



Competition and tree crowns: A neighborhood analysis of three boreal tree species

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ARTICLE INFO

Article history:

Received 29 October 2009

Received in revised form 16 January 2010

Accepted 18 January 2010

Keywords:

Competition

Crown length

Crown radius

Distance-dependent Individual-based models

Neighborhood models

Tree crown

ABSTRACT

Competition for canopy space is a fundamental structuring feature of forest ecosystems and remains an enduring focus of research attention. We used a spatial neighborhood approach to quantify the influence of local competition on the size of individual tree crowns in north-central British Columbia, where forests are dominated by subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta*) and interior spruce (*Picea glauca* × *engelmannii*). Using maximum likelihood methods, we quantified crown radius and length as functions of tree size and competition, estimated by the species identity and spatial arrangement of neighboring trees. Tree crown size depended on tree bole size in all species. Given low levels of competition, pine displayed the widest, shortest tree crowns compared to the relatively long and narrow crowns found in spruce and fir. Sensitivity to crowding by neighbors declined with increasing tree height in all but the pine crown radius model. Five of the six selected best models included separate competition coefficients for each neighboring tree species, evidence that species generally differ in their competitive effects on neighboring tree crowns. The selected crown radius model for lodgepole pine, a shade-intolerant species, treated all neighbors as equivalent competitors. In all species, competition from neighbors exerted an important influence on crown size. Per-capita effects of competition across different sizes and species of neighbors and target trees varied, but subalpine fir generally displayed the strongest competitive effects on neighbors. Results from this study provide evidence that species differ both in their response to competition and in their competitive influence on neighbors, factors that may contribute to maintaining coexistence.

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1. Introduction

Plant community structure is shaped by competitive interactions among individuals (Harper, 1977; Barnes et al., 1998). In forests, outcomes of these interactions determine the size and position of individual tree crowns in the canopy, which in turn influence tree light interception, photosynthetic capacity, growth and survival (Pacala et al., 1996). Tree crowns collectively constitute the forest canopy (Purves et al., 2007), the primary determinant of subcanopy light levels (Canham et al., 1999) and resulting understorey seedlings and sapling dynamics in northern temperate and boreal forests (Kobe and Coates, 1997; Wright et al., 1998). Competitive interactions among individual canopy trees are therefore critical to nearly all aspects of forest ecology.

Understanding how canopy trees interact is critical to forest ecosystem management as well as to ecology. Recent changes in management goals have led to increasing interest in maintaining structural and compositional complexity in managed forests (e.g., Kohm and Franklin, 1997; Burton et al., 2003; Puettmann et al., 2009). Alternatives to monocultural, even-aged forestry practices generally involve management of mixed species and/or multiple tree cohorts (e.g., Harvey et al., 2002; Bauhus et al., 2009; Kuuluvainen, 2009) and encompass a nearly infinite number of possible variations of species, sizes and spatial arrangements of residual trees (Papaik and Canham, 2006). Predicting stand development in complex forests therefore requires a detailed understanding of tree crown structure and its variation with tree size, species, and local neighborhood competition.

The plasticity of plant growth in response to competition is well established (e.g., Weiner et al., 1990; Jack and Long, 1991; Weiner and Thomas, 1992; Takahashi, 1996; Muth and Bazzaz, 2003; Vincent and Harja, 2008). However, many previous studies have modelled tree crowns as simple functions of diameter or height (e.g., O'Brien et al., 1995; Pacala et al., 1996; Gill et al., 2000; Grote, 2003). Where crown size is predicted based on allometric equations alone, crown dimensions tend to be overestimated in crowded forests and underestimated in sparse stands, leading to biased predictions of understorey light levels and seedling growth

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and survival rates (Astrup, 2006). Thus, a comprehensive model of tree crowns requires the inclusion of competition effects (e.g., Purves et al., 2007; Davies and Pommerening, 2008).

In this study we characterise tree crown structure using neighborhood analysis, an approach that assumes plant communities can be understood as a collection of individuals interacting in a spatial manner over restricted distances (Stoll and Weiner, 2000; Gratzler et al., 2004; Canham and Uriarte, 2006). Previous neighborhood analyses have examined annual plant growth (Weiner, 1982; Watkinson et al., 1983), adult tree growth (e.g., Canham et al., 2004; Uriarte et al., 2004a; Papaik and Canham, 2006; Coates et al., 2009), seedling and sapling demography (Uriarte et al., 2004b) and tree mortality rates (Uriarte et al., 2004a; Thorpe et al., 2008) as functions of local “neighborhood” conditions, which incorporate the size, distance, species, and density of neighbors. A benefit of neighborhood analysis is that it allows explicit testing of the hypothesis that species differ in their competitive effects, an issue central to debate surrounding Hubbell's (2001) neutral theory.

The specific objectives of this study were: (i) to determine how subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.), lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) and interior spruce (the complex of white spruce [*Picea glauca* (Moench) Voss] and Engelmann spruce [*Picea engelmannii* Parry ex Engelm.]) crown dimensions vary with tree bole size; (ii) to quantify the effect of crowding by neighbors on crown size in the three study species; and (iii) to determine whether the species identity of neighbors influences competitive effects on tree crowns.

2. Materials and methods

2.1. Study site and field sampling

Field sampling was conducted near Smithers, British Columbia, Canada (54°35'N, 126°55'W), in the sub-boreal spruce forest zone (Meidinger and Pojar, 1991). Study sites were located in upland areas of typical nutrient and moisture availability that spanned a range of forest ages and densities and were dominated by combinations of lodgepole pine, subalpine fir and interior spruce, with very minor components of trembling aspen (*Populus tremuloides* Michx.), black cottonwood (*Populus balsamifera* ssp. *Trichocarpa* Torr. and Gray), western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) and black spruce (*Picea mariana* [Mill.] B.S.P.).

We collected data in 15 sites, with plots ranging in size from 0.07 to 0.22 ha. For all trees ≥ 5 cm diameter at breast height (dbh: 1.3 m), we measured dbh, height, species, spatial position (x - y coordinates), crown length and crown radius. We estimated crown length as the average of four measurements of height of lowest live branch, taken in each cardinal direction, subtracted from total tree height. Crown areas were obtained by digitizing crown outlines on georectified 5-cm resolution aerial photographs using GIS software (Manifold System 8.0, 2008, Manifold Net Ltd.). Outlines were subsequently verified in the field and we derived radii estimates from crown area values, assuming circular crown shapes. In total we took crown measurements of 2391 trees, including 524 subalpine fir, 1029

lodgepole pine and 813 interior spruce (Table 1). Other sampled species – trembling aspen, black cottonwood, western hemlock and black spruce – were not sufficiently abundant to include as target species in the analysis but were included as neighbors.

