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## Do position and species identity of neighbours matter in 8–15-year-old post harvest mesic stands in the boreal mixedwood?

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### ABSTRACT

Neighbourhood competition indices (NCI), where position and species identity of neighbours are known, have been used to investigate growth and competitive interactions among adult trees. In this study, we used NCI in 8–15-year-old stands following clear-cutting in a boreal mixedwood forest of eastern Canada to improve our understanding of early successional forest dynamics. Trees of increasing diameter from the center ( $\geq 1$  cm) to the edge ( $\geq 5$  cm) were mapped in twenty-five circular 450 m<sup>2</sup> plots. Target trees (DBH  $\geq 1$  cm) were sampled in plot center to determine their annual radial stem growth. For each species, we compared a set of growth models using either a spatially explicit NCI or a non-spatial competition index. Both types of indices estimated a species-specific competition coefficient for each pair of competitor–target species. NCI were selected as the best competition model for all target species although differences in variance explained relative to the non-spatial index were small. This likely indicates that competition occurs at the local level but that the high density and the relative uniformity of these young stands creates similar neighbourhoods for most trees in a given stand. The effective neighbourhood radius for competitors varied among species and was smaller for shade tolerant species. Intraspecific neighbours were the strongest competitors for most species. Aspen (*Populus tremuloides*) was a weak competitor for all species as opposed to balsam fir (*Abies balsamea*) which was a strong competitor in all cases. These results are in contradiction with some widely used forest policies in North America (e.g. free-to-grow standards) that consider broadleaf species, such as aspen, as the strongest competitors. For these early successional forests, the decision regarding the use of spatial or non-spatial competition indices should rest on the intended use. For even-age management, spatial indices might not justify their use in high-density stands but they are needed for the simulation of novel harvest techniques creating complex stand structure.

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### 1. Introduction

In boreal mixedwood forests, naturally regenerating post-harvest stands originate from seedlings and saplings left from the previous forest undergrowth (Haeussler and Bergeron, 2004) or emerge from seed sources (Tierney and Fahey, 1998) as well as root and stump sprouts (Frey et al., 2003). These multiple sources create dense even-sized pioneer stands that are not necessarily representative of the future forest. The prediction of the future composition

of these stands from regeneration surveys executed shortly after harvests is often inaccurate due to the lack of understanding of species-specific growth and mortality dynamics (Ruel et al., 1998; Dubois et al., 2006). These dynamics are controlled in part by plant interactions (Tilman, 1988; Woods, 2000) and, although the net outcome of these interactions can range from negative (competition) to positive (facilitation), a net negative balance is usually observed (Callaway and Walker, 1997).

Consequently, numerous indices, spatially explicit or not, have been developed to estimate the effect of competition on tree growth. Spatially explicit indices are often considered better growth predictors (Larocque, 2002; Stadt et al., 2007), but similar predictive power for both types of indices is often found when stands exhibit a uniform density (Lorimer, 1983; Filipescu and Comeau, 2007). Most of these indices are not mechanistic and do not allow for the partitioning of above- (light) and below-ground (nutrients and water) competition. Recent studies that included

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explicit calculation of the shading caused by neighbours to competition measurements resulted in an improved predictive power of the models (Canham et al., 2004; Stadt et al., 2007; Coates et al., 2009). The calculation of shading requires species-specific knowledge of crown allometry and shading properties not readily available for most species. In the northern hemisphere, competitors located to the south of a target tree block more light due to the sun trajectory and could be stronger competitors for light (Liefers et al., 2002). The use of a simple function modifying the competitive effect of competitors as a function of their cardinal direction could serve as a surrogate to shading calculation when information necessary for the latter are lacking.

It has long been hypothesized that the identity of neighbouring species is an important factor in the characterization of their competitive effect (Bella, 1971). While the debate around species functional equivalence is still active on theoretical grounds (e.g. Hubbell, 2005; Pueyo et al., 2007), studies that have looked for differences in competitive effect found no compelling evidence for it among tropical species (Uriarte et al., 2004), but at times found striking differences among temperate and boreal species (Canham et al., 2006; Papaik and Canham, 2006). It remains unclear if these observed differences also exist in young even-age stands and how this could affect measures of competition and their predictive power. Moreover, several recent studies have shown that tree species can modify important ecological traits as they grow (Claveau et al., 2002; Delagrangue et al., 2004; Valladares and Niinemets, 2008), which make extrapolating ecological traits from one developmental stage to another difficult. It is therefore likely that the competitive effects among tree species can also change in the different developmental stage of the stand.

The last few decades of industrial forestry have created a large quantity of regenerating young stands in the boreal mixedwood landscape for which an understanding of the competition dynamics among pioneer species is lacking. On a management perspective, this knowledge is needed to evaluate present competition indices and, if needed, develop new ones that would allow better growth predictions. Indeed, Free-To-Grow standards (FTG) now in use in many places throughout North America to assess competition intensity in regenerating stands have been shown to lack precision (Liefers et al., 2007). Efficient tree growth models are needed for the development of new forest simulators to evaluate the effects of present and new logging techniques on future stands' structure and composition. This project aims at developing tree growth models and their competition sub-parts for four widespread tree species of the boreal mixedwood forest (hereafter referred to as target species): pin cherry (*Prunus pensylvanica*), aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*) and balsam fir (*Abies balsamea*). To evaluate the efficacy of the models, we used information theoretic methods to: (1) compare non-spatial and spatial competition indices to predict tree growth in young stands, (2) evaluate whether the cardinal direction of neighbours changes their competitive effect, and (3) assess whether competitive effects vary with species identity. The present study brings much needed insight into the functioning of dense young regenerating boreal mixedwoods using advanced neighbourhood dynamics and information theory methods, which was never attempted before.

