional stages and competitive neighbourhoods were not robust enough for growth predictions across a wide range of successional stages.

The most general objective of the current study was to assess above-ground (shoot) and below-ground (root) competitive effects and responses across an entire guild of co-occurring tree species. Manipulative field studies with annual plants and short-lived perennials have shown that shoot and root competition are not necessarily independent processes (e.g. Cahill 1999, 2002). Destructive studies with tree seedlings and saplings have also demonstrated and separated above- and below-ground competitive effects in forests (e.g. Coomes & Grubb 1998). For field studies of adult trees, it is not feasible to separate root and shoot competition by these types of manipulative or destructive experiments. In this study, our objective was to develop robust statistical models capable of separating the relative effects of above- and below-ground competition across a wide range of successional stages and competitive neighbourhoods within a guild of temperate forest tree species. Our analyses explicitly partition the competitive effects of neighbours into the effects of shading (above-ground competition) versus the residual effects of 'crowding', which is assumed to reflect primarily below-ground or root competition. The analyses also provide empirical estimates of per capita competition coefficients that quantify the relative magnitude of the crowding effect of species *i* on species *j*.

Our specific objectives were (i) to predict the potential maximum tree growth for a given set of climatic and edaphic conditions, as a function of tree species and size; (ii) to quantify variation among species within the guild in their competitive responses to neighbours, as a function of both above-ground competition (shading) versus below-ground competition (crowding); and (iii) to compare the species within the guild in terms of the magnitude of their below-ground competitive effects on neighbouring trees.

Methods

STUDY SITES AND FIELD SAMPLING

The research was conducted within the moist cold subzone of the Interior Cedar-Hemlock (ICHmc) biogeoclimatic zone of British Columbia (Banner *et al.* 1993). Forests of this region represent a transition between the interior and coastal forests of Northwestern British Columbia (Pojar *et al.* 1987). Mature natural forests in the ICH zone are dominated by western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), but have a diverse tree species mix with western redcedar (*Thuja plicata* (Donn ex D. Don in Lamb), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.), hybrid spruce [the complex of white spruce (*Picea glauca* [Moench] Voss), Sitka spruce (*P. sitchensis* [Bong.] Carr.) and occasionally Engelmann spruce (*P. engelmannii* Parry ex Engelm.)], paper birch (*Betula papyrifera* Marsh.), trembling aspen (*Populus*

Table 1. Samples sizes and mean, minimum and maximum d.b.h. (cm) for the study species

Species	Common name	*n*	Mean	Minimum	Maximum
Tsuga heterophylla	Western hemlock	245	29.9	6.1	103.9
Thuja plicata	Western redcedar	192	25.1	6.0	69.5
Abies amabilis	Amabilis fir	91	28.2	6.5	76.7
Abies lasiocarpa	Subalpine fir	95	15.4	4.0	45.4
Picea hybrid*	Hybrid spruce	196	22.0	4.3	59.1
Pinus contorta	Lodgepole pine	93	18.7	3.7	43.2
Populus tremuloides	Trembling aspen	101	20.1	4.0	47.3
Betula papyrifera	Paper birch	149	17.5	1.8	42.1
Populus balsamifera ssp. *trichocarpa*	Cottonwood	39	21.1	8.0	63.0

*A complex of *Picea glauca*, *P. sitchensis* and *P. engelmannii*.

tremuloides Michx.), and black cottonwood (*Populus balsamifera* ssp. *trichocarpa* Torr. & Gray). Subalpine fir is typically replaced by amabilis fir (*Abies amabilis* Dougl. ex Forbes) at higher elevations. Morainal parent materials dominate the area, ranging in texture from loamy sand to clay loam. Eluviated Dystric Brunisols, Orthic Dystric Brunisols and Orthic Humo-Ferric Podzols are the most common soils.

We sampled across a wide range of stand ages, disturbance histories, tree species composition and competitive neighbourhoods to obtain a data set that allowed analysis of all dominant tree species (nine) found in the ICH zone (Table 1). A core set of measurements were taken at 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), but sampling also occurred at sites throughout the ICH zone. The Date Creek sample sites are fully described in Canham *et al.* (2004). Briefly, they were in experimental plots in mature and old-growth stands that were either undisturbed or subject to two levels of partial cutting (30% or 60% basal area removal). Our sampling 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, but only in the two dominant age-classes found at Date Creek. Because of the small sample sizes for species other than western hemlock and western redcedar, only those two species were reported on in our earlier study (Canham *et al.* 2004).

We added 19 additional stem-mapped plots to the eight original sites used by Canham *et al.* (2004). The location of all trees > 2 m tall were mapped. Mapped areas varied from 0.1 to 1 ha in size. Species, (d.b.h., 1.3 m) and condition (live or dead) were recorded for each mapped tree. Species composition of each mapped area varied widely depending on stand age and disturbance history (Appendix S1). Sample trees were selected to have a minimum 15 m radius of mapped neighbours on all sides. A total of 1201 target growth trees were cored, with sample sizes of the nine study species varying between 39 and 245 (Table 1). Increment cores were taken at 1.3 m height. The average radial growth (mm year⁻¹) over the last 5 years was used as the response variable.

ANALYSIS

Our analysis is an extension of the spatially explicit models of tree competition outlined in Canham *et al.* (2004). As in our previous studies, the observed radial growth (*RG*) of a target tree is analyzed as a function of: (i) the potential growth of a hypothetical 'free grow-ing' tree (*PRG*), (ii) the size (d.b.h.) of the tree, (iii) the degree of shading, and (iv) crowding of trees by neighbours:

$$RG = PRG \times \text{Size Effect} \times \text{Shading Effect} \times \text{Crowding Effect} \quad (1)$$

RG and *PRG* are in units of mm year⁻¹, and the remaining three terms on the right hand side of Eqn 1 are scalars ranging from 0 to 1 that act to reduce potential growth. As in other recent studies (Canham *et al.* 2004, 2006), we use a lognormal function for the shape of the size effect:

$$\text{Size Effect} = e^{-1/2\left[\frac{\ln(\text{d.b.h.}/\delta)}{\sigma}\right]^2} \quad (2)$$

where δ is the d.b.h. (of the target tree) at which *PRG* occurs, and σ determines the breadth of the function. This function is flexible enough that for the effective range of adult trees the shape can be monotonically increasing (i.e. when δ is very large), decreasing (i.e. when δ is very small), or have a single 'hump' and a skew to the left when δ is within the normal range of d.b.h. (Canham *et al.* 2004).