2.2. Data analysis

To quantify the influence of competition on tree crown size, we analysed crown radius and length as functions of tree diameter or height and neighborhood competition. Our analytical approach follows from previous distance-dependent analyses of competition in which growth of a target tree is predicted as a function of neighbor tree abundance, size and distance from the target (e.g., Bella, 1971; Lorimer, 1983; Weiner, 1984; Canham et al., 2004; Coates et al., 2009). For this study, we used a neighborhood approach to examine the influence of competition on crown radius and crown length. We analysed each species separately and tested a set of seven candidate models.

The simplest model tested, the ‘size only’ scenario (Tables 2a and 2b, model 1), uses target tree bole size as the sole predictor variable. Crown radius is predicted as a function of target tree dbh and crown length is predicted as a function of target tree height. The size only scenario assumes that crown radius and crown length of a target tree increase nonlinearly with dbh and height respectively:

$$\text{Crown radius} = \zeta_R(1 - e^{-\delta_R \text{dbh}}) \quad (1a)$$

$$\text{Crown length} = \zeta_L(1 - e^{-\delta_L \text{height}}) \quad (1b)$$

where ζ and δ are estimated parameters and the subscripts R and L distinguish between crown radius and crown length model parameters.

For the six remaining candidate models, crown radius and crown length are predicted as functions of neighborhood competition as well as dbh and height respectively. Crown dimensions increase nonlinearly with diameter or height but exhibit an exponential decline with increasing neighborhood competition:

$$\text{Crown radius} = \zeta_R(1 - e^{-\delta_R \text{dbh}}) e^{-\eta_R \text{NCI}} \quad (2a)$$

$$\text{Crown length} = \zeta_L(1 - e^{-\delta_L \text{height}}) e^{-\eta_L \text{NCI}} \quad (2b)$$

where η is an estimated parameter and NCI is a neighborhood competition index. The six models that include competitive effects each incorporate a different formulation of NCI in Eqs. (2a) and (2b). These NCI equations (Eqs. (3a)–(3f)) represent three scientific hypotheses about how neighborhood competition influences crown size. We tested each hypothesis twice, using dbh and then height as the measure of neighbor tree size. This allowed us to determine whether the size-related competitive effects neighbors exert on target trees are better described by their diameter or height. For all NCI calculations, only those individuals located within 10 m of a target tree were considered potential neighbors. We selected a neighborhood radius *a priori*, rather than estimating a specific parameter, since we assumed competitive effects on tree crowns would occur over a relatively small scale (an assumption confirmed

Table 1
Sample sizes and ranges of tree dbh and height in the three study species.

Species	Common name	<i>n</i>	Mean dbh (cm)	Minimum dbh (cm)	Maximum dbh (cm)
<i>Abies lasiocarpa</i>	Subalpine fir	524	15.8	5.4	40.3
<i>Pinus contorta</i>	Lodgepole pine	1029	18.7	5.1	45.3
<i>Picea glauca</i> × <i>engelmannii</i>	Interior spruce	813	14.4	5.0	42.3
Species	Common name	<i>n</i>	Mean height (m)	Minimum height (m)	Maximum height (m)
<i>Abies lasiocarpa</i>	Subalpine fir	524	12.8	4.4	29.4
<i>Pinus contorta</i>	Lodgepole pine	1029	17.1	5.1	27.7
<i>Picea glauca</i> × <i>engelmannii</i>	Interior spruce	813	11.7	4.8	29.2

Table 2a

ΔAIC_c and R^2 for the set of candidate crown radius models. The model with the lowest AIC_c ($\Delta AIC_c = 0$) is highlighted in bold.

Model description	Model number	Equation numbers	Size measure in NCI	Species					
				Subalpine fir		Lodgepole pine		Interior spruce	
				ΔAIC_c	R^2 (%)	ΔAIC_c	R^2 (%)	ΔAIC_c	R^2 (%)
Size only	1	1a	n/a	133	37.3	391	62.6	216	57.4
Equivalent competitors	2	2a and 3a	dbh	37.4	44.2	168	71.5	49.2	63.8
	3	2a and 3b	Height	41.5	44.0	0	75.9	87.0	61.6
Species-specific, size-indep. NCI	4	2a and 3c	dbh	3.55	49.8	68.1	73.9	0.417	65.4
	5	2a and 3d	Height	1.85	50.1	7.16	75.9	9.34	64.8
Full model	6	2a and 3e	dbh	5.25	50.0	70.4	74.1	2.66	65.6
	7	2a and 3f	Height	0	50.4	7.20	76.0	0	65.8

Table 2b

ΔAIC_c and R^2 for the set of candidate crown length models. The model with the lowest AIC_c ($\Delta AIC_c = 0$) is highlighted in bold.

Model description	Model number	Equation numbers	Size measure in NCI	Species					
				Subalpine fir		Lodgepole pine		Interior spruce	
				ΔAIC_c	R^2 (%)	ΔAIC_c	R^2 (%)	ΔAIC_c	R^2 (%)
Size only	1	1b	n/a	160	51.9	974	3.54	339	61.4
Equivalent competitors	2	2b and 3a	dbh	75.8	61.3	558	34.6	128	70.2
	3	2b and 3b	Height	69.7	31.3	105	58.2	108	69.2
Species-specific, size-indep. NCI	4	2b and 3c	dbh	34.9	66.1	310	48.0	76.8	70.8
	5	2b and 3d	Height	4.64	67.5	95.8	58.3	38.4	71.1
Full model	6	2b and 3e	dbh	36.4	66.0	244	52.2	41.7	71.1
	7	2b and 3f	Height	0	68.7	0	61.2	0	73.4

by our results: see Section 3.4) and because this reduced the number of target trees in the dataset with incomplete mapped neighborhoods.

In all NCI equations, the influence of individual neighboring trees ($j = 1 \dots n$) of species s ($i = 1 \dots s$) found within 10 m of a target tree increases with size and decreases with distance from the target tree, t (Canham et al., 2004; Coates et al., 2009). The simplest competition hypothesis tested, the 'equivalent competitors' scenario (Tables 2a and 2b, models 2 and 3), assumes no differences among species in their competitive effects on target tree crowns:

$$NCI_t = \sum_{i=1}^s \sum_{j=1}^n \frac{dbh_{ij}^\alpha}{distance_{ij}^\beta} \quad (3a)$$

$$NCI_t = \sum_{i=1}^s \sum_{j=1}^n \frac{height_{ij}^\alpha}{distance_{ij}^\beta} \quad (3b)$$

where α and β are estimated parameters. The shape of the neighbor tree size effect is determined by α while β describes the slope at which the competitive influence of a neighboring tree declines with its distance to the target tree.

