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The relative dominance hypothesis explains interaction dynamics in mixed species *Alnus rubra*/*Pseudotsuga menziesii* stands

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Summary

1 We used repeated measurements of tree growth and population-level and neighbourhood conditions from three mixed *Alnus rubra*/*Pseudotsuga menziesii* forests in the Pacific Northwest, USA to investigate why previous results regarding the importance of neighbourhood competition as a determinant of plant growth were inconsistent.

2 We propose that relative dominance of a particular species determines the importance of neighbourhood interactions, and tested whether growth performance of both species at various stand ages agrees with this relative dominance hypothesis.

3 Neighbourhood and relative dominance interaction indices were modified to accommodate two-species mixtures and were incorporated into a growth model predicting relative diameter growth rates. The corrected Akaike Information Criterion (AIC_c) was used to identify the optimum interaction measures and model forms for each species and measurement period.

4 Interaction indices reflecting the size of a tree relative to the population were the best predictors of growth of the dominant (i.e. taller) species and neighbourhood interaction indices of the subordinate species.

5 Performance of interaction measures as predictors of relative growth rates in our study varied in agreement with the relative dominance hypothesis for both species and on all sites. Results from other studies suggest that the hypothesis may explain growth performances on a species and individual plant level and for a variety of life forms.

6 These findings suggest that the spatial scale of plant interactions is influenced by the size structure of plant populations. The relative dominance hypothesis offers a framework to provide insight into the mechanism of competition, based on the relative performance of competition indices.

Key-words: *Alnus rubra*, competition index, competitive asymmetry, neighbourhood competition, plant interaction, *Pseudotsuga menziesii*, relative dominance, relative growth rate, Akaike information criterion

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Introduction

The importance of plant–plant interactions in plant community structure and development has been well recognized (Yoda *et al*. 1963; Harper 1977; Tilman 1988; Duncan 1991; Peterson & Squiers 1995; Oliver & Larson 1996). These interactions may have positive effects on growth and survival through processes such as facilitation (for examples in forest ecosystems, see Binkley 1983; Walker & Chapin 1987; Peterson & Squiers 1995) or negative effects through processes such as competition for resources (e.g. Ford 1975) and allelopathy (Williamson 1990). The predominant mode of interaction between trees in forest communities is, however, generally considered to be competition for resources (Oliver & Larson 1996). In many cases, early differences in size among trees due to variation in their emergence time (Connolly & Wayne 1996), their early growth rates (Turner & Rabinowitz 1983) and/or environmental heterogeneity (Hartgerink & Bazzaz 1984) are magnified as stands develop and competition for resources intensifies. In particular, inequalities in height within a population can result in the pre-emption of resources (e.g. light) by

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larger individuals, thus exacerbating the differences in growth rates among interacting trees (Cannell *et al.* 1984). Such competitive relationships, in which larger individuals obtain a disproportionate amount of available resources and suppress the growth of smaller individuals, have been referred to as size-asymmetric (Schwinning & Weiner 1998) and often lead to an increasingly positive correlation between the size of a tree relative to the population and its growth rate (Ford 1975; Cannell *et al.* 1984; Schmitt *et al.* 1987).

While size is often related to resource capturing capacity in populations in which competition is asymmetric (Ford & Diggle 1981; Miller & Werner 1987; Goldberg 1990; Schwinning & Weiner 1998), the amount of competition a tree experiences is also a function of the sizes and proximities of its neighbours (Mack & Harper 1977; Weiner 1982, 1984; Silander & Pacala 1985; Goldberg 1987). The influence of neighbourhood competition on plant growth has been well documented (e.g. Bella 1971; Weiner 1984; Penridge & Walker 1986; Peterson & Squiers 1995). However, our understanding of the relationship between this concept (referred to hereafter as the importance of competition *sensu* Weldon & Slauson 1986) and a plant's size relative to the population is limited. For example, several authors examining competition in populations with varied size structures have noted that measures of neighbourhood competition have only been able to explain the variation in growth of the smaller individuals in the population (e.g. Cannell *et al.* 1984; Kubota & Hara 1995; McLellan *et al.* 1997). In these studies, the effects of neighbourhood competition on larger individuals have been minimal, suggesting that the importance of neighbourhood competition as a determinant of tree growth may vary according to an individual's relative size. While neighbourhood measures incorporating the effects of size-asymmetrical competition have been developed to account for this variation (e.g. Penridge & Walker 1986; Thomas & Weiner 1989; Tomé & Burkhart 1989; Schwinning & Weiner 1998; Purves & Law 2002), these measures have assumed that neighbourhood competition is equally important for all individuals in a population irrespective of their size (Thomas & Weiner 1989).

The influence of plant size is further complicated. In populations in which competition is asymmetric, large individuals often obtain a disproportionate share of resources and suppress the growth of smaller individuals (e.g. Connolly & Wayne 1996). Under these conditions, the amount of resources available to smaller individuals within the population is strongly related to the amount of neighbourhood competition from larger neighbours only (Thomas & Weiner 1989; Schwinning & Weiner 1998). Although the amount of resources available to dominant individuals may also be affected by neighbourhood competition, only weak relationships have been observed in several studies between measures of neighbourhood competition and the growth of larger individuals (Cannell *et al.* 1984) or taller species (Kubota & Hara 1995; McLellan *et al.* 1997; Wagner & Radosevich 1998). This suggests that the superior resource capturing capacity of a dominant plant may be a more important determinant of its growth than neighbourhood competition (Wagner & Radosevich 1998). The changes to population and neighbourhood conditions that result from differences in long-term growth rates among interacting individuals and stochastic events could also lead to changes in the importance of neighbourhood competition over time (e.g. Daniels *et al.* 1986; Stoll *et al.* 1994). We propose the 'relative dominance hypothesis', which states that changes in the relative dominance of a particular species may result in changes in the importance of neighbourhood interactions over time. Repeated measurements of tree growth and population-level and neighbourhood conditions from three mixed *Alnus rubra* Bong./*Pseudotsuga menziesii* [Mirb.] Franco (nomenclature follows Hitchcock & Cronquist 1976) forests in the Pacific Northwest, USA are used to test this hypothesis.