Canham *et al.* (2004) presented an empirical method of calculating the shading of a target tree by neighbours, and we use the same method here. For our purposes, 'shading' is the percent of incident, seasonal total photosynthetic photon flux density blocked by neighbours. The calculations are based on a spatially explicit model of light transmission, parameterized specifically for the species at our study sites (Canham *et al.* 1999). The calculations use tree allometry, grown geometry and light extinction characteristics of each of the tree species (reported in Canham *et al.* 1999) to determine the areas of the sky around each target tree that are blocked by neighbours, and then weight those areas of the sky by a sky brightness distribution calculated for our study sites (see Canham *et al.* 2004 for details). The shading effect is then assumed to reduce potential growth following a negative exponential function:

$$\text{Shading Effect} = e^{-S \times \text{Shading}} \quad (3)$$

The parameter *S* measures the sensitivity of the target tree to shading: at *S* equals zero, the target tree is insensitive to shading.

Our analysis of the effects of crowding follows from the long tradition of distance-dependent analyses of competition, in which tree growth is analyzed as a function of the sizes and distances to neighbouring trees (e.g. Bella 1971; Hegyi 1974; Lorimer 1983; Wimberly & Bare 1996; Vettenranta 1999; Berger & Hildenbrandt 2000; Canham *et al.* 2004, 2006; Uriarte *et al.* 2004a,b; Stadt *et al.* 2007). The net effect of a neighbouring 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 neighbour, and as an inverse function of the distance to the neighbour. Most previous studies have assumed that all species of competitors are equivalent. In our analysis, the net effect of an

individual neighbour 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 $i = 1 \ldots s$ species and $j = 1 \ldots n$ neighbours of species s within a maximum radius (R) of the target tree, a Neighbourhood Competition Index (*NCI*) specifying the net crowding effect of the neighbours on the target tree is given by (Canham *et al.* 2004):

$$NCI = \sum_{i=1}^{S} \sum_{j=1}^{n} \lambda_i \frac{(\text{d.b.h.}_{ij})^\alpha}{(\text{distance}_{ij})^\beta} \qquad (4)$$

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 d.b.h. and the distance to the neighbour, respectively, on *NCI*. Because of our ability to explicitly incorporate estimates of shading in our analyses, we interpret our 'crowding' term (Eqn 1) as primarily a measure of below-ground competition. Our analysis also estimates *R*, as a fraction of the maximum neighbourhood radius of 15 m (the limit allowed by the size of our mapped plots and transects). To keep the number of parameters in the model manageable, α, β and *R* were assumed to be identical for all species of neighbours.

We have an *a priori* interest in quantifying interspecific variation in per capita effects of crowding by different species of neighbours. This is motivated by our interest in understanding the consequences for timber yield of designing silvicultural systems that manage for specific mixtures of species in local neighbourhoods. This issue is also relevant to recent debates about neutral theory in ecology in contrast to niche differentiation as a means to explain coexistence among species. In recent studies from species-rich tropical forests (Uriarte *et al.* 2004a,b, 2005), the most parsimonious models typically lump many species of neighbours as equivalent competitors. This appears to be largely a function of the very small samples of any given species of neighbour as a result of very high tree species diversity in those forests. For comparison with those studies, we also tested three different groupings of neighbouring species in Eqn 4: (i) a model in which all species were considered equivalent (i.e. fixing λ = 1 regardless of the species of neighbour); (ii) a model that calculated a separate λ for conspecifics and a single, separate λ for all heterospecific neighbours; and (iii) a model that calculated one λ for all neighbours of conifer species and a separate λ for all neighbours of deciduous species.

We assume that growth declines as a negative exponential function of *NCI*:

$$\text{Crowding Effect} = e^{-C \times NCI} \qquad (5)$$

Canham *et al.* (2004) used a simpler, linear reduction in growth with increasing crowding, but that formulation requires truncating the function at some level of *NCI* to prevent predictions of negative growth. Other recent studies have tested for a sigmoidal reduction in growth with increasing crowding (Uriarte *et al.* 2004a,b; Canham *et al.* 2006), but have consistently found that the simple exponential decline provides the best fit to the data, so we did not test a sigmoidal model here.

We also tested a variant of Eqn 5 in which the effect of crowding on target tree growth varied as a function of target tree d.b.h. This effect is independent of the underlying effect of target tree size on potential growth (Size Effect, in the absence of competition). This allowed us to test whether a given level of crowding had a greater effect on smaller (or larger) target trees (Canham *et al.* 2004). To test this, we allowed the exponential decay term (*C*) in Eqn 5 to vary as a function of target tree size (d.b.h.):

$$C = C' \times \text{d.b.h.}^\gamma \qquad (6)$$

If $\gamma = 0$ there is no variation in sensitivity to crowding as a function of target tree size. If $\gamma < 0$, then sensitivity to crowding declines as target tree d.b.h. increases (i.e. smaller trees suffer a greater reduction in growth from a given level of crowding than do larger trees). If $\gamma > 0$, then larger trees are more sensitive to a given level of crowding than smaller trees.

PARAMETER ESTIMATION AND COMPARISON OF ALTERNATE MODELS

Growth of each of the nine species was analyzed separately. For each analysis, the regression models described by Eqns 1–6 require estimation of $n + 10$ parameters for *n* species or groups of competitors. 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 parameter estimation was done using software written specifically for this study using Delphi for Windows (Borland Software Corp.). Residuals were normally distributed, and unlike our earlier studies (Canham *et al.* 2004, 2006), the variances were uniform across the range of predicted values. We used asymptotic, two-unit support intervals (Edwards 1992) to assess the strength of evidence for individual maximum likelihood parameter estimates. A two-unit support interval is roughly equivalent to a 95% support limit defined using a likelihood ratio test. 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.

Our likelihood approach uses two different methods to assess the strength of evidence for (and magnitude of) different processes incorporated in our models. In many cases, the parameter estimates themselves provide the basis for determining the magnitude of the effect of a given process. For example, if the maximum likelihood estimate for parameter *S* in Eqn 3 is effectively zero, then there is no effect of shading by neighbours on the growth of a target tree species. We have also used formal model comparison methods, parameterizing alternate models with and without specific terms, and have then used the Akaike Information Criterion corrected for small sample size (AIC_{corr}) to incorporate both parsimony and likelihood in comparing alternate models. In addition to the different groupings of species of neighbours described above to simplify the number of distinct λ parameters, we used formal model comparison in three additional cases. First, we tested whether there was evidence that sensitivity to crowding varied as a function of the target tree d.b.h., by comparing models including γ in Eqn 6 versus models omitting this term. Then we tested three simpler models in which we dropped: (i) shading, (ii) crowding, or (iii) shading plus crowding, leaving size as the only term modifying predicted potential growth.

Since both shading and crowding are functions of the distributions of neighbours, it is unavoidable that there is some degree of collinearity in the above- and below-ground competition experienced by individuals within a given target tree species. The correlation among calculated levels of shading and the crowding term ranged from very low ($r = 0.05$ for spruce) to relatively high (0.91 for amabilis fir), but even when high, there was considerable scatter among individuals, and the models converged without difficulty. Our method of model comparison, in which simpler models were fit using only shading or crowding alone, further helps guard against spurious inclusion of both above- and below-ground effects.

