Sugar maple (*Acer saccharum* Marsh.) growth is influenced by close conspecifics and skid trail proximity following selection harvest

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A B S T R A C T

In this study, we quantified the effects of local neighbourhood competition, light availability, and proximity to skid trails on the growth of sugar maple (*Acer saccharum* Marsh.) trees following selection harvest. We hypothesized that growth would increase with decreasing competition and increasing light availability, but that proximity to skid trails would negatively affect growth. A total of 300 sugar maples were sampled ~10 years after selection harvesting in 18 stands in Témiscamingue (Québec, Canada). Detailed tree and skid trail maps were obtained in one 0.4 ha plot per stand. Square-root transformed radial growth data were fitted to a linear mixed model that included tree diameter, crown position, a neighbourhood competition index, light availability (estimated using the SORTIE light model), and distance to the nearest skid trail as explanatory variables. We considered various distance-dependent or -independent indices based on neighbourhood radii ranging from 6 to 12 m. The competition index that provided the best fit to the data was a distance-dependent index computed in a 6 m search radius, but a distance-independent version of the competition index provided an almost equivalent fit to data. Models corresponding to all combinations of main effects were fit to data using maximum likelihood, and weighted averages of parameter estimates were obtained using multimodel inference. All predictors had an influence on growth, with the exception of light. Radial growth decreased with increasing tree diameter, level of competition and proximity to skid trails, and varied among crown positions with trees in suppressed and intermediate positions having lower growth rates than codominants and dominants. Our results indicate that in selection managed stands, the radial growth of sugar maple trees depends on competition from close (≤6 m) conspecific neighbours, and is still affected by proximity to skid trails ~10 years after harvesting. Such results underscore the importance of minimizing the extent of skid trail networks by careful pre-harvest planning of trail layout. We also conclude that the impact of heterogeneity among individual-tree neighbourhoods, such as those resulting from alternative spatial patterns of harvest, can usefully be integrated into models of post-harvest tree growth.

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1. Introduction

Modelling the response of tree growth to partial harvesting in structurally complex forest stands presents a host of challenges (Peng, 2000; Puettmann et al., 2008a; Coates et al., 2009). In such stands, trees are of different size and age, and occupy various positions in the canopy. Moreover, partial harvest tends to maintain or favour heterogeneous conditions in terms of residual tree density (Grushecky and Fajvan, 1999), and light availability (Beaudet et al., 2002) and hence in neighbourhood competition. Therefore, an individual-tree approach should be favoured to model post-harvest growth response in such stands (Pretzsch, 1995).

Individual-tree growth models generally include as predictors a suite of tree characteristics such as tree size, vigour and/or crown position, as well as variables accounting for variation in competition levels experienced by individual trees. These variables can consist of stand-level characteristics such as residual stand basal area or density, or individual-tree competition indices. Among the latter, some are non-spatial in nature, in the sense that they do not aim at representing the competitive environment of a target tree in a spatially explicit neighbourhood, but rather as its relative situation in the stand (e.g., ratio between target-tree dimension and stand-level measures: Kiernan et al., 2008). Others can be considered spatially explicit in that they describe a target-tree neighbourhood within a given search radius and some indices

account for the distance to competing neighbours leading to distance-dependent indices (Stadt et al., 2007).

Obviously, the most appropriate approach to account for variation in competition level will depend on the ecological and silvicultural context. For instance, several studies found that distance-dependent competition indices did not perform better than distance-independent indices. However, most of such studies (according to Busing and Mailly, 2004; Stadt et al., 2007) were performed in stands where the spatial distribution of trees tended to be regular (e.g., plantations), and it has been argued that spatially explicit distance-dependent competition indices would be more likely to perform well in irregular stands where clustering of trees is common (Mailly et al., 2003; Busing and Mailly, 2004).

In recent years, increasing computer power and availability of light models have facilitated the use of computationally demanding light interception indices as an alternative or complement to conventional competition indices in growth models (e.g., MacFarlane et al., 2002; Mailly et al., 2003; Canham et al., 2004; Stadt and Lieffers, 2000; Astrup et al., 2008; Coates et al., 2009). However, mixed results have been reported regarding the usefulness of light indices compared to competition indices as predictors of tree growth. For instance, Mailly et al. (2003) found that indices computed from virtual hemispherical images did not yield better growth prediction than simpler distance-dependent competition indices. Similarly, Stadt et al. (2007) reported that the performance of the light indices was intermediate to poor when compared to conventional competition indices. Other investigators have explored the possibility of simultaneously using light and conventional competition indices as a way to partition competitive effects into below-ground (competition index) and above-ground (light interception) components. Such approaches allowed inferring on ecological processes such as competitive exclusion and species coexistence from growth rates (Canham et al., 2004; Coates et al., 2009).

While partial harvest modifies the competitive environment of residual trees, harvest operations have other effects that could enhance or diminish the possible benefits of reduced neighbourhood competition. During partial harvest, machinery traffic often leads to soil disturbance and compaction (Grigal, 2000), and residual trees near skid trails often suffer from root damage, as well as from impaired root development and water uptake (Startsev and McNabb, 2001; Nadezhdina et al., 2006; Komatsu et al., 2007). Such an impact is generally restricted to skid trails and areas nearby (Malo, 2008; Puettmann et al., 2008b; Roberts and Harrington, 2008). The stresses associated with skid trail disturbances are often reported to reduce stand productivity (Grigal, 2000), individual-tree growth, and survival (Murphy, 1983; Helms and Hipkin, 1986; Heninger et al., 2002; Puettmann et al., 2008b; Thorpe et al., 2008). However, most studies that have examined the effect of skid trails on tree growth and survival have focused on planted or natural regeneration (e.g., Murphy, 1983; Helms and Hipkin, 1986; Heninger et al., 2002; Puettmann et al., 2008b), while much fewer have evaluated the impact of skid trail proximity on residual mature tree growth and survival. Among the latter, equivocal results were obtained ranging from increased growth rates of trees located near skid trails (Roberts and Harrington, 2008), to absence of any effect (Hartmann and Messier, 2008; Hartmann et al., 2008), to a negative impact of skid trail proximity on residual tree survival (Thorpe et al., 2008).