Methods

STUDY SPECIES AND SITES

Alnus rubra and *Pseudotsuga menziesii* commonly co-occur throughout the Pacific Northwest and the interactions between these two species at different stages of forest development have received a great deal of attention (e.g. Puettmann *et al.* 1992; Shainsky & Radosevich 1992). Mixed forests of these two species provide an excellent test system for examining the relative dominance hypothesis due to the differences in their growth rates and resource requirements. *A. rubra* is a fast-growing, early successional species that is often able to attain its mature height within 40 years (Newton & Cole 1994). Its ability to fix nitrogen also provides an opportunity to investigate positive (i.e. facilitation) as well as negative (i.e. competition) interactions (Binkley 1983). In contrast, *P. menziesii* is a long-lived, early to late-successional species and, although intial growth rates are less than *A. rubra*, it is able to maintain height growth for up to two hundred years (Curtis *et al.* 1974). The mixed *Alnus rubra*/*Pseudotsuga menziesii* stands studied consisted of two established replacement series studies at the Cascade Head and H.J. Andrews Experimental Forests in western Oregon, USA, and a natural stand at Delezene Creek in western Washington, USA (see Table 1 for locations and climatic and soil properties).

EXPERIMENTAL DESIGN

The experimental design of the Cascade Head (CH) and H.J. Andrews (HJA) study sites is a replacement series (de Wit 1960; Jolliffe 2000) consisting of six proportions (0 : 100, 10 : 90, 30 : 70, 50 : 50, 75 : 25, and 100 : 0%) of *A. rubra* and *P. menziesii* replicated three times at each site in a randomised, complete block design (Fuentes-Rodríquez 1994). These sites were prepared for planting by clearcutting and slash burning in 1984

Table 1 Locations and climatic and site characteristics of the study areas

Study site/location	Lat. N, Long. W	Soil drainage class/texture	Soil parent material	Elevation (m)	Mean minimum temperature (°C)	Mean maximum temperature (°C)	Precipitation (cm)
Cascade Head Experimental Forest, Oregon, USA	45°05′ N, 124°00′ W	Well-drained, fine loams*	Basalt	150–330	2.2	20.9	250
H.J. Andrews Experimental Forest, Oregon, USA	44°14′ N, 122°10′ W	Well-drained, coarse loams†	Andesite	500–800	−8.5	26.9	230§
Delezene Creek, Oakville, Washington, USA	46°56′ N, 123°24′ W	Well-drained, fine loams‡	Sandstone	60–130	1	21.5	250¶

*Shipman (1997).
†Patching (1987).
‡Pringle (1986).
§Halpern (1989).
¶WRCC (2001).

and were planted in 1986 with 2-year old *A. rubra* and 1-year old *P. menziesii* seedlings on a 3 × 3 m, grid. Each plot consisted of 9 rows with 9 seedlings and species were intermixed (Fuentes-Rodríquez 1994). Three additional replicates of the replacement series were established at each site with *P. menziesii* planted in 1986, but *A. rubra* planting delayed until the fifth year. It is important to note that, despite the initial grid-based spacing, random mortality and variation in seedling placement, as well as the differences in timing of alder plantings, created a range of spatial and size conditions in these plots.

The stand at Delezene Creek (DC) is a naturally regenerated, even-aged mixture of *A. rubra* and *P. menziesii* that was inventoried repeatedly from 1952 to 1978 by students from University of Washington and again in 1990 by D.E. Hibbs and K.J. Puettmann. A complete stem map of the 1-ha study area was created in 1959. At the time of initial measurement (1952), the stand was 30 years old. Other tree species were present at all three study sites, including *Tsuga heterophylla* and *Picea sitchensis.* However, these species occurred at very low frequencies and were only found as understorey seedlings or saplings.

FIELD SAMPLING

On the replacement series sites, trees were measured in 15 × 15 m plots in the centre of each replicate (the outer two rows were left as unmeasured buffers), with the CH and HJA sites contributing 33 and 30 plots, respectively. Species, diameter at breast height (D), total tree height, height to base of live crown and crown diameter (average of 2 perpendicular crown diameter measurements) were recorded for each tree in 1991, 1992, 1993, 1995, 1998 and 2001. The stands were 15 years old at the time of last measurement. Locations of trees were mapped in the summer of 2001 and converted to metric coordinates. For multiple stemmed individuals, stump location and breast height location of each stem were recorded and a single value of diameter at breast height was calculated by summing the basal areas at breast height of each stem and deriving the D represented by the total basal area.

For the DC site, species and D were recorded for each tree in 1952, 1957, 1961, 1965, 1969, 1975, 1978 and 1990. At each date, height measurements were taken from a subset of trees representative of the range of tree sizes for *P. menziesii* and *A. rubra* in the stand. We estimated missing heights using ratio estimation (Som 1996). The stand was harvested after the final measurement in 1990.

INTERACTION INDICES

Intra- and inter–specific interaction indices, designed to represent various aspects of the nature and degree of interaction between trees, were calculated for each tree at each site and measurement period. The set of indices listed in Table 2 was selected based on their successful performance in previous studies examining competitive interactions in forest stands (e.g. Biging & Dobbertin 1992; Richardson *et al*. 1999) and to represent a range of complexity (e.g. distance independent and dependent, relative diameter or crown sizes of neighbouring trees). These indices were modified to accommodate two-species mixtures allowing for separation of intra- and inter–specific interactions on individual tree growth.

Interaction indices (IIs) selected were categorized into two broad classes (Table 2). Neighbourhood (N) interaction indices (referred to as 'proximity indices' in the recent review by Weigelt & Jolliffe 2003) were calculated from various characteristics of neighbouring trees and were used to characterize the influence of neighbourhood interactions on the resources available for tree growth (**B**, **BE**, **H**, **L**, and **R** in Table 2). Neighbouring trees were defined as trees within a radius centred on the focal tree except for the **BE** index, where a circular area of influence (A_i) was constructed for all trees using crown diameter measurements. In contrast to the other neighbourhood interaction indices, **BE** defined the influence of a neighbouring tree on the resources available to a focal tree as a function of the degree of overlap between its area of influence and that of the focal tree. In addition, the ratio of diameters between neighbouring trees was also utilized in the **BE** index to represent size–symmetrical interactions. Bella (1971) incorporated a scaling exponent into this term to express

Table 2 Neighbourhood (N) and relative dominance (RD) interaction indices used to characterize tree–tree interactions. All interaction indices have been modified to separate intra- and inter–specific interactions