## 2. Methods

### 2.1. Study area and sites

Our research was conducted in the vicinity of La Tuque, Quebec, Canada (47°27'N, 72°47'W) in the balsam fir - yellow birch bioclimatic domain of the boreal mixedwood forest zone (Saucier et al., 2009). The landscape is dominated by low hills with thick glacial

**Table 1**

Sample size (*n*), species shade tolerance index (*I*) where 9 is very intolerant and 1 very tolerant (Humbert et al., 2007), mean and maximum DBH (in cm) of each target species.

Species	<i>n</i>	<i>I</i>	Mean DBH	Maximum DBH
Pin cherry	318	9	1.8	6
Aspen	442	9	3	7.5
Paper birch	367	7	2.7	7.7
Balsam fir	328	3	3.4	12

tills (Robitaille and Saucier, 1998). The mean annual temperature is 3.4 °C and the mean annual precipitation is 940 mm (25% falling as snow) (La Tuque weather station, Environment Canada).

We sampled 25 sites based on the following criteria. Each site was clearcut 8–15 years prior to the study (between 1993 and 1999), was representative of the dominant forest composition of the region and had to contain individuals of at least one of the four target species. The sites were characterised by mesic conditions, thick soil deposits of average textural class, and the potential to develop mixedwood canopies at maturity. Stands where pre-commercial thinning had occurred were excluded, as were plantations. Moreover, sample sites had to present a homogeneous topography and be devoid of residual trees with DBH >15 cm. Plots were located at 40 m perpendicular from forest roads to minimize edge effects.

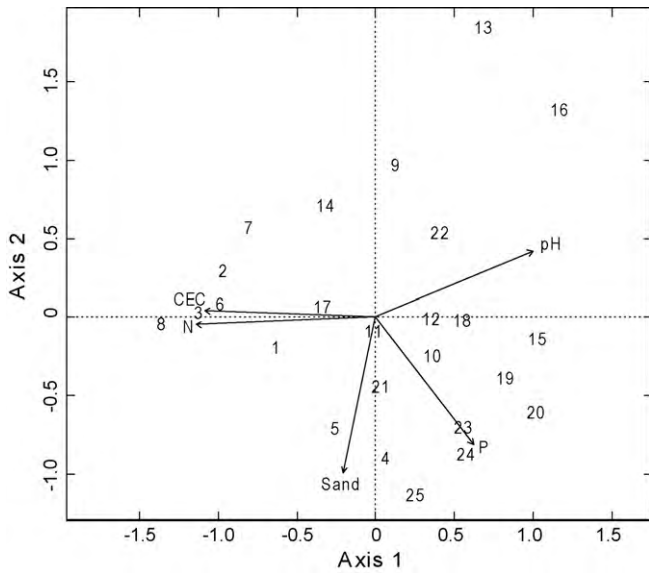
### 2.2. Data collection

All plots were sampled during the 2007 and 2008 summers. The exact position of all individuals of large shrub and tree species (hereafter only referred to as trees) with a diameter at breast height (1.30 m, DBH) ≥ 5 cm were identified and mapped in a 12 m radius (species, DBH, azimuth and distance from plot center). The same measurements were made for trees with a DBH ≥ 3 cm within a 9 m radius and within a 7 m radius for trees with DBH ≥ 1 cm. DBH was measured to the closest mm (averaged over two orthogonal measurements), azimuth was determined to 0.5° precision using a Suunto-14D compass (Vantaa, Finland) affixed to a monopod located at plot center. Given the high density of the stands, distance to center was measured to a 0.1 m precision with a Vertex III ultrasound device (Haglöf Sweden AB, Langsele, Sweden).

Up to 20 individuals of each of the four target species with DBH ≥ 1 cm located within 5 m of the plot center were sampled for growth analysis at each plot using three steps (Table 1). (1) Lines were drawn on the ground from plot center in each cardinal direction. (2) For each cardinal direction the five individuals closest to the line were selected. (3) When fewer than five trees were available in a given cardinal direction, more trees were sampled in the next cardinal direction turning clockwise until the sample size was reached or all available trees for a given species on that plot had been selected.

The crown width of each target tree was measured in two orthogonal directions and averaged. Target trees were cut 10 cm above ground and disks were collected from stumps. Disks were oven dried (50 °C for 48 h) and sanded to 320 grit. Using a tree-ring measuring table (0.01 mm precision, Velmex Inc., Bloomfield, NY), annual radial growth was assessed by averaging tree-ring width measured in two directions separated by 90–180°. Average yearly growth of the four last complete years of growth, ignoring the last incomplete ring, was used for analysis.

On each plot, composite mineral soil samples were taken at 3 m from plot center in the four cardinal directions, each consisting of three combined samples taken 1 m apart, 10–20 cm beneath the organic layer. For each sample, pH, extractable N and P, cation exchange capacity (CEC) and soil texture (fractions of sand, silt and



**Fig. 1.** Principal component analysis (PCA) of the soil characteristics of the 25 sample plots (numbers). Axes 1 and 2 explained 53% and 21% of the variance, respectively. “Sand”: % of sand content; “N”: N concentration; “P”: P concentration; “CEC”: cation exchange capacity. Plot scores on axis 1 were used as an environmental gradient in growth models.

clay) were evaluated following established protocols (McKeague, 1978; Mehlich, 1984; Carter, 1993).

2.3. Data analysis

2.3.1. Growth models

Our analysis is based on the models developed by Canham et al. (2006) and Papaik and Canham (2006). For each species, analyses were conducted to determine the best radial growth (hereafter, growth) model in mm/year from a set of alternate models. The models predict growth as a function of potential growth (PotG) affected by a combination of three scalar components (values between 0 and 1). The three components are: target tree size effect, plot effect and crowding effect (Eq. (1)) (Canham et al., 2006; Papaik and Canham, 2006).

$$\text{growth} = \text{PotG} \times \text{size effect} \times \text{plot effect} \times \text{crowding effect} \quad (1)$$

PotG is a parameter estimated by the analysis and corresponds to the average growth of a tree of optimal size, growing in the absence of competition in the best plot conditions (Canham et al., 2004).