Although many studies have assumed that different species exert equivalent competitive effects on their neighbors, recent research shows strong evidence for species-specific differences in competitive effects on target tree growth (e.g., Canham et al., 2004; Uriarte et al., 2004a; Coates et al., 2009). To determine whether species differences extend to crown dimensions, we tested a form of NCI that includes a species-specific competition coefficient, λ :

$$NCI_t = \sum_{i=1}^s \sum_{j=1}^n \lambda_i \frac{dbh_{ij}^\alpha}{distance_{ij}^\beta} \quad (3c)$$

$$NCI_t = \sum_{i=1}^s \sum_{j=1}^n \lambda_i \frac{height_{ij}^\alpha}{distance_{ij}^\beta} \quad (3d)$$

Here, the net competitive effect of an individual neighbor is multiplied by the competition coefficient λ_i , which is estimated separately for each species s ($i = 1 \dots s$). We refer to these as the 'species-specific, size-independent NCI' models (Tables 2a and 2b, models 4 and 5).

Finally, in the 'full model' (Tables 2a and 2b, models 6 and 7), NCI includes species-specific competition effects in addition to a parameter that allows the competitive influence of neighbors to decline as target tree diameter or height increases (i.e., asymmetric competition: Thomas and Weiner, 1989). In this model, large trees are less sensitive to crowding than smaller trees: given the same number, sizes and species of neighboring trees, larger target trees are associated with a lower NCI:

$$NCI_t = \left(\sum_{i=1}^s \sum_{j=1}^n \lambda_i \frac{dbh_{ij}^\alpha}{distance_{ij}^\beta} \right) e^{-\gamma dbh} \quad (3e)$$

$$NCI_t = \left(\sum_{i=1}^s \sum_{j=1}^n \lambda_i \frac{height_{ij}^\alpha}{distance_{ij}^\beta} \right) e^{-\gamma height} \quad (3f)$$

where γ is an estimated parameter.

2.2.1. Parameter estimation and model selection

We used maximum likelihood methods to fit the seven candidate models to the data using software written specifically for this study in the C programming language. A simulated annealing algorithm (Press et al., 1992) was implemented to search for parameter values that would maximize the log-likelihood of the observed dataset. Residuals were lognormally distributed and we used Akaike's Information Criterion corrected for small sample size (AIC_c) as our model selection tool (Burnham and Anderson, 2002). We assessed model fit using R^2 values and used slopes of the regression lines between predicted and observed values of crown radius and length (intercept = 0) to assess model bias, where an unbiased model has a slope of 1.

Confidence intervals were obtained by randomly sampling parameter values of the best model to obtain 100 000 sets of parameters and their associated log-likelihoods. Parameter sets whose deviance ($2(L - L_{\max})$), exceeded the critical value of the χ^2 distribution ($\alpha = 0.05$, $df = 1$) were excluded. We selected the maximum and minimum values from the remaining parameter sets as the 95% confidence intervals (Hilborn and Mangel, 1997).

3. Results

3.1. Model selection and goodness of fit

The full model was selected as the best crown radius model for fir and spruce and as the best crown length model for all three species. In this model, neighborhood competition (NCI) depends on neighbor tree height and species, and the effective NCI declines with increasing target tree height (Tables 2a and 2b, model 7). For pine crown radius, the equivalent competitors model in which height is used as the neighbor tree size proxy in NCI calculations (Table 2a, model 3) was most parsimonious. Selected models and their associated maximum likelihood parameter estimates (Tables 3a and 3b) provided a good fit to the data and produced unbiased predictions: R^2 values ranged from 50 to 76% (Tables 2a and 2b) and slopes of predicted versus observed crown dimensions fell between 0.99 and 1.01 (Fig. 1).

Only two alternate crown radius models were associated with substantial support ($\Delta AIC_c < 2$; Burnham and Anderson, 2002). Both of these were species-specific, size-independent NCI models. For fir, the model in which neighbor tree height was used in NCI calculations was associated with more support (Table 2a, model 5; $\Delta AIC_c = 1.8$) while there was more support for the neighbor tree dbh model for spruce (Table 2a, model 4; $\Delta AIC_c = 0.4$). No alternate model for pine crown radius was associated with any real support, as all ΔAIC_c values were greater than 7. For crown length, the only model associated with a ΔAIC_c value lower than 5 was the species-

specific, size-independent NCI model for fir (Table 2b, model 5; $\Delta AIC_c = 4.6$). No other crown length model was associated with any support, as all ΔAIC_c values were greater than 30 (Table 2b).

3.2. Effects of tree bole size on crown dimensions and sensitivity to crowding

Crown size was strongly influenced by tree bole size. We illustrated these effects by calculating predicted crown dimensions across a range of dbh and height values while NCI remained fixed at zero (Fig. 2). It should be noted, however, these predicted values for crown size are extrapolated from our data and represent predictions for well-spaced, rather than truly competition-free, trees, since all trees in our dataset were located in forests.

For all species, crown radius was strongly dependent on tree dbh. Well-spaced fir and spruce trees showed a similar pattern of increasing crown radius with diameter up to a plateau of ~2 m at 30–40 cm dbh. Small size-class pine (5–15 cm) were associated with crown radius predictions similar to fir and spruce, but large, well-spaced pines were expected to support crowns up to 50% wider than their fir and spruce counterparts (Fig. 2a). Similarly, tree height had a large influence on crown length. Fir and spruce showed comparable patterns of near-linearly increasing crown length across the observed range of tree heights, with spruce expected to support slightly longer crowns for a given height (Fig. 2b). Well-spaced 4 m tall fir and spruce trees were associated with crown length predictions of 3.0 and 3.5 m respectively, while 29 m tall trees (the largest in the dataset) were predicted to support 19.8 and 21.2 m long crowns for fir and spruce respectively. All well-spaced pine trees taller than 15 m were associated with shorter predicted crown lengths than equivalent spruce or fir trees (Fig. 2b), likely a result of the species' shade intolerance, which results in self-pruning of low branches. The tallest pines in the dataset, 28 m, were expected to support 12.7 m long crowns.

Table 3a

Maximum likelihood parameter estimates (and 95% confidence intervals) for the best crown radius model (see Table 2a) for each of the three study species.

Parameter	Species		
	Fir	Pine	Spruce
ζ_R	2.245 (2.209, 2.279)	5.376 (5.115, 5.987)	2.069 (2.048, 2.146)
δ_R	0.0558 (0.0514, 0.0586)	0.0185 (0.0161, 0.0196)	0.0636 (0.0610, 0.0655)
η_R	0.130 (0.0829, 0.212)	1.0×10^{-6} (5×10^{-7} , 3×10^{-6})	0.000145 (9.3×10^{-5} , 0.00019)
α	0.0863 (0.0310, 0.185)	3.743 (3.439, 4.010)	2.075 (1.983, 2.152)
β	1.550 (1.505, 1.586)	1.441 (1.279, 1.609)	1.587 (1.341, 1.623)
λ_{fir}	0.562 (0.338, 1.18)	n/a	6.305 (4.301, 7.888)
λ_{pine}	0.0132 (0.0065, 0.0203)	n/a	1.480 (0.8128, 2.374)
λ_{spruce}	0.140 (0.0518, 0.500)	n/a	2.331 (1.110, 3.544)
γ	0.00996 (0.00435, 0.0235)	n/a	0.0463 (0.0307, 0.0589)
σ^2 (variance)	0.0698 (0.0656, 0.0773)	0.0784 (0.0725, 0.0867)	0.0424 (0.0385, 0.0486)

Table 3b

Maximum likelihood parameter estimates (and 95% confidence intervals) for the best crown length model (see Table 2b) for each of the three study species.