Table 2. AIC (corrected for small sample size) and R^2 of alternate models. The Full Models fit separate competition coefficients (λ) for all nine species of neighbours. The model with the lowest AIC is highlighted in bold

Species	n	AIC – full models		AIC – reduced models			R^2			
		With γ	Without γ	Equivalent competitors	Shading + size	Size only	Size only (%)	Shading + size (%)	Equivalent Competitors (%)	Full model* (%)
Hemlock	245	**454.2**	472.4	475.3	522.9	694.5	27.2	64.2	71.8	76.2
Cedar	192	**275.1**	303.6	364.2	412.9	541.7	2.3	50.6	63.8	79.6
Amabilis fir	91	160.8	165.0	**138.0**	154.5	235.8	64.1	85.6	89.5	89.9
Subalpine fir	95	232.4	227.4	**218.7**	238.8	282.9	2.6	40.2	56.2	63.1
Spruce	196	509.1	**508.7**	520.0	524.3	640.4	28.0	60.6	63.1	68.7
Pine	93	214.5	213.3	**210.6**	210.7	265.6	45.2	70.4	73.3	79.0
Aspen	101	177.4	182.8	**166.2**	172.3	186.9	3.0	17.8	31.2	42.6
Birch	149	**290.2**	290.8	299.9	336.7	438.1	30.4	65.2	74.8	79.9
Cottonwood	39	157.0	153.9	**115.0**	116.0	121.0	33.9	45.7	61.6	67.9

*R^2 of the best full model (lowest AIC for full models with or without γ).

Results

MODEL COMPARISON AND EVALUATION

All of the models produced unbiased estimates of growth (i.e. slopes of predicted versus observed growth were all very close to 1.0) and the models explained a high percentage of the variation in the data (Table 2; R^2 for the best full model ranged from 43% to 90%). Alternate, simpler models that eliminated the effects of either crowding, or crowding plus shading, were always a far worse fit to the data than models that included both crowding and shading effects (Table 2; see both AIC_{corr} and R^2). The alternate models that grouped species of neighbours into a single estimated competition coefficient (λ) were better (lower AIC_{corr}) for the five species with the smallest sample size ($n \leq 101$). In each of these cases, the 'equivalent' competitor model was superior to a model that either contrasted: (i) intra- versus interspecific competitors, or (ii) conifer versus angiosperm competitors (AIC not shown). For all four of the species with samples sizes of *c.* 150 or more individuals, however, the model that estimated separate competition coefficients for all nine species of neighbours was the best model. We take this as evidence that species do indeed differ in their competitive effects, but that there is a minimum sample size needed to discriminate between them.

EFFECTS OF TREE SIZE ON POTENTIAL RADIAL GROWTH AND SENSITIVITY TO CROWDING

While our data set includes trees with relatively little shading or crowding, the predicted potential radial growth rates (*PRG*) are simply the intercepts of the function given by Eqn 1 (i.e. the predicted radial growth when crowding and shading both = 0), and thus represent an extrapolation from our data. They are also the growth rates predicted for a tree of optimal size (i.e. a target tree with d.b.h. = δ, Eqn 2). The predicted potential radial growth rates were remarkably similar among eight of the nine species, ranging from 4.4 mm year^{-1} in birch to 5.9 mm year^{-1} in spruce (Table 3a). The support
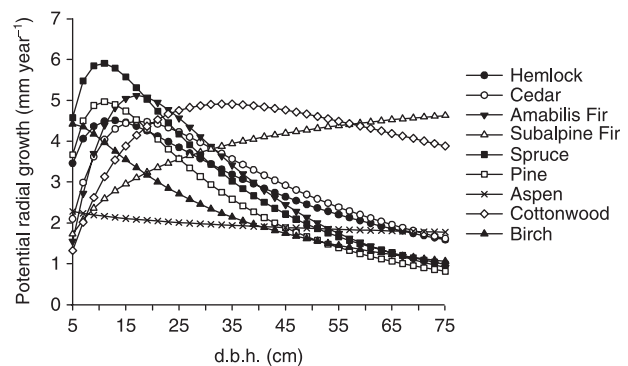

Fig. 1. Predicted potential radial growth (mm year^{-1}) as a function of size (d.b.h., in cm) for each of the nine species in the absence of shading or crowding effects.

intervals were extremely narrow, indicating strong support in the data for these estimates (Table 3a). The one exception to this pattern was aspen, with a low potential growth rate of 2.4 mm year^{-1} (Table 3a).

There was a strong size-dependency in potential growth as a function of target tree size (i.e. for a completely released tree) (Fig. 1). Six of the nine species showed an optimal size between 5 and 20 cm d.b.h., with a moderately strong decline in potential growth as d.b.h. increased (Fig. 1). The exceptions were: aspen, which had relatively uniform (and low) potential growth across the range of adult tree sizes; cottonwood, which showed a predicted maximum potential growth at 33.5 cm d.b.h. and subalpine fir, in which potential tree growth was predicted to increase throughout the range of observed adult tree sizes (Fig. 1).

There was evidence that sensitivity to crowding varied as a function of the size of the target tree for five of the nine species: hemlock, redcedar, amabilis fir, aspen and birch (i.e. $\gamma \neq 0$, Eqn 6, Table 3b). These results for hemlock and redcedar are in contrast to our earlier study based on a more restricted range of stand structure (Canham *et al.* 2004). The three conifers showed a fundamentally different pattern of sensitivity

Table 3. (a) Maximum likelihood parameter estimates and two-unit support intervals (below, in italics) for the best full model (with or without γ; see Table 2) for each of the nine study species

Species		Variance	PRG	C	S	R
Hemlock	MLE	0.304	4.509	1.205	0.505	0.876
	Two-Unit S.I.	*0.294–0.334*	*4.464–4.554*	*1.105–1.305*	*0.405–0.605*	*0.867–0.885*
Cedar	MLE	0.201	4.488	2.983	0.240	0.936
	Two-Unit S.I.	*0.191–0.211*	*4.443–4.578*	*2.883–3.083*	*0.140–0.340*	*0.926–0.945*
Amabilis fir	MLE	0.206	5.119	8.066	0.366	0.537
	Two-Unit S.I.	*0.187–0.216*	*5.067–5.170*	*7.866–8.166*	*0.266–0.466*	*0.532–0.542*
Subalpine fir	MLE	0.400	4.990	54.632	0.000	0.442
	Two-Unit S.I.	*0.390–0.410*	*4.940–5.040*	*54.086–56.271*	*0.000–0.100*	*0.437–0.446*
Spruce	MLE	0.636	5.911	0.059	1.642	1.000
	Two-Unit S.I.	*0.626–0.646*	*5.852–5.970*	*0.000–0.159*	*1.542–1.742*	*0.990–1.000*
Pine	MLE	0.339	4.969	39.881	1.150	0.675
	Two-Unit S.I.	*0.329–0.379*	*4.919–5.019*	*39.482–41.476*	*1.050–1.250*	*0.668–0.682*
Aspen	MLE	0.214	2.440	0.682	0.000	0.996
	Two-Unit S.I.	*0.184–0.224*	*2.415–2.465*	*0.582–0.782*	*0.000–0.100*	*0.986–1.000*
Birch	MLE	0.297	4.422	10.901	0.471	0.959
	Two-Unit S.I.	*0.287–0.317*	*4.378–4.510*	*10.465–11.010*	*0.371–0.571*	*0.949–0.969*
Cottonwood	MLE	0.473	4.908	7.562	0.159	0.761
	Two-Unit S.I.	*0.463–0.533*	*4.859–5.006*	*7.362–7.662*	*0.059–0.259*	*0.754–0.769*