Source	Symbol	Interaction Index (II)	Type
Biging & Dobbertin (1992)	**B**	$B_{i1} = \left[\sum_{j_1=1}^{n_1}\left(\frac{V_{j1}/V_{i1}}{L_{i1j1}}\right)\right] + \left[\sum_{j_2=1}^{n_2}\left(\frac{V_{j2}/V_{i1}}{L_{i1j2}}\right)\right]$	N
Bella (1971)	**BE**	$BE_{i1} = \left[\sum_{j_1=1}^{n_1}\left(\frac{O_{i1j1}}{A_{i1}}\right)\left(\frac{D_{j1}}{D_{i1}}\right)^b\right] + \left[\sum_{j_2=1}^{n_2}\left(\frac{O_{i1j2}}{A_{i1}}\right)\left(\frac{D_{j2}}{D_{i1}}\right)^b\right]$	N
Glover & Hool (1979)	**G**	$G_{i1} = \left[\left(\frac{B_{i1}}{\bar{B}_1}\right) + \left(\frac{B_{i1}}{\bar{B}_2}\right)\right] \Big/ 2$	RD
Hegyi (1974)	**H**	$H_{i1} = \left[\sum_{j_1=1}^{n_1}\left(\frac{D_{j1}/D_{i1}}{L_{i1j1}}\right)\right] + \left[\sum_{j_2=1}^{n_2}\left(\frac{D_{j2}/D_{i1}}{L_{i1j2}}\right)\right]$	N
Lorimer (1983)	**L**	$L_{i1} = \left[\sum_{j_1=1}^{n_1}\left(\frac{D_{j1}}{D_{i1}}\right)\right] + \left[\sum_{j_2=1}^{n_2}\left(\frac{D_{j2}}{D_{i1}}\right)\right]$	N
Richardson *et al.* (1999)	**R**	$R_{i1} = \left[\frac{1}{H_{i1}^2}\frac{1}{n_1}\sum_{j_1=1}^{n_1}(H_{j1})^2(Af_{j1})\right] + \left[\frac{1}{H_{i1}^2}\frac{1}{n_2}\sum_{j_2=1}^{n_2}(H_{j2})^2(Af_{j2})\right]$	N
Wykoff *et al.* (1982)	**W**	$W_{i1} = \left[\sum_{\substack{j_1=1 \\ D_j>D_i}}^{p_1}(D_{j1})^2 0.00007854\right] + \left[\sum_{\substack{j_2=1 \\ D_j>D_i}}^{p_2}(D_{j2})^2 0.00007854\right]$	RD

A_i = area of influence of focal tree *i*.
Af_j = arc fraction of neighbour *j*'s crown, defined as: $Af_j = \{2 \times \tan^{-1}(R_j/L_{ij})/360\}$.
L_{ij} = distance between neighbour *j* and focal tree *i*.
R_j = crown radius of neighbour *j*.
b = scaling exponent (1.0, 1.5, 2.0).
$\bar{B}$ = basal area of tree with mean D within a stand.
B_i = basal area of focal tree *i*.
D_i = diameter at breast height of focal tree *i*.
D_j = diameter at breast height of neighbour tree *j*.
H_i = height of focal tree *i*.
H_j = height of neighbour tree *j*.
n = total number of neighbours.
O_{ij} = area of influence overlap between focal tree *i* and neighbour *j*.
p = total number of trees in the population.
V_i = crown volume of focal tree *i*.
V_j = crown volume of neighbour tree *j*.
1, 2 = species.

the degree to which resources were shared disproportionately, i.e. size-asymmetrically (*sensu* Schwinning & Weiner 1998). Based on findings of past research (e.g. Bella 1971; Holmes & Reed 1991; Biging & Dobbertin 1992), we used **BE** indices with scaling exponents set at 1, 1.5, and 2.

Relative dominance (RD) interaction indices were computed from characteristics of all trees within a given stand, rather than just those of neighbours. As a result, they serve as an expression of the size of an individual tree relative to the overall population. Glover & Hool's (1979) index (**G** in Table 2) uses the ratio of the basal area of the focal tree relative to that of a tree whose D has the same value as the mean for the population. This index assumes that the interactions experienced by a focal tree are strictly a function of its relative size (i.e. perfect size symmetry *sensu* Schwinning & Weiner 1998) and does not therefore incorporate a measure of density. A second relative dominance index, **W**, developed by Wykoff *et al.* (1982) assumes that the focal tree interacts only with trees in the population that are larger than it. In contrast to **G**, this index also includes a measure of density (of larger individuals), as basal areas of all trees larger (in basal area) than the focal tree were summed.

Measurements taken at CH and HJA sites allowed calculation of all the various indices, but only indices using D (to characterize tree size) and intertree distances could be calculated at DC (**G**, **H**, **L**, and **W** in Table 2). Only single stemmed trees were used as focal individuals in calculation of the interaction indices, but multiple stemmed individuals were considered as neighbours. To avoid plot edge biases, only trees occurring at least 3 m from the measurement plot border at the CH and HJA sites and at least 9 m from the study site border at the DC site were selected as focal trees. However, all trees within the study sites were considered as neighbours in calculating the interaction indices.

A set of search radii was used to determine neighbouring trees (with the exception of **BE**, which utilized the area of overlap). For the CH and HJA sites, the maximum radii were restricted to 4.5 m to make use of as many trees as possible while avoiding neighbourhoods that extended beyond the plot borders. We used the central tree in each plot, for which we could calculate the largest neighbourhood, to investigate whether this was a restrictive assumption and compared results of analyses using search radii of 3.0, 4.5, and 6.0 m. Search radii of 3.0, 4.5, 6.0, 7.5, 9.0, and 11.5 m were used in the calculation of the neighbourhood indices for the DC study site.

ANALYSIS

The relative diameter growth rate (*RGR*) was selected as a measure of performance (i.e. of the response to interactions experienced by the focal tree). *RGR* was calculated for each measurement period as:

$$RGR = \frac{\ln D_2 - \ln D_1}{t_2 - t_1} \qquad \text{eqn 1}$$

where D_1 and D_2 are the diameters at the beginning (t_1) and end (t_2) of the measurement period. This measure accounts for initial size at the beginning of a measurement period, thus allowing for a more accurate assessment of the relative importance and intensity of tree–tree interactions at different stages of stand development (Ford & Sorrensen 1992).

A growth model, which incorporated intra- and inter–specific interactions, was developed to evaluate the intensity and importance of tree–tree interactions over each measurement period. The main growth model used was:

$$RGR_i = \beta_0 + \beta_1 \cdot \ln(II_{11}) + \beta_2 \cdot \ln(II_{12}) + \beta_3 \cdot \ln(II_{11} \cdot II_{12}) + \varepsilon \qquad \text{eqn 2}$$

where II_{11} and II_{12} are the intra- and inter–specific interaction indices (without units) at the beginning of the growth interval, $II_{11} \cdot II_{12}$ is the statistical interaction between intra- and inter–specific interaction indices, and ε is the error term. In addition to the full model (Equation 2), models only incorporating intra or inter–specific interactions were evaluated for each growth interval and interaction index using mixed linear regression analyses performed in SAS (PROC MIXED; SAS Institute 1999). It is important to note that the choice of growth models using these interaction indices is determined by the study conditions. For example, Richardson *et al.* (1999) used an exponential growth model as their data were limited to very young seedlings, which have been shown to exhibit exponential growth. Consequently, the absolute results of comparisons in any study cannot be directly compared with results of other studies. Instead, any comparison of different studies should be limited to relative performances, and this assumes proper choice of models in all studies as evidenced by residual analysis. With one exception (**W** interaction index for *P. menziesii* years 6–9 at HJA), non-linearity and non-homogeneous variance was corrected by logarithmic transformation of independent variables in the growth models. Spatial correlation between trees in each plot was accounted for by including a power spatial correlation structure in each of the models (SP(POW); SAS Institute, Inc. 1999). This structure accounts for the covariance between trees due to spatial location based on the *x*-y coordinates of each tree. For the CH and HJA study sites, random plot effects were also incorporated into the models to account for variation in growing conditions across plots.