In temperate northern hardwoods of the north-eastern United States and eastern Canada, uneven-aged sugar maple stands are a dominant forest component (Godman et al., 1990). The selection silvicultural system is widely used in such forests (Nyland, 1998; Bédard and Majcen, 2003) and involves the periodic removal of individual or small groups of trees across diameter and age classes at regular intervals. This silvicultural system seeks to maintain a specific diameter- and age-class distribution, to provide long-term consistency in yield, and to create or maintain favourable conditions for residual tree growth and regeneration (Smith et al., 1997; Nyland, 1998). While several recent studies examined the growth response of sugar maple following selection harvest (Jones and Thomas, 2004; Forget et al., 2007; Fortin et al., 2008; Kiernan et al., 2008), few included individual-tree competition indices, and none accounted for the possible influence of skid trail proximity on tree growth.

In this study, our main objective was to determine the effects of local neighbourhood competition, light availability, and the long-term effect of proximity to skid trails on sugar maple individual-tree growth following selection harvest. We hypothesized that growth would increase with decreasing competition and increasing light availability, but that proximity to skid trails would reduce growth. A secondary objective was to identify the attributes of the competitive neighbourhoods that have a significant impact on sugar maple growth through a comparison of several competition indices.

2. Methods

2.1. Study sites

The study sites were located approximately 60 km southeast of the city of Témiscaming (46°43′N, 79°04′W), Québec, Canada. The region is part of the western sugar maple-yellow birch bioclimatic domain, where the growing season is usually 170–180 days long. Mean annual temperature varies from 2.5 to 5.0 °C, and mean annual precipitation is 900 mm (snowfall ca. 25% of total) (Robitaille and Saucier, 1998).

In 2004 and 2005, 18 plots of 0.4 ha (50 m × 80 m) were established in uneven-aged northern hardwood stands that had been harvested by selection cuts in 1993 or 1994 (Table 1). All plots were located on level ground or on gentle slopes with good to moderate drainage, on ferro-humic podzols with underlying thin tills of glacial origin. The selection cuts aimed primarily at removing trees of low quality and vigour to increase overall post-harvest stand quality and reduce subsequent losses to mortality, as well as to maintain an uneven-aged structure in the residual stand. The pre-harvest BA ranged from 21 to 33 m²/ha (28 m²/ha on average), while post-harvest BA ranged from 14 to 24 m²/ha (20 m²/ha on average) (Table 1). The removal rate was ~24% of stand basal area (BA) and was generally well distributed across diameter classes. Tree felling was done manually with chainsaws and whole trees were moved to forest roads with cable skidders. Skid trails were spaced approximately 15 m apart but spacing was not constant along the trail path. Thus, some areas were more affected by machinery traffic than others.

In the post-harvest stands, sugar maple (Ms) made up 74% of total BA, yellow birch (By, Betula alleghaniensis Britton) about 14%, American beech (Ba, Fagus grandifolia Ehrh.) roughly 4%, balsam fir (Fb, Abies balsamea [L.] P. Mill.) 3%, whereas white spruce (Sw, Picea glauca [Moench] Voss), red oak (Qr, Quercus rubra L.), red maple (Mr, Acer rubrum L.), eastern hemlock (He, Tsuga canadensis [L.] Carr.), and eastern white cedar (Cw, Thuja occidentalis L.) occurred in lower proportions (Table 1). Sugar maple stands in the study region have undergone several forest tent caterpillar (FTC, Malacosoma disstria Hubner) defoliations and the most recent ones occurred in 1986–1992, and in 1999–2002 (Hartmann and Messier, 2008).

2.2. Tree mapping

All live and standing dead trees ≥9.1 cm DBH (diameter at breast height, 1.3 m above ground), and all stumps were mapped in the 18 plots. To perform the mapping, a plot was divided lengthwise in two halves. The resulting center line served as the

Table 1
Characteristics of the 18 study plots, which were all from stands harvested through selection cutting in 1993 or 1994. Basal area (BA), tree density and species proportions are for stems with DBH > 9 cm. Post-harvest BA, density, and species proportion are as measured at the time of sampling (i.e., 11 years after harvest), while pre-harvest values are estimated based on our mapping and diameter measurement of stumps and dead trees.

Site number	Site	Harvest year	BA (m²/ha)		Tree density (stems/ha)		Skid trails (% of plot area)	Species proportion (%, post-harvest)								
			Pre-harvest	Post-harvest	Pre-harvest	Post-harvest		Ms	By	Ba	Fb	Sw	Qr	Mr	He	Cw
1	ART_01	1993	28	21.3	528	430	8.9	42	22	9	20	0	6	1	0	0
2	BOB_01	1994	24	18.5	480	433	15.2	71	18	0	7	2	0	0	0	2
3	BOB_02	1994	31	23.7	443	388	21.2	89	11	0	0	0	0	0	0	0
4	BOB_03	1994	32	23.2	450	378	16.4	96	4	0	0	0	0	0	0	0
5	BOB_04	1994	28	21.6	483	430	15.6	82	18	0	0	1	0	0	0	0
6	BOB_05	1994	33	24.1	393	313	15	80	9	0	0	0	2	0	9	0
7	CHY_01	1993	28	20.8	395	343	14.5	90	7	3	0	0	0	0	0	0
8	CHY_02	1993	26	14	360	250	14.5	54	14	23	2	6	1	0	0	0
9	CHY_03	1993	27	20.3	345	278	16.9	81	5	9	0	2	1	2	0	0
10	CHY_04	1993	31	23.3	455	373	16.1	61	7	17	4	5	1	5	0	0
11	CHY_05	1993	26	20.1	480	398	16.8	65	21	0	3	5	1	4	0	0
12	HWD_01	1993	28	20.5	515	425	16.8	77	14	0	1	4	0	0	1	4
13	MCK_01	1994	25	20.1	503	455	13.6	97	1	1	0	0	0	1	0	0
14	MCK_02	1994	29	21.3	358	305	14.3	84	3	7	2	0	3	0	2	0
15	MMW_01	1993	26	18.5	535	425	14.6	86	13	0	0	0	0	0	1	0
16	MMW_02	1993	31	20.9	428	315	10.7	75	7	2	0	0	9	7	1	0
17	MMW_03	1993	23	17.3	410	348	10.2	70	20	0	5	2	0	0	0	2
18	MMW_04	1993	21	16.1	488	408	9.6	37	52	0	6	3	0	0	0	3
Mean			27.6	20.3	447	372	14.5	74	14	4	3	2	1	1	1	1
Min			21.0	14.0	345	250	8.9	37	1	0	0	0	0	0	0	0
Max			33.0	24.1	535	455	21.2	97	52	23	20	6	9	7	9	4