Table 3. (b) Maximum likelihood parameter estimates and two-unit support intervals (below, in italics) for the best full model (with or without γ; see Table 2) for each of the nine study species

Species		α	β	δ	σ	γ
Hemlock	MLE	2.420	0.976	12.396	1.245	–0.999
	Two-Unit S.I.	*2.395–2.444*	*0.966–0.985*	*12.272–12.892*	*1.195–1.295*	*–1.009–0.989*
Cedar	MLE	1.901	0.766	17.529	1.017	–0.810
	Two-Unit S.I.	*1.882–1.920*	*0.758–0.773*	*17.179–17.704*	*0.967–1.067*	*–0.818–0.802*
Amabilis fir	MLE	2.301	0.537	17.107	0.796	–0.645
	Two-Unit S.I.	*2.278–2.324*	*0.531–0.553*	*16.936–17.449*	*0.746–0.846*	*–0.651–0.638*
Subalpine fir	MLE	3.414	0.215	199.942	2.533	
	Two-Unit S.I.	*3.380–3.448*	*0.213–0.217*	*195.943–200.000*	*2.483–2.583*	
Spruce	MLE	0.733	0.000	10.509	1.039	
	Two-Unit S.I.	*0.726–0.762*	*0.000–0.026*	*10.404–10.929*	*0.989–1.089*	
Pine	MLE	3.570	0.109	10.988	1.012	
	Two-Unit S.I.	*3.534–3.606*	*0.083–0.111*	*10.878–11.208*	*0.962–1.062*	
Aspen	MLE	0.033	0.000	0.521	6.217	1.040
	Two-Unit S.I.	*0.031–0.035*	*0.000–0.002*	*0.421–0.621*	*6.155–6.279*	*1.030–1.051*
Birch	MLE	0.943	0.148	5.304	1.566	0.808
	Two-Unit S.I.	*0.934–0.962*	*0.146–0.164*	*5.204–5.504*	*1.516–1.616*	*0.800–0.832*
Cottonwood	MLE	2.384	0.000	33.559	1.175	
	Two-Unit S.I.	*2.360–2.431*	*0.000–0.006*	*32.217–33.895*	*1.125–1.275*	

than the two angiosperms: for all three conifers, the estimates of γ were negative (ranging from –0.8 to –1.0, Table 3b), indicating that smaller d.b.h. target trees were more sensitive to crowding than larger trees. In contrast, the estimates of γ for the two angiosperms were both positive (birch: γ = 0.8; aspen: γ = 1.0). Thus, larger trees of these two species were more sensitive to crowding than smaller trees.

EFFECTS OF DISTANCE TO NEIGHBOURS ON DEGREE OF CROWDING

The Neighbourhood Competition Index (*NCI*) sums the crowding effects of all neighbouring trees within a fraction *R* of the maximum neighbourhood radius of 15 m. The value of

the β parameter determines the decline (if any) in the below-ground effect of a neighbour with increasing distance from a target tree. Together, *R* and β define the effective neighbourhood for a given target tree species (the 'zone of perception' of Burton 1993) (Fig. 2). For eight of the nine species (all species except spruce), the *R* parameters (and their support limits) were less than 1.0 (Table 3a), indicating that the 15 m search radius was sufficient to capture the effective range of below-ground competitive interactions between neighbouring trees. For the three most shade tolerant species (hemlock, redcedar and amabilis fir), the β parameters were large (0.53–0.97), indicating that the effects of neighbours declined as an inverse linear or square root function of distance from the target tree (Fig. 2). Thus, the three most shade tolerant species also had
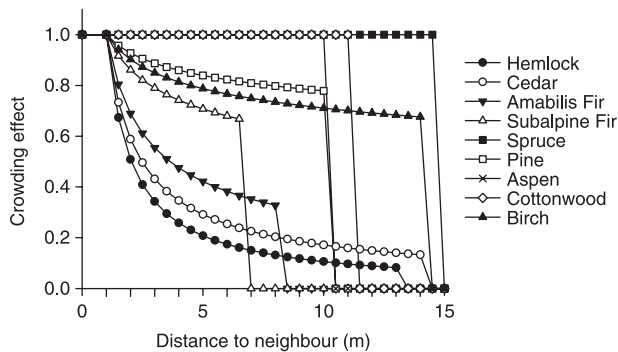
Fig. 2. Effect of distance to a neighbour (of any species) on the crowding effect of the neighbour, for the nine study species. The functions combine the effects of parameter *R* (Table 3a) and β (Table 3b).

the smallest effective neighbourhood within which they were sensitive to the below-ground effects of neighbours (Fig. 2), suggesting that shade tolerance is also correlated with tolerance of below-ground competition within this guild of nine species. For the remaining six species, the estimates of β were close to zero (Table 3b), indicating that there was very little decline in the net effect of a neighbour within the fraction *R* of the 15 m maximum neighbourhood radius (Fig. 2). For spruce, the maximum likelihood estimate of *R* was 1.0, and the β parameter estimates were effectively zero. Thus, it is likely that for this species, the effective neighbourhood radius exceeds the 15 m limit used in the analysis.

EFFECTS OF SIZE OF NEIGHBOURS ON DEGREE OF CROWDING

The exponent α in *NCI* (Eqn 4) controls the scaling of the effects of neighbouring tree size (d.b.h.) on *NCI* (and hence, on target tree radial growth). The estimates of α for the nine species varied dramatically (Table 3b). For aspen, the estimate was effectively zero, indicating that aspen responds simply to the density of neighbours, regardless of their size. For spruce and birch, the estimates were < 1, indicating that the below-ground effects of neighbours increased at a rate that was less than a linear function of neighbour d.b.h. For the three most shade tolerant species (hemlock, redcedar and amabilis fir) and for cottonwood, the estimates of α ranged from 1.9 to 2.4, suggesting that the crowding effects of neighbours were scaled to their basal area (i.e. d.b.h.²), and hence, roughly proportional to the biomass of the neighbouring tree. For subalpine fir and lodgepole pine, the maximum likelihood estimates were > 3, indicating that target trees of these species are disproportionately sensitive to the presence of very large neighbours.