For each measurement period, a set of models containing all possible interaction indices was constructed. The corrected Akaike Information Criterion, AIC_c, was used to determine the best index and neighbourhood size for each measurement period and to test the relative fit of each model (Burnham & Anderson 1998). AIC_c is derived from the maximum log-likelihood estimate and number of parameters in a given model, rewarding models for goodness of fit and imposing penalties for multiple parameters. Smaller AIC_c values indicate better models and AIC_c values are ranked according to the difference between the AIC_c value for a given model (AIC_{ci}) and the lowest AIC_c value in a given set of models (AIC_{cmin}): $\Delta_i = AIC_{ci} - AIC_{cmin}$. The difference value, Δ_i, allows a strength of evidence comparison among the models, where increasing Δ_i values correspond with decreasing probability of the fitted model being the best approximating model in the set (Anderson *et al.* 2000). As a rule of thumb, models with $\Delta_i \leq 2$ have considerable support and should be considered when making inferences about the data (Burnham & Anderson 2001).

To approximate the probability of a model being the best in a given set, the Δ_i values were used to calculate Akaike weights (w_i) using the following formula (Burnham & Anderson 1998):

$$w_i = \frac{\exp(-\Delta_i/2)}{\sum_{r=1}^{R} \exp(-\Delta_{ir}/2)} \qquad \text{eqn 3}$$

where w_i is the Akaike weight for model *i* and *R* is the number of models in the set. Although performances are only reported in this paper for well supported models (i.e. $\Delta_i \leq 2$), w_i values calculated using all Δ_i values provide an approximation of how other models in the set performed relative to the best selected models.

A null model was included in each set of candidate models to determine the importance of interactions on relative growth rates over the measurement period. The null model stated that the relative growth rate over a given measurement period was solely a function of the spatial correlation among trees in a given population and the model did not therefore include any terms describing tree–tree interactions. Models incorporating measures of interaction that had lower Δ_i values than the null model indicated situations where tree–tree interactions were more important than other unmeasured factors, such as genetic variation and environmental heterogeneity, which also affect relative diameter growth rates (Weldon & Slauson 1986).

In cases in which the best models for the CH and HJA sites contained neighbourhood interaction indices, the appropriate neighbourhood size was determined by fitting models for the central tree in each plot using neighbourhood radii of 3.0, 4.5 and 6.0 m and comparing the Δ_i values. If the models using 3.0 and/or 4.5 m radii were ranked higher than the models with larger neighbourhoods (i.e. 6.0 m) it was assumed that the neighbourhood sizes used in our analyses were appropriate for the site and species.

Results

The density, height, and diameter of *A. rubra* and *P. menziesii* in the young (CH and HJA) and mature (DC) stands for all measurements are shown in Figure 1. On average, *A. rubra* in the young stands had larger heights than *P. menziesii*, whereas *P. menziesii* was taller in the mature stand (Fig. 1). Diameter at breast height followed a similar pattern (Fig. 1). Very little mortality occurred in the young stands (Fig. 1), but roughly 30% of the *A. rubra* and 22% of the *P. menziesii* in the mature stand died between ages 30–68 (sample sizes for D in Fig. 1c).

ANALYSIS OF TREE–TREE INTERACTIONS

The null models for both species and in all measurement periods had Δ_i values greater than 2.0 indicating that tree–tree interactions and the other measured factors were important to the relative growth rates of *A. rubra* and *P. menziesii* in both young and mature stands.

Specific spatial information, i.e. neighbour tree distances, did not improve our ability to characterize the nature of interaction in these stands. With few exceptions, models employing a neighbourhood interaction index that did not weight neighbour tree influence by proximity (**L**, **BE** in Table 2) and/or models containing

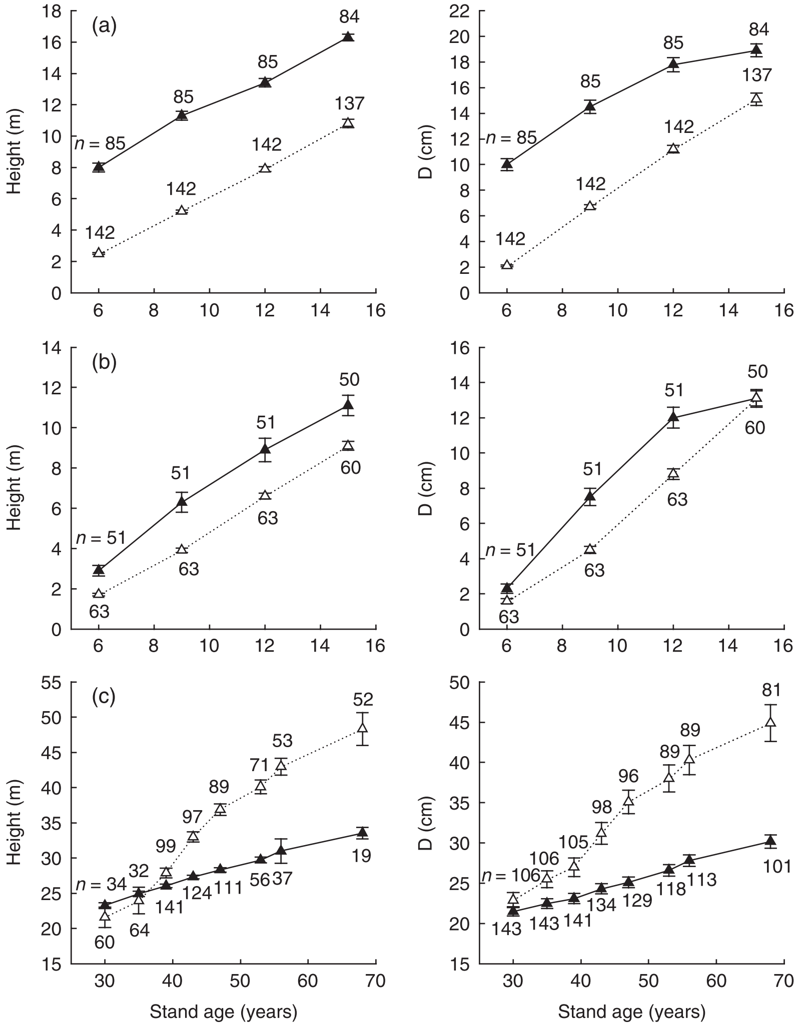

Fig. 1 Mean height and diameter at breast height (D) of *Alnus rubra* (▲) and *Pseudotsuga menziesii* (△) over time at the (a) Cascade Head (CH), (b) H.J. Andrews (HJA), and (c) Delezene Creek (DC) study sites. Error bars represent standard errors and *n* gives the number of observations in a sample (Note: height was only measured on a subset of trees representing a range of tree sizes at the DC study site).

