# Individual-tree basal area growth models for jack pine and black spruce in northern Ontario

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Individual-tree models of five-year basal area growth were developed for jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* (Mill.) BSP) in northern Ontario. Tree growth data were collected from long-term permanent plots of pure and mixed stands of the two species. The models were fitted using mixed model methods due to correlated remeasurements of tree growth over time. Since the data covered a wide range of stand ages, stand conditions and tree sizes, serious heterogeneous variances existed in the data. Therefore, the coefficients of the final models were obtained using weighted regression techniques. The models for the two species were evaluated across 4-cm diameter classes using independent data. The results indicated (1) the models of jack pine and black spruce produced similar prediction errors and biases for intermediate-sized trees (12–28 cm in tree diameter), (2) both models yielded relatively large errors and biases for larger trees (> 28 cm) than those for smaller trees, and (3) the jack pine model produced much larger errors and biases for small-sized trees (< 12 cm) than did the black spruce model.

Key words: mixed models, repeated measures, model validation

Les modèles de croissance de la surface terrière pour une période de cinq ans par arbre individuel ont été élaborés pour le pin gris (*Pinus banksiana* Lamb.) et l'épinette noire (*Picea mariana* (Mill.) BSP) du nord de l'Ontario. Les données de croissance des arbres ont été recueillies dans des parcelles permanentes à long terme situées dans des peuplements purs et mélangés des deux espèces. Les modèles ont été ajustés au moyen de méthodes de modèles mixtes à cause du remesurage corrélé de la croissance des arbres au cours du temps. Compte tenu que les données couvraient un grand ensemble d'âges de peuplement, d'états du peuplement et de tailles d'arbres, d'importantes variances hétérogènes existaient au sein des données. En conséquence, les coefficients des modèles finaux ont été obtenus au moyen de techniques pondérées de régression. Les modèles pour les deux espèces ont été évalués pour des classes de diamètre de 4 cm au moyen de données indépendantes. Les résultats indiquent (1) que les modèles pour le pin gris et l'épinette noire ont produit des erreurs de prédiction et des biais semblables pour les arbres de taille intermédiaire (12 à 28 cm de diamètre), (2) que les modèles ont généré des erreurs et des biais relativement importants pour les arbres plus imposants (> 28 cm) que pour les arbres de plus petits diamètres et (3) que le modèle pour le pin gris a généré des erreurs et des biais beaucoup plus importants pour les arbres de petits diamètres (< 12 cm) que dans le cas du modèle pour l'épinette noire.

Mots-clés: modèles mixtes, mesures répétées, validation du modèle

## Introduction

Tree diameter is the easiest and most commonly measured tree attribute. Along with height growth and mortality data, diameter growth data are needed to estimate volume growth and to evaluate the type of product that can be obtained from individual trees and forest stands (Hann and Larsen 1991). Therefore, tree diameter or basal area growth models have traditionally been



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used as one of the primary growth equations in forest growth and yield prediction systems. Over the past several decades, a number of individual-tree diameter or basal area growth models have been developed for a variety of tree species (e.g., Belch-



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er et al. 1982, Wykoff et al. 1982, Hilt 1983, Ritchie and Hann 1985, Monserud and Sterba 1996, Cao 2000, Lessard et al. 2001). Since tree diameter increment and basal area increment are mathematically related, the decision to model either variable is based on convenience (Vanclay 1994). Empirical studies offer no evidence of any difference in the precision of estimating future tree diameter from either diameter or basal area increment equations (West 1980, Shifley 1987). However, some authors prefer to model basal area growth because it is more linearly related to tree volume growth than diameter growth (e.g., Hokka and Groot 1999).