2.3.2. Size effect

The empirical effect of target tree size (DBH) on potential growth was modelled using a lognormal function (Eq. (2)):

$$\text{size effect} = e^{-0.5(\ln(\text{DBH})/\delta/\sigma)^2} \quad (2)$$

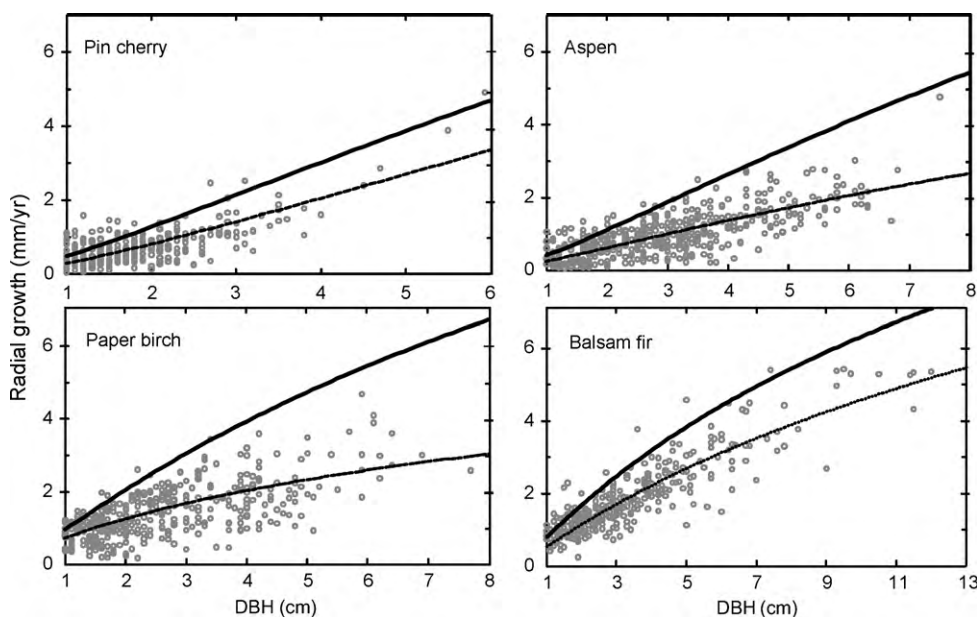
where  $\delta$  is the estimated DBH at which PotG occurs and  $\sigma$  is the parameter that determines the breadth of the function.  $\delta$  and  $\sigma$  are parameters estimated by the analysis. Over the data range, this function can monotonically increase (when  $\delta >$  maximum DBH) or decrease (when  $\delta <$  minimum DBH) or have a single hump and be skewed to the left (when  $\delta$  is within the DBH range).

2.3.3. Plot effect

We used principal component analysis (PCA) to summarise soil differences across plots within the MASS package of the R statistical software (R Foundation for Statistical Computing, Vienna, Austria). Plot pH, CEC, % sand content and log-transformed [P] and [N] were

**Table 2** Difference in AICc ( $\Delta\text{AIC}_c$ ) and of alternate growth models with respect to the best model for each target species, and  $R^2$  of each model.  $\Delta\text{AIC}_c$  (0 by definition) and  $R^2$  of the best models are highlighted in bold. Models from left to right are the size only, the size effect + plot effect model and size effect + plot effect + crowding effect models varying in crowding effect component where “BA” is the stand basal area, “NCl” is the neighbourhood crowding index, “NCl<sub>cd</sub>” is the NCI including the cardinal direction of neighbours, “equi” is the equivalent competitor model and “full” is the competition model assigning different competitive effects to each neighbouring species. Akaike weights ( $\omega_i$ ) are also presented for the three “full” competition models ( $\omega_i < 0.001$  for all other models).

Species	Size only		+Plot		+Crowding		NCl <sub>cd</sub> (equi)		NCl (equi)		BA (full)		NCl (full)				
	$\Delta\text{AIC}_c$	$R^2$	$\Delta\text{AIC}_c$	$R^2$	$\Delta\text{AIC}_c$	$R^2$	$\Delta\text{AIC}_c$	$R^2$	$\Delta\text{AIC}_c$	$R^2$	$\Delta\text{AIC}_c$	$\omega_i$	$\Delta\text{AIC}_c$	$\omega_i$	$R^2$		
Pin cherry	37.2	0.541	23.9	0.572	67.1	0.501	23.3	0.6	18.3	0.601	5.8	<0.001	13.5	0.645	0	~1	<b>0.653</b>
Aspen	165.3	0.543	122.7	0.589	34.2	0.673	35.2	0.683	25.6	0.688	9.7	0.008	11.3	0.004	0	0.989	<b>0.72</b>
Paper birch	210.7	0.448	168.1	0.514	153.3	0.538	79.3	0.634	74	0.635	9.8	0.007	5.7	0.708	0	<b>0.939</b>	<b>0.71</b>
Balsam fir	50.9	0.778	45	0.784	46.4	0.784	41.3	0.796	30.6	0.8	40	<0.001	15.7	0.821	0	~1	<b>0.824</b>



**Fig. 2.** Radial growth as a function of target tree DBH for four species. Solid lines are predicted growth rates from the best model when environmental condition are optimal and without competition. Dashed lines are predicted growth rates from the ‘size-only’ model.

used as inputs in the PCA. Plot scores on the first PCA axis were used to represent an environmental gradient. We compared models with or without the effect of the environmental gradient on growth to determine if such an effect existed (Eq. (3), Canham et al., 2006; Papaik and Canham, 2006):

$$\text{plot effect} = e^{-0.5(\text{axis}_p - K_0/K_b)^2} \quad (3)$$

where  $\text{axis}_p$  is the plot score on the first axis of the PCA,  $K_0$  is the estimated position along the gradient where maximum growth occurs and  $K_b$  is the estimated breadth of the function. This function can produce sigmoid curves or a Gaussian distribution depending on the parameter values.