Table 3 AIC_c model comparisons of selected models (i.e. $\Delta_i \leq 2.00$) for quantifying the effects of intra- and inter–specific interactions on *Pseudotsuga menziesii* relative growth rates over the measurement periods examined (years 6–9, 9–12, and 12–15) in the young stands (CH and HJA)

Site	Y[a]	II[b]	Radius	Model[c]	K[d]	AIC_c[e]	Δ_i[f]	w_i[g]
CH	6–9	**G**	–	Intra-specific	5	−317.9	0.00	0.67
		G	–	Intra-specific, interspecific, intra × interspecific	7	−316.5	1.44	0.32
	9–12	**BE 1***	A_i^{γ}	Inter-specific	5	−505.5	0.00	0.24
		BE 1.5	A_i	Inter-specific	5	−504.6	0.93	0.16
	12–15	**R**	4.5	Intra-specific	5	−537.5	0.00	0.17
		B	4.5	Inter-specific	5	−536.1	1.39	0.09
HJA	6–9	**G**	–	Intra-specific, interspecific, intra × interspecific	7	−99.4	0.00	0.98
	9–12	**L**	3.0	Intra-specific, interspecific, intra × interspecific	7	−213.5	0.00	0.25
		L	4.5	Intra-specific, interspecific, intra × interspecific	7	−213.1	0.34	0.21
	12–15	**BE 2**	A_i	Intra-specific, interspecific, intra × interspecific	7	−329.7	0.00	0.17
		BE 1.5	A_i	Intra-specific, interspecific, intra × interspecific	7	−329.5	0.24	0.15
		BE 1	A_i	Intra-specific, interspecific, intra × interspecific	7	−329.2	0.55	0.13
		B	4.5	Intra-specific	5	−329.1	0.63	0.13
		B	3.0	Intra-specific	5	−328.9	0.80	0.12
		B	4.5	Intra-specific	5	−328.8	0.89	0.11
		L	4.5	Intra-specific, interspecific, intra × interspecific	7	−328.5	1.19	0.10
		B	3.0	Intra-specific, interspecific, intra × interspecific	7	−327.7	1.99	0.06

*Scaling exponent (1.0, 1.5, 2.0).
[γ] Area of influence of focal tree.
[a] Measurement period.
[b] Interaction index (*II*) used to measure intra- and inter–specific interactions (see Table 2).
[c] Parameters included in growth model.
[d] Total number of model parameters including the intercept, variance, and covariance parameters.
[e] Corrected Akaike Information Criterion.
[f] Difference between model AIC_c value and minimum AIC_c value.
[g] Probability of model being the best in a given set.

a relative dominance interaction index (**G** and **W**) were more likely to be the best model in the set (i.e. $\Delta_i < 2$) than those weighting neighbour influence by distance (**B**, **H**, and **R** in Table 2). We found no differences in the ranking of interaction indices selected for predicting relative growth rates when the power spatial correlation structure was removed (data not shown), suggesting that these results are not a consequence of accounting for spatial correlation in these models.

In the young stands, several of the best models for both species contained the neighbourhood interaction index (**BE**) that used the area of influence (A_i) (Tables 3 and 4). Weighting of **BE** for size–asymmetrical interactions was unnecessary as there was no distinguishable difference between the fit of models with the three different scaling exponents, indicating perfect size-symmetry (*sensu* Schwinning & Weiner 1998). Evaluations of appropriate neighbourhood sizes using the central trees in CH and HJA plots indicated that neighbourhoods with a 3.0 m and 4.5 m radius were appropriate in these young stands (Table 5). However, these results should be interpreted cautiously due to the small sample size. The range of neighbourhood sizes used in the mature stand was also appropriate, as all neighbourhood interaction indices included in the set of best models had neighbourhood sizes less than the maximum neighbourhood size employed (≤ 11.5 m) (Tables 6 and 7).

It is interesting to note that there was strong evidence, for both species, that effects of inter–specific interactions were not exclusively additive to effects of intra–specific

Table 4 *AIC_c* model comparisons of selected models for quantifying the effects of intra- and inter–specific interactions on *Alnus rubra* relative growth rates over the measurement periods examined (years 6–9, 9–12, and 12–15) in the young stands (CH and HJA). For definitions of symbols see Table 3

Site	Y	II	Radius	Model	K	*AIC_c*	Δ_i	w_i
CH	6–9	**W**	–	Intra-specific	5	–316.7	0.00	0.33
		W	–	Inter-specific	7	–315.8	0.88	0.21
	9–12	**G**	–	Intra-specific, interspecific, intra × interspecific	7	–360.4	0.00	0.68
	12–15	**L**	3.0	Inter-specific	5	–256.5	0.00	0.24
		L	4.5	Inter-specific	5	–256.1	0.34	0.21
		BE 2.0	A_i	Inter-specific	5	–255.4	1.10	0.14
HJA	6–9	**G**	–	Intra-specific, interspecific, intra × interspecific	7	–94.4	0.00	0.63
		G	–	Intra-specific	5	–93.3	1.09	0.36
	9–12	**G**	–	Intra-specific	5	–144.0	0.00	0.44
	12–15	**L**	3.0	Intra-specific, interspecific, intra × interspecific	7	–105.6	0.00	0.18
		L	4.5	Intra-specific, interspecific, intra × interspecific	7	–105.1	0.50	0.14

Table 5 Evaluations of appropriate neighbourhood sizes for *Pseudotsuga menziesii* and *Alnus rubra* occurring in the plot centres at the CH and HJA sites. For definitions of symbols see Table 3