Parameter	Species		
	Fir	Pine	Spruce
ζ_L	93.88 (89.55, 96.77)	14.04 (13.90, 15.42)	62.25 (60.06, 70.22)
δ_L	0.00817 (0.00783, 0.00826)	0.0865 (0.0764, 0.0951)	0.0143 (0.0122, 0.0148)
η_L	7.2×10^{-5} (4.9×10^{-5} , 0.00012)	6.0×10^{-6} (5.3×10^{-6} , 1.0×10^{-5})	0.000127 (9.2×10^{-5} , 0.00014)
α	2.480 (2.341, 2.678)	3.835 (3.774, 4.018)	2.964 (2.819, 3.053)
β	1.425 (1.307, 1.614)	1.126 (0.991, 1.272)	1.309 (1.209, 1.379)
λ_{fir}	2.573 (0.959, 3.472)	1.182 (0.576, 1.594)	0.619 (0.544, 1.32)
λ_{pine}	0.511 (0.217, 0.811)	1.283 (0.623, 1.593)	0.209 (0.148, 0.428)
λ_{spruce}	0.161 (0.106, 0.537)	0.295 (0.0694, 0.0478)	0.431 (0.215, 0.757)
γ	0.0285 (0.0126, 0.0397)	0.0845 (0.0717, 0.0920)	0.0464 (0.0348, 0.0590)
σ^2 (variance)	4.169 (3.810, 4.509)	4.888 (4.529, 5.448)	2.403 (2.304, 2.522)

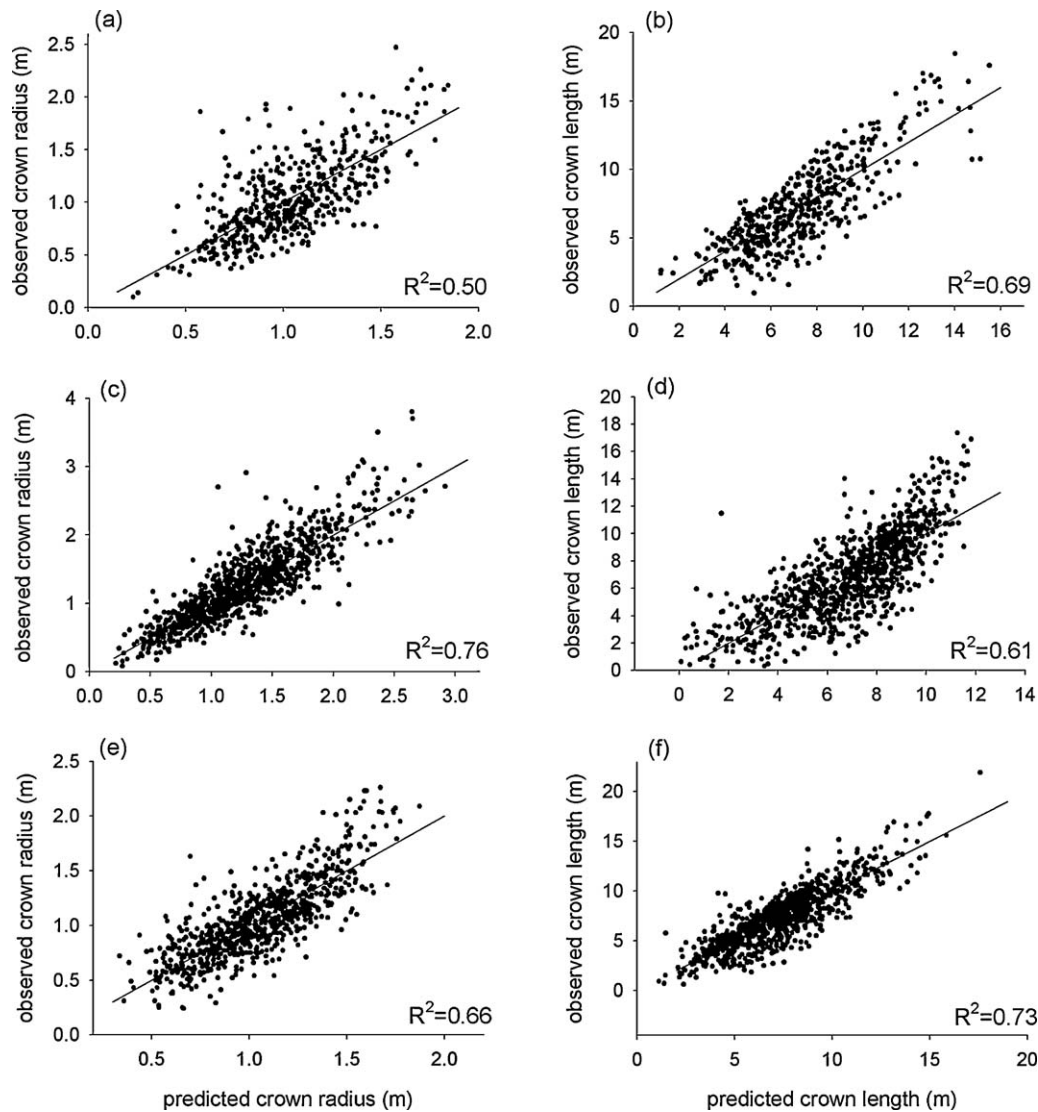


Fig. 1. Goodness of fit of the selected best models (see Tables 2a and 2b and 3a and 3b) for: (a) subalpine fir crown radius, (b) subalpine fir crown length, (c) lodgepole pine crown radius, (d) lodgepole pine crown length, (e) interior spruce crown radius and (f) interior spruce crown length. Lines represent 1:1 relationships between predicted and observed crown dimensions.

For all models except pine crown radius, there was evidence that taller trees were less sensitive to crowding than their shorter counterparts (i.e., $\gamma > 0$; Eq. (3f); Tables 3a and 3b), but the magnitude of sensitivity decline varied across species and crown dimensions. At a given level of crowding, increases in target tree height from 12 to 24 m were associated with declines in effective NCI of 11 and 43% for fir and spruce crown radius respectively and of 29, 64, and 43% for fir, pine and spruce crown length respectively. This indicates that sensitivity to crowding followed shade-tolerance rankings, with pine showing the steepest reductions in NCI with increasing tree height while the most modest declines were found for fir.

3.3. Influence of neighbor tree size on NCI

The parameter α (Eqs. (3a)–(3f)) determines the effect of neighbor tree height on NCI, where values near zero indicate that target trees respond to the density of neighbors, values near 1 suggest that competitive effects scale linearly with tree height, and values > 2 indicate that competitive effects of neighbors increase nonlinearly with height. The α estimate for fir crown radius was

0.086, suggesting that fir crown radii respond to neighbor tree density rather than height. In all other models, α estimates were greater than 2 (range: 2.1–3.8, Tables 3a and 3b), demonstrating an exponential increase in competitive effects with neighbor tree height.