Note: Ms: sugar maple; By: yellow birch; Ba: American beech; Fb: balsam fir; Sw: white spruce; Qr: red oak; Mr: red maple; He: eastern hemlock; Cw: eastern white cedar.

y-coordinate of the plot. Perpendicular distances from this line to individual trees (or stumps) were measured using a Hägloff Vertex III® hypsometer and a forester's compass. The DBH of all trees was recorded and their crown class was determined based on relative tree position in the canopy (MRNQ, 2002). Four crown classes were considered: dominant trees (D) with crowns reaching above the upper component of the main canopy of the stand, codominants (C) are within two-thirds to five-sixths of the height of dominants, intermediate trees (I) are within half to two-thirds of the height of dominants, and suppressed trees (S) are no more than half the height of dominant trees. For stumps, diameter at stump height (~0.5 m above ground) was measured and converted to DBH using existing conversion tables (MRNFPQ, 2003). Such measurements were used to estimate pre-harvest stand densities and BA (Table 1).

2.3. Skid trail mapping and calculation of distance to nearest skid trail

Skid trails originating from the 1993 to 1994 harvests were identified and mapped in each plot. Because harvesting took place >10 years prior to sampling, subsequent understory vegetation development and litter accumulation rendered skid trail identification difficult in some cases. A set of criteria was used to ensure accurate identification: (i) presence of openings (mainly linear ones) in the forest canopy, (ii) presence of ruts, (iii) presence of wounds at the base of trees, (iv) presence in the undergrowth of species that are usually associated with higher light levels and soil disturbance (e.g., yellow birch, pin cherry [*Prunus pensylvanica* L.f.], poplars [*Populus* sp.]), (v) presence of adjacent stumps, (vi) absence of obstacles (e.g., boulders, escarpments), (vii) machinery constraints (e.g., turning radius), and (viii) general concordance with the trail network and stand features. Based on the above criteria, skid trails were mapped with reference to tree positions. Only clearly identifiable trails were considered for further analysis. Due to the recovery of the forest floor and vegetation, we could not directly measure trail width. As a result, we estimated it to 4 m based on machinery dimensions and field observations. Based on tree- and skid trail-maps and using GIS software (ArcGIS 9.2, Esri® GIS and Mapping Software, Redlands, CA), we computed for each

sugar maple target tree its distance to the closest skid trail (DIST.TRAIL). We also calculated the proportion of each plot area affected by skid trails (Table 1).

2.4. Radial growth measurements

Three increment cores were taken on all sugar maple trees with DBH between 19.1 cm and 49.0 cm, and located within a 26 m × 56 m subplot in the main plots. Hence, the subplots were surrounded by a 12 m buffer of mapped trees for computations of neighbourhood competition indices (NCI, see below). Trees with DBH <19.1 cm and >49.0 cm were excluded from sampling to avoid juveniles or senescent trees. A total of 300 sugar maple trees were sampled.

Increment cores were progressively sanded down to grain 400 to allow a clear identification of the final cell layer in each tree-ring. Tree-rings were measured to the nearest 0.001 mm using a computer-assisted micrometer equipped with a microscope. In most cases, at least two of the three increment cores taken per tree were readable and used for growth measurements. We obtained a single growth chronology per tree by averaging tree-level measurements to account for intra-tree variability of radial increment due to growing conditions or leaning (Kienholz, 1930; Peterson and Peterson, 1995).

Among these chronologies, a subsample from 29 dominant trees was used to construct a master chronology. We used the COFECHA software (Holmes, 1983; Grissino-Mayer, 2001) to progressively add highly correlated (e.g., r-values ≥0.3, Tardif et al., 2001) tree-ring series to the already existing ones. The final master chronology had an overall cross-correlation coefficient of 0.479. We matched tree-rings of the remaining trees with calendar years by cross-dating tree-ring series and master chronology based on (i) visual examination of marker years (mainly severe growth declines in 1971 and 1988), and (ii) cross-correlation coefficients of chronology segments with the master chronology. COFECHA assisted in detecting missing or false rings in individual segments of tree-ring series. In suspect cases, we identified missing or false rings on the cores and added (for zero growth) or removed these

from the series accordingly. Corrected series were then run again in COFECHA to verify the cross-correlation with the master chronology.

2.5. Competition indices

The level of neighbourhood competition encountered by tree i was quantified using variants of the following neighbourhood competition index (NCI):

$$\text{NCI}_i = \frac{\sum_{j=1}^{N}(\text{DBH}_j)^{\alpha}/(\text{dist}_{ij})^{\beta}}{1000} \tag{1}$$

where DBH_j is the DBH (in cm) of a neighbour tree j located at distance dist_{ij} (in m) from target tree i, for neighbours located at $\text{dist}_{ij} \leq$ than the maximum search radius R (in m) and having a DBH ≥ 9.1 cm. Forty-eight variants of NCI were considered based on all possible combinations of three α values (0, 1, or 2), four β values (0, 0.5, 1, or 2) and four R values (6, 8, 10, or 12 m). Hence, the NCI either corresponded to the count, the sum of the diameter, or the sum of the squared diameter of all competitors located within a search radius R, weighted (or not) by either the square-root of the distance, the distance, or the squared distance between the target tree i and competitor j.