### 2.3.4. Crowding effect

The effect of increasing competition, as measured by a competition index, is assumed to decrease the growth of target trees following a negative exponential function (Eq. (4)):

$$\text{crowding effect} = e^{-C \times (\text{competition index})} \quad (4)$$

where  $C$  is a parameter estimated by the analysis that determines the steepness of the decline in growth with increasing competition. Parameter  $C$  is dependent on competition scale which itself depends on species-specific parameters estimate ( $\alpha$  and  $\beta$ , see below) and, therefore, cannot be compared between species (Coates et al., 2009).

### 2.3.5. Competition models

Models using two spatial and one non-spatial competition indices were then compared. The first two models were the spatially explicit NCI model (NCI, Eq. (5)) developed by Canham et al. (2004) and our modified version that included the effect of the cardinal direction of neighbours (NCI<sub>cd</sub>, Eq. (6)). For both these NCI models, the total neighbourhood competitive effect is measured by summing the ratio of the effect of DBH to distance of the  $j$  individuals of each of  $i$  species (or group of species) within a fraction “ $R$ ” of the potential neighbourhood.  $R$  is an estimated parameter that determines the fraction of the potential neighbourhood affecting growth (the “effective neighbourhood”). This potential neighbour-

hood consist of a 7 m radius area, centered on the target tree. It includes any neighbour trees fitting a defined size limit which increases with distance from the center (DBH  $\geq 1$  cm within the first 2 m radii, DBH  $\geq 3$  cm neighbours within 4 m and DBH  $\geq 5$  cm within 7 m). The size of the potential neighbourhood is the maximum allowed by our sampling design. The effect of size and distance of neighbours are determined by the  $\alpha$  and  $\beta$  exponents respectively, both estimated by the analysis (Canham et al., 2004).  $\lambda_i$  is described below.

$$\text{NCI} = \sum_{i=1}^s \sum_{j=1}^n \lambda_i \frac{(\text{DBH}_{ij})^\alpha}{(\text{distance}_{ij})^\beta} \quad (5)$$

NCI<sub>cd</sub> (Eq. (6)) included a sinusoidal function that estimated the variation of neighbour competition effect depending on the cardinal direction from the target tree:

$$\text{NCI}_{cd} = \frac{\sum_{i=1}^s \sum_{j=1}^n \lambda_i ((\sin(A_{ij} + \varphi) + 1 + \nu)/(2 + \nu)) (\text{DBH}_{ij})^\alpha}{(\text{distance}_{ij})^\beta} \quad (6)$$

where  $A_{ij}$  is a neighbour cardinal direction (in radians) relative to north, and  $(\varphi + \pi/2)$  is the cardinal direction where maximum competition occurs (sine function = 1). Parameter  $\nu$  determines the minimal value that occurs at the opposite ( $180^\circ$ ) of  $(\varphi + \pi/2)$ . Function values are symmetric at  $(\varphi + \pi/2) \pm A$ .

Stand basal area (BA, Eq. (7)) is a non-spatial competition index that sums the squared DBH of all trees (DBH > 1 cm) within a 7 m radius from plot center. BA was chosen among many non-spatial competition indices as it is routinely gathered in forest surveys. It was also found to be among the best competition model to predict tree growth of mature aspen and paper birch (Stadt et al., 2007).

$$\text{BA} = \sum_{i=1}^s \sum_{j=1}^n \lambda_i (\text{DBH}_{ij})^2 \quad (7)$$

For each competition model, we also tested for differences in competitive effect among species or groups of species with the addition of one species-specific competition coefficient ( $\lambda_i$ ) per species or group of species  $i$  (full competitors model) and compared

that to another model where the effect of all neighbour species was considered equal ( $\lambda$  fixed to 1, equivalent competitors model). Six  $\lambda$ 's were included in the full model, one for each of the four target species, and the remaining species grouped under "other conifers" (4 species) or "other broadleaves" (10 species) (Annex A). This was done because most species, except for the target species, were rare and their effects could not be estimated individually. To facilitate the comparison between competitive effects of species in the full model,  $\lambda_i$  values were rescaled as a fraction of the strongest competitive species or group  $i$  (Canham et al., 2004).

#### 2.4. Parameter estimations and model evaluations

Model parameter values and asymptotic 2-unit support intervals (SI) were estimated using simulated annealing (Goffe et al., 1994). This was performed using software specifically written for this study with Delphi 6 for Windows (Borland Software Corporation, Cupertino, CA). For each species, models were compared using Akaike information criterion corrected for small sample size ( $AIC_c$ , Burnham and Anderson, 2002). A smaller  $AIC_c$  indicates a model that is better supported by the data. The absolute difference between  $AIC_c$  values ( $\Delta AIC_c$ ) of competing models is a relative measure of support of the model by the empirical data (Burnham and Anderson, 2002). We also computed Akaike weight ( $\omega_i$ ) for alternate models using  $AIC_c$ :

$$\omega_i = \frac{e^{-0.5\Delta_i}}{\sum_{r=1}^R e^{-0.5\Delta_r}}$$

where  $\Delta_i$  is  $\Delta AIC_c$  between the best model and the  $i$ th model and  $R$  is the number of models used in the analysis. Akaike weights are measures of the relative strength of evidence for competing models that can be interpreted as the probability of that model being selected best if analysis were repeated using independent samples from the same population (Burnham and Anderson, 2002).

Lower and upper SI were determined for each parameter by varying parameter values up and down while keeping all other parameters constant until global  $AIC_c$  for the model had changed by two units (Edwards, 1992). To evaluate model performance two goodness of fit measures were used: (1) the slope of the linear regression between predicted and observed radial growth with a zero intercept was used as a measure of bias, and (2)  $R^2 = 1 - (sse/sst)$  was used to calculate the coefficient of determination. Residuals were assumed to be normally distributed and this was incorporated in the analysis by estimating an additional parameter (Canham et al., 2004).