3.4. Influence of distance between target tree and neighbors

The neighborhood competition index (NCI) sums the competitive effects of neighboring trees located within 10 m of a target, and the parameter β (Eqs. (3a)–(3f)) determines the shape of the decline in competitive influence of neighboring trees with distance. Competitive effects of neighbors declined steeply with distance from the target tree, and estimates of β varied little among species (Tables 3a and 3b). The competitive influence of neighbors declined slightly less steeply for crown length than for crown radius. For example, a neighbor located 2 m away from a target tree had on average 4 times the competitive impact on crown radius of a neighbor tree 5 m away (Fig. 3a), while for crown length, a neighbor located 2 m from the target tree exerted an average of 3.2 times the competitive impact of a neighbor 5 m from the target (Fig. 3b).

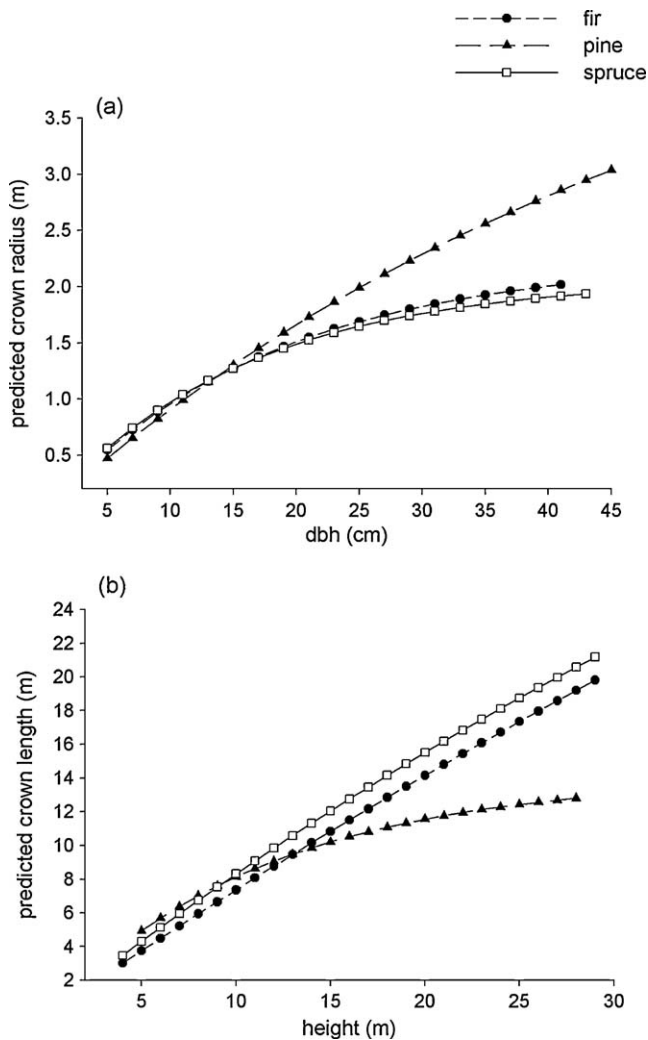


Fig. 2. Predicted crown dimensions at low competition levels ($NCI = 0$) for the three study species across their observed size ranges. (a) Crown radius as a function of dbh. (b) Crown length as a function of tree height.

3.5. Influence of neighbor species identity on competitive effects

There was good evidence for species-specific competitive effects in all models except for pine crown radius (Tables 2a and 2b). For fir and spruce crown radius models, the species-specific competition coefficient (λ) was largest for fir, followed by spruce and then pine (Table 3a), indicating that competitive strength of neighbors for these species ranked fir > spruce > pine. Fir was also the strongest competitor in the fir crown length model, followed by pine and then spruce (Table 3b). For pine crown length, pine neighbors exerted slightly larger competitive effects than did fir, while spruce competition was weakest (Table 3b). Finally, the λ values for spruce crown length followed the same rank order as for spruce crown radius (Table 3b). Thus, fir was generally the strongest competitor and was most influenced by intraspecific competition. Interspecific competition was most important for spruce, while species-specific differences in competitive effects were least apparent in the pine crown models.

3.6. Illustrating competitive effects on crown dimensions

Competition played a critical role in determining crown size in all three study species. The parameter η (Eqs. (2a) and (2b)) controls sensitivity to neighborhood competition, but differences in α and β estimates led to wide variation in the scale of NCI among models, and

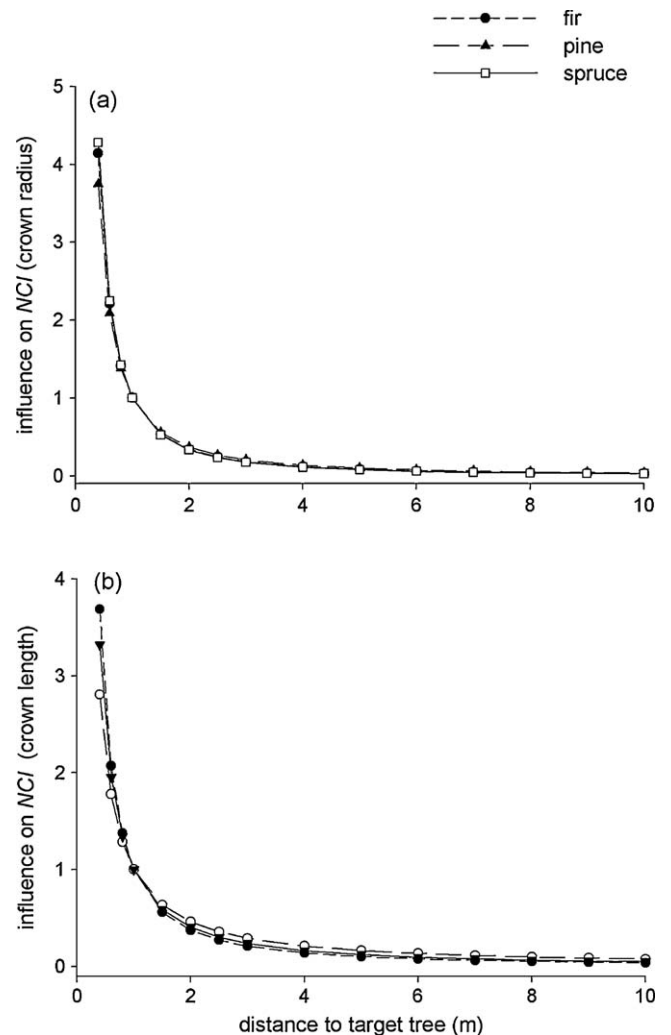


Fig. 3. The effect of distance between a neighbor and a target tree on the competitive impact of that neighbor on (a) crown radius and (b) crown length ($1/\text{distance}^\beta$; see Eqs. (3a)–(3f)). β estimates can be found in Tables 3a and 3b.

therefore direct comparisons of η are not appropriate. Instead, we present comparisons of several scenarios of neighborhood competition and their predicted effects on crown dimensions. To do this, we calculated predicted crown radius and length for each species in four basic scenarios: (i) a mid-sized target tree surrounded by mid-sized neighbors, (ii) a large target tree surrounded by large neighbors, (iii) a mid-sized target tree surrounded by large neighbors, and (iv) a large target tree surrounded by mid-sized neighbors. For each competitive scenario, we calculated predicted crown dimensions for both a monospecific and a mixed-species case. We used the λ (competition coefficient) values estimated for conspecific neighbors to calculate NCI for monospecific scenarios. In the mixed-species scenarios, we assumed an equal fir–pine–spruce mix and calculated NCI using the mean λ value of the three neighbor species for each species and crown dimension (see Tables 3a and 3b for λ values).

