Predicting basal area increment in a spatially explicit, individual tree model: a test of competition measures with black spruce

Daniel Mailly, Sylvain Turbis, and David Pothier

Abstract: A current trend in the development of forest stand models is to use spatially explicit, individual-tree information to simulate forest dynamics with increased accuracy. By adding spatial information, such as tree coordinates, crown shape, and size, it is hypothesized that the computation of the model's driving function is improved over traditional competition indices, especially when simulating multistoried stands. In this paper, we want to test whether computationally demanding competition indices outperform traditional indices in predicting mean basal area increment. The study was undertaken in old, uneven-aged black spruce (*Picea mariana* (Mill.) BSP) stands in northeastern Quebec, Canada. The predictability of individual tree growth rates was related to crown dimensions and other stand and tree variables measured in the field. Data were collected from 90 trees coming from stands of varying site quality (range 9.6–16.5 m height at 50 years, age taken at 1 m) and age (range 66–257 years). Hegyis's distance-dependent competition index was found to be the most strongly correlated competition measure (r = 0.57) with mean basal area growth of the last 20 years. This value, 12% higher than the value obtained from the best distance-independent competition index (r = 0.45), clearly shows that precision gains can be achieved when estimating basal area increment with spatial indices in black spruce stands. Using indices computed from virtual hemispherical images did not prove superior to simpler distance-dependent indices based on their individual correlations with basal area increment. When included in a basal area increment model for the last 20 years of growth, however, the gains in precision were comparable to Hegyi's competition index. This indicates that indices derived from a hemispherical approach have some value in spatially explicit forest simulations models but that further tests using younger stands are needed to confirm this result in black spruce stands.

Résumé : La tendance actuelle dans la mise au point de modèles à l'échelle du peuplement forestier consiste à employer de l'information spatialement explicite à partir d'arbres pris individuellement afin de simuler la dynamique des forêts avec une précision accrue. En ajoutant de l'information spatiale telle que la localisation des arbres, la forme et la dimension des houppiers, on présume que le calcul de la fonction motrice du modèle est améliorée par rapport aux indices de compétitions traditionnels, particulièrement pour la simulation de peuplements pluri-étagés. Dans cet article, nous voulons tester si les indices de compétition qui sont particulièrement coûteux en temps de calcul informatique surpassent les indices traditionnels en précision pour prédire l'accroissement moyen en surface terrière. L'étude a été entreprise dans de vieux peuplements d'épinette noire de structure inéquienne (*Picea mariana* (Mill.) BSP) localisés dans le Nord-Est du Québec, au Canada. La prévisibilité des différents taux de croissance des arbres a été reliée à la dimension des houppiers et à d'autres variables du peuplement et à des mesures d'arbres prises sur le terrain. Des données ont été recueillies sur 90 arbres provenant de peuplements de diverses qualités de station (écart allant de 9,6 à 16,5 m de haut à 50 ans, âge pris à 1 m) et différents âges (écart allant de 66 à 257 ans). L'indice de compétition dépendant des distances de Hegyi s'est avéré la mesure de compétition la mieux corrélée (r = 0,57) avec l'accroissement moyen en surface terrière des 20 dernières années. Cette valeur, 12 % plus haute que la valeur obtenue à partir du meilleur indice de compétition indépendant des distances (r = 0,45), démontre clairement que des gains de précision peuvent être réalisés en estimant l'accroissement moyen en surface terrière avec des indices de type spatial dans des peuplements d'épinette noire. L'emploi d'indices de compétition calculés à partir d'images hémisphériques virtuelles ne s'est pas avéré meilleur que l'utilisation d'indices de compétition dépendants des distances, plus simples, si on se base sur leurs corrélations avec l'accroissement moyen en surface terrière. Lorsqu'inclus dans un modèle d'accroissement moyen en surface terrière au cours des 20 dernières années, cependant, les gains en précision pour le modèle étaient comparables à ceux obtenus avec l'indice de compétition de Hegyi. Ceci indique que les indices dérivés d'une approche hémisphérique ont une certaine valeur dans les modèles de simulation forestière spatialement explicites, mais également que d'autres essais avec de plus jeunes peuplements sont nécessaires pour confirmer ce résultat pour les peuplements d'épinette noire.

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Introduction

Black spruce (*Picea mariana* (Mill.) BSP) is a ubiquitous tree species in boreal landscapes of northern North America and is the most important commercial tree species in Quebec. Stands of black spruce originate from fire or through clear-cutting and, in some cases, from old horse logging. Both even-aged and uneven-aged structures may be found, and in general these structures include abundant advance growth, generally from layers (Morin and Gagnon 1992). Tree harvesting in these forests is generally done using the traditional clear-cutting method with protection of advance regeneration, either in cutblock areas or in strips (Pothier 2000).

Recently, alternative harvesting methods have been introduced in eastern Canada with the aim of preserving tall saplings, thus leaving well-regenerated stands (Hökkä and Groot 1999). Such logging methods can be fully mechanized and can help maintain an uneven-aged structure in these forests by carefully leaving small merchantable trees in the residual stand. This poses, however, a challenge to growth modelling. It is currently done using the province's system of equations for yield prediction (Pothier and Savard 1998). The system is based on variable-density yield tables, which are normally used for relatively pure, even-aged stands.

The lack of an adequate tool to simulate and predict growth and yield in uneven-aged stands of black spruce led us to look for an alternative approach. A distance-dependent modelling approach that uses competition indices was chosen on the basis that it can handle mixed stands or uneven-aged stands better than nonspatial models (Pukkala et al. 1994; Pretzsch 1995). Distance-dependent competition indices have been widely used and tested in the past (Tomé and Burkhart 1989; Biging and Dobbertin 1992, 1995; Wimberly and Bare 1996; Vettenranta 1999), often with mitigated success (Vanclay 1994). Simple measures of stand density or basal area have, in many cases, been as good in predicting tree growth increment as more sophisticated indices that take into account intertree distances along with crown shape and size (Lorimer 1983; Vanclay 1994).