### 3. Results

#### 3.1. Environmental gradient

Plot pH, CEC, % and content and log-transformed [P] and [N] were used as inputs in the PCA to order our plots along an environmental gradient using soil factors known to influence tree growth (Brais et al., 1996; Pinno et al., 2009) (Fig. 1). The first axis of the PCA was positively associated with pH and negatively with [N] and CEC while containing 53% of the total variance. Plot scores on axis 1 were then used as an environmental gradient in growth models. Stand density was not a function of plot scores on axis 1 (linear regression,  $p = 0.22$ ) so plot and crowding effects were considered independent.

#### 3.2. Model evaluation

All models produced unbiased estimates of growth (slope of predicted vs. observed growth =  $1 \pm 0.005$ ). For all species, the best

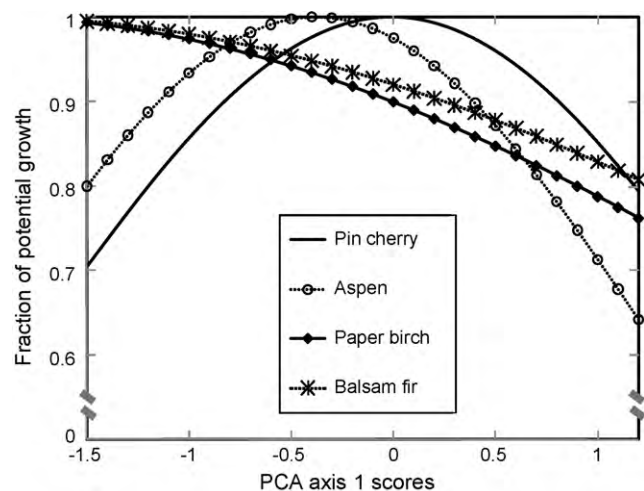
growth model included size, plot, and crowding effects ( $\omega_i \geq 0.939$ ) and explained a substantial part of the variance ( $R^2 = 0.653\text{--}0.824$  depending on target species, Table 2). NCI was a better competition model than the  $NCI_{cd}$  for all species ( $\Delta AIC_c \geq 5.7$ ). Moreover, differences in competitive effects of neighbours due to their cardinal direction as estimated with  $NCI_{cd}$  were always low (<2%) suggesting a weak effect, if any. The NCI was also a better competition model than the simpler BA model ( $\Delta AIC_c \geq 5.8$ ). The differences in predictive power between these models were small for all species ( $\Delta R^2 \leq 0.032$ ) and correlations between their respective predicted growths varied among target species from 0.971 to 0.985. The slope (0.969–1.054) and the intercept (–0.049 to 0.056) of the orthogonal regressions also suggest that growth predicted by both models were similar, although long term impact on simulations are unknown. In all cases, full competition models that allowed different competitive effects for each neighbouring tree species were a better fit than the equivalent competitor models ( $\Delta AIC_c \geq 18.3$ , Table 2).

#### 3.3. Size effect

For all tree species, the best model predicted a monotonic increase in potential growth with increasing tree size over our data range (Fig. 2). All target trees save for a few exceptions had a DBH < 10 cm which is under the reported size where maximum PotG occurs for most species (Uriarte et al., 2004; Canham et al., 2006; Papaik and Canham, 2006; Coates et al., 2009). Due to our small size range, estimates for PotG (Eq. (1)) and  $\delta$  (Eq. (2)) were above 17 mm/year and 120 cm respectively for all species and likely not representative of "true" values. Therefore, size dependant growth curves should not be extrapolated much beyond the sampled size range (Fig. 2).

#### 3.4. Plot effect

For all species, the best model included a plot effect, as measured by plot scores on axis 1 of the PCA. The maximum estimated potential growth for paper birch and balsam fir occurred at the end of the gradient with higher [N] and CEC and declined by 24 and 19% respectively at the opposite end. Maximum potential growth for aspen and pin cherry occurred towards the middle of the gradient with respective maximum reduction of their potential growth of 36 and 30% (Fig. 3).



**Fig. 3.** Fraction of the predicted radial growth (determined by tree size and species) as a function of plot scores (axis 1 of the PCA, Fig. 1) as estimated by the best model for each species. Higher CEC and [N] and more acidic soils are associated with negative axis 1 scores.

**Table 3**

Estimated parameter values for the best model of each species. SI (*italic*) is the 2 AICc units asymptotic support interval for each parameter.

Target species	R	$\alpha$	$\beta$	C	$K_1$	$K_2$
Pin cherry	6.48	1.02	0.28	0.8	-0.01	1.78
<i>SI</i>	<i>6.41–6.54</i>	<i>1.01–1.04</i>	<i>0.28–0.37</i>	<i>0.7–0.9</i>	<i>-0.01–0.04</i>	<i>1.76–1.9</i>
Aspen	7	0.54	0	0.11	-0.38	1.68
<i>SI</i>	<i>6.95–7</i>	<i>0.57–0.55</i>	<i>0–0</i>	<i>0.01–0.21</i>	<i>-0.39–-0.38</i>	<i>0.66–1.74</i>
Paper birch	4.82	1.53	0.24	3.54	-2	4.33
<i>SI</i>	<i>4.77–4.86</i>	<i>1.52–1.55</i>	<i>0.24–0.27</i>	<i>3.44–3.64</i>	<i>-2–-1.98</i>	<i>4.29–4.38</i>
Balsam fir	3.23	1.04	0.14	0.6	-2	4.89
<i>SI</i>	<i>3.19–3.26</i>	<i>1.02–1.04</i>	<i>0.13–0.21</i>	<i>0.5–0.7</i>	<i>-2–-1.98</i>	<i>4.84–4.94</i>

3.5. Crowding effect

3.5.1. Effect of neighbouring tree species

The strongest competitive effect ( $\lambda$ ) was from intraspecific neighbours for all species except for aspen for which balsam fir was the strongest. Balsam fir was always a strong competitor ( $\lambda \geq 0.8$ ) as opposed to aspen which was generally a weak one ( $\lambda \leq 0.28$ ). Competitive effects of pin cherry ( $\lambda = 0.03–0.99$ ), paper birch ( $\lambda = 0.01–1$ ) and other conifers ( $\lambda = 0.37–1$ ) were highly variable depending on target species identity. In all cases, the competitive effects of other broadleaf species was about half that of the strongest competitor ( $\lambda = 0.3–0.65$ ). Most of the relationships were highly asymmetric which implies that the competitive effect of species “a” on species “b” was different than the effect of “b” on “a”. The  $\lambda$  estimates of the BA models (not shown) were well correlated ( $r = 0.88$ ) to those of the NCI models.