Because several studies have found that the effects of competition on tree growth may depend on competitor species (e.g., Canham et al., 2006; Zhao et al., 2006; Stadt et al., 2007; Coates et al., 2009), we also computed versions of the NCI which accounted for intra- versus inter-specific competition. We initially considered using a more detailed representation of inter-specific competition (i.e., based on individual competitor species or smaller groups of species), but species other than sugar maple were scarcely represented in our data set (i.e., sugar maple comprised ~68% of all trees) and therefore needed to be grouped to ensure adequate sample size. In the present paper, we use the term NCI.Sm to denote neighbourhood competition indices from sugar maple neighbours only, NCI.Oth to denote competition indices from other species only, and NCI.all to denote competition indices from both conspecific and heterospecific neighbours. This increased the number of NCI to 144 (48 NCI.all, 48 NCI.Sm, and 48 NCI.Oth).

2.6. Estimation of crown light environment using the SORTIE light model

An estimate of each tree's (post-harvest) light environment was obtained using the light module of SORTIE (v. 4.1), an individual-tree spatially explicit model of forest dynamics (Pacala et al., 1993, 1996). Using the SORTIE light module requires parameterising three species-specific allometric relationships (tree height vs. DBH, crown radius vs. DBH, and crown depth vs. tree height) and providing species-specific crown openness values. Such parameters were available from the same study region and type of sites for the two most abundant species (Ms and By, Lefrançois, 2006; Lefrançois et al., 2008) which together accounted for 89% of all trees in our plots. For most of the remaining species, we used parameters from Canham et al. (1994), Beaudet et al. (2002), Beaudet (2004), and Poulin and Messier (2007). When parameters were not available for some species (4% of all trees), we assigned parameters from similar species (e.g., for *Fraxinus nigra* Marsh., we used *F. americana* L. parameters from Beaudet, 2004). For standing dead trees, a percentage of crown openness of 75% and 60% was used for deciduous and conifer species, respectively, based on Poulin and Messier (2007). Tree coordinates, DBH, and species identification of all live and standing dead trees mapped in the plots were fed into SORTIE to create post-harvest stem maps. Light

availability was computed for each sugar maple target tree at a height corresponding to $0.75 \times$ crown height, as the seasonally averaged percentage of incident photosynthetic photon flux density (PPFD) that penetrates through the canopy (gap light index [GLI], Canham, 1988).

2.7. Statistical analyses

2.7.1. NCI selection

We first determined which of all possible NCI would be the most appropriate predictor of radial growth by fitting linear mixed models of radial growth as a function of each NCI:

$$\text{radial growth}_{ik}^{0.5} = \beta_0 + \beta_1 \text{NCI}_{ik} + Zb_k + \varepsilon_{ik} \tag{2}$$

and

$$\varepsilon_{ik} \sim N(0, \sigma^2)$$

The response variable, radial growth$_{ik}$, was the (square-root transformed to homogenize variances) annual radial growth (in mm) of tree i at site (plot) k averaged over the 8th, 9th and 10th years following harvest (2001–2003 and 2002–2004 for the 1993 and 1994 selection cuts, respectively). Note that different time windows (from 1 to 5 years) were tested for averaging growth rates but without major differences in the outcome of the analyses. The β parameters in Eq. (2) were estimated as fixed effects, whereas the term Zb_k was estimated as a random effect and corresponded to random intercepts (one for each plot). Thus, our model yielded two variance components, one for the variability between plots (associated to the random intercepts) and one for the intra-site variability (i.e., the error term ε_{ik}). Both the error term and random intercepts are assumed to be normally distributed with zero mean and variance σ^2. Model diagnostics did not indicate substantial departure from these assumptions. We estimated the parameters of the linear mixed effect models using the `lme` function from the `nlme` library (v.3.1-89, Pinheiro et al., 2008) in the R software (Version 2.7.0, R Core Development Team, 2008). Given that our analytic strategy included model selection, we fit the models using maximum likelihood (Pinheiro and Bates, 2000). We selected the NCI which provided the best fit, i.e., the lowest AICc (Akaike's Information Criterion [AIC] corrected for small sample sizes, Burnham and Anderson, 2002). As a result, a single version of NCI was retained for further analysis.

2.7.2. Regression modelling

As in the NCI selection procedure, we used linear mixed models to estimate radial growth as a function of DBH, crown position, distance to nearest skid trail, crown light environment and competition from neighbouring trees. Plots were incorporated as a random effect. This yielded the following full model:

$$\begin{aligned}\text{radial growth}_{ik}^{0.5} = {} & \beta_0 + \beta_1 \text{DBH}_{ik} + \beta_2 \text{CROWN.POS}_{ik} \\ & + \beta_3 \text{DIST.TRAIL}_{ik} + \beta_4 \text{GLI}_{ik} + \beta_5 \text{NCI}_{ik} \\ & + Zb_k + \varepsilon_{ik}\end{aligned} \tag{3}$$

where radial growth$_{ik}^{0.5}$ was the (square-root transformed to homogenize variances) annual radial growth (in mm) of tree i at plot k averaged over the 8th, 9th and 10th years following harvest, DBH_{ik} was the diameter (cm) of tree i in plot k, CROWN.POS_{ik} and DIST.TRAIL_{ik} were categorical variables describing, respectively, the crown class and the distance class of tree$_{ik}$ to the nearest skid trail. Distances to the nearest skid trail were grouped into five 6 m classes (corresponding to the minimum neighbourhood radius) to allow detecting a potential non-linear relationship between square-root transformed radial growth rates and skid trail distances. GLI_{ik} (%) was the crown light availability, and NCI_{ik}

was the neighbourhood competition index selected in the previous section.

2.7.3. Multimodel inference

We estimated parameters of a total of 31 models which represented all combinations of main effects (except for the intercept-only model) of the five predictor variables DBH, CROWN.POS, DIST.TRAIL, GLI and NCI. Model averaging yielded a weighted average for each parameter based on the Akaike (AICc) weight of each model in which the corresponding term was present (Burnham and Anderson, 2002). This enabled the computation of unconditional 95% confidence intervals for the parameters of interest. Parameters with confidence intervals excluding 0 were deemed good predictors of square-root transformed radial growth.