More recently, efforts have been made to use detailed light simulation as a process-oriented competition index in growth models for forest management (Brunner and Nigh 2000) or in forest succession models (Canham et al. 1999). Light modelling is seen as a promising approach, since the amount of light absorbed and net primary production are highly correlated (e.g., Jarvis and Leverenz 1983; Wang et al. 1991). Estimating the amount of light absorbed by a tree crown during a growth period is computationally demanding, however, and the task of implementing it into a simulation model raises questions as to whether it is warranted for the purpose of yield forecasts for uneven-aged black spruce stands.

We do not know of any other study where distance-independent, distance-dependent, and light competition indices were compared with each other in their capacity to predict tree growth increment in old, uneven-aged stands. This study was undertaken to test the hypothesis that competition indices that more explicitly take into account the spatial distribution of trees in uneven-aged stands would be better correlated with tree growth increment than nonspatial indices. A second objective was to identify a competition index that in combination with other independent variables, best describes basal area increment in old, uneven-aged black spruce stands.

Materials and methods

Data

Twenty-six sample plots were established north of the Manicouagan reservoir in the province of Quebec during the summer of 2000 (Fig. 1), in an area that lies in the Black Spruce – Moss biogeoclimatic domain (Robitaille and Saucier 1998). The stands were selected for sampling if they were representative of the forest inventory database for the area, the overstory was dominated by black spruce, there was no evidence of recent disturbance, the stand composition and site type were uniform within the stand, and the stand was accessible by road or by helicopter. As a result of these constraints, no random selection procedures were applied in choosing stands or in locating plots within stands.

One square plot (20 × 20 m, 0.04 ha) was established within each selected stand. In establishing the plot, the following data were recorded for every tree whose diameter at breast height (DBH; 1.30 m) was greater than 7.0 cm: species, canopy class, DBH, and live crown ratio (10% classes). Within the plots, each tree's polar coordinates were measured using a laser rangefinder (Impulse™) equipped with a MapStar™ electronic compass module (Laser Technology Inc., Colorado) levelled on a surveyor tripod.

A subset of trees was selected for coring and height measurement following a method similar to the one described in B.C. Ministry of Forests (2000). For each tree, total height and height to crown base, four crown radii (measured in metres for each north, south, east, and west compass directions) as well as tree age and radial increment were measured. To determine the radial growth, one or two increment cores were taken at 1 m height from selected trees using an increment borer. The cores were sanded and subsequently analysed using the WINDENDRO™ measuring system (Guay et al. 1992). The radial growth from the last 5 and 20 years were converted into basal area growth ($cm^2 \cdot year^{-1}$). Basic data on the stands measured are given in Table 1.

Analysis approach

In the present study, a selection of nine competition indices were tested for inclusion in a predictive model of basal area increment. These ranged from simple indices such as density and basal area of competitor trees to more complex indices such as canopy and light indices derived from hemispherical images (Table 2). All competition indices except those estimated from hemispherical images were computed using a specific program written in the Delphi™ programming language (Borland, California). The search radius (R) for inclusion of competitor trees was set to 3.5 times the mean crown radius (Lorimer 1983) of canopy trees in these stands (1.1 m), which resulted in a search radius of 4 m used throughout the study. A tree was considered to be a potential competitor when its DBH was found to be equal or greater than two thirds of the DBH of the subject tree. An exception to these rules is the computation of Schütz's index (Schütz 1989), which uses a special distance for including competitor trees in the neighbourhood of a subject tree (cf. Table 2

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Fig. 1. Map showing locations of the study stands around the Manicouagan reservoir, Quebec, Canada.