3.5.2. Effect of the position and size of neighbours

There was a highly significant linear relationship ( $R^2 = 0.62$ ,  $p < 0.0001$ ) between three crown width and DBH. Therefore, when  $\alpha = 1$  the competition effect of neighbours scales proportionally to their crown radius. An estimated  $\alpha$  value of 0 means that the competitive effect of neighbours is solely dependent on their density and an  $\alpha$  value of 2 indicates that the competitive effect of neighbours is proportional to their basal area. For all target species, there was a positive relationship between the size of neighbours and their competitive effect. The increase in competitive effect with DBH was weak in the model for aspen ( $\alpha \sim 0.5$ ), proportional to the crown radius of neighbours for balsam fir and pin cherry ( $\alpha \sim 1$ ) and stronger for paper birch ( $\alpha \sim 1.5$ ).

Except for aspen, the size of the effective neighbourhood was smaller than the maximum 7 m allowed by the sampling design (Table 3) indicating that the mapped neighbourhood was large enough to include all significant competitors. There was a strong correlation ( $r = -0.97$ ) between species shade tolerance ranks (Table 1) and the estimated radius of their effective neighbourhood. This result indicates that shade intolerant species are influenced by more distant neighbours than shade tolerant species. Within the effective neighbourhood, the decline of the competitive effect of

increasingly distant neighbours was null or near null in all cases ( $\beta \sim 0$ , Table 3).

4. Discussion

Even though the “size-only” model was least supported by the data for all species, this simple model still explained a large fraction of the variance (Table 2; Fig. 2). The only other published results for a size only model using this type of analysis explained far less variance than ours (average  $R^2 = 0.23$  vs. 0.58), even though the performances of their complete models were similar to ours (average  $R^2 = 0.72$  vs. 0.73) (Coates et al., 2009). Our sites were very homogenous in terms of tree age and size, resulting in low variability in stand structure whereas in Coates et al. (2009) stands were of different age and disturbance histories. Small size differences in homogenous stands should be an indication of a tree’s relative status in the canopy and its ability to compete for light, thus explaining the difference in variance explained by both studies.

4.1. Competition in young stands

For all species, we found no decrease in competitive effects of neighbours with increasing distance ( $\beta \sim 0$ ) within their respective effective neighbourhoods. It is possible that the small estimated  $\beta$  values are artefacts of the sampling method used that included only larger neighbours as we moved further from the target tree and, therefore, could not account, for example, for the effect of small neighbours with DBH < 3 cm beyond 2 m. Even so, our results indicate that the competitive effect is more constant with distance than the linear relation often assumed in competition indices (e.g. Hegyi, 1974) and are in agreement with other NCI studies (Canham et al., 2006; Papaik and Canham, 2006). The most variable element among target species was the size of the effective neighbourhood which was larger for shade intolerant species. This trend was also observed for young conifers in western Canada (Simard and Sachs, 2004) and could be the result of the higher resource requirements (light, water and/or nutrients) of shade intolerant species.

There were important differences in species-specific competitive effects ( $\lambda$ ) and the most consistent pattern was that all species

**Table 4**

Estimated interspecific competition coefficient ( $\lambda$ ) of each pair of target (row) and competitor (column) species for the best model of each species. SI (*italic*) is the 2 AICc unit asymptotic support interval for each parameter. Intraspecific  $\lambda$  are highlighted in bold.

Target species	Competitor species					
	Pin cherry	Aspen	Paper birch	Balsam fir	Other conifers	Other broadleaves
Pin cherry	<b>0.99</b>	0	0.01	1	0.4	0.65
<i>SI</i>	<i>0.97–1</i>	<i>0–0</i>	<i>0–0.01</i>	<i>0.99–1</i>	<i>0.4–0.41</i>	<i>0.64–0.65</i>
Aspen	0.03	<b>0.28</b>	0.79	1	0.37	0.56
<i>SI</i>	<i>0.03–0.12</i>	<i>0.28–0.29</i>	<i>0.78–0.81</i>	<i>0.99–1</i>	<i>0.37–0.44</i>	<i>0–1</i>
Paper birch	0.41	0.09	<b>1</b>	0.8	1	0.5
<i>SI</i>	<i>0.36–0.42</i>	<i>0.09–0.09</i>	<i>0.99–1</i>	<i>0.79–0.81</i>	<i>0.99–1</i>	<i>0.49–0.5</i>
Balsam fir	0.33	0.06	0.45	<b>1</b>	0.7	0.3
<i>SI</i>	<i>0.32–0.39</i>	<i>0.06–0.07</i>	<i>0.41–0.45</i>	<i>0.99–1</i>	<i>0.68–0.71</i>	<i>0.29–0.71</i>

except aspen were stronger competitor to their conspecific neighbours than to other species. Aspen was the weakest competitor of the four target species (Table 4) and was also a weak competitor among the nine studied species of Coates et al. (2009). Moreover, at a given size, the predicted growth of aspen was generally similar or lower to the predicted growth of the other species (Fig. 2). Taken together, these elements suggest that the high occurrence of aspen in these stands is driven by a high fecundity and intensive production of roots suckers after clear-cut (Frey et al., 2003) rather than a strong competitive capacity.