In recent years, different statistical techniques have been applied to estimate the coefficients of linear or nonlinear forest growth and yield models, including diameter or basal area increment equations. Stage and Wykoff (1993) demonstrated how

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to construct a model for different types of unexplained variations, such as variance within and between stands, measurement variance, and time-serial correlation, in estimates of periodic tree increment. Several authors used a mixed model approach to account for correlation of errors in longitudinal data for tree and stand level models (Gregoire et al. 1995, Gregoire and Schabenberger 1996, Fang and Bailey 2001, Hall and Bailey 2001). Zhang et al. (1997) developed a simultaneous equation system to provide compatible estimates for individual tree diameter increment and total stand basal area increment. McDill and Ameties (1993) and Cao (2000) proposed different approaches for estimating annual diameter growth from periodic measurements. Rose and Lynch (2001) applied seemingly unrelated regression (SUR) to estimate the restricted parameters of a tree basal area growth model that accounts for tree interdependency within a plot.

Individual tree diameter or basal area increment is often modeled using either a composite model or a potential / modifier model. A composite model predicts tree diameter or basal area growth as a function of tree attributes (such as tree size, crown ratio, vigour and local competition) and stand level variables (such as age, site index, stand density, and site characteristics) (West 1980, Wykoff 1990, Hann and Larsen 1991, Vanclay 1994, Monserud and Sterba 1996, Hokka and Groot 1999). For example, the following composite model was developed from the Bertalanffy growth function (Vanclay 1994):

$$ln(\Delta d^{k}) = \beta_{0} + \beta_{1}ln(d) + \beta_{2}d^{k} + \beta_{3}E + \beta_{4}C + \varepsilon$$

where  $\Delta d$  is tree diameter increment (annual or periodic); d is initial tree diameter; In is natural logarithm; k is a constant (typically k=1 or 2); E represents a combined effect of environmental variables that commonly include stand habitat type, location, elevation, slope and aspect; C describes the competition among trees and is estimated from tree crown size, competition index, and relative tree size;  $\beta_0$  is the intercept coefficient,  $\beta_1$  and  $\beta_2$  are the slope coefficients for tree diameter  $d, \beta_3$  is the vector of regression coefficients for the environmental variables,  $\beta_4$  is the vector of regression coefficients for the competition variables; and  $\epsilon$  is the model error term.

In contrast, a potential / modifier model takes a form of:

## Growth = Potential Growth $\times$ Modifier

where the potential growth function represents the maximum growth attainable for a tree, and the modifier function represents deviation from the potential due to competition (Quicke et al. 1994). Theoretically, the potential growth function sets an upper limit size that a given tree cannot exceed (Hahn and Leary 1979). The potential growth function and modifier function are usually a function of tree size, crown ratio and a local competition index (Leary and Holdaway 1979). Some researchers consider that the potential/modifier model is more biologically explainable than the composite model approach (e.g., Zhang et al. 1997). Others find that this approach poses several difficulties (e.g., Vanclay 1994). One difficulty is the arbitrary nature of the definition of trees representing maximum attainable growth. Some authors use open-grown trees (e.g., Amateis et al. 1989), while others use the proportion of the fastest-growing trees present in the data (e.g., Teck and Hilt 1991, Schroder et al. 2002). The potential growth function and modifier function are usually constructed in separate steps using appropriate data sets (Belcher *et al.* 1982, Shifley 1987, Amateis *et al.* 1989, Teck and Hilt 1991). An alternative approach of combining the potential growth and modifier functions into one model is also proposed based on Chapman-Richards or logistic functions in recent years, in which the model coefficients of both functions can be estimated simultaneously (Murphy and Shelton 1996, Bitoki *et al.* 1998, Murphy and Graney 1998, Lynch *et al.* 1999, Huebschmann *et al.* 2000). Comparison studies have shown that the two types (composite models and potential / modifier models) of the diameter or basal area increment models performed essentially the same over the range of conditions tested (Shifley 1982, 1987, Wykoff and Monserud 1988, Wykoff 1990).

Jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* (Mill.) BSP) are small- to medium-sized conifer tree species widely distributed throughout the Canadian boreal forest region (OMNR 2000). They are an important source of pulpwood, lumber, and round timber in Canada and are dominant conifer species in the boreal and northern regions of Ontario. For example, jack pine contributes 17% of species composition in the boreal forest region and 8% in the Great Lakes – St. Lawrence (central) forest region. In these two regions, jack pine occupies about 5.9 millions hectares and has about 720 millions cubic meters in gross total volume. Black spruce accounts for 64% of Ontario's coniferous growing stock and 80% of the annual allowable cut and represents important economical activities through the boreal forest region (OMNR 2000).

To date, studies have been conducted on stand density management, growth response to silvicultural treatment and tree diameter-height relationships for the two species in Ontario (Newton and Jolliffe 1998, Peng et al. 2001, Zhang et al. 2002, Peng et al. 2004). However, there have been very limited efforts to develop individual-tree diameter or basal area growth models for jack pine and black spruce. We are aware of only one study for developing an individual-tree basal area growth model for black spruce in second-growth peatland stands in northeastern Ontario (Hokka and Groot 1999). But the growth patterns of black spruce are different for peatland and upland stands (Viereck and Johnston 1990). Therefore, the objectives of this research were (1) to construct a composite model of individual-tree basal area growth for both jack pine and black spruce in northern Ontario, (2) to validate the models using independent data, and (3) to compare the models for the two species across diameter classes.

### **Data and Methods**

Data used in this study were acquired from the permanent plots established and measured by Kimberly Clark Limited in the Longlac—Geraldton area of Ontario. The stands naturally originated during the 1790 to 1923 period. A total of 119 permanent plots were established between 1952 and 1965. At the first measurement, 22 188 trees were measured for diameter at breast height at 1.37 m (DBH). The average DBH was 12.65 cm and varied between 1.3 and 61.2 cm. Jack pine and black spruce were two major tree species, occupying 31.3% and 48.6% in number of trees, respectively. Other tree species included white spruce (*Picea glauca* (Moench) Voss) (1% in number of trees), balsam fir (*Abies balsamea* (L.) Mill.) (2.4%), paper birch (*Betula papyrifera* Marsh.) (5.7%), balsam popular (*Populus balsamifera* L.) (1.2%), trembling

Table 1. Summary statistics of stand variables at the beginning of the first measurement for the 78 plots used for model development

Stand Variables	Mean	Standard Deviation	Minimum	Maximum
Stand total age (year)	82.4	26.2	34	139
Trees per hectare	2451	1169	1001	6462
Mean tree diameter (cm)	13.45	2.99	7.43	20.71
Quadratic mean diameter (cm)	14.26	3.00	7.77	21.80
Mean tree height (m)	12.7	2.5	7.3	18.7
Stand top height <sup>a</sup> (m)	19.2	2.0	13.3	23.0
Stand basal area (m <sup>2</sup> /ha)	34.47	7.41	16.6	48.5
Jack pine site index <sup>b</sup> (m)	16.54	2.51	11.8	25.1
Black spruce site index <sup>b</sup> (m)	15.88	4.23	8.8	30.0

<sup>a</sup>Stand top height is the average tree height of the 100/ha largest trees in diameter.

aspen (*Populus tremuloides* Michx.) (9.8%), and other minor species. Remeasurements were taken at various growth intervals that varied from one to 16 years. Five-year growth intervals represented 78% of the measurements. Only 6% of the measurements were 10-year growth intervals. Other time intervals represented less than 3% each. To obtain consistent growth periods for model development, the following criteria were used to select plots: (1) a plot should have at least three consecutive five-year growth intervals, and (2) a plot should be a pure jack pine or black spruce stand (i.e., 75% or higher in total basal area of jack pine or black spruce, respectively), or a mixed jack pine and black spruce stand (i.e., the sum of the two species' total basal area was 75% or higher). The plots with other tree species as dominant species were not used in this study. As a result, seventy-eight (78) plots were selected with 4501 jack pine trees and 7139 black spruce trees present at the time of plot establishment. These plots covered a range of stand conditions. For example, stand total age varied from 34 to 139 years, stand density ranged from 1000 to more than 6400 trees per hectare, stand quadratic mean diameter was 14.26 cm (7.8 – 21.8 cm), and jack pine site index ranged from 11 to 25 m, while black spruce site index ranged from 9 to 30 m (Table 1). In general, jack pine trees were relatively larger in mean tree size at the beginning of the first measurement and had better basal area growth over the first five-year growth period than black spruce (Table 2).