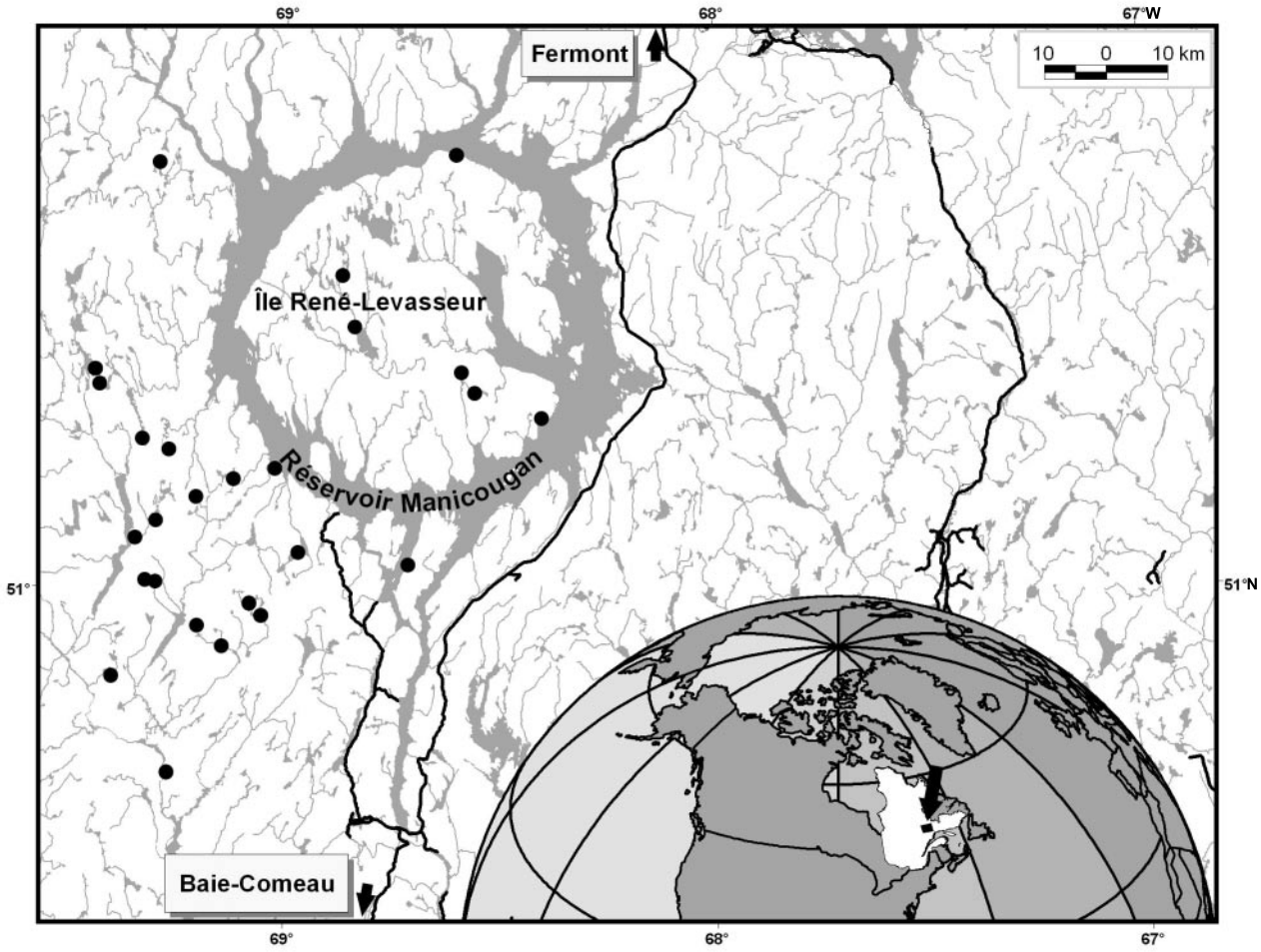


Table 1. Summary statistics for black spruce dominated stands (N = 26).

Variable	Mean	Minimum	Maximum	SD
Stand age (years)	149	66	257	50
Site index (m at 50 years, age at 1 m)	12.9	9.6	16.5	1.7
Stand density (stems·ha^{-1})	3633	875	7500	1643
Stand basal area (m^2·ha^{-1})	22.1	10.8	36.0	7.2
Stand volume (m^3·ha^{-1})	98.0	39.7	190.9	49.4

Note: Volume was estimated using local height–diameter curves and Perron's (1983) tables. SD, standard deviation.

for details). Only black spruce trees that were located within a 12 × 12 m subplot centred inside the plots were selected as subject trees to avoid using edge-bias compensation (Radtke and Burkhart 1998) when computing competition indices. This resulted in 90 subject trees among which there were 7 dominants, 28 codominants, 39 intermediates, and 16 suppressed trees.

When computing competition indices derived from virtual hemispherical images, all trees having a DBH >7.0 cm located within the plot were represented. The crown of black spruce trees was modelled as a rocket (a cone of 25% of the crown length perched on a cylinder 75% of the crown length; Stadt and Lieffers 2000), whereas a solid cone was used for all other conifers and an ellipsoid for broadleaf species. A computer program written in Visual Basic™ was used to convert tree lists into a file format compatible with Persistance of Vision (PovRay™, www.povray.org), a ray-tracing program that allows the conversion of rendered images into 180° fisheye images without or with plot translation (Turbis et al. 2002). While generating the image, the camera was positioned at two thirds of the crown length from the subject tree top (Burger 1939*a*, 1939*b*), which was removed from the tree list for that purpose, and no plot translation was used (Radtke and Burkhart 1998). The upper crown is often called the "light crown", i.e., an area where the tree receives most of the light and, therefore, the most important part of the crown for growth measures (Biging and Dobbertin 1995). Since PovRay™ is a ray-tracing pro-

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Table 2. List of competition indices.

Index	Name	Definition[a]	References
Distance-independent indices			
1	Nn	Number of neighbours j (trees situated at less than R metres, on a per-hectare basis)	
2	SBA	Sum of the basal areas of the neighbours j situated at less than R metres, on a per-hectare basis: $\mathrm{SBA} = \sum_{j=1}^{n} \mathrm{BA}_j$	Steneker and Jarvis 1963
3	C18	Sum of DBH_j of the neighbours j situated at less than R metres, divided by the subject tree DBH_i: $\mathrm{C18} = \frac{\sum_{j=1}^{n} D_j}{D_i}$	Lorimer 1983
Distance-dependent indices			
4	C14	Sum of the ratios between the competitor j and subject tree i DBH, divided by the square root of the ratio between the distance separating the competitor j with subject tree i and the search radius: $\mathrm{C14} = \sum_{j=1}^{n} \frac{D_j / D_i}{\sqrt{\mathrm{DIST}_{ij} / R}}$	Lorimer 1983
5	DCI	Hegyi's diameter-distance competition index, for neighbours j situated at less than R metres: $\mathrm{DCI} = \sum_{j=1}^{n} \left(\frac{D_j}{D_i} \times \frac{1}{\mathrm{DIST}_{ij}} \right)$	Hegyi 1974
6	Schütz	Schütz's index, equals to the sum of the vertical and horizontal competition components:[b] $\text{Schütz} = \sum_{j=1}^{n} \left[k \frac{H_j - H_i}{\mathrm{CR}_j + \mathrm{CR}_i} + \left(0.5 - \frac{E_{ij}}{\mathrm{CR}_j + \mathrm{CR}_i} \right) \right]$	Schütz 1989; Ung et al. 1997
Hemispherical-image indices			
7	CO	Canopy openness, percentage of open sky seen from beneath a forest canopy	Frazer et al. 1999
8	LAI_5	Effecitve leaf area index integrated over the zenith angle 0–75°	Welles and Norman 1991
9	TSF	Total site factor, ratio between total radiation (diffuse and direct components) received under and above the canopy	Frazer et al. 1999