Free-to-grow (FTG) standards are very simple field assessments in respect to a threshold level of competition that should not reduce the normal height development of a target tree. They are used in several regions of North America to determine whether further treatments (e.g. thinning) are warranted to improve the establishment of a vigorous regrowth of commercial tree species following harvest. For example in the province of Quebec, as elsewhere in Canada (Liefers et al., 2007), FTG standards consider commercial broadleaf species, such as aspen, to be stronger competitors than conifers (MRNF, 2002). Therefore, height and proximity criteria relative to target trees are more severe for these competing species than they are for competing conifers. The abundance of aspen (42% of all stems on our plots) in the boreal mixedwood often results in few trees considered FTG and to the prescription of clearing of broadleaf trees to release conifers from competition. Our results suggest that, at least for naturally established balsam fir, aspen is the weakest competitor in young stands. The high variance and asymmetry in species competitive effects also highlight the importance of developing species-specific competition indices.

The sampled young stands were characterized by a high tree density ranging from roughly 8500 to 40,000 trees/ha in which tree position is probably greatly influenced by colonisation processes (e.g. localisation of seeds and root suckers). These elements resulted in stands with relative homogeneous tree distribution and similar neighbourhoods around trees. This likely explains why the gain in predictive power of NCI models relative to BA models was small (Table 2). Tree mortality in the stands was low (2%) and our sampling was performed before the self-thinning phase where the density, especially of the early successional species like aspen and pin cherry, will diminish greatly (Mallik et al., 1997; Fahey et al., 1998). It is unclear if trees' neighbourhood will differ more importantly following this phase and increase the difference in the predictive power of the NCI and BA competition models.

The small difference between the NCI and the BA models in young dense stands is important because measuring stand BA of each species is much faster than mapping all of the trees in a stand which is required to compute NCI. In the context of broad scale management, predictions of yield and composition of stands need to be performed over a large territory for many species mixtures and edaphic conditions. For young homogeneous stands, the development of simple BA models could free resources that could then serve to parameterise growth models for more species and stand conditions. If the goal is to model the development of stands with more complex structures (e.g. following strip cutting), spatially explicit NCI should be used as they perform better at the individual level and can incorporate spatial variability.

Forest management models often predict yield from species-specific growth curves that are calibrated from pure stands (CEGFQ, 2004). The individual growth of each species is then applied *pro rata* of their abundance in a mixed-species stand to obtain total yield. This has been shown to produce biased predictions as it does not take into account variations in species competitive effects (Balandier et al., 2006) with important consequences in mixedwood stands populated by several tree species differing markedly in their competitive effects. Ultimately, growth models like those developed here could be used in novel forest

simulators to create a range of potential growth curves for any particular stand composition.

## 5. Conclusion

Growth of saplings of the major tree species of the boreal mixedwood in young dense stands can be effectively predicted from models that include the effects of tree size, plot and competition by neighbours. In these stands, species competitive effect varied importantly and we believe that competition indices like FTG standards should be reviewed and adapted to factor in the relative competitiveness of each species of competitor. The impact of the competitive interactions on growth is best measured from the neighbourhood of each tree although competition measurements at the stand level are also good growth predictor due to uniformity of the stands. The choice between both types of indices should depend on the intended use. For even-age stand management, the BA model is much less expensive and time consuming to develop and appears to be adequate for homogeneous regenerating stands but the NCI model, by taking into account the immediate surroundings of each tree, is more appropriate for complex stands. Subsequent analysis should aim at determining how both types of indices perform after stands self-thinning phase and if mortality could be predicted from competition calculation.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2010.06.037.

## References

- Balandier, P., Collet, C., Miller, J.H., Reynolds, P.E., Zedaker, S.M., 2006. Designing forest vegetation management strategies based on the mechanisms and dynamics of crop tree competition by neighbouring vegetation. *Forestry* 79, 3–27.
- Bella, I.E., 1971. A new competition model for individual trees. *Forest Science* 17, 364–372.
- Brais, S., Brazeau, M., Brown, J.-L., Camiré, C., Paré, D., Robitaille, A., 1996. Géologie, dépôts de surface et sols forestiers. In Manuel de Foresterie. Les presses de l'université Laval, Saint-Nicolas, Canada, 5–95.
- Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.
- Callaway, R.M., Walker, L.R., 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* 78, 1958–1965.
- Canham, C.D., LePage, P.T., Coates, K.D., 2004. A neighborhood analysis of canopy tree competition: effects of shading versus crowding. *Canadian Journal of Forest Research* 34, 778–787.
- Canham, C.D., Papaik, M.J., Uriarte, M., McWilliams, W.H., Jenkins, J.C., Twery, M.J., 2006. Neighborhood analysis of canopy tree competition along environmental gradients in New England forests. *Ecological Applications* 16, 540–554.
- Carter, M.R., 1993. Soil Sampling and Methods of Analysis. Lewis publishers.
- CEGFQ, 2004. Commission d'étude sur la gestion de la forêt publique québécoise, ISBN 2-550-43626-1. Québec: Les publications du Québec.
- Claveau, Y., Messier, C., Comeau, P.G., Coates, K.D., 2002. Growth and crown morphological responses of boreal conifer seedlings and saplings with contrasting shade tolerance to a gradient of light and height. *Canadian Journal of Forest Research* 32, 458–468.

