# Developing and Evaluating Tree Height-Diameter Models at Three Geographic Scales for Black Spruce in Ontario

**Changhui Peng,** *Ministry of Natural Resources, Ontario Forest Research Institute, 1235 Queen Street East, Sault Ste. Marie, ON P6A 2E5, Canada;* **Lianjun Zhang,** *Faculty of Forestry, State University of New York, College of Environmental Science and Forestry, One Forestry Drive, Syracuse, NY 13210;* **Xiaolu Zhou** *and* **Qinglai Dang,** *Faculty of Forestry and the Forest Environment, Lakehead University, 955 Oliver Road, Thunder Bay, ON P7B 5E1, Canada; and* **Shongming Huang,** *Forest Management Division, Land and Forest Service, Alberta Environment, 9920-108 Street, Edmonton, AB T5K 2M4 Canada*

**ABSTRACT:** *A total of 11,612 black spruce trees were measured from permanent sample plots across the boreal and central regions of Ontario and were used to fit the well-known Chapman-Richards growth model at provincial, regional, and ecoregional scales. The results suggest that the height-diameter relationships of black spruce vary with different geographic regions and scales. There were significant variations in height-diameter relationships for black spruce between boreal and central regions as well as among some of the seven ecoregions. The ecoregion-based height-diameter models presented here will provide more accurate predictions for tree height and, consequently, tree volume than these models developed at both provincial and regional scales. Furthermore, the heterogeneity of tree species should be considered in developing and applying ecoregion-based height-diameter models for predicting local tree height. North. J. Appl. For. 21(2):83–92.*

**Key Words:** Permanent sample plot, Chapman-Richards growth function, ecoregion, forest management.

**B**lack spruce (*Picea mariana* (Mill.) B.S.P.) is a wide-ranging, abundant conifer of the northern part of North America. It is the most important pulpwood species in Canada (Farrar 1995) and is one of the dominant species in the boreal and central regions of Ontario. Black spruce accounts for 64% of Ontario's coniferous growing stock and 80% of the annual allowable cut and represents an important economical species throughout the boreal forest region (Ontario Ministry of Natural Resources 2000). Recently, the Ontario growth and yield program has identified an urgent need to develop and evaluate local tree height-diameter equations for estimating tree height, and consequently tree volume. This information is required by forest resources managers to produce accurate yield estimations for the decisionmaking process of ecologically based forest management (Ontario Ministry of Natural Resources 1997, Ontario Ministry of Natural Resources 2000).

The relationship between tree height and diameter is one of most important elements of boreal forest structure. Total tree height and diameter at breast height (1.3 m above ground) outside bark are two essential forest inventory measures. They can be used to estimate timber volume, site index, and other important variables in forest growth and yield, succession, and carbon budget models (Spurr 1952, Botkin et al. 1972, Kurz et al. 1992, Vanclay 1994). In practice, tree diameters can be easily measured in the field at little cost, while tree heights are relatively more difficult and time-consuming to obtain. A common way to deal with

NOTE: Changhui Peng can be reached at (514) 987-3000 ext. 1056#, peng.changhui@uqam.ca. Dr. Peng's current address is Institute des Science de l'Environnement/Department des Sciences Biologiques, Université du Québec à Montréal, Case Postale 8888, Succ Centre-ville, Montréal, H3C 3P8, Canada. The authors thank K. Zhou for assistance on the permanent sample plot data set and mapping location and P. Uhlig for providing the updated Ecoregion Map of Ontario. We are grateful to the three anonymous reviewers for their valuable comments and suggestions on the manuscript. This work was supported in part by the Forest Growth and Yield Program of the Ontario Ministry of Natural Resources and the Sustainable Forest Management Network of Centre of Excellence (NCE-SFM) and CFCAS. X. Zhou acknowledges receipt of a postdoctoral fellowship from Lakehead University. 

the problem is to use an established height-diameter model to predict tree heights from field measurements of tree diameters. Accurate prediction of tree heights is thus critical in forest inventory, model simulation, and management decisionmaking (Curtis 1967, Botkin et al. 1972). Recently, 25 nonlinear, height-diameter models have been developed for nine major tree species, including black spruce, of Ontario's boreal forests (Peng 1999, Peng et al. 2001a). In these studies, the Chapman-Richards model is identified as one of the best model forms for all species across the entire study region in Ontario. However, height-diameter relationships depend heavily on local environmental conditions and vary within a large geographic region. The existing province-based models fail to account for the effects of variable climatic and ecological factors on tree height-diameter relationships within the different ecological regions and thus are only appropriate for making height predictions on a broad provincial basis. To date, there is no ecoregion-based tree height-diameter model available for black spruce in Ontario. Applying the provincial models to local ecological sites may result in biased prediction for tree heights. For example, Zhang et al. (2002) used provincial height-diameter model to predict jack pine tree height in each ecoregion in Ontario. They found that the provincial model underestimated tree heights from 1 to 10% and overestimated tree height from 2 to 7% for jack pine. Furthermore, the ecoregion-based height-diameter models are needed to help forest managers better understand the nature of various relationships that characterize, differentiate, and influence the development of forest ecosystem (Huang 1999, Huang et al. 2000, Peng et al. 2001b).

The objectives of this study were: (1) to develop tree height-diameter models for black spruce at provincial, regional, and ecoregional scales in Ontario; (2) to compare the different height-diameter relationships among different geographic scales; and (3) to evaluate the consequences and biases resulting from the use of height-diameter models in ecoregions for which they were not parameterized.

## Data, Models, and Methods

### Data and Study Area

A total of 11,612 black spruce tree heights were collected from permanent sample plots across the boreal and central regions of Ontario (Hayden et al. 1995). All sampled trees were measured for diameter at breast height (dbh) outside bark and total height (H). Forked trees or those with damaged tops were excluded from the analysis. The study area was assigned to seven ecoregions in the boreal and central regions of Ontario, namely 3E, 3S, 3W, 4E, 4S, 4W, and 5E (Figure 1). The boreal region covers five ecoregions, including 3E, 3S, 3W, 4S, and 4W, while the central region contains only ecoregions 4E and 5E. Theses ecoregions are characterized by broad climatic patterns (e.g., temperature and precipitation), soil moisture and nutrient regimes, growing season length, and vegetation types, and provide comprehensive information about the changes in species-ecoregion relationships along ecological and macroclimatic gradients within Ontario. Detailed analysis of climatic characteristics for each ecoregion can be found in Mackey et al. (1996). The summary statistics of diameter and total height for black spruce trees are provided for each ecoregion, the