Species	Site	Y	n^h	II	Radius	K	*AIC_c*	Δ_i	w_i
Pseudotsuga menziesii	CH	12–15	13	**R**	4.5	5	–20.2	0.00	0.33
			13	**R**	3.0	5	–19.4	0.83	0.21
			13	**R**	6.0	5	–19.3	0.97	0.19
			13	**B**	4.5	5	–18.1	2.16	0.10
			13	**B**	3.0	5	–18.0	2.23	0.10
			13	**B**	6.0	5	–17.5	2.69	0.07
	HJA	9–12	12	**L**	4.5	5	–10.6	0.00	0.65
			12	**L**	3.0	5	–8.1	2.49	0.18
			12	**L**	6.0	5	–8.0	2.65	0.17
	HJA	12–15	10	**B**	3.0	5	–3.6	0.00	0.27
			10	**B**	4.5	5	–3.6	0.00	0.27
			10	**B**	6.0	5	–3.0	0.61	0.14
			10	**L**	3.0	5	–2.6	1.03	0.14
			10	**L**	4.5	5	–2.6	1.03	0.15
			10	**L**	6.0	5	2.6	6.18	0.03
Alnus rubra	CH	12–15	14	**L**	3.0	5	–21.3	0.00	0.60
			14	**L**	4.5	5	–20.1	1.20	0.33
			14	**L**	6.0	5	–16.6	4.68	0.07
	HJA	12–15	13	**L**	4.5	5	–8.2	0.00	0.38
			13	**L**	3.0	5	–8.0	0.18	0.36
			13	**L**	6.0	5	–7.6	0.60	0.26

[h] Number of centre trees used in regression.

interactions. Not only did the best models contain the interaction terms (Tables 3, 4, 6, and 7) but, in several cases in the young stands, parameters for intra–specific interactions had a positive sign when predicting on *P. menziesii* relative growth rates (e.g. years 12–15 at CH, Table 3, Intra–specific interaction parameter = 0.018 ± 0.012). These positive parameter estimates may be a function of multicollinearity, i.e. the interactions from *P. menziesii* are less negative relative to interactions from *A. rubra* in the young stands.

INTERACTION DYNAMICS

Alnus rubra

The importance of neighbourhood interactions compared to that of size relative to the population as predictors of relative growth rates varied between the young and mature stands. In general, size relative to the population was a better predictor of *A. rubra* relative growth rates in young stands, as the majority of best

Table 6 AIC_c model comparisons of selected models for quantifying the effects of intra- and inter–specific interactions on *Pseudotsuga menziesii* relative growth rates over the measurement periods (years 30–35, 35–39, 39–43, 43–47, 47–53, 53–56, and 56–68) examined in the mature stand (DC). For definitions of symbols see Table 3

Y	II	Radius	Model	K	AIC_c	Δ_i	w_i
30–35	**H**	4.5	Intra-specific, interspecific, intra × interspecific	6	−1076.8	0.00	0.30
	G	–	Intra-specific, interspecific, intra × interspecific	6	−1076.7	0.11	0.29
	H	3.0	Intra-specific, interspecific, intra × interspecific	6	−1075.8	1.00	0.18
35–39	**H**	9.0	Intra-specific	4	−777.5	0.00	0.54
39–43	**L**	9.0	Intra-specific	4	−593.2	0.00	0.26
	H	9.0	Intra-specific, interspecific, intra × interspecific	6	−593.0	0.20	0.23
	H	7.5	Intra-specific, interspecific, intra × interspecific	6	−591.6	1.57	0.12
43–47	**G**	–	Intra-specific, interspecific, intra × interspecific	6	−560.0	0.00	0.64
47–53	**W**	–	Inter-specific	4	−583.8	0.00	0.40
	W	–	Intra-specific, interspecific, intra × interspecific	6	−583.4	0.41	0.32
	G	–	Intra-specific, interspecific, intra × interspecific	6	−583.1	0.64	0.29
53–56	**W**	–	Inter-specific	4	−560.1	0.00	0.46
56–68	**W**	–	Inter-specific	4	−550.7	0.00	0.70

models used relative dominance interaction indices (Table 4). It is important to note that the high performance of the relative dominance interaction index **W** over the earliest measurement period (years 6–9) at the CH site suggests that population density was also influencing *A. rubra* relative growth rates, whereas the selection of the relative dominance interaction index **G** over the same period at the HJA site suggests that only size determinined growth rates here (Table 4). The positive inter–specific interaction effects on *A. rubra* relative growth rates over years 12–15 at the CH site (e.g. Tables 4, **L** with 3.0 m radius, Inter–specific interaction parameter = 0.037 ± 0.021) and the negative intra- and inter–specific interactions over the same period at the HJA site (e.g. Tables 4, **L** with 3.0 m radius, Intra–specific interaction parameter = −0.017 ± 0.021 and Inter–specific interaction parameter = −0.087 ± 0.015) indicate increased intensity of neighbourhood interactions from other large *A. rubra* at the CH site and from codominants of both species at HJA. These increases coincide with the shift in the nature of interactions from the population to the neighbourhood-level (Table 4).

There was strong evidence that neighbourhood interactions were more important to *A. rubra* relative growth rates in the mature stand as all the best models used neighbourhood interaction indices (Table 7). Similar to the young stands, the importance of neighbourhood interactions in the mature stand was expressed during the periods *A. rubra* occupied codominant and subordinate canopy positions (Fig. 1c).

Pseudotsuga menziesii

In general, neighbourhood interactions were also important for *P. menziesii* relative growth rates in young stands (the majority of best models used neighbourhood interaction indices, Table 3). However, over the earliest measurement period examined (years 6–9) the index using size relative to the population was more important than neighbourhood or population–level interactions (the best models contained the interaction index, **G**, Table 3). In the mature stand, the importance of size relative to the population compared to neighbourhood interactions changed as *P. menziesii* attained a dominant canopy position. During periods where heights of the two species were similar (years 30–43, Fig. 1c), neighbourhood interactions were a better predictor of *P. menziesii* relative growth rates (Table 6). However, once *P. menziesii* had attained a dominant canopy position (years 43–68, Fig. 1c), size relative to the population became a better predictor of relative growth rates, with all of the best models using relative dominance interaction indices (Table 6).