2.7.4. Impact of skid trails on growth rates

We predicted the square-root of radial growth rates for the sampled trees using model-averaged parameter estimates obtained from multimodel inference. To investigate the impact of excluding information on skid trails in growth estimations, we compared, within each distance class, back-transformed growth rate estimates based on models without the DIST.TRAIL term with predictions based on models containing the term. We computed the prediction bias within distance class d as

$$\text{prediction bias}_d \ (\%)$$

$$= \frac{\sum_{i=1}^{k} \frac{\text{Pred(no DIST.TRAIL)}_{id} - \text{Pred(DIST.TRAIL)}_{id}/}{\text{Pred(DIST.TRAIL)}_{id}}}{k} \times 100 \qquad (4)$$

where the prediction bias is the average ratio (expressed as a percentage) of the difference between individual predicted growth rates (of tree i within distance class d) based on models excluding the term DIST.TRAIL [Pred(no DIST.TRAIL)] minus growth predictions from models containing the term DIST.TRAIL term [Pred(DIST.TRAIL)], over the predictions with DIST.TRAIL, and divided by the total number of trees (k) within distance class d.

3. Results

Of the 144 versions of NCI we considered, the one which provided the best fit to the data (i.e., lowest AICc) was based on a summation of conspecific neighbours' squared diameter within a 6 m radius around each target tree, weighted by the square-root of their distance (NCI.Sm with $\alpha = 2$ and $\beta = 0.5$, Fig. 1). However, the model with the best NCI had an AICc weight of only 0.16 and four other NCI had AICc weights between 0.05 and 0.10 (Table 2). All of these five best NCI were based on conspecific neighbours (NCI.Sm) and most (four out of five) were computed within the smallest neighbourhood radius (6 m). All of the five best NCI comprised some measure of neighbours' dimension (diameter, squared or
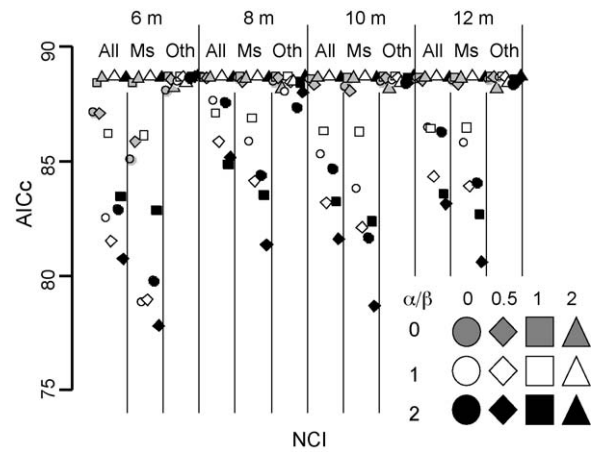

Fig. 1. AICc values obtained from mixed models of square-root transformed radial growth as a function of the 144 versions of NCI considered for different search radii under the three different scenarios: (1) all neighbours included (All), (2) only conspecific sugar maple (Ms), (3) only heterospecific (Oth) neighbours. Symbols with different shapes and shadings represent combinations of α and β values used to compute the NCI indices.

Table 2
Parameter values of neighbourhood competition indices (NCI) which provided the best fit (AICc weights > 0.05) to growth data (among the 144 tested versions), where R (in m) is the search radius, α and β are exponents as defined in Eq. (1), NCI type indicates whether the competition index accounted for conspecific neighbours only (NCI.Sm) or neighbours of all species (NCI.all), AICc, ΔAICc and AICc weights and squared correlation coefficient (SCC) between observed and predicted values.

R (m)	α	β	NCI type	AICc	ΔAICc	AICc weight	SCC
6	2	0.5	NCI.Sm	77.821	0	0.159	0.255
10	2	0.5	NCI.Sm	78.684	0.863	0.103	0.263
6	1	0	NCI.Sm	78.856	1.035	0.094	0.256
6	1	0.5	NCI.Sm	78.955	1.134	0.090	0.254
6	2	0	NCI.Sm	79.809	1.988	0.058	0.251

not), with three out of five having $\alpha = 2$, and two having $\alpha = 1$ (Fig. 1). Three of the best NCI accounted for variation in the distance of individual neighbours to subject tree (with $\beta = 0.5$), but two did not ($\beta = 0$) (Fig. 1). The five best NCI had together a cumulative AICc weight of 0.51 (Table 2). Squared correlation coefficients of observed versus predicted values of individual models ranged between 0.217 and 0.263 and, within the best five NCI models, between 0.251 and 0.263 (Table 2).

Ten out of 31 regression models had AICc weights >0.01. They all contained the DBH term, and nine models contained the NCI term, whereas CROWN.POS and GLI were each present in six, and DIST.TRAIL in five of the 10 models (Table 3). The model with the lowest AICc had an AICc weight of 0.23 and the first six models

Table 3
Results of model selection based on AICc showing number of parameters (K), AICc, ΔAICc (compared to model with lowest AICc), AICc weights and cumulative AICc weights. Only models with AICc weights > 0.01 are shown for brevity.

Model	K	AICc	ΔAICc	AICc weight	Cumulative AICc weight
Intercept + DBH + CROWN.POS + GLI + NCI	9	62.689	0.000	0.231	0.231
Intercept + DBH + CROWN.POS + DIST.TRAIL + GLI + NCI	13	62.711	0.022	0.228	0.459
Intercept + DBH + CROWN.POS + DIST.TRAIL + NCI	12	62.887	0.197	0.209	0.668
Intercept + DBH + CROWN.POS + NCI	8	64.053	1.363	0.117	0.784
Intercept + DBH + CROWN.POS + GLI	8	64.734	2.045	0.083	0.867
Intercept + DBH + CROWN.POS + DIST.TRAIL + GLI	12	65.917	3.228	0.046	0.913
Intercept + DBH + GLI + NCI	6	67.070	4.381	0.026	0.939
Intercept + DBH + DIST.TRAIL + GLI + NCI	10	67.944	5.254	0.017	0.956
Intercept + DBH + DIST.TRAIL + NCI	9	68.588	5.899	0.012	0.968
Intercept + DBH + NCI	5	68.926	6.237	0.010	0.978

Table 4
Model-averaged parameter estimates and their 95% confidence interval (CI). Parameter estimates in bold correspond to terms for which CI excluded 0. Note that the intercept term codes for CROWN.POS of codominant trees and for DIST.TRAIL of trees within 0–6 m from the nearest skid trail.