It is always desirable to validate a prediction model using independent data sets. Among the 41 plots (= 119 - 78) that were not used for constructing the models, pure or mixed jack pine and black spruce plots (24 plots) were identified according to the second criterion for the model development data mentioned above. These plots were not used for developing the models mainly because they did not have three consecutive five-year intervals. For example, the plot 78 was a pure black spruce stand with four repeated measurements that were 10year, 5-year, 5-year and 8-year time intervals. Then individual five-year growth intervals were obtained from these plots for both jack pine and black spruce. A total of 1995 five-year growth intervals were collected for jack pine and a total of 3565 five-year growth intervals were collected for black spruce trees. Table 3 indicated that the size and growth of the trees in the validation data set were compatible with those in the model development data set.

A composite model was chosen to regress the dependent variable, five-year basal area increment (m<sup>2</sup>) of individual trees

(BAG), to available tree and stand predictor variables. These predictor variables were the measurements at the beginning of a five-year growth interval. They included tree DBH (cm), the sum of the basal area (m<sup>2</sup>/ha) in trees with DBHs larger than the subject tree's DBH (BAL), stand mean diameter (cm) (MDBH), stand quadratic mean diameter (cm) (QMD), stand density (i.e., number of trees per hectare) (N), the total basal area of the plot (m<sup>2</sup>/ha) (Stand-BA), mean tree height (m), stand top height (m) (i.e., the average height of the 100/ha largest trees in diameter), species site indices (m) based on Payandeh (1977) (SI), and stand total age (year). However, tree crown information was not available in the data. Thus, tree crown size and related stand variables such as crown competition factor (CCF) were not used in this study. These predictor variables, along with their various transformations, interactions, and combinations as suggested in the literature (e.g., Hann and Larsen 1991), were tested in a multiple linear regression model with the significant level of  $\alpha = 0.05$ . Non-significant variables were removed in the modeling process, resulting in the following model for both species:

$$\ln(BAG + 1) = \beta_0 + \beta_1 \cdot \ln(DBH) + \beta_2 \cdot DBH^2$$
$$+\beta_3 \cdot BAL + \beta_4 \cdot \left(\frac{BAL}{DBH}\right) + \beta_5 \cdot \left(\frac{QMD}{DBH}\right) \quad [1]$$
$$+\beta_6 \cdot SI + \beta_7 \cdot (Stand - BA) + \varepsilon$$

where  $\beta_0 \sim \beta_7$  are regression coefficients to be estimated, and  $\epsilon$  is the model error term. Equation [1] was fitted for jack pine trees and black spruce trees separately.

Mixed model method was used to estimate the regression coefficients ( $\beta_0 \sim \beta_7$ ) in equation [1] using PROC MIXED in SAS (SAS Institute, Inc. 2001) because the tree growth was repeated measurement (Gregoire *et al.* 1995). Different error covariance structures were evaluated to find the desirable fit based on Akaike Information Criterion (AIC), Schwarz's Bayesian Criterion (BIC), and Likelihood Ratio Test (LRT) (Gregoire *et al.* 1995, Littell *et al.* 1996). Both AIC and BIC are essentially log likelihood values penalized for the number of parameters estimated. BIC imposes a heavier penalty than AIC. The error covariance structure with the smallest values of AIC and BIC is considered most desirable. LRT is a  $\chi^2$  test that can be used to determine whether it is necessary to model the covariance structure of the data at all.