[a] D_i, diameter at breast height of subject tree i; D_j, diameter at breast height of competitor tree j; R, search radius (= 3.5 × mean crown radius of canopy trees, m); K, constant in Schütz's index (0.65); H_i, height of subject tree i; H_j, height of competitor tree j; DIST_{ij}, distance between subject tree i and competitor j; BA_j, basal area of competitor tree j; CR_i, crown radius (m) of subject tree i; CR_j, crown radius (m) of competitor tree j; E_{ij}, distance (m) between crown extremities of subject tree i and competitor tree j.

[b] Note that a neighbour is considered a competitor only if $E_{ij} \leq 0.5(\mathrm{CR}_j + \mathrm{CR}_i) + K(H_j - H_i)$.

gram rather than a sophisticated light model, a special texture imitating the foliage of conifer trees was applied to the generated tree crowns. Tests were made with the Gap Light Analyser (GLA) program (Frazer et al. 1999) to adjust the texture so that it would filter a similar amount of light when compared with real, average canopy trees. Images of 600 × 600 pixels in size were generated by PovRay™ and further analysed with GLA to derive canopy and light indices.

Statistics

The growth model used in this study is a multiple regression model (cf. also Wykoff 1990; Wimberly and Bare 1996; Jõgiste 2000) between basal area increment (mean Δg, $\mathrm{cm}^2 \cdot \mathrm{year}^{-1}$, ln transformed) and four independent variables that were found to be highly correlated with Δg: DBH, diameter at breast height (cm); age, the subject tree's age (years); LCR, the live crown ratio (%); and SI, the plot site index (height in metres at 50 years, age at 1 m; Pothier and Savard 1998):

$$[1] \qquad \ln \Delta g = b_0 + b_1(\mathrm{DBH}) + b_2(\mathrm{age}) + b_3(\mathrm{LCR}) + b_4(\mathrm{SI})$$

To assess the performance of alternative competition indices in improving the value of the growth function, each

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competition index was added independently to the multiple regression model as a first step to test them in the context of basal area growth modelling:

$$[2] \quad \ln \Delta g_5 = b_0 + b_1(\mathrm{DBH}) + b_2(\mathrm{age}) + b_3(\mathrm{LCR}) + b_4(\mathrm{SI}) + b_5(\mathrm{CI})$$

where $\ln \Delta g_5$ is the natural logarithm of mean basal area increment for the last 5 years of growth and CI is the value of the competition index used (cf. Table 2). Because the trees used in this study were fairly old (mean stand age of 149 years; Table 1) and growing at a high latitude, the basal area increment of only the last 5 years was suspected to be affected by climatic variations in addition to competition and ageing. Therefore, a second regression model was used to relate the natural logarithm of mean basal area increment for the last 20 years of growth and the independent variables:

$$[3] \quad \ln \Delta g_{20} = b_0 + b_1(\mathrm{DBH}) + b_2(\mathrm{age}) + b_3(\mathrm{LCR}) + b_4(\mathrm{SI}) + b_5(\mathrm{CI})$$

The models were fitted using the JMP version 4.0 statistical software, using the stepwise forward multiple regression procedure with P value to enter set at 0.10 and P value to leave set at 0.05. Testing for multicollinearity was done by inspecting the leverage plots and by using the Mallow's statistic, C_p, to retain only the significant variables (SAS Institute Inc. 2000).

To compare the value of the growth model without and with the competition index, the mean square error reduction (MSER) relative to no competition index (Biging and Dobbertin 1995; Schröder and von Gadow 1999) was calculated using

$$[4] \quad \mathrm{MSER} = \left[1 - \left(\frac{\mathrm{MSE}_2}{\mathrm{MSE}_1}\right)\right] \times 100$$

where MSE_1 is the mean square error of the basic eq. 1 and MSE_2 is the mean square error of the basic eqs. 2 or 3, respectively.

Results

Hegyi's (1974) distance-dependent competition index (DCI) was found to be well correlated (r = –0.49 and r = –0.57) with basal area increment for the 1995–1999 and 1980–1999 growth periods considered, respectively (Table 3). Lorimer's (1983) C14 distance-dependent index was also well correlated with basal area increment, although the values were slightly lower (r = –0.44 and r = –0.51; Table 3). In both cases, higher correlations were obtained when considering the last 20 years growth period instead of the last 5 years.

The inclusion of Hegyi's (1974) distance-dependent competition index (DCI) into eqs. 2 and 3 resulted in the highest MSER among all competition indices, i.e., 5.82 and 9.84% for the 1995–1999 and 1980–1999 growth periods considered, respectively, (Table 4). The second highest MSER for the 1995–1999 growth period was obtained using Lorimer's (1983) C14 distance-dependent index (MSER 3.25%), whereas LAI_5 resulted in the second highest MSER for the 1980–1999 growth period (MSER 7.98%; Table 4). As for the correlations between basal area increment and competition indices, the higher MSER values were obtained when considering the last 20 years growth period instead of the last 5 years. In a few cases, the inclusion in the model of a competition index resulted in slight reductions in the MSER (Table 4), indicating that some competition indices were not correlated with the unexplained variance of the multiple regression model.

Table 3. Correlation between basal area increment (ln transformed, $\mathrm{cm}^2 \cdot \mathrm{year}^{-1}$) averaged for 1995–1999 and 1980–1999 and the competition indices.