INTERSPECIFIC VARIATION IN SENSITIVITY TO CROWDING

Because of differences among target tree species in the scaling of *NCI* to neighbour size and distance (α and β), the absolute
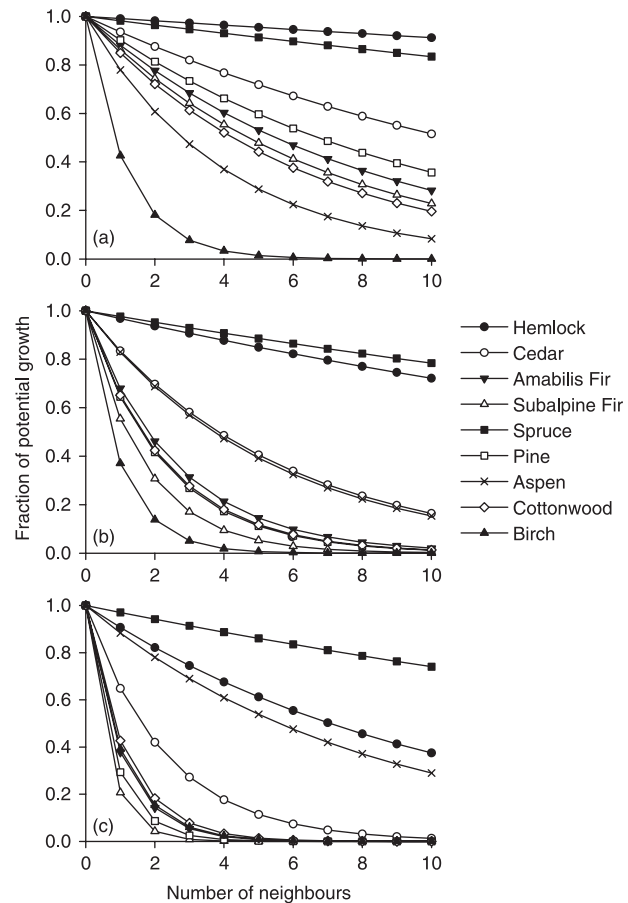

Fig. 3. The crowding effects of neighbours on each of the nine target tree species, as a function of the number of neighbours for three different cases. (a) 20 cm d.b.h. neighbours 7 m away from a 40-cm d.b.h. target tree. (b) 30 cm d.b.h. neighbours 7 m away from a 30-cm d.b.h. target tree. (c) 40 cm d.b.h. neighbours 7 m away from a 20-cm d.b.h. target tree.

scale of *NCI* varies among the different species. Thus, the absolute magnitude of the *C* parameter cannot be used to assess the relative sensitivity to crowding among the nine species. Rather, we have plotted the predicted reduction in growth for each species as a function of the numbers of neighbours of the strongest competitor (i.e. λ = 1) of a specified size (d.b.h.) at a specified distance from the target tree (Fig. 3a–c). For the five species for which γ was not equal to 0, the calculations also take into account the target tree size. Because of differences among species in the α, β and γ parameters, there is no single ranking of relative sensitivity to crowding among the nine species. Figure 3 presents three simple cases: (i) a large target tree surrounded by smaller neighbours, (ii) a neighbourhood in which both the target and the neighbours are the same size, and (iii) a case where the target tree is smaller than the neighbours. In all three cases, hemlock and spruce are the least sensitive to crowding, but their relative rank switches, with hemlock being the least sensitive when it is larger than its neighbours, but more sensitive to crowding than spruce when it is smaller than its neighbours. The sensitivity of the other four conifer species to crowding varies

dramatically among the three scenarios, with all four species more sensitive when their size declines relative to their neighbours (because of the combined effects of α and γ). Overall, the three deciduous species were among the most sensitive to crowding, and birch was consistently the most sensitive to crowding of the deciduous species. When the target tree is larger than the neighbours, all of the conifers are consistently less sensitive to crowding than the three deciduous species (Fig. 3a).

INTERSPECIFIC VARIATION IN SENSITIVITY TO SHADING AND THE RELATIVE EFFECTS OF ABOVE- VERSUS BELOW-GROUND COMPETITION

The average proportion of incident growing season radiation blocked by neighbours ranged from a low of 25% in lodgepole pine target trees, to a high of 63% in western redcedar, but the samples for each species contained individuals from a very broad range of levels of shading. The sensitivity to shading among the six conifer species was generally correlated with their shade tolerance (Fig. 4) (Kobe & Coates 1997). Spruce and pine were the most sensitive to the effects of shading by neighbouring trees (Fig. 4). The one anomaly among the conifers was subalpine fir, which is only a moderately shade tolerant species as a sapling (Kobe & Coates 1997), but for which the maximum likelihood estimate of S was effectively zero, indicating no decline in growth of adult trees of this species as a function of shading (given that the effects of crowding are also included in the model). The results for the three angiosperms were also unexpected. Juveniles of the three deciduous species are quantitatively less shade tolerant than the entire conifer species, based on analysis of sapling mortality in the same region by Kobe & Coates (1997). Our analysis of adult tree growth, however, indicates that after taking into account the effects of crowding, there was little or no additional reduction in growth of adults due to levels of shading experienced by trees of these three deciduous species. For two of the least shade tolerant species – lodgepole pine and
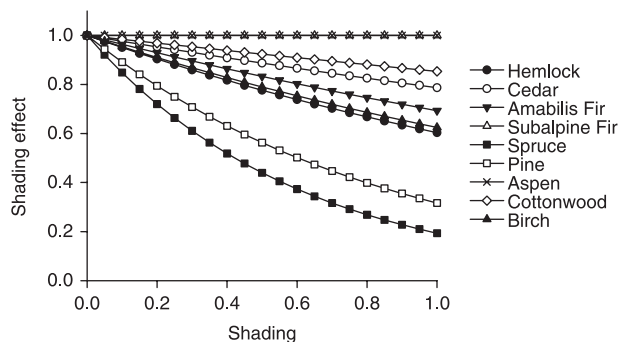

Fig. 4. Predicted decline in potential growth of a target tree of the nine study species, as a function of the degree of shading by neighbours. 'Shading' is the fraction of seasonal total global radiation intercepted by neighbours within 15 m of the target tree.

cottonwood – a model using shading but not crowding performed almost as well as the simplest model that incorporated crowding (and much better than a model based on crowding alone; AIC not shown) suggesting that most of the effect of neighbours can be attributed to shading for those two species.