The models were validated using two statistics. The mean  $(\overline{e})$  of the prediction errors  $(m^2)$  were computed as follows:

$$\overline{e} = \frac{\sum_{i=1}^{m} \left( BAG_i - B\widehat{A}G_i \right)}{m}$$
[2]

where  $BAG_i$  is the observed five-year tree basal area growth; and  $B\hat{A}G_i$  is the predicted five-year tree basal area growth from equation [1], i = 1, 2, ..., m, and m is the number of observations in the model validation data. The prediction bias is defined as

$$Bias(\%) = \frac{\overline{e}}{\overline{BAG}} \times 100$$
 [3]

<sup>&</sup>lt;sup>b</sup>Site indices were computed based on Payandeh (1977).

Table 2. Summary statistics of tree variables at the beginning of the first measurement for jack pine and black spruce

	Jack Pine (n = 4501)				Black Spruce $(n = 7139)$			
Tree Variables	Mean	Std	Min	Max	Mean	Std	Min	Max
Tree diameter (cm)	14.7	5.1	2.0	36.1	11.35	4.5	1.3	30.2
Five-year diameter growth (cm)	0.61	0.48	0.0	3.4	0.51	0.47	0.0	5.3
Tree basal area (m <sup>2</sup> )	0.019	0.013	0.0003	0.1024	0.012	0.0086	0.0001	0.0716
Five-year basal area growth (m <sup>2</sup> )	0.0016	0.0015	0.0	0.0125	0.001	0.001	0.0	0.0089
$BAL^a$	17.45	9.32	0.0	43.63	26.03	10.79	0.0	47.93

<sup>&</sup>lt;sup>a</sup>BAL is the sum of the basal area (m<sup>2</sup>/ha) in trees with DBHs larger than the subject tree's DBH.

Table 3. Summary statistics of the five-year growth intervals of jack pine and black spruce trees for model validation

	Jack Pine				Black Spruce			
Tree Variables	Mean	Std	Min	Max	Mean	Std	Min	Max
Tree diameter (cm)	16.95	5.0	5.3	39.9	12.92	5.0	1.8	37.3
Five-year diameter growth (cm)	0.69	0.61	0.0	3.8	0.56	0.49	0.0	4.1
Tree basal area (m <sup>2</sup> )	0.025	0.014	0.0022	0.125	0.015	0.0112	0.0003	0.109
Five-year basal area growth (m <sup>2</sup> )	0.002	0.002	0.0	0.0172	0.001	0.001	0.0	0.0113
BALa	19.23	10.26	0.0	41.55	28.04	10.81	0.0	53.29

<sup>&</sup>lt;sup>a</sup>BAL is the sum of the basal area (m<sup>2</sup>/ha) in trees with DBHs larger than the subject tree's DBH.

Table 4. Model fitting statistics of the different error covariance structures for equation [1]

Jack Pine					Black Spruce							
Criterion	AR(1)	ARH(1)	ARMA(1,1)	UN	OLS	Final <sup>d</sup> Model	AR(1)	ARH(1)	ARMA(1,1)	UN	OLS	Final <sup>d</sup> Model
AICa	-161722	-161782	-161721	-161942	-161257	-167984	-264746	-264878	-265668	-266046	-263924	-272284
$BIC^b$	-161658	-161691	-161650	-161793	-161170	-167835	-264677	-264781	-265599	-265887	-263852	-273224
LRT <sup>c</sup>	485.88	553.32	486.21	731.76	_	-1019.20	824.11	964.19	1746.34	2149.88	-	-2957.75
p-value	< 0.0001	< 0.0001	< 0.0001	< 0.0001	-	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	-	< 0.0001

<sup>&</sup>lt;sup>a</sup>AIC is Akaike Information Criterion.

where  $B\overline{A}G_i$  is the mean of observed tree basal area growth. To evaluate the model prediction error and bias across tree sizes, all trees in the validation data were grouped into 4-cm diameter classes. Average prediction error and bias were calculated for each diameter class.