3.6.1. Competitive effects on crown radius

Predicted crown radius decreased with increasing numbers and sizes of neighbors for all study species. Fir was most sensitive to competition from conspecific neighbors, and thus its predicted crown radius declined more steeply across monospecific (Fig. 4a, c, e and g) than mixed-species (Fig. 4b, d, f and h) competitive gradients. Spruce displayed the opposite pattern, with steeper reductions in predicted crown radius found in mixed-species (Fig. 4b, d, f and h) compared to conspecific (Fig. 4a, c, e and g) competition scenarios.

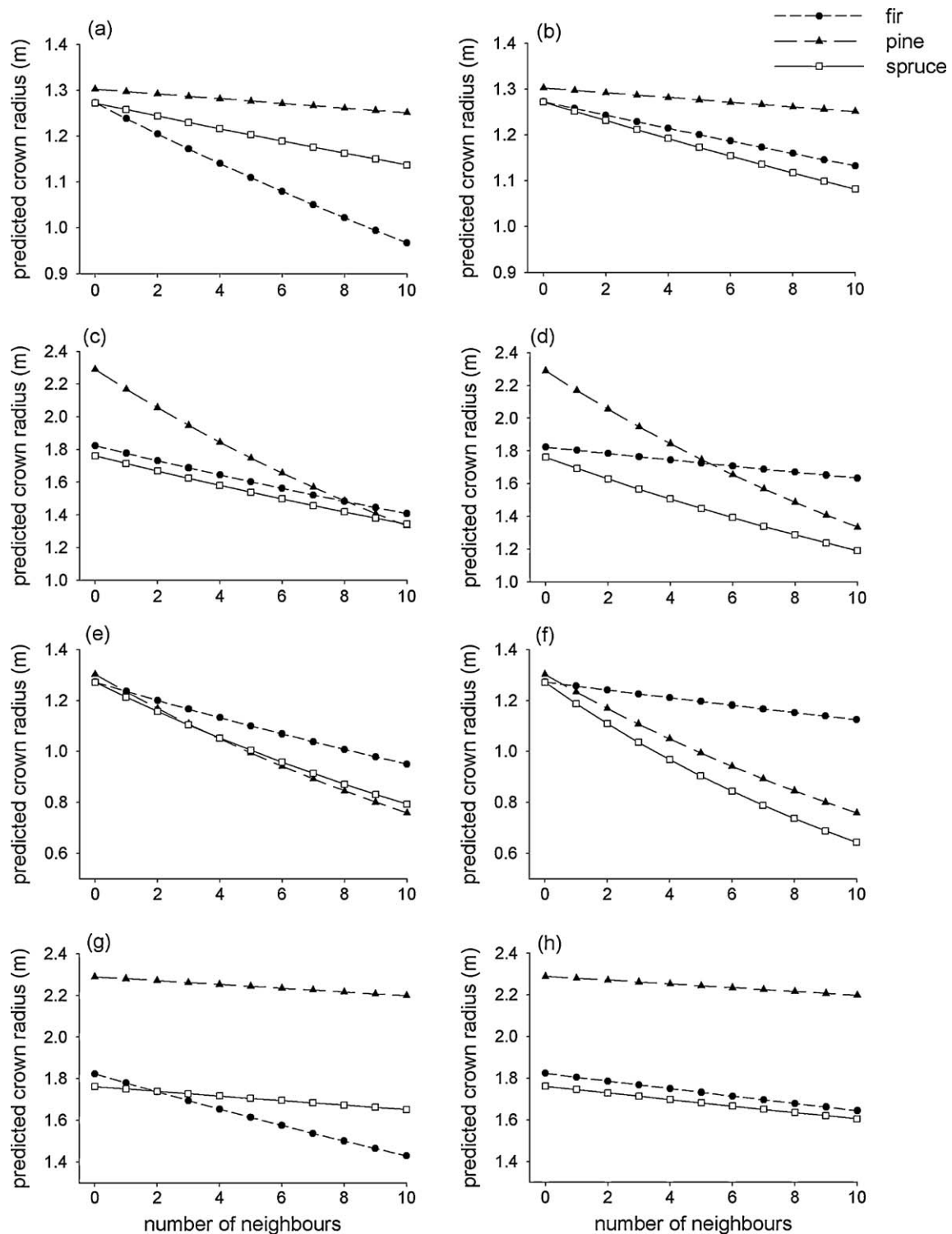


Fig. 4. Predicted crown radius across a range of competitive gradients in the three study species. In left column panels (a, c, e and g), neighbors are conspecifics. Right column panels (b, d, f and h) depict mixed-species scenarios, where species composition of neighbors is split equally among fir, pine and spruce. Specific competitive scenarios include: (a and b) 12-m tall neighbors 2 m from a 12-m tall, 15-cm dbh target tree, (c and d) 24-m tall neighbors 2 m from a 24-m tall, 30-cm dbh target tree, (e and f) 24-m tall neighbors 2 m from a 12-m, 15-cm dbh target tree. (g and h) 12-m tall neighbors 2 m from a 24-m, 30-cm dbh target tree.

Because the selected best model for pine did not include species-specific competitive effects, pine crown radius predictions were equivalent in monospecific and mixed-species scenarios (Fig. 4).

Specific responses to competition varied across species and competitive scenarios. For the case of a 12-m tall target tree surrounded by 12-m conspecific neighbors, pine showed the least sensitivity to increasing neighbor density, followed by spruce and

then fir (Fig. 4a). In the equivalent mixed-species case, spruce showed the steepest declines in predicted crown radius (Fig. 4b). The scenario in which 24-m tall target trees were surrounded by 24-m tall neighbors was associated with the largest reductions in predicted crown radius across the competition gradient, with a mean predicted reduction of 0.60 m for the monospecific and 0.57 for the mixed-species cases (Fig. 4c and d). On a proportional basis,

the largest reductions were found in the scenario in which 12-m tall neighbors were surrounded by 24-m tall neighbors, where mean crown radii predictions declined by 35 and 34% across the competitive gradient in the monospecific and mixed-species cases respectively (Fig. 4e and f). Pine generally displayed the steepest declines in predicted crown radius with increasing neighborhood competition from 24-m tall neighbors (Fig. 4c–f). No species was particularly sensitive to competition from 12-m tall neighbors surrounding a 24-m tall target (Fig. 4g and h), but the steepest decline in predicted crown radii was found for fir surrounded by conspecific neighbors (Fig. 4g).