As Figs 3 and 4 illustrate, there was a wide range of variation both among species and among individuals within species in the magnitude of the reduction in potential growth due to shading versus crowding. Sensitivities to both shading and crowding clearly vary as a function of the species and size of the target tree (Figs 3 and 4). However, they also vary as a function of not just the total number, size, distance to, and identity of the neighbours, but also as a function of the spatial configuration of neighbours around the tree (since shading of direct beam radiation is directional). Since our goal was the development of robust empirical models rather than inference about population means, our samples of each species are not representative of any particular population, but it is instructive to compare the relative magnitude in reduction in potential growth due to shading versus crowding for the nine species (Fig. 5). For all species except the two least shade tolerant conifers
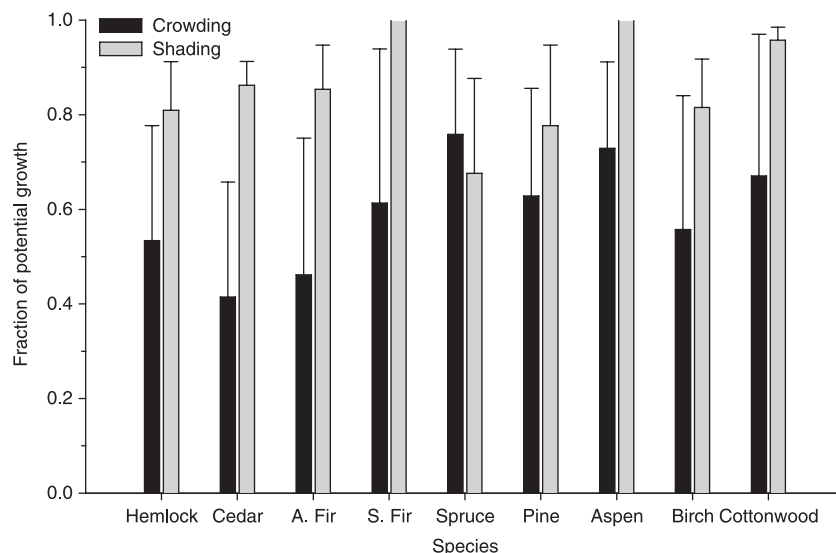

Fig. 5. The average growth of target trees of each of the nine study species, as a fraction of potential growth, due to the effects of crowding or shading alone. Error bars are standard deviations. Subalpine fir and trembling aspen were effectively insensitive to shading (C approximately 0; Table 3a).

Table 4. The matrix of interspecific competition coefficients (λ) estimated from the best full model (see Table 2). The values in each row are the effects of the row species on the column species. The species are ordered from shade tolerant to intolerant. The intraspecific competition coefficients (diagonals) are underlined. The strongest competition coefficients (> 0.75) are indicated in bold. The coefficients are relativized so that λ for the strongest competitor of a given species is equal to 1

	Hemlock	Cedar	Amabilis fir	Subalpine fir	Spruce	Pine	Aspen	Cottonwood	Birch
Hemlock	**1.000**	0.132	0.220	0.219	**1.000**	0.000	0.090	0.175	0.176
Cedar	0.638	0.243	0.004	**1.000**	0.200	0.198	0.286	0.073	0.040
Amabilis fir	0.289	**1.000**	0.140	0.643	0.000	0.502	0.000	0.387	**1.000**
Subalpine fir	0.678	0.124	**0.851**	0.459	0.271	0.345	0.000	**1.000**	0.191
Spruce	0.118	0.000	0.000	0.000	0.000	0.154	0.000	0.054	0.032
Pine	0.000	0.000	0.021	0.317	0.111	0.183	0.000	0.000	0.133
Aspen	0.000	0.000	0.089	0.115	0.000	**1.000**	0.140	**0.948**	0.057
Cottonwood	0.366	0.104	0.559	0.284	0.000	0.041	**1.000**	0.064	**0.813**
Birch	0.127	0.000	**1.000**	**0.933**	0.321	0.178	0.239	0.000	0.315

(spruce and pine), reduction in growth due to crowding was much larger than the average reduction due to shading (Fig. 5). Moreover, within those two species the magnitude of reduction in growth of an individual due to shading was uncorrelated with the magnitude of reduction due to crowding (Pearson correlation coefficients 0.05 and 0.26 for spruce and pine, respectively). In contrast, the effects of shading and crowding were strongly correlated among individuals for the three most shade tolerant conifers (r = 0.91, 0.78 and 0.66 for amabilis fir, hemlock and redcedar, respectively).

VARIATION IN THE PER CAPITA EFFECTS OF CROWDING BY DIFFERENT SPECIES OF NEIGHBOURS

Our analysis allows us to estimate the matrix of per capita effects of crowding (below-ground competition) by species i on species j (i.e. the matrix of λ values) (Table 4). Most of the individual pairwise interactions were strongly asymmetric (i.e. the effect of species A on B was much larger or smaller than the effect of B on A). As in two recent studies using similar methods for temperate forests of the Northeastern United States (Canham *et al.* 2006; Papaik & Canham 2006), the matrix has a surprisingly large number of low values, indicating that there were many pairs of species for which a neighbour of species i had little effect on growth of a neighbour of species j via crowding (i.e. given that the effects of shading are taken into account). Almost two-thirds (64%) of the elements reflect very weak effects of crowding (i.e. λ < 0.25, where 1.0 represents the per capita effects of the strongest competitor among the nine possible species of neighbour). Only 16% of the elements were what we would consider 'strong' effects of crowding (λ > 0.75). Thus, while the magnitude of reduction in growth due to crowding was greater on average than the reduction in growth due to shading (Fig. 5), the crowding effects on any individual target tree species appear to be due to proximity to species of neighbours from a very specific (and small) subset of its strong competitors within the guild (Table 4).

The support intervals for the individual estimates of λ were generally very narrow, indicating strong support within the data for the estimates (data not shown). While the pairwise interactions were generally strongly asymmetric, there was no simple ranking of competitive dominance across all nine species (Table 4). There was, however, a consistent ranking of competitive dominance among the three most shade tolerant species (amabilis fir > redcedar > hemlock) that mirrors the shade tolerance ranking for the three species as measured by Kobe & Coates (1997; with unpublished data using the same methods for amabilis fir).

For the late-successional dominant species in these forests (western hemlock), conspecific neighbours had the strongest per capita crowding effects. For all of the other species, however, the strength of intraspecific crowding (i.e. below-ground competition) was generally quite low (0.00–0.46). The row averages in the matrix can be used as an approximate ranking of the relative strength of a species as a below-ground competitor (i.e. via crowding). On this basis, aspen and spruce both had very low average per capita effects on other species, while amabilis fir and cottonwood had the highest average effects on crowding (Table 4). Three of the most common early successional species in these forests – spruce, pine and aspen – all had a single species of competitor that had strong crowding effects on them (hemlock, aspen and cottonwood, respectively), while all other species of neighbours had little effect via crowding.