	1995–1999		1980–1999	
Competition index	r	p	r	p
Nn	–0.31	0.003	–0.25	0.019
SBA	–0.01	0.911	–0.02	0.844
C18	–0.39	<0.001	–0.45	<0.001
C14	–0.44	<0.001	–0.51	<0.001
DCI	–0.49	<0.001	–0.57	<0.001
Schütz	–0.15	0.147	–0.31	0.003
CO	0.06	0.591	0.21	0.050
LAI_5	–0.21	0.052	–0.35	0.001
TSF	0.14	0.198	0.29	0.006

Note: See Table 2 for details of the competition indices.

Fitting eq. 2 using the stepwise forward procedure resulted in a model that explained approximately 64% of the variation between ln Δg for the 1995–1999 growth period (Table 5). The LCR was the most significant predictor (partial R^2 = 0.38) followed by site index (partial R^2 = 0.10). The parameters for LCR and SI were positive, indicating that they were positively correlated with basal area increment. The contribution of DCI to the model was modest (partial R^2 of approximately 5.4%; Table 5). The whole model contained all five variables (LCR, SI, DCI, age, and DBH) that had significant coefficients ($P < 0.05$; Table 5, Fig. 2*a*).

Fitting eq. 3 using the stepwise forward procedure resulted in a model that explained approximately 70% of the variation in ln Δg for the 1980–1999 growth period (Table 6). Unlike fitting eq. 2, four independent variables (LCR, SI, age, and DBH) were entered into the model before Hegyi's DCI. The contribution of DCI to the model was also modest (partial R^2 of approximately 4.2%; Table 6). As for eq. 2, the whole model contained all five variables that had significant coefficients ($P < 0.05$; Table 6, Fig. 2*b*).

Discussion

The distance-dependent competition indices DCI and C14 performed better than the nonspatial indices or the hemispherical images indices based on their correlation with basal area increment or their reduction in MSE. We expected that using a more sophisticated competition index would prove superior to other indices, which do not take tree locations or crown length and size into account. An exception to this rule was the Schütz's index whose correlation with basal area increment was similar to using only neighbourhood density as a competition index.

We had also expected that most of the competition indices used in this study would be highly correlated with basal area

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Table 4. Mean square error reduction (MSER) relative to no competition index for the multiple regression between basal area increment (ln transformed, $cm^2 \cdot year^{-1}$) averaged for 1995–1999 and 1980–1999.

	1995–1999			1980–1999		
Competition index	Adjusted R^2	MSE[a]	MSER (%)[b]	Adjusted R^2	MSE	MSER (%)
None	0.595	0.2385	0.00	0.642	0.1788	0.00
Nn	0.606	0.2321	2.71	0.642	0.1790	–0.11
SBA	0.591	0.2408	–0.96	0.640	0.1802	–0.78
C18	0.600	0.2351	1.44	0.646	0.1771	0.95
C14	0.608	0.2308	3.25	0.657	0.1714	4.15
DCI	0.618	0.2247	5.82	0.678	0.1612	9.84
Schütz	0.590	0.2413	–1.18	0.647	0.1764	1.33
CO	0.590	0.2412	–1.10	0.650	0.1748	2.23
LAI_5	0.597	0.2370	0.64	0.671	0.1645	7.98
TSF	0.593	0.2393	–0.32	0.663	0.1685	5.75

[a]Mean square error.
[b]Mean square error reduction (%) relative to the regression model with no competition index.

Table 5. (A) Stepwise regression for the model of ln Δg_5 for 1995–1999 ($cm^2 \cdot year^{-1}$) and (B) the independent variables.

(A) Stepwise regression.

Step	R^2	Sequential SS	P	Variables added
1	0.384	20.12	<0.001	LCR
2	0.475	4.73	<0.001	LCR, SI
3	0.529	2.84	0.002	LCR, SI, DCI
4	0.594	3.41	<0.001	LCR, SI, DCI, age
5	0.640	2.39	0.002	LCR, SI, DCI, age, DBH

(B) Independent variables.

Variable	Estimate	SE	t	P
Intercept	–2.4408	0.4460	–5.47	<0.001
LCR	0.0149	0.0031	4.85	<0.001
SI	0.1463	0.0329	4.44	0.002
DCI	–0.0577	0.0231	–2.50	0.014
Age	–0.0066	0.0014	–4.89	<0.001
DBH	0.0415	0.0127	3.26	<0.001

Note: Results from stepwise regression using the forward procedure (P to enter was 0.10, and P to leave was 0.05). SS, sum of squares; P, probability value; LCR, live crown ratio; SI, site index; DCI, distance competiton index; age, tree age; DBH, diameter at breast height.

increment, since black spruce trees in uneven-aged stands often have a nonrandom or clumped distribution. Increasing the search radius to 6 or 8 m and using plot edge-bias compensation with plot translation did not improve the correlations with basal area increment (data not shown). The fact that a search radius set at 3.5 times the mean crown radius of canopy trees (in our case, $R = 4$ m) worked well is consistent with Lorimer (1983) who recommends such a rule for most applications. In his study, Lorimer (1983) found that (*i*) this distance appears to be long enough to assess important variations in local stocking near the subject tree, (*ii*) the correlation of the competition index with growth was close to the observed maximum, and (*iii*) yet it is a short enough distance that in many stands it could be used on small plots (≤0.08 ha) without losing too many trees to the border zone. Unlike Lorimer (1983), however, the distance-independent competition index C18 was inferior to the distance-dependent C14 or Hegyi's (1974) DCI, suggesting that in our study, traditional distance-independent indices proved inferior to distance-dependent indices. Other studies have also found Hegyi's DCI to be on par or superior to other competition indices (Alemdag 1978; Pukkala and Kolström 1987; Holmes and Reed 1991). Hegyi's DCI is an index that uses distance from subject to competitor as denominator, thereby giving a greater weight to closer competitors (Wimberly and Bare 1996). This supports the hypothesis that significant competitive stress on individual trees may be induced only by the ring of competitor trees immediately surrounding the subject tree crown (Cole and Lorimer 1994). Results from our study suggests that DCI is a suitable index to use in nonrandom or clumped distributions such as those found in old, uneven-aged black spruce stands.