Table 7 AIC_c model comparisons of selected models for quantifying the effects of intra- and inter–specific interactions on *Alnus rubra* relative growth rates over the measurement periods (years 30–35, 35–39, 39–43, 43–47, 47–53, 53–56, and 56–68) examined in the mature stand (DC). For definitions of symbols see Table 3

Y	II	Radius	Model	K	AIC_c	Δ_i	w_i
30–35	**L**	4.5	Intra-specific	4	−1321.6	0.00	0.17
	L	7.5	Intra-specific	4	−1321.6	0.05	0.17
	L	3.0	Intra-specific	4	−1321.6	0.05	0.17
	L	6.0	Intra-specific	4	−1321.5	0.14	0.16
	L	7.5	Intra-specific, interspecific, intra × interspecific	6	−1320.0	1.65	0.08
35–39	**L**	6.0	Intra-specific, interspecific, intra × interspecific	6	−1107.5	0.00	0.72
39–43	**L**	3.0	Intra-specific	4	−1001.0	0.00	0.16
	L	6.0	Intra-specific	4	−1000.4	0.56	0.12
	L	9.0	Intra-specific	4	−1000.2	0.76	0.11
	L	7.5	Intra-specific	4	−1000.0	0.97	0.10
	L	9.0	Intra-specific	4	−999.9	1.10	0.09
	L	7.5	Intra-specific, interspecific, intra × interspecific	6	−999.6	1.38	0.08
43–47	**L**	4.5	Intra-specific, interspecific, intra × interspecific	6	−981.7	0.00	0.29
	L	6.0	Intra-specific, interspecific, intra × interspecific	6	−980.7	0.99	0.18
	L	4.5	Intra-specific	4	−979.7	1.94	0.11
47–53	**L**	6.0	Intra-specific	4	−927.1	0.00	0.17
	L	4.5	Intra-specific	4	−926.7	0.38	0.14
	L	7.5	Intra-specific	4	−925.4	1.71	0.07
53–56	**L**	7.5	Inter-specific	4	−886.3	0.00	0.12
	L	6.0	Inter-specific	4	−885.5	0.82	0.08
	L	4.5	Inter-specific	4	−885.1	1.24	0.06
	L	3.0	Intra-specific	4	−884.5	1.80	0.05
	L	9.0	Inter-specific	4	−884.3	1.99	0.04
56–68	**L**	11.5	Inter-specific	4	−541.7	0.00	0.29
	L	11.5	Intra-specific, interspecific, intra × interspecific	6	−541.4	0.33	0.25

NEIGHBOURHOOD SIZE

The optimal extent of neighbourhoods for prediction of focal tree growth increased over time (stand age and/or tree size) for both species (Tables 3, 4, 6, and 7). For example, neighbourhood size resulting in best models for *P. menziesii* in the mature stand at age 30 was roughly 4.5 m (Table 6), increasing to 9.0 m at age 35 and over (Table 6). In general, in the mature stand good models for predicting *A. rubra* relative growth rates over the earlier years (30–43) included neighbourhood interaction indices with radii ranging from 3.0 to 9.0 m (Table 7) but, by age 56 and over the neighbourhood size had increased to 11.5 m for all such models (Table 7). However, during some measurement periods, the fits of models using different neighbourhood sizes were very similar, such as for years 9–12 for *P. menziesii* at the HJA site (Table 3). This suggests there was no distinguishable difference between neighbourhood interactions at different scales during that particular interval.

ALTERNATIVE EXPLANATIONS

We investigated alternative explanations for the relatively poor performance of models incorporating neighbourhood interactions as compared to models with relative dominance measures, including whether performance of the interaction indices was influenced by a mathematical artefact (i.e. using diameter vs. squared diameter, P. Couteron, personal communication) or the use of inappropriate neighbourhood sizes (Burton 1993).

Two additional interaction indices, **H′** and **L′**, were evaluated to test for a mathematical artefact due to using squared diameters (in **G** and **W**) vs. diameters (in **H** and **L**). The **H′** and **L′** indices were calculated in a similar fashion as indices **H** and **L**, but using squared diameters. With the exception of *A. rubra* in the mature stand, there was no evidence that models containing **H′** and **L′** became the best models in the set, suggesting that the mathematical transformation is not influencing our results. However, the prevalence of **L′** in the majority of best models for predicting *A. rubra* relative growth rates

Table 8 AIC_c model comparisons of selected best models using additional interaction indices for quantifying the effects of intra- and inter–specific interactions on *Alnus rubra* relative growth rates over the measurement periods examined in the mature stand (DC). **L′** was calculated in a similar fashion as index **L** but using squared diameters. For additional definitions of symbols see Table 3

Y	II	Radius	Model	K	AIC_c	Δ_i	w_i
30–35	**L′**	4.5	Intra-specific	4	−1325.9	0.00	0.27
	L′	7.5	Intra-specific	4	−1324.2	1.68	0.12
35–39	**L**	6.0	Intra-specific, interspecific, intra-X interspecific	6	−1107.5	0.00	0.22
	L′	6.0	Intra-specific, interspecific, intra-X interspecific	6	−1107.3	0.20	0.20
	L′	4.5	Intra-specific	4	−1107.1	0.39	0.19
	L′	6.0	Intra-specific	4	−1106.2	1.30	0.12
39–43	**L′**	3.0	Intra-specific	4	−1004.8	0.00	0.25
	L′	6.0	Intra-specific, interspecific, intra-X interspecific	6	−1003.3	1.50	0.12
43–47	**L**	4.5	Intra-specific, interspecific, intra-X interspecific	6	−981.7	0.00	0.17
	L	6.0	Intra-specific, interspecific, intra-X interspecific	6	−980.7	0.99	0.10
	L′	4.5	Intra-specific, interspecific, intra-X interspecific	6	−980.4	1.24	0.09
	L′	4.5	Intra-specific	4	−979.7	1.93	0.06
	L	4.5	Intra-specific	4	−979.7	1.94	0.06
	L′	6.0	Intra-specific, interspecific, intra-X interspecific	6	−979.2	1.97	0.06
47–53	**L′**	6.0	Intra-specific	4	−928.9	0.00	0.15
	L′	7.5	Intra-specific	4	−928.4	0.51	0.12
	L′	4.5	Intra-specific	4	−928.2	0.77	0.10
	L	6.0	Intra-specific	4	−927.0	1.84	0.06
	L′	9.0	Intra-specific	4	−927.3	1.91	0.06
53–56	**L**	7.5	Inter-specific	4	−886.3	0.00	0.07
	L′	6.0	Inter-specific	4	−886.2	0.14	0.07
	L	6.0	Inter-specific	4	−885.5	0.82	0.05
	L′	4.5	Inter-specific	4	−885.5	0.82	0.05
	L′	3.0	Intra-specific	4	−885.5	0.87	0.05
	L	4.5	Inter-specific	4	−885.1	1.24	0.04
	L	3.0	Intra-specific	4	−884.5	1.80	0.03
	L	9.0	Inter-specific	4	−884.3	1.99	0.03
56–68	**L′**	11.5	Intra-specific, interspecific, intra-X interspecific	6	−542.5	0.00	0.24
	L	11.5	Inter-specific	4	−541.7	0.77	0.16
	L	11.5	Intra-specific, interspecific, intra-X interspecific	6	−541.4	1.09	0.14
	L′	11.5	Inter-specific	4	−539.6	1.53	0.11

in the mature stand suggests that weighting the relative dominance of the focal tree improved our ability to predict relative growth rates (Table 8).