We examined the robustness of the estimates of λ to idiosyncrasies of the data set by creating 10 randomly selected subsamples containing *c.* 75% of the observations for both hemlock and redcedar, and then repeated the analysis for each random subset for each of these two species. As might be expected, the consistency of the estimates of λ ranged from very high, generally for species that were well represented as neighbours, to low, particularly for rarer species (Appendix S2).

Discussion

We believe that our extensive sample of stand conditions (27 sites) specifically designed to cover a wide range of successional stages, disturbance histories, tree species compositions and competitive neighbourhoods, was critical for robust prediction of tree growth rates and competitive interactions in these forests. In our earlier study (Canham *et al.* 2004; based on a much more restricted range of stand conditions), we were

able to explain 33% of the variation in growth of a sample of western hemlock trees, and 59% in western redcedar. This increased to 76% and 80%, respectively, with the broader sampling. Results were equally good for the other seven tree species found in interior cedar-hemlock forests, none of which we were able to estimate in the original, more restricted, sample at the Date Creek research site (Canham *et al.* 2004). Beyond the improvement in goodness-of-fit and the associated reduction in prediction error, the broader range of stand conditions represented in the current sample gives us much more confidence in the use of the resulting functions in stand simulation models such as SORTIE/BC (Coates *et al.* 2003).

UNCOVERING THE EFFECTS OF TREE SIZE ON POTENTIAL GROWTH AND SENSITIVITY TO CROWDING

There is very little consensus on the theoretical expectations for the shapes of the functions in Fig. 1 (i.e. Muller-Landau *et al.* 2006; Russo *et al.* 2007). One of the limitations of most previous analyses of size–growth relationships is that the studies use realized growth, rather than an estimate of potential growth in the absence of competition. Since small individuals are much more likely to experience higher levels of shading, and since our results illustrate that for at least some species, smaller individuals are more sensitive to the effects of crowding, failure to correct for the effects of competition will generally lead to biased underestimates of the potential growth of smaller stems.

We selected the lognormal function 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 it could accommodate a wide range of shapes, depending on the estimated parameters δ and σ. In the earlier Date Creek study (Canham *et al.* 2004), the shape of the function was strongly influenced by the successional status of our study sites. Specifically, most of the small diameter trees in that sample had been subjected to prolonged suppression. When released, they still showed relatively low growth rates, leading us to interpret what are likely to have been the effects of past suppression (Wright *et al.* 2000) as low potential growth rates. In our current study, we specifically sampled young stands (15–25 years-old) with moderate density. We also emphasized sampling of large diameter trees of each species in old forests (Table 1). This had a significant impact on the prediction of parameter estimates for the fundamental relationship between tree size and potential growth. Predicted maximum growth rates of hemlock and redcedar increased, and diameter at which maximum growth occurred (δ) decreased dramatically compared to values reported in Canham *et al.* (2004). This highlights the importance of the distribution of sampling effort for data collection in studies using model selection methods (Canham & Uriarte 2006). In complex ecological systems such as mixed-species forests, it is critical to sample the breadth of successional stages and growing conditions.

Determining the correct shape of the size effect term in Eqn 1 has important implications for the simulation of the effects of partial harvesting regimes using models such as

SORTIE/BC (Coates *et al.* 2003). To properly fit the size effect term in Eqn 1 it is important to have a well-balanced data set of both tree sizes and competitive neighbourhoods. It appears that it is equally important to have both fast-growing, small diameter trees to estimate maximum growth rates and large diameter older trees to get the shape of the tail correct. In the subalpine fir sample, there were few trees greater than 45 cm d.b.h. and this may account for the atypical shape of that species growth function (Fig. 1).

It is widely believed that smaller trees will be more sensitive to below-ground competition than larger trees (e.g. Hegyi 1974), but there are ample studies suggesting that there is no relationship between size and sensitivity to competition, and we know of no theory that precludes a pattern in which larger trees are more sensitive than smaller trees. We found examples of each of these three possible patterns of target tree sensitivity to crowding among the nine tree species in the interior cedar-hemlock forests we studied. In our more restricted, original sample from Date Creek, there was no evidence that target trees of hemlock and redcedar were more sensitive to crowding when they were small (Canham *et al.* 2004). The inclusion of a broader sample of conditions experienced by small stems in the current study provides evidence that smaller stems of both hemlock and redcedar (and the other shade tolerant species in the system, amabilis fir) are more sensitive to crowding than larger stems (negative values of γ, Table 3b). Unlike the three most shade tolerant conifers (hemlock, redcedar and amabilis fir), subalpine fir, pine, spruce and cottonwood showed no size sensitivity to crowding. There was also evidence that larger trees of birch and aspen were more sensitive to crowding than smaller ones. Our results indicate that sensitivity to crowding does fluctuate with tree size but that the size of tree most affected by neighbours also varies among tree species. These results suggest that there is no simple size hierarchy in sensitivity to crowding (i.e. below-ground competition) across all species.

BELOW-GROUND ZONES OF INFLUENCE AND THE SCALING OF CROWDING EFFECTS WITH NEIGHBOUR SIZE AND DISTANCE

Our analysis allows us to estimate the maximum effective neighbourhood size for below-ground competition (R, as a fraction of 15 m, the maximum neighbourhood radius allowed by the data) for each tree species. Except for spruce, the distance within which neighbours had measurable crowding effects on target tree growth (i.e. the 'zone of perception' of Burton 1993) was less than 15 m (Fig. 2). Our approach also allows estimation of α, the parameter relating neighbour d.b.h. to its below-ground competitive effect, and β, the parameter controlling the decline in neighbour effect with distance from the target tree, rather than requiring that they be set arbitrarily as in most previous studies. Many previous studies using distance-dependent competition indices have assumed that $\beta = 1$ (i.e. that competitive effect declines as the inverse of the distance to the neighbour) (e.g. Hegyi 1974; Stoll *et al.* 1994). Our results suggest that there is considerable

variation among species in the decline in the crowding effects of neighbours with increasing distance (Fig. 2). For all of the nine species we examined, the maximum likelihood estimates of β were < 1, and in some cases were effectively zero (Table 3b, Fig. 2). For the three most shade tolerant species (hemlock, redcedar and amabilis fir), the β parameters were relatively large (0.53–0.97), indicating that the effects of neighbours declined as an inverse linear or square root function of distance from the target tree. For the remaining six species, the estimates of β were < 0.25, suggesting little decline in the net below-ground effect of a neighbour within the maximum range of the effective competitive neighbourhood.