Competition indices based on virtual hemispherical images did not generally prove superior to other indices based on their individual correlation with basal area increment. An exception to this generalization was the inclusion of LAI_5 and TSF in the basal area increment model for the 1980–1999 period, which resulted in MSE reductions of 7.98 and 5.75%, respectively, i.e., second and third after Hegyi's (1974) DCI (9.84%). It appears that using an index that takes into account only DBHs and distances from competitors was more able to capture competitive effects than indices using crown shapes and distances such as those estimated by hemispherical images. One possible explanation may be the difficulty experienced in the field to measure and assess the crown dimensions of old black spruce trees. Such trees often have misshapen crowns, sometimes with foliage located only on one half or one third of the crown. The use of symmetrical crown shapes (rocket, cone, ellipsoid) in the ray-tracing program may have overestimated crown size in some cases, thereby influencing the computation of LAI_5, openness, or TSF from the virtual hemispherical images. Calculating canopy light and structural indices for several sample points per tree at the crown surface (e.g., Brunner and Nigh 2000) instead of only one might have yielded better correlations between basal area increment and hemispherical canopy indices. The computation of light indices

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Fig. 2. Residuals for eqs. 2 and 3 plotted versus predicted values.

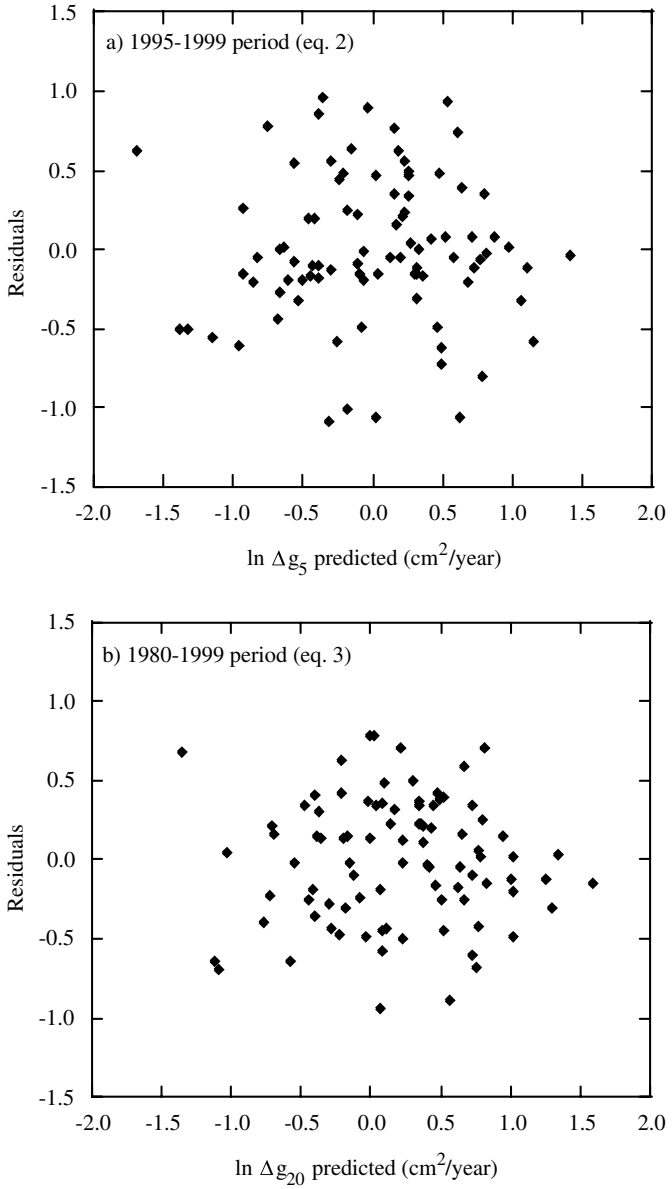


Table 6. (A) Stepwise regression for the model of ln Δg_{20} for 1980–1999 ($cm^2 \cdot year^{-1}$) and (B) the independent variables.

(A) Stepwise regression.

Step	R^2	Sequential SS	P	Variables added
1	0.345	15.36	<0.001	LCR
2	0.523	7.89	<0.001	LCR, DBH
3	0.618	4.23	<0.001	LCR, DBH, age
4	0.658	1.81	0.002	LCR, DBH, age, SI
5	0.700	1.66	0.002	LCR, DBH, age, SI, DCI

(B) Independent variables.

Variable	Estimate	SE	t	P
Intercept	–1.7428	0.3778	–4.61	<0.001
LCR	0.0114	0.0026	4.36	<0.001
DBH	0.0595	0.0108	5.53	<0.001
Age	–0.0066	0.0011	–5.78	<0.001
SI	0.1003	0.0279	3.60	0.001
DCI	–0.0627	0.0196	–3.21	0.002

Note: Results from stepwise regression using the forward procedure (P to enter was 0.10, and P to leave was 0.05); SS, sum of squares; P, probability value; LCR, live crown ratio; SI, site index; DCI, distance competiton index; age, tree age (years); DBH, diameter at breast height.

from a spatially explicit light model (e.g., Brunner 1998; Stadt and Lieffers 2000) might also have provided better correlations with tree growth, however this was not tested.