- Coates, K.D., Canham, C.D., LePage, P.T., 2009. Above- versus below-ground competitive effects and responses of a guild of temperate tree species. *Journal of Ecology* 97, 118–130.
- Delagrèze, S., Messier, C., Lechowicz, M.J., Dizengremel, P., 2004. Physiological, morphological and allocational plasticity in understory deciduous trees: importance of plant size and light availability. *Tree Physiology* 24, 775–784.
- Dubois, J., Ruel, J.C., Elie, J.G., Archambault, L., 2006. Dynamique et estimation du rendement des strates de retour après coupe totale dans la sapinière à bouleau jaune. *Forestry Chronicle* 82, 675–689.
- Edwards, E.W., 1992. The framework of inference in Likelihood. Johns Hopkins University Press, Baltimore, USA.
- Fahey, T.J., Battles, J.J., Wilson, G.F., 1998. Responses of early successional northern hardwood forests to changes in nutrient availability. *Ecological Monographs* 68, 183–212.
- Filipescu, C.N., Comeau, P.G., 2007. Competitive interactions between aspen and white spruce vary with stand age in boreal mixedwoods. *Forest Ecology and Management* 247, 175–184.
- Frey, B.R., Lieffers, V.J., Landhäusser, S.M., Comeau, P.G., Greenway, K.J., 2003. An analysis of sucker regeneration of trembling aspen. *Canadian Journal of Forest Research* 33, 1169–1179.
- Goffe, W.L., Ferrier, G.D., Rogers, J., 1994. Global optimization of statistical functions with simulated annealing. *Journal of Econometrics* 60, 65–99.
- Haeussler, S., Bergeron, Y., 2004. Range of variability in boreal aspen plant communities after wildfire and clear-cutting. *Canadian Journal of Forest Research* 34, 274–288.
- Hegyi, F., 1974. A simulation model for managing jack-pine stands. In: Fries, J. (Ed.), *Growth Models for Tree and Stand Simulation*. Royal College of Forestry, Stockholm, pp. 74–90.
- Hubbell, S.P., 2005. Neutral theory in community ecology and the hypothesis of functional equivalence. *Functional Ecology* 19, 166–172.
- Humbert, L., Gagnon, D., Kneeshaw, D., Messier, C., 2007. A shade tolerance index for common understory species of northeastern North America. *Ecological Indicators* 7, 195–207.
- Larocque, G.R., 2002. Examining different concepts for the development of a distance-dependent competition model for red pine diameter growth using long-term stand data differing in initial stand density. *Forest Science* 48, 24–34.
- Lieffers, V.J., Pinno, B.D., Stadt, K.J., 2002. Light dynamics and free-to-grow standards in aspen-dominated mixedwood forests. *Forestry Chronicle* 78, 137–145.
- Lieffers, V.J., Stadt, K.J., Feng, Z., 2007. Free-to-grow regeneration standards are poorly linked to growth of spruce in boreal mixedwoods. *Forestry Chronicle* 83, 818–824.
- Lorimer, C.G., 1983. Tests of age-independent competition indices for individual trees in natural hardwood stands. *Forest Ecology and Management* 6, 343–360.
- Mallik, A.U., Bell, F.W., Gong, Y., 1997. Regeneration behavior of competing plants after clear cutting: implications for vegetation management. *Forest Ecology and Management* 95, 1–10.
- McKeague, J.A., 1978. *Manuel de méthodes d'analyse des sols*, 2ème édition. Société canadienne de la science du sol, Ottawa, Canada.
- Mehlich, A., 1984. Mehlich 3 soil test extractant: a modification of Mehlich 2. *Communications in Soil Science and Plant Analysis* 15, 1409–1416.
- MRNF, 2002. *Normes d'inventaire forestier*, édition 2002. Ministère des Ressources Naturelles et de la Faune du Québec - Direction des inventaires forestiers, Québec, Qc.
- Papaik, M.J., Canham, C.D., 2006. Multi-model analysis of tree competition along environmental gradients in southern New England forests. *Ecological Applications* 16, 1880–1892.
- Pinno, B.D., Thomas, B.R., Bélanger, N., 2009. Predicting the productivity of a young hybrid poplar clone under intensive plantation management in northern Alberta, Canada using soil and site characteristics. *New Forests*, 1–15.
- Pueyo, S., He, F., Zillio, T., 2007. The maximum entropy formalism and the idiosyncratic theory of biodiversity. *Ecology Letters* 10, 1017–1028.
- Robitaille, A., Saucier, J.P., 1998. *Paysages régionaux du Québec méridional*. Les publications du Québec, Québec, Canada.
- Ruel, J.C., Quillet, F., Plusquellec, R., Ung, C.H., 1998. Évolution de la régénération de peuplements résineux et mélangés au cours des 30 années après coupe à blanc mécanisée. *The Forestry Chronicle* 74, 428–443.
- Saucier, J.P., Grondin, P., Robitaille, A., Gosselin, J., Morneau, C., Richard, P.J.H., Brisson, J., Sirois, L., Leduc, A., Morin, H., Thiffault, E., Gauthier, S., Lavoie, C., Payette, S., 2009. *Écologie forestière*. In: Multimondes, É. (Ed.), *Manuel de foresterie*. Ordre des ingénieurs forestiers du Québec, Québec, Qc, Canada, pp. 165–316.
- Simard, S.W., Sachs, D.L., 2004. Assessment of interspecific competition using relative height and distance indices in an age sequence of seral interior cedar-hemlock forest in British Columbia. *Canadian Journal of Forest Research* 34, 1228–1240.
- Stadt, K.J., Huston, C., Coates, K.D., Feng, Z., Dale, M.R.T., Lieffers, V.J., 2007. Evaluation of competition and light estimation indices for predicting diameter growth in mature boreal mixed forests. *Annals of Forest Science* 64, 477–490.
- Tierney, G.L., Fahey, T.J., 1998. Soil seed bank dynamics of pin cherry in a northern hardwood forest, New Hampshire, U.S.A. *Canadian Journal of Forest Research* 28, 1471–1480.
- Tilman, D., 1988. *Plant Strategies and the Dynamics and Structure of Plant Communities*. Princeton University Press, Princeton, NJ, USA.
- Uriarte, M., Condit, R., Canham, C.D., Hubbell, S.P., 2004. A spatially explicit model of sapling growth in a tropical forest: Does the identity of neighbours matter? *Journal of Ecology* 92, 348–360.
- Valladares, F., Niinemets, A., 2008. Shade tolerance, a key plant feature of complex nature and consequences. *Annual Review of Ecology, Evolution, and Systematics*, 237–257.
- Woods, K.D., 2000. Dynamics in late-successional hemlock-hardwood forests over three decades. *Ecology* 81, 110–126.