3.6.2. Competitive effects on crown length

The effects of competition on crown length (Fig. 5) for the most part mirrored crown radius results, with decreases in crown length predicted for all three species as neighbor tree height and density increased. Crown length of fir, and to a lesser extent pine, declined most steeply with increasing competition from conspecific neighbors, while spruce crown length was most sensitive to interspecific competition. Pine was associated with the shortest crown length predictions in most scenarios, but it was not usually the most sensitive species to increasing competition. In the monospecific scenarios, relative sensitivity to competition among the three species varied depending on the particular competitive situation (Fig. 5a, c, e and g) while in the mixed-species cases, spruce was generally most sensitive to increasing neighborhood competition (Fig. 5b, d, f and h).

Across the competition scenarios considered, the largest decreases in crown length predictions were found as the density of 24-m tall neighbors surrounding a 24-m tall target tree increased (Fig. 5c and d). In these scenarios, average crown length predictions across the competitive gradient declined by 9.4 and 7.3 m for monospecific and mixed-species cases respectively. The largest proportional declines in predicted crown radius occurred across the competition gradient in which a 12-m tall target tree was surrounded by 24-m tall neighbors, where average crown length predictions declined 81 and 68% in monospecific and mixed-species cases respectively.

4. Discussion

Competition for canopy space is a key structuring feature of forest ecosystems (Oliver and Larson, 1996). Results from this study provide insight into how competition among individuals influences tree canopy structure in the boreal forest. We found strong evidence for species differences in crown dimensions and in responses to increasing neighborhood competition. With the exception of one model, neighbor species identity influenced competitive effects on target trees, and sensitivity to crowding from neighbors decreased with increasing target tree height. Neighborhood competition depended on the size, species and distance of neighbors, and each species and crown dimension exhibited a slightly different response to competition. The wide variation in crown responses to competition across tree sizes and species highlights the complexity of competitive interactions, even in a relatively species-poor ecosystem, and suggests that differences in responses to competition may contribute to maintaining species diversity.

This study was carried out in part to develop a spatially explicit crown model for the forest simulation model SORTIE-ND.⁴ Crown dimensions in SORTIE-ND are currently predicted as a function of tree diameter or height alone and do not incorporate neighborhood conditions. This can lead to overestimated light availability in open stands and underestimated light levels in dense forests (Astrup, 2006). The selected best crown models in this study were associated

with high R^2 values, ranging from 50 to 74% of the variation in crown dimensions, while models that considered size as the only predictor of were associated with R^2 values from 3.5 to 63% (Tables 2a and 2b and Fig. 1). We expect that incorporating neighborhood-dependent crown models into SORTIE-ND will greatly improve the accuracy of modelled crown size and will lead to more realistic predictions of understorey light availability and corresponding sub-canopy tree dynamics across a wide range of forest densities.

4.1. Further model development

We are confident in the crown models we developed in this study since parameters were estimated using data from over 2000 trees, models were unbiased, and model fits were good (Fig. 1). However, there is potential for further model development. We used only two parameters – crown length and crown radius – to represent tree crowns, while trees in forests have irregularly shaped crowns. More realistic models of crown shape have been developed recently (Purves et al., 2007; Strigul et al., 2008). Our models also assume that crowns are centred on the stem, but previous research has shown that trees develop asymmetric crowns in order to avoid competition by neighbors (Muth and Bazzaz, 2003). While the assumptions that tree crowns are cylindrical and symmetrical afforded us computational simplicity both with the current analysis and follow-up simulation modeling, future research could address those factors which may contribute to model inaccuracy.

4.2. Neighbor tree size and distance scaling effects

Studies of the effect of competition on adult-tree growth generally use diameter as the size measure of neighboring competitors (Lorimer, 1983; Canham et al., 2004; Uriarte et al., 2004a). We compared pairs of NCI formulations to test whether using neighbor tree dbh or height in the numerator (Eqs. (3a)–(3f)) provided a better approximation of competitive effects on tree crowns. All selected models used height as the proxy for neighbor tree size, suggesting that competitive effects on tree crown size are better described by neighbor tree height than by diameter. This may also be true for competitive effects on tree growth. Height is not usually included as a potential predictor variable because it is more difficult than dbh to measure in the field, but it may be a better descriptor of competitive relationships among canopy trees.

Many previous studies have arbitrarily defined relationships between neighbor tree size and distance and their competitive effects on target trees (e.g., Bella, 1971; Stoll et al., 1994) but our analytical approach allowed us to estimate these scalar relationships (Eqs. (3a)–(3f): α and β). We found evidence that fir crown radius is influenced more by the density than the size of neighboring trees ($\alpha < 1$; Table 3a) while competitive effects on pine and spruce radius and on crown length in all species increased exponentially with neighbor tree height ($\alpha > 2$; Tables 3a and 3b). Alpha values ~ 2 are common for adult-tree growth analyses (Canham et al., 2004; Uriarte et al., 2004a) but studies that estimate α for several species often find a wide range of parameter estimates (Uriarte et al., 2004a; Papaik and Canham, 2006; Coates et al., 2009).

Estimates of β (Eqs. (3a)–(3f); Tables 3a and 3b), the parameter that determines the shape of the decline in competitive influence with distance, were remarkably similar across the three species for both crown dimensions (Fig. 3). We found steep declines in the influence of neighbors with increasing distance from the target tree, particularly for crown radius. Neighbors located within 2 m of the target tree exhibited by far the strongest competitive effects on tree crowns. Trees 2–4 m from the target tree also exerted some competitive influence, while the competitive effects of neighbors

⁴ www.sortie-nd.org.