# Results and Discussion Model fitting

Repeated measurements from permanent plots are correlated over time, e.g., at least three consecutive five-year remeasurements in the model development data. It is reasonable to assume that the correlations between observations decrease with temporal distance. Appropriate specification of the error covariance structure of the data is an important part of the model identification process (Gregoire et al. 1995). Four commonly used covariance structures were evaluated to find the desirable specification: first-order autoregressive (AR(1)), heterogeneous first-order autoregressive (ARH(1)), first-order autoregressive moving average (ARMA(1,1)), and completely general or unstructured (UN) (Littell et al. 1996). They were compared by three of the model-fitting criteria computed by PROC MIXED (SAS Institute, Inc. 2001). Table 4 showed that, for both jack pine and black spruce, the LRT tests of different covariance structure were all highly significant, indicating the gain over incorrectly using Ordinary Least Squares (OLS) (i.e., assuming independency between consecutive observations). As a result, the specifications of covariance structure addressed the bias in the standard error of parameter estimates. Table 4 also indicated that, among the four alternative specifications, the completely general or unstructured error structure (UN) was the most desirable one since it produced the smallest AIC and BIC and had the largest LRT for both jack pine and black spruce (Table 4).

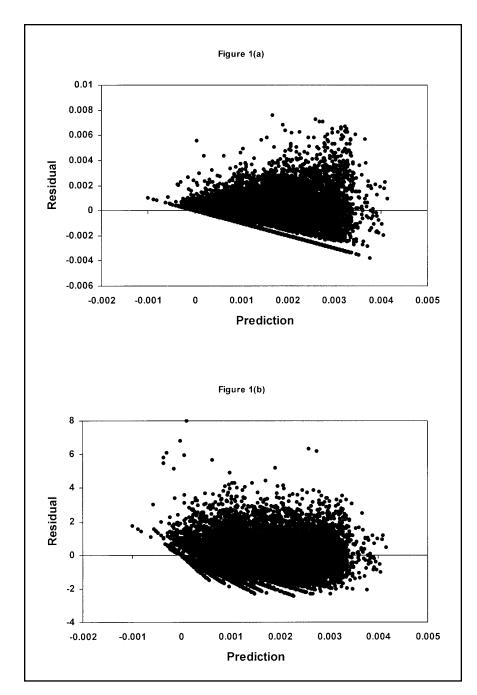
Therefore, the unstructured error covariance structure was used to fit equation [1] for the two species. However, the residual plots revealed that there were heterogeneous variances existing for both jack pine (Fig. 1(a)) and black spruce (Fig. 2(a)). Then the variances of the model residuals were computed for 2-cm DBH classes and the reciprocal of these variances was used as the weight to re-fit equation [1], resulting in the final model. The residual plots of the final models were significantly improved for the heterogeneous variance (Fig. 1(b) and 2(b)). The final models had the smallest AIC and BIC, and the largest LRT (Table 4). The different statistics associated with the parameter estimates indicated that the coefficients for the final model for both jack pine and black spruce were highly significant, except the  $\beta_7$  coefficient for the predictor variable Stand-BA in the jack pine model (Table 5).

The logarithmic transformation of the dependent variable (BAG) in equation [1] stabilizes variance, provides a good fit, and can be easily fitted using linear regression (Vanclay 1994). In general, the predictor variables in the model (equation [1]) represent (1) tree size attribute (e.g., DBH), (2) tree position attribute (e.g., BAL, BAL/DBH, QMD/DBH), (3) site productivity attribute (e.g., SI), (4) stand size attribute (e.g.,

<sup>&</sup>lt;sup>b</sup>BIC is Schwarz's Bayesian Criterion.

<sup>&</sup>lt;sup>c</sup>LRT is Likelihood Ratio Test.

<sup>&</sup>lt;sup>d</sup>The final model was fitted using the unstructured error covariance structure (UN) and weight regression techniques.



**Fig. 1.** Residual plots of the model for jack pine: (a) residual plot of unweighted model, and (b) residual plot of weighted model (final model).