Term	Estimate	CI lower	CI upper
Intercept	**1.4719**	1.2692	1.6746
DBH	**−0.0096**	−0.0152	−0.0041
CROWN.POS (suppressed)	**−0.2081**	−0.3497	−0.0664
CROWN.POS (intermediate)	**−0.0973**	−0.1821	−0.0126
CROWN.POS (dominant)	−0.0553	−0.1390	0.0284
DIST.TRAIL (6–12 m)	−0.0154	−0.0830	0.0522
DIST.TRAIL (12–18 m)	**0.1065**	0.0153	0.1977
DIST.TRAIL (18–24 m)	0.0327	−0.1280	0.1935
DIST.TRAIL (24–30 m)	0.1843	−0.0719	0.4406
GLI	0.0010	−0.0001	0.0021
NCI	**−0.0562**	−0.1016	−0.0109

accounted for >90% of the cumulative AICc weight (Table 3). Moreover, although the GLI term was present in the best model, its exclusion from the model did not increase greatly the AICc (Table 3, see ΔAICc < 2).

Multimodel inference showed that unconditional confidence intervals of the parameters for DBH, some CROWN.POS, some DIST.TRAIL, and NCI excluded zero, which was not the case for GLI, indicating that GLI did not contribute much to explaining variation in sugar maple growth (Table 4). Radial growth rates declined with increasing DBH and competition, and with decreasing distance to skid trails (Table 4 and Fig. 2). Growth rates were lower in suppressed and intermediate trees than in codominants and dominants (Table 4 and Fig. 2).

Residuals of predicted values from averaged parameter estimates were approximately normally distributed. The regression intercept and slope of observed versus predicted values were significantly different ($p < 0.05$) from zero and one, respectively, indicating that the model overestimated low growth rates and underestimated high growth rates (Fig. 3). The squared correlation coefficient of observed versus predicted values was 0.324.

Predicted radial growth rates of trees in the close vicinity of skid trails (0–6 m and 6–12 m) were lower than growth rates of trees at greater distances (Table 4). When DIST.TRAIL was excluded from models, predicted growth rates for trees within 0–6 m and within 6–12 m were 2.4% and 5.1% greater, respectively, than predictions based on models containing DIST.TRAIL (Table 5). At greater distances, excluding information on skid trails led to an underestimation of predicted growth rates of 13.3% (12–18 m), 3.7% (18–24 m) and 17.9% (24–30 m) (Table 5).

4. Discussion

### 4.1. Comparing neighbourhood competition indices

The neighbourhood competition index (NCI) that provided the best fit to sugar maple growth was a distance-dependent index computed from the summation of the squared DBH of conspecific neighbours located within 6 m of subject trees, weighted by the square-root of their distance. However, as noted above, the best NCI led to a model that had a relatively low AICc weight and four other NCI yielded models with very similar fit to data.

A common characteristic of the five best NCI was that they were solely based on information about conspecific neighbours. Given the low proportion of species other than sugar maple in the study stands (Table 1), it is understandable that an account of only heterospecific neighbours would not adequately describe the competitive environment of sugar maple target trees. However, it is interesting to observe that ignoring heterospecific neighbours
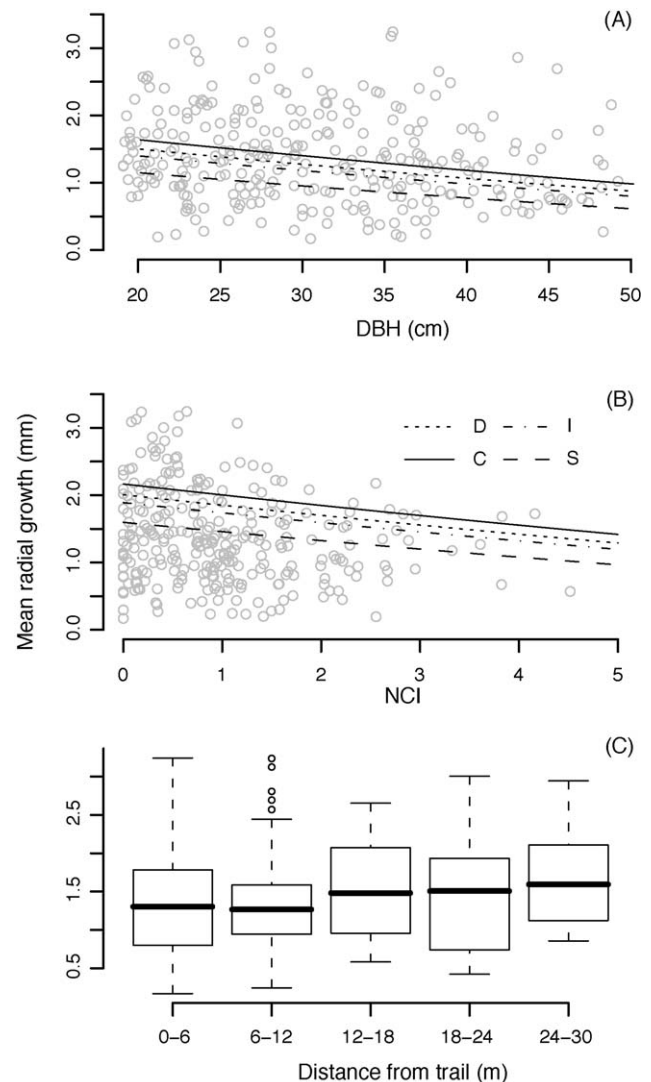
Fig. 2. Scatterplots of observed radial growth (mm) as a function of the good predictor variables DBH (A) and NCI (B) with linear relationships shown for following crown classes: suppressed [S]: dashed line; intermediate [I]: dot-dashed line; codominant [C]: solid line; dominant [D]: dotted line. (C) Boxplot of observed radial growth (mm) as a function of distance (five 6 m distance classes) from the nearest skid trail (DIST.TRAIL). Boxes indicate the first and third quartile, the bold horizontal line within the boxes indicates the median. Whiskers span across the whole data range (excluding outliers) and dots are data points beyond 1.5 times the interquartile range (i.e., difference between first and third quartiles) and are considered outliers.