Many previous studies have assumed that competitive effects of neighbours scale linearly with their d.b.h. (i.e. that α = 1) (e.g. Bella 1971; Hegyi 1974, see Biging & Dobbertin 1995 for a review of competition indices). We found no evidence to support this assumption in our data. There were striking differences in the estimates of α among the nine species, ranging from values near zero, to greater than three. Thus, for different species of 'target' trees, the net crowding effect of neighbours ranged from being proportional simply to neighbour density (regardless of size; i.e. α = 0), to cases where target trees were disproportionately sensitive to the very largest neighbours (i.e. α > 3). It is worth pointing out that it would be plausible to assume that the values of α and β could, in principle, vary for different species of neighbours, rather than to estimate a single value of each exponent for all species of neighbours. Except in very low diversity forests, however, the sample sizes needed to estimate two additional parameters for each species of neighbour would be prohibitively large.

DISCRIMINATING BETWEEN BELOW- VERSUS ABOVE-GROUND COMPETITION

While the magnitude of the effects of crowding (below-ground) were generally much stronger than the effects of shading (above-ground) for canopy trees in these forests, the mechanisms that underlie the shading effects are clearly much better understood. The competitive 'effects' component of shading (i.e. amount of shade cast by an individual) is an obvious function of the crown dimension and light transmission characteristics of a neighbour (Canham *et al.* 1999), and the spatial location of the neighbour relative to the target tree. The aggregate effects of all nearby neighbours on the shade experienced by a target tree, however, are effectively homogenized across all of the neighbours. In practical terms, variation in the shade experienced by a target tree is controlled by the absence of neighbours (i.e. canopy gaps), rather than by the details of the identities and sizes of neighbours. The competitive 'responses' to shading – i.e. the ecophysiological basis for variation in growth as a function of light – are also well understood, and reflect well-documented differences in the shade tolerances of these nine species (Kobe & Coates 1997).

Our understanding of the crowding effects is much more phenomenological. Our methods obviously do not allow us to identify any particular resource that is being competed for, and do not even preclude the possibility that the below-ground interaction is not direct resource competition rather than some negative effect of neighbours mediated by soil microbial communities or pathogens (i.e. Booth 2004). Even if the interaction is resource-based, there is ample evidence that the effects of neighbouring trees on soil resource availability can be controlled by 'supply-side' effects of ecosystem processes such as litterfall chemistry rather than simply by 'demand-side' effects of resource depletion via nutrient uptake (i.e. Finzi *et al.* 1998). Moreover, there is no reason to believe that there is only one resource being competed for below-ground within this guild of trees, or that the same mechanism (i.e. direct resource exploitation, microbially mediated effects, or canopy tree–soil ecosystem processes) underlies each of the pairwise interaction coefficients in Table 4.

Despite our uncertainty in the mechanistic basis for the crowding effects, the striking variation in the strength of per capita below-ground effects of different species of neighbours has implications for both ecological theory and forest management. We have not attempted a formal analysis of reciprocity and transitivity of the competition matrix (*sensu* Freckleton & Watkinson 2001b) because our analysis focuses only on predicting adult tree growth (rather than population growth rate). Nonetheless, there was a clear competitive hierarchy among the three late successional, shade tolerant species in these forests with amabilis fir > western redcedar > western hemlock. This ranking of competitive dominance in below-ground interactions among adults of these three species actually matched the ranking of effective shade tolerance of juveniles (Kobe & Coates 1997, and additional unpublished results for amabilis fir). Those rankings, however, are inversely correlated with the relative abundance of these three species in interior cedar-hemlock forests, where western hemlock is typically the most abundant and amabilis fir the least abundant of the three species in late successional stands (Coates *et al.* 1997).

Conclusions

Our results highlight the complexity of the strength of competitive effects and responses within this guild of temperate tree species. We found strong evidence for variation in tree-size specific sensitivity to crowding, which varied by broad shade-tolerance rankings within this guild of trees. This suggests that competitive hierarchies are not necessarily fixed over the life cycle of a tree. Our results demonstrate a high degree of predictability in the growth of all of the species from knowledge of the configuration of trees within the immediate neighbourhood of an individual, reflecting the highly local spatial scale of both above- and below-ground interactions within these forests. The species-specific crowding effects and the attendant reduction in growth experienced by an individual varied in a complex way depending on the identity of neighbouring trees, their proximity and their size. Spatial dynamics were thus particularly important in these forests.

Holt & Barfield (2003) suggest that one of the major goals of both theoretical and empirical studies is to understand the combined effects of temporal and spatial heterogeneity in

determining the realized structure of ecological communities. Both heterogeneity and species trade-offs are important for species coexistence through niche differentiation (Chesson 2000; Kneitel & Chase 2004), although coexistence can also be promoted by species-specific responses to a spatially or temporally varying environment through the storage effect (Kelly & Bowler 2002; Sears & Chesson 2007). On the other hand, Hubbell (2001) has developed a 'neutral' model which assumes that species have equal per capita fitness and that niche differentiation is unimportant. Our study of competition in a guild of trees could be seen as providing support for both views. For example, models that treated neighbours as equivalent in their competitive effects were the most parsimonious for five species, but these were the species with the smallest sample sizes. For the remaining species, the best models estimated separate competition coefficients for all nine species of neighbours. We take this as evidence that species do indeed differ in their below-ground competitive effects, but that analysis based on small sample sizes can come to the false conclusion that species have equivalent competitive effects.

The population and community dynamics of this guild of trees arise out of temporal and spatial variation in the environment interacting with disturbance, dispersal and competition. Analysis of the dynamics of these forests with a spatially explicit simulation model (Coates *et al.* 2003) indicates that the dominance of western hemlock reflects a whole suite of life-history traits, including fecundity, seed dispersal and seedling establishment (Wright *et al.* 1998b; LePage *et al.* 2000; Coates 2002). While the ranking of competitive interactions among adult trees may not translate directly into predictions of the relative abundance of species, or directly explain mechanisms of species coexistence, the models tested in this study and the strength and pattern of individual parameter estimates (e.g. intra- and interspecific competition, Table 4) provide robust empirical estimates of competitive interactions that clearly play a role in both population dynamics and species coexistence.

The results of our study have direct implications for managing complex forests and the design of silvicultural practices that seek to optimize yield by minimizing both above- and below-ground effects on adult tree growth (Coates *et al.* 2003; Pretzsch 2005; Canham *et al.* 2006). Our predictive empirical models can be used to evaluate the effects different levels and spatial configurations of proposed harvests on the growth of residual trees. Managing for patchiness in forest structure is a well-established idea in partial harvesting silviculture. More generally, the diverse competitive interactions found in this study suggest the potential benefits of managing for patchiness in the composition of local neighbourhoods within forests.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Location, disturbance history, stand age at time of sampling, plot size, number of mapped trees, species composition and number of sample trees at each stem mapped study site used in the analysis.

Appendix S2 Test of the consistency of the estimates of the per capita competition coefficients (λ) for the effects of the nine species on the growth of western hemlock and western redceder.

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