Results using the central trees in the CH and HJA plots had consistently indicated that the neighbourhood size was appropriate (see above). However, we also plotted the residuals from a variety of models with different neighbourhood sizes over individual tree size and found no detectable pattern (data not shown).

Discussion

The results from the three study sites support the relative dominance hypothesis, which states that the importance (*sensu* Weldon & Slauson 1986) of neighbourhood interactions varies with competitive status (i.e. size relative to the population). The differences in importance of neighbourhood interactions observed in this study appeared to be linked to changes in the relative dominance in height of *A. rubra* and *P. menziesii* in the young and mature stands. When tree–tree interactions were occurring, neighbourhood interactions were a better predictor of individual tree growth for species with subordinate and codominant positions (i.e. heights) in the population, whereas expressions of relative dominance (i.e. tree size relative to the population) were better predictors of individual tree growth for species with dominant heights. The results of this study suggest that interactions were perfectly size-symmetric (*sensu* Schwinning & Weiner 1998), thus linking the size of a tree relative to the population to its resource capturing capacity (Ford & Diggle 1981; Miller & Werner 1987; Goldberg 1990). Obviously, the relationships predicted by the relative dominance hypothesis only apply to conditions in which plants are interacting and will not hold true in low density stands of small plants, such as those observed over the earliest measurement period in the young stands.

While other studies investigating species interactions have been limited to investigations of shorter time periods, their findings also support the relative dominance hypothesis. For example, in another conifer/broadleaf mixture, the taller tree species, *Liquidambar styraciflua*, had a significant effect on the resources available to the subordinate species, *Pinus taeda*, whereas *P. taeda* did not significantly affect the resources available for *L. styraciflua* (Zutter *et al*. 1997). These findings suggest that the size of the dominant species, *L. styraciflua*, relative to the population was the most important factor determining its growth, whereas the growth of the subordinate species, *P. taeda*, was strongly affected by the neighbouring *L. stryraciflua*. Similar results were also found in a removal experiment of herbaceous and grassy species, in which the growth of the tallest species, *Plantago lanceolata* and *Sanguisorba minor*, were not significantly affected by competition from the subordinate species, *Briza media*, *Carex caryophllea* and *Lotus corniculatus* (McLellan *et al*. 1997). In addition, longer-term studies of neighbourhood competition have also noted that individual tree sizes, rather than neighbourhood conditions, become better predictors of growth as over time the height of the focal species increasingly exceeds the height of the neighbouring vegetation (e.g. Wagner & Radosevich 1998).

Studies that investigated aspects of this phenomenon in monocultures also support the relative dominance hypothesis and suggest that this hypothesis may also apply to individuals within a population. For example, Cannell *et al*. (1984) noted a weak relationship between measures of neighbourhood interactions and the relative growth rates of individuals with dominant heights in monocultures of *Picea sitchensis* and *Pinus contorta*. Competitive status, as quantified by height relative to the population, was able to explain significantly more variation in the growth of dominant individuals than measures of neighbourhood interactions (Cannell *et al*. 1984). Also, an examination of size hierarchy development in monocultures of *Tagetes patula* found that the dominant individuals in the population all shared higher relative growth rates (Ford 1975). On the other hand, there was a great deal of variation in relative growth rates among subordinate individuals (Ford 1975). These independent findings from a variety of species and study conditions all fit within the predictions of the relative dominance hypothesis, confirming that dominant plants were less affected by neighbourhood interactions than subordinate individuals.

The strong relationships between relative dominance and the growth of dominant individuals observed in this and other studies are presumably due to the greater access to available resources for a plant of a dominant size, i.e. due to a competitive advantage. In this study, the inherent height growth patterns of *A. rubra* and *P. menziesii* resulted in each species having a height advantage at a different stage of development. Within the constraints of inherent growth patterns, trees with greater heights (i.e. a size advantage) at a given point in stand development appear to have greater access to available resources (Connolly & Wayne 1996) and were thus less affected by neighbourhood interactions. However, the interactions were size-symmetrical (*sensu* Schwinning & Weiner 1998), indicating that the differences in performance were directly proportional to size differences. This pattern was found for both species and in both the young and mature stands.

It is important to recognize the limitations of the methods used in this study for testing the relative dominance hypothesis (e.g. Thomas & Weiner 1989). At the CH and HJA study sites, the relative dominance interaction indices may have been performing similarly to a neighbourhood interaction index due to the small plot sizes. However, the strong relationships between tree growth and neighbourhood interaction indices using 3.0 and 4.5 m neighbourhoods in several of the measurement periods, along with the results of the tests using the central trees at each site, suggest that interactions with first order neighbours were most important. In addition, the mean crown diameter estimates for these sites over the periods examined (2.6, 3.8, and 4.3 m at years 6, 9, and 12, respectively, at the CH study site and 1.6, 3.3, and 3.9 m at years 6, 9, and 12, respectively, at the HJA study site) also suggest that interactions were occurring primarily with direct neighbours. For the DC study site, the lack of a complete census of tree heights limits our ability to reach unequivocal conclusions on their relative dominance although the similarity between the trends in D and height (Fig. 1c) over time suggest that similar patters are also valid in this stand (Fig. 1c).

As with limitations due to neighbourhood sizes, the use of inappropriate measures of neighbourhood interactions (Thomas & Weiner 1989) could not explain our results. We used a variety of measures and statistically selected the best fitting models. Also, while the layout of the studies were not optimal for testing the importance of including inter–tree distances in interaction indices, the significance of the strong relationships between neighbourhood interactions and tree growth in the majority of measurement periods suggested that we included the most appropriate measures of neighbourhood interactions. We therefore believe that relative dominance, expressed in tree height, is likely to drive the trends observed.

Conclusions

Results from three different mixed species stands supported the relative dominance hypothesis and demonstrate the influence of relative dominance on the importance of neighbourhood interactions in forest communities. While other authors have recognized the importance of accounting for the social status of individual trees when predicting growth (Tomé & Burkhart 1989; Dhôte 1994), the results of our study provide a framework for future work evaluating the relationship between relative dominance and the importance of neighbourhood competition. Although a two-species mixture was used in this study, it is likely that the relationships predicted by the relative dominance hypothesis are appropriate for individuals within a population and for communities composed of numerous species. The documentation of similar trends in perennial plant communities, suggests that the application of this hypothesis may not be restricted to interactions between tree species. The relationships between relative dominance in height and neighbourhood interactions described here are presumably due to the importance of competition for light, but alternative measures, such as rooting depth (e.g. Manning & Barbour 1988), may be needed in environments in which competition for below-ground resources is more important.

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