tended to improve model fit (see NCI.Sm vs. NCI.all, Fig. 1). Such a result suggests that competition by conspecific neighbours is more detrimental than competition by other species. An alternative explanation is that the presence of a few heterospecific neighbours might positively influence sugar maple growth, which would partially counteract the negative effect of intra-specific competition and might explain why model fit would improve when ignoring heterospecific neighbours. Such a positive influence of heterospecific neighbours could result from higher litter decomposition and nutrient return rates in mixed-species than in single-species litter (Gartner and Cardon, 2004). In this study, we only investigated the difference between conspecific and heterospecific competitors. Nonetheless, our results generally agree with those from several recent studies that reported significant differences in species' competitive ability, and concluded that accounting for species identity of neighbours when computing competition
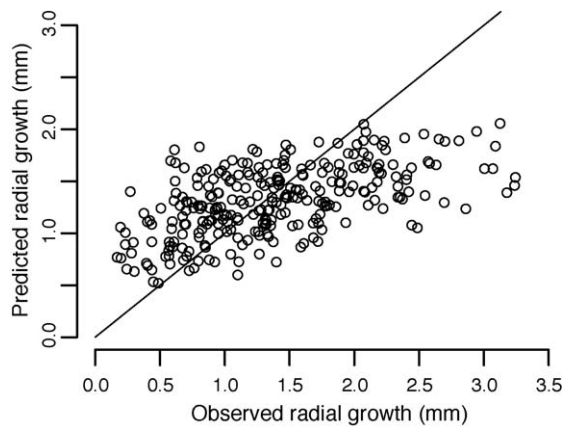
Fig. 3. Predicted vs. observed radial growth rates. Predictions are based on the model-averaged parameter estimates. The line indicates the 1:1 relationship between predicted and observed radial growth rates.

Table 5
Average growth rate estimate per distance class (d) based on averaged predictions from models containing or not the term DIST.TRAIL and average percentage individual (tree-level) prediction biases per distance class (d) when the DIST.TRAIL term is excluded from model.

Distance class, d (m)	Average growth estimate (mm)		Prediction bias (%)
	With DIST.TRAIL	Without DIST.TRAIL	
0–6	1.276	1.303	2.4
6–12	1.275	1.335	5.1
12–18	1.476	1.282	−13.3
18–24	1.370	1.322	−3.7
24–30	1.653	1.360	−17.9
All classes	1.314	1.312	−0.6

indices generally improved predictions of tree growth (Canham et al., 2006; Zhao et al., 2006; Stadt et al., 2007; Coates et al., 2009).

Another relatively clear trend emerging from our comparison of alternate NCI was that the smallest of the four radii provided the best description of the competitive neighbourhood for sugar maple trees (four of the five best NCI were based on a 6 m radius). Lorimer (1983) found that a neighbourhood radius of 3.5 times the average crown radius of overstory trees yielded best model fit. In our study plots, overstory (dominant and codominant) trees had an average DBH of approximately 35 cm. This measure translates into an estimate of average crown radius of 1.7 m, based on allometric relationships between stem and crown diameter (Beaudet et al., 2002). Applying Lorimer's findings to our data, we obtain a neighbourhood radius of 5.95 m.

The β values of 0.5 or 0 found in, respectively, three and two of the five best NCI, indicate that the impact of neighbours, within that relatively small neighbourhood, did not decline rapidly with increasing distance from a target tree. In contrast, many distance-dependent competition indices have assumed that the effect of neighbours declined with the inverse of their distance (i.e., $\beta = 1$, e.g., Hegyi, 1974; Daniels, 1976; Lorimer, 1983; Daniels et al., 1986). The presence of two distance-independent NCI (i.e., with $\beta = 0$) among the five best NCI indicates little support for the use of distance-dependent indices. Although our subsequent analyses were undertaken using the best NCI (a distance-dependent index) the impact on the fit of the relationship would not have been large had we used a distance-independent competition index. The performance of distance-dependent versus distance-independent competition indices is a subject that has raised considerable interest over the last decades. Mixed results have been reported regarding which type of competition indices performs best. Some studies reported clear evidence of better performance of distance-dependent indices in

some contexts (e.g., Mailly et al., 2003). However, others reported that while distance-dependent indices performed well, distance-independent indices were almost as effective (Stadt et al., 2007). In some situations, the additional effort and expense required to obtain data (i.e., inter-tree distances) for developing forest growth models based on distance-dependent competition measures might not be justified (Wimberly and Bare, 1996). However, substituting stand-level data with plot-level data can be used to compute spatial distance-independent competition measures for growth predictions while limiting sampling effort and expense.

Finally, our comparison of numerous NCI versions indicated that all of the five best NCI comprised some measure of neighbours' size, indicating that the impact of neighbours on sugar maple growth tends to increase linearly with their diameter or scales to their basal area. This relationship reflects the asymmetric nature of competitive interactions among individuals of different sizes for resources such as soil nutrients where individuals get a share of resources that is proportional to their size (Schwinning and Weiner, 1998). Although all neighbours contribute to the perceived competition of target trees, bigger ones contribute more than smaller ones.

4.2. Growth model

4.2.1. Effect of tree size and crown position

As in most empirical models of tree growth, our model contained a term relating to tree size (DBH). Radial growth is usually not linearly related with tree stem diameter (LeBlanc, 1990) and several studies used non-linear relationships in their models (e.g., log-normal function to relate radial growth to DBH in Canham et al., 2004, 2006; Coates et al., 2009). However, visual examination of square-root transformed growth rates as a function of DBH in our study showed that the relationship was relatively linear for the range of DBH included in the sample (~20–50 cm).

Tree crown position was also found to be an important predictor of sugar maple tree growth with suppressed and intermediate positions having lower growth rates than codominant and dominant ones. Lorimer (1983) pointed out that growth prediction requires some information regarding the crown class or competitive status of the subject tree, especially when growth is predicted following some change in the competitive environment (e.g., harvesting).

4.2.2. Effects of competition and crown light environment

In this study, the NCI was a better predictor of sugar maple growth than the crown-level light conditions (GLI). Although the NCI used in this study accounted for both taller and smaller neighbours, the GLI was influenced by taller neighbours only. The better fit obtained with the NCI compared to the GLI indicates that sugar maple square-root transformed radial growth is mostly affected by competitive interactions involving resource depletion by neighbours of all sizes, implying that factors beyond light interaction were involved. This explanation is consistent with the high nutrient demand of sugar maple (St.Clair et al., 2008), and with its strong responsiveness to variation in soil nutrient availability (Moore and Ouimet, 2006). Because interactions with neighbours' root systems are probably occurring in a limited area around target trees, it is not surprising that the best fit was obtained with a NCI based on the smallest neighbourhood.

Another explanation of the poor performance of GLI on predicting growth might be related to the limited precision in our estimates of crown light environment. This may be due to: (i) some assumptions in the light model, such as that of symmetrical crowns with cylindrical shape, (ii) the use of allometric equations to predict tree height and crown dimensions from measured DBH (since tree height and crown dimensions were not directly measured in our study plots), and (iii) the need to use parameters

from studies in regions outside our study area for some species. Similar concerns have been mentioned by Mailly et al. (2003) and Stadt et al. (2007) regarding the precision and intermediate performance of the light indices they used to model tree growth.

4.2.3. Effect of skid trail proximity

It is well recognized that forest harvesting leads to soil disturbance and alteration of soil physical properties (Grigal, 2000), but the duration of such negative impact has been little investigated. Our results suggest that negative impacts on tree growth occur in a zone up to 12 m around skid trails and that these impacts extend at least 10 years after harvest in selection cut stands. Similarly, Hartmann et al. (2008) observed increased soil penetration resistance in the same study sites indicating soil compaction in skid trails 11 years after selection cutting. The negative impact of skid trail proximity on residual tree growth might be due to root damage incurred by trees located near the trails, as well as to impaired post-harvest root development of residual trees in compacted soil. In a selection harvested sugar maple stand in southern Quebec, Malo (2008) observed reduced fine root growth in both primary and secondary skid trails. Obviously, reduced fine root growth could lead to reduced overall tree growth although Hartmann and Messier (2008) could not find support for this relationship in the analysis of their factorial design.

Tree growth predictions that do not account for skid trails may both under- or overestimate actual growth rates. This could happen if post-harvest yield is estimated from forest inventory sample plots within an unbalanced sampling design with proportionally more trees either close to or far from skid trails than actually encountered in the field. Our data set was obtained from very large sample plots (0.4 ha) and we consider it a representative sample of actual skid trail distances, because there was no important overall prediction bias (0.6%) when information on skid trails was ignored. However, forest inventory plots are usually of smaller size (e.g., 400 m^2) and this could lead to an unbalanced sampling distribution of skid trail distances and hence to prediction bias.

Soil disturbance in skid trails, and its negative consequences on residual tree growth, can persist for several years (e.g., Puettmann et al., 2008b). Thus, care should be taken to minimize soil disturbance by using appropriate techniques and equipment, as well as by minimizing the extent of the skid trail network (Grigal, 2000). In the 18 stands sampled in this study, the percentage of the area affected by skid trails ranged from 9 to 21%, with an average of 14.5% (Table 1). Lower values can generally be achieved through careful pre-harvest planning of the trails layout (Nyland, 1994; Dwyer et al., 2004; Germain and Munsell, 2005). Since consequences can be important even after a single machinery pass (Murphy, 1983; Wang et al., 2007; Malo, 2008), the trail layout should be planned so as to concentrate the effects and to avoid spreading trails throughout a stand (Grigal, 2000).

4.2.4. Model performance

The squared correlation coefficient of 0.324 between predicted versus observed values is, albeit not very high, in the same range as values obtained in natural hardwood forests (Lorimer, 1983). However, our model overestimates low growth rates and under-estimates high growth rates (Fig. 3). A potential explanation for the bias of our model predictions could be that some determinant of growth, such as variation among trees in terms of genetic potential or tree age, is lacking in the model.

Radial growth rates are known to vary with tree age (Duchesne et al., 2003) but tree age is difficult to measure. Although stem diameter is sometimes interpreted as a surrogate measure of tree age, the diameter–age relationship may be weak and levels off with increasing diameter (Leak, 1985; Kenefic and Nyland, 1999) and the usefulness of estimating tree age from diameter has been questioned

altogether (McClaran and Bartolome, 1990). Consequently, the inclusion of stem diameter in our models may not accurately represent the functional form of the diameter–age relationship and our growth estimates could suffer from this deficiency.

5. Conclusions

In the recent years, there has been an increasing interest towards the development of silvicultural practices that would better allow preserving and enhancing the structural complexity of forests (Puettmann et al., 2008a). Such silvicultural practices include variable retention and partial cuts of various sorts. This study confirms earlier reports that have indicated the importance of local neighbourhood characteristics to individual-tree growth (e.g., Canham et al., 2004, 2006; Coates et al., 2009). Our results also suggest that the negative effects were mainly from below-ground interaction with conspecifics. It is well recognized that a better understanding of the effect of gaps, and patchiness in general, and individual-tree response to this within-stand structural hetero-geneity is required to evaluate appropriately the effect of different silvicultural options (Coates et al., 2003). The study also confirmed the long-term negative influence of skid trails on residual tree growth, further stressing the importance of minimizing machinery movement within stands. Effective planning of partial harvest could benefit from the use of individual-tree spatially explicit models that explore the effects of different levels and spatial configuration of harvest, including skid trail network layout, on residual tree growth (Coates et al., 2003).

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