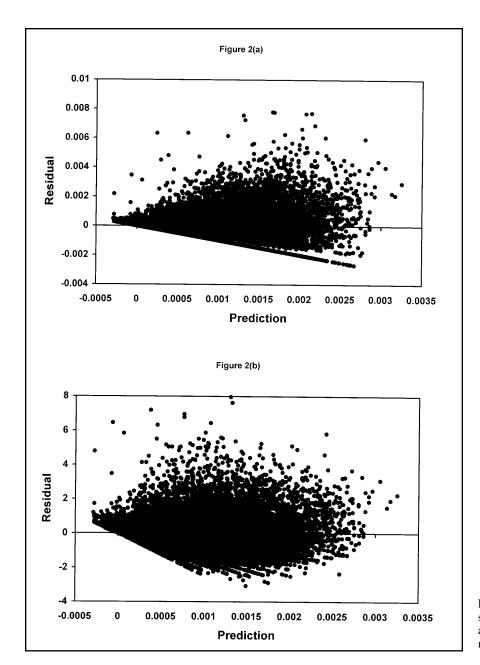
QMD), and (5) stand density attribute (e.g., Stand-BA) (Hann and Larsen 1991). A shortcoming of the model was that it lacked tree vigour attributes (e.g., crown ratio) since they were not available in the data.

Among the predictor variables, BAL is considered as a distance-independent index of trees' competitive position. It was evident that the  $\beta_3$  coefficients were negative, indicating a suppressed tree (larger BAL) would have less basal area growth than that of a dominant tree (smaller BAL). Since the  $\beta_6$  coefficients for SI were positive for both models, a plot with a higher site index would produce better tree basal area growth. The negative  $\beta_7$  coefficients for Stand-BA indicated that a denser stand would produce less tree basal area growth. Conceptually, BAL indirectly quantifies the competition effect from above (large-sized competitors) whereas Stand-

BA indirectly quantifies the competition effect from both above and below (large- and small-sized competitors). Table 5 suggested that a strong asymmetric competitive effect for jack pine and to a lesser degree for black spruce because the  $\beta_3$  (-0.00008) for BAL of the jack pine model was four times larger in magnitude than the one (-0.00002) for the black spruce model, and the  $\beta_7$  coefficient for Stand-BA of the jack pine model was not statistically significant. The results were consistent with many other studies (e.g., Wykoff 1990, Hann and Larsen 1991).

## **Model evaluation**

The final models of the two species were validated using the independent data set (Table 3). The mean prediction errors (m<sup>2</sup>) and bias (%) were computed by equations [2] and



**Fig. 2.** Residual plots of the model for black spruce: (a) residual plot of unweighted model, and (b) residual plot of weighted model (final model).

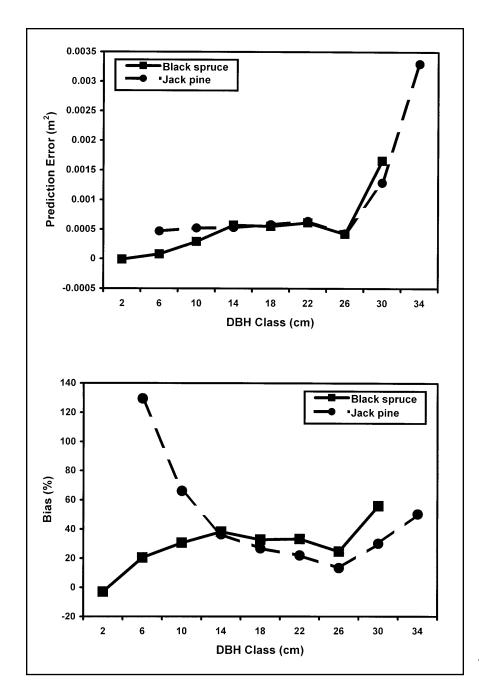
[3]. For jack pine the overall mean prediction error was  $0.00097 \, (m^2)$  and the overall bias was 47%. For black spruce the overall mean prediction error was  $0.000452 \, (m^2)$  and the overall bias was 29%.