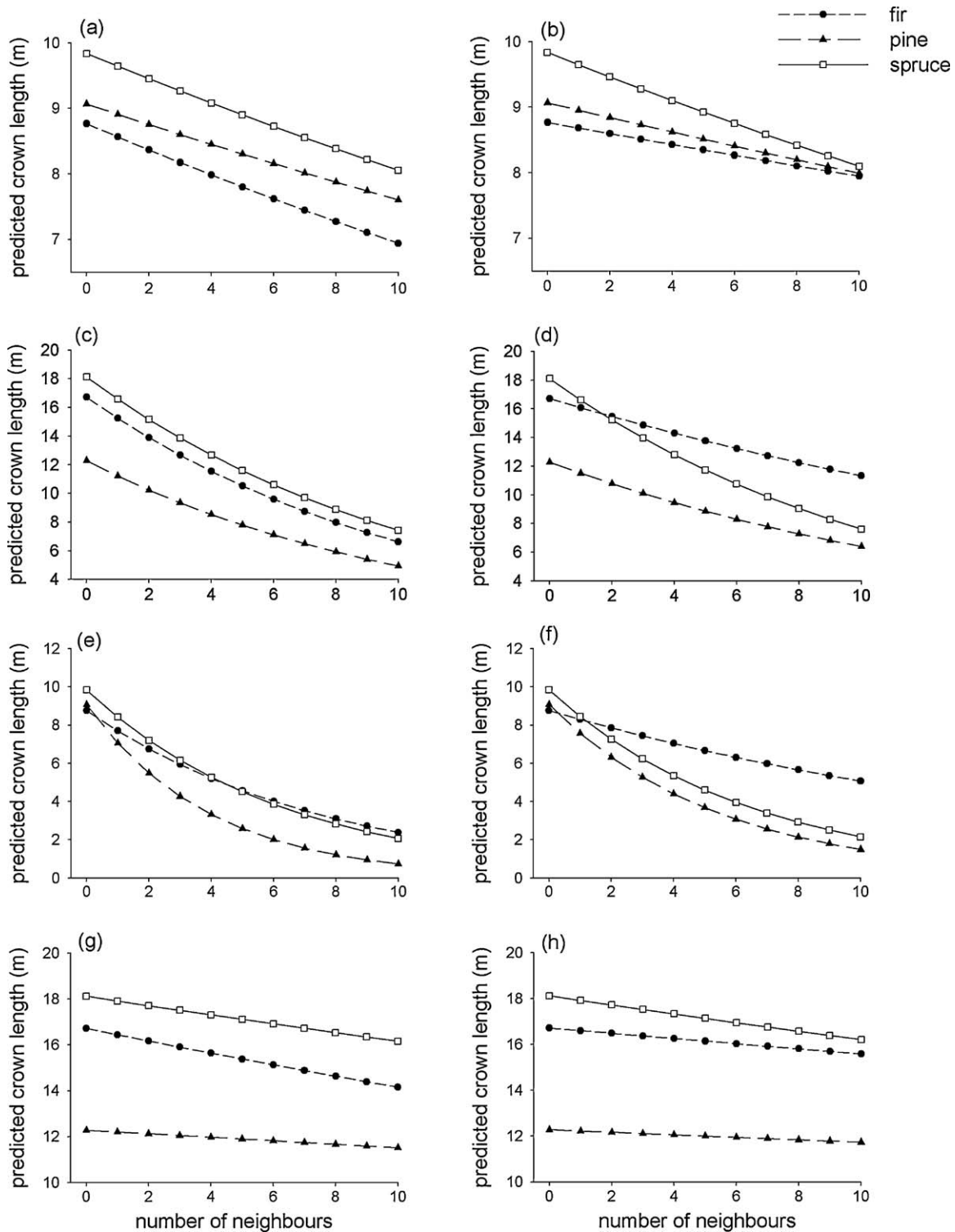


Fig. 5. Predicted crown length across a range of competitive gradients in the three study species. Left column panels (a, c, e and g) depict scenarios in which target and neighbor trees are conspecifics. In right column panels (b, d, f and h), neighbors are split equally among fir, pine and spruce. Specific competitive scenarios include: (a and b) 12-m tall neighbors 2 m from a 12-m tall target tree, (c and d) 24-m tall neighbors 2 m from a 24-m tall target tree, (e and f) 24-m tall neighbors 2 m from a 12-m target tree, (g and h) 12-m tall neighbors 2 m from a 24-m target tree.

located further than 4 m away from the target were negligible. Thus crown dynamics in boreal trees are very local in nature. Neighborhood analyses of adult-tree growth generally show a much larger range in β estimates across species and a larger distance over which neighboring trees exert competitive effects on target trees (e.g., Uriarte et al., 2004a; Coates et al., 2009). This likely reflects the larger spatial extent over which competition for

water and soil nutrients occurs compared to competition for canopy space (i.e., size of root plates vs. tree crowns).

4.3. Neighbor species identity

For all models except pine crown radius, we found compelling evidence for species-specific differences in competitive effects, as

has been demonstrated in previous neighborhood analyses of tree growth (Uriarte et al., 2004a; Canham et al., 2006; Papaik and Canham, 2006; Coates et al., 2009). Studies that include multiple species often show evidence for differences in per-capita competitive effects in some species and for functional equivalence of neighbors in others, particularly those with small sample sizes (e.g., Uriarte et al., 2004a, 2004b; Canham et al., 2006; Coates et al., 2009). The species associated with a functional equivalence of neighbors model in this study, lodgepole pine, was the most abundant in our dataset and so this result is not an artefact of insufficient data. Instead, we believe it is a result of pine's shade intolerance, where competition from any neighbor, regardless of species, affects pine crown radius. The species identity of neighbors did influence competitive effects on pine crown length, but pine crown length was overall less sensitive to competition than pine crown radius. This is likely because pine tends to self-prune lower branches. For both spruce and fir crown models, competitive effects depended on species identity of neighbors, and in all cases fir showed the largest competition coefficient. Intraspecific competition was therefore most important in fir, while spruce experienced the largest competitive effects from interspecific neighbors.

For models that included species-specific competition coefficients (λ), our results mirrored findings from a recent study of adult-tree growth (Coates et al., 2009). This study quantified competitive effects of subalpine fir, lodgepole pine and interior spruce among others and found that for all three species, the competitive ranking of neighbors was fir > pine > spruce. While our results were more varied across species and crown dimensions, fir was generally the most competitive species. Similar findings from studies of crown size and diameter growth support the notion that growth follows the acquisition of canopy space.

4.4. Management implications

Results from this study provide new tools for understanding and predicting development of complex forests, and demonstrate how detailed information on species interactions can be used to inform the design of forest management prescriptions. Silvicultural treatments that maintain residual trees of varying sizes, species, and spatial configurations are becoming commonplace, but our understanding of how complex stands will develop over long time scales remains weak. Implementing results from this study into spatially explicit, individual-based models will allow managers to explore the long-term effects of recently developed silvicultural prescriptions. A manager could explore, for example, how dispersed versus aggregated retention patterns influence understory light levels and regeneration dynamics across a range of stands with varying species compositions.

Although the pattern was not entirely consistent, we found that trees growing in dense neighborhoods were generally associated with larger predicted crowns in mixed-species scenarios than in monocultures. This may result from differences in crown shapes, which could allow greater partitioning of canopy space when stands contain species mixtures, and may lead to improved forest productivity overall. Future simulation modeling research could aim to quantify how tree size, density, species composition and spatial pattern affect individual-tree and stand productivity.

Acknowledgements

Funding for this study was provided by British Columbia's Forest Sciences Program. We thank Megan Adams, Matthew Bryan, Erica Close, Tlell Glover, and Beth Henderson for their field assistance.

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