Our results with the distance-dependent Schütz's index contrast with the findings of Ung et al. (1997) who found Schütz's index to be superior to the distance-dependent indices of Arney (1973) or Monserud and Ek (1977). Ung et al. (1997) found a correlation of –0.81 between Schütz's index and the logarithm of basal area increment of the last 5 years of growth in an uneven-aged black spruce stand. Unlike our study, however, their stand was relatively younger (~77 years old) compared with our mean stand age (149 years old), was growing in a relatively milder climate (48°N) compared with the mean site latitude in our study (51°N), and had only 16 observations.

The fact that this study was conducted in old, uneven-aged stands may have concealed the true value of using sophisticated competition indices based on crown shape and size or estimated from hemispherical images. Most studies using competition indices are conducted on relatively young and even-aged stands (e.g., Barclay and Layton 1990; Schröder and von Gadow 1999; Brunner and Nigh 2000) that are leaving the stem exclusion stage or entering the understory reinitiation stage (sensu Oliver 1981). Basal area increment normally declines when trees enter the senescence phase, and during this period, sophisticated competition indices may be of little added value in explaining tree growth. Factors other than competition such as ageing and climatic fluctuations very likely outweigh competition per se in some old trees, and this may explain why basal area increment of the last 20 years of growth was better correlated with competition than for the last 5 years.

Live crown ratio was found to be the single most important variable of eqs. 2 and 3, i.e., for the 1995–1999 and 1980–1999 growth periods considered, respectively. The live crown ratio is related to crown shape and size, which in turn reflect the competitive ability of the tree and, consequently, its photosynthetic capacity and bole volume increment (Raulier et al. 1996). As Lorimer (1983) pointed out, growth cannot be predicted from stem spatial pattern alone and requires some indication of the crown class or competitive status of the subject tree, especially when predicting recovery from competition when a competitor is removed (e.g., by thinning, Vanclay 1994).

Conclusion

Hegyi's (1974) distance-dependent competition index was found to be the most well-correlated competition measure (r = 0.57) with mean basal area growth of the last 20 years. This value, 12% higher than the value obtained from the best distance-independent competition index, clearly shows that precision gains can be achieved when estimating basal area increment with spatial indices in black spruce stands.

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Using indices computed from virtual hemispherical images did not prove superior to simpler distance-dependent indices based on their individual correlations with basal area increment. When included in the basal area increment model for the 1980–1999 growth period, however, the gains in precision were comparable to Hegyi's distance-dependent competition index. This indicates that indices derived from a hemispherical approach have some value in spatially explicit forest simulations models but that further tests using younger stands are needed to confirm this result in black spruce stands.

The fact that the live crown ratio was found to be the single most important variable in the basal area increment models suggests that this variable is worth measuring. Estimating, to the nearest 10%, the live-crown length of all living tagged trees in an inventory plot is a standard procedure in some places (e.g., B.C. Ministry of Forests 2000), and we strongly recommend it being implemented in any forest inventory procedures aimed at collecting data for growth modelling

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References

Alemdag, I.S. 1978. Evaluation of some competition indexes for the prediction of diameter increment in planted white spruce. Can. For. Serv. For. Manag. Inst. Inf. Rep. FMR-X-108.

Arney, J.D. 1973. Tables for quantifying competitive stress on individual trees. Can. For. Serv. Pac. For. Res. Cent. Inf. Rep. BC-X-78.

Barclay, H.J., and Layton, C.R. 1990. Growth and mortality in managed Douglas fir: relation to a competition index. For. Ecol. Manage. **36**: 187–204.

B.C. Ministry of Forests. 2000. Establishing permanent sample plots in natural stands — June 2000. B.C. Ministry of Forests, Resources Inventory Branch, Victoria, B.C.

Biging, G.S., and Dobbertin, M. 1992. A comparison of distance-dependent competition measures for height and basal area growth of individual conifer trees. For. Sci. **38**: 695–720.

Biging, G.S., and Dobbertin, M. 1995. Evaluation of competition indices in individual tree growth models. For. Sci. **41**: 360–377.

Brunner, A., and Nigh, G. 2000. Light absorption and bole volume growth of individual Douglas-fir trees. Tree Physiol. **20**: 323–332.

Brunner, A. 1998. A light model for spatially explicit forest stand models. For. Ecol. Manag. **107**: 19–46.

Burger, H. 1939*a*. Der Kronenaufbau gleichalteriger Nadelholzbestande. Schweiz. Anst. Forstl. Versuchswesen. Mitt. **21**: 5–57.

Burger, H. 1939*b*. Baumkrone und Zuwachs in zwei hiebsreifen Fichtenbestanden. Schweiz. Anst. Forstl. Versuchswesen. Mitt. **21**: 147–176.

Canham, C., Coates K.D., Bartemucci, P., and Quaglia, S. 1999. Measurement and modeling of spatially explicit variation in light transmission through interior cedar–hemlock forests of British Columbia. Can. J. For. Res. **29**: 1775–1783.

Cole, W.G., and Lorimer, C.G. 1994. Predicting tree growth from crown variables in managed northern hardwood stands. For. Ecol. Manage. **67**: 159–175.

Frazer, G.W., Canham, C.D., and Lertzman, K.P. 1999. Gap Light Analyzer (GLA): imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, user's manual and program documentation. Simon Fraser University, Burnaby, B.C., and the Institute of Ecosystem Studies, Millbrook, New York.

Guay, R., Gagnon, R., and Morin, H. 1992. A new automatic and interactive tree ring measurement system based on a line scan camera. For. Chron. **68**: 138–141.