To evaluate the model performance across tree sizes, the computed prediction errors and bias were averaged over 4-cm diameter classes and illustrated in Fig. 3. The final models of the two species performed similarly for intermediate-sized trees between 12 cm and 28 cm. The jack pine model produced large prediction errors for small-sized trees. It produced more than 100% bias for trees less then 8 cm in diameter (Fig. 3(b)). It is probably due to the nature of the species (Rudolph and Laidly 1990). Jack pine is one of the most shade-intolerant species. Sapling jack pine trees are sensitive to shade and competition and may have large variations in basal area growth. The jack pine model also produced relatively large bias for large-sized trees because jack pine stands begin to disintegrate after 80 years

on the best sites and after 60 years on the poor sites (Rudolph and Laidly 1990) causing larger variation in basal area growth. On the other hand, the final model of black spruce yielded much smaller prediction errors and bias for small-sized trees (Fig. 3). Black spruce is a shade-tolerant species and is fairly common as an understory tree in pine stands. It can survive without serious loss of vigour under shade and the growth may have less variation across smaller tree sizes (Viereck and Johnston 1990). Similar to the jack pine model, the black spruce model also produced relatively larger prediction error and bias for large-sized trees than it did for small- and intermediate-sized trees.

#### Conclusion

In this study, individual-tree models of five-year basal area growth were developed for jack pine and black spruce in northern Ontario. Tree growth data were collected from longterm permanent plots of pure and mixed stands of the two species.



**Fig. 3.** Validation of the final models of jack pine and black spruce: (a) prediction error (m<sup>2</sup>), and (b) bias (%).

		Jack Pine			Black Spruce	
Coefficient	Estimate	Std Error	p-value	Estimate	Std Error	p-value
$\beta_0$	-0.00440	0.000287	< 0.0001	-0.00316	0.000141	< 0.0001
$3_1^{\circ}$	0.00239	0.000132	< 0.0001	0.00208	0.000070	< 0.0001
$\beta_2$	-0.0000011	0.000000	< 0.0001	-0.0000022	0.000000	< 0.0001
$3_3^2$	-0.00008	0.000003	< 0.0001	-0.00002	0.000001	< 0.0001
$3_4$	0.000456	0.000029	< 0.0001	0.000149	0.000009	< 0.0001
3,	-0.00022	0.000043	< 0.0001	0.00015	0.000015	< 0.0001
$3_6^{\circ}$	0.000039	0.000003	< 0.0001	0.00005	0.000002	< 0.0001
$\beta_7$	-0.0000023	0.000002	< 0.2285	-0.00004	0.000002	< 0.0001

Large variation in tree growth existed in the data that covered a wide range of stand ages, stand conditions and tree sizes. Explanatory variables used to predict the basal area periodic increment were tree initial DBH, the sum of the basal area in trees larger than the subject tree as an index of trees' competitive position, stand quadratic mean diameter, species site index, and stand total basal area. Mixed model methodology was applied to fit the models to account for the correlated model errors due to repeated measures of tree growth. Since the data had strong heterogeneous variances across tree sizes, the coefficients of the final models for the two species were obtained by weighted regression techniques. The model validation indicated that the two models produced similar prediction errors and biases for intermediate-sized trees, and yielded relatively larger errors and biases for larger trees than for smaller trees. However, the jack pine model produced much larger errors and biases for small-sized trees than the black spruce model.

Although tree diameter growth model is a key component in many forest growth and yield prediction systems, it would have restricted applicability without other model components such as height growth, ingrowth, mortality, and regeneration. Hopefully, these model components will be developed in the future. Thus a reliable prediction system will be available for managing the jack pine and black spruce stands in the region.

## Acknowledgments

The authors thank the Associate Editor and two anonymous reviewers for their valuable suggestions and helpful comments on the manuscript. This work was supported by the Network Center of Excellent for SFM (NCE-SFM) at the University of Alberta, Canadian Foundation for Climate and Atmosphere Sciences (CFCAS), and Canada Research Chair program.

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