Hegyi, F. 1974. A simulation model for managing jack-pine stands. *In* Proceedings, Growth Models for Tree and Stand Simulation, IUFRO S4.01–4. *Edited by* J. Fries. Department of Forest Yield, Royal College of Forestry, Stockholm, Sweden. pp. 74–87.

Hökkä, H., and Groot, A. 1999. An individual-tree basal area growth model for black spruce in second-growth peatland stands. Can. J. For. Res. **29**: 621–629.

Holmes, M.J., and Reed, D.D. 1991. Competition indices for mixed species northern hardwoods. For. Sci. **37**: 1338–1349.

Jarvis, P.G., and Leverenz, J.W. 1983. Productivity of temperate, deciduous and evergreen forests. *In* Ecosystem processes: mineral cycling, productivity and man's influence. *Edited by* O.L. Lange, P.S. Nobel, C.B. Osmond, and H. Ziegler. Physiol. Plant Ecol. 4. pp. 233–280.

Jõgiste, K. 2000. A basal area increment model for Norway spruce in mixed stands in Estonia. Scand. J. For. Res. **15**: 97–102.

Lorimer, C.G. 1983. Tests of age-independent competition indices for individual trees in natural hardwood stands. For. Ecol. Manage. **6**: 343–360.

Monserud, R.A., and Ek, A.R. 1977. Prediction of understorey tree height growth in northern hardwood stands. For. Sci. **23**: 391–400.

Morin, H., and Gagnon, R. 1992. Comparative growth and yield of layer- and seed-origin black spruce (*Picea mariana*) stands in Quebec. Can. J. For. Res. **22**: 465–473.

Oliver, C.D. 1981. Forest development in North America following major disturbances. For. Ecol. Manage. **3**: 153–168.

Perron, J.-Y. 1983. Tarif de cubage général — volume marchand brut. Ministère de l'Énergie et des Ressources du Québec, Québec, Que.

Pothier, D. 2000. Ten-year results of strip clear-cutting in Quebec black spruce stands. Can. J. For. Res. **30**: 59–66.

Pothier, D., and Savard, F. 1998. Actualisation des tables de production pour les principales espèces forestières du Québec. Direction des inventaires forestiers, ministère des Ressources Naturelles du Québec, Québec, Que.

Pretzsch, H. 1995. Zum Einfluss des Baumverteilungsmusters auf den Bestandeszuwachs. Allg. Forst Jagdztg. **166**: 190–201.

Pukkala, T., and Kolström, T. 1987. Competition indices and the prediction of radial growth in Scots pine. Silva Fenn. **21**: 55–67.

Pukkala, T., Vettenranta, J., Kolstrom, T., and Miina, J. 1994. Productivity of mixed stands of *Pinus sylvestris* and *Picea abies*. Scand. J. For. Res. **9**: 143–153.

Radtke, P.J., and Burkhart, H.E. 1998. A comparison of methods for edge-bias compensation. Can. J. For. Res. **28**: 942–945.

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Raulier, F., Ung, C.-H., Ouellet, D., and Ung, C.H. 1996. Influence of social status on crown geometry and volume increment in regular and irregular black spruce stands. Can. J. For. Res. **26**: 1742–1753.

Robitaille, A., and Saucier, J.-P. 1998. Paysages régionaux du Québec méridional. Les Publications du Québec, Sainte-Foy, Que.

SAS Institute Inc. 2000. JMP statistical discovery software. Statistics and graphics guide. SAS Institute Inc., Cary, N.C.

Schröder, J., and von Gadow, K. 1999. Testing a new competition index for maritime pine in northwestern Spain. Can. J. For. Res. **29**: 280–283.

Schütz, J.-P. 1989. Zum Problem der Konkurrenz in Mischbeständen. Schweiz. Z. Forstwes. **140**: 1069–1083.

Stadt, K.J., and Lieffers, V.J. 2000. MIXLIGHT: a flexible light transmission model for mixed-species forest stands. Agric. For. Meteorol. **102**: 235–252.

Steneker, G.A., and Jarvis, J.M. 1963. A preliminary study to assess competition in a white spruce – trembling aspen stand. For. Chron. **39**: 334–336.

Tomé, M., and Burkhart, H.E. 1989. Distance-dependent competition measures for predicting growth of individual trees. For. Sci. **35**: 816–831.

Turbis, S., Mailly, D., and Pothier, D. 2002. ADAGE: un logiciel d'analyse et de description de placettes d'inventaire forestier. Direction de la recherche forestière, ministère des Ressources naturelles du Québec, Québec, Que. Note Rech. For. 116.

Ung, C.-H., Raulier, F., Ouellet, D., and Dhôte, J.-F. 1997. L'indice de compétition interindividuelle de Schütz. Can. J. For. Res. **27**: 521–526.

Vanclay, J.K. 1994. Modelling forest growth and yield. Applications to mixed tropical forests. CAB International, Wallingford, Oxon, U.K.

Vettenranta, J. 1999. Distance-dependent models for predicting the development of mixed coniferous forests in Finland. Silva Fenn. **33**: 51–72.

Wang, Y.P., Jarvis, P.G., and Taylor, C.M.A. 1991. PAR absorption and its relation to above-ground dry matter production of Sitka spruce. J. Appl. Ecol. **28**: 547–560.

Welles, J.M., and Norman, J.M. 1991. Instrument for indirect measurement of canopy architecture. Agron. J. **83**: 818–825.

Wimberly, M.C., and Bare, B.B. 1996. Distance-dependent and distance-independent models of Douglas-fir and western hemlock basal area growth following silvicultural treatment. For. Ecol. Manage. **89**: 1–11.

Wykoff, W.R. 1990. A basal area increment model for individual conifers in the northern Rocky Mountains. For. Sci. **36**: 1077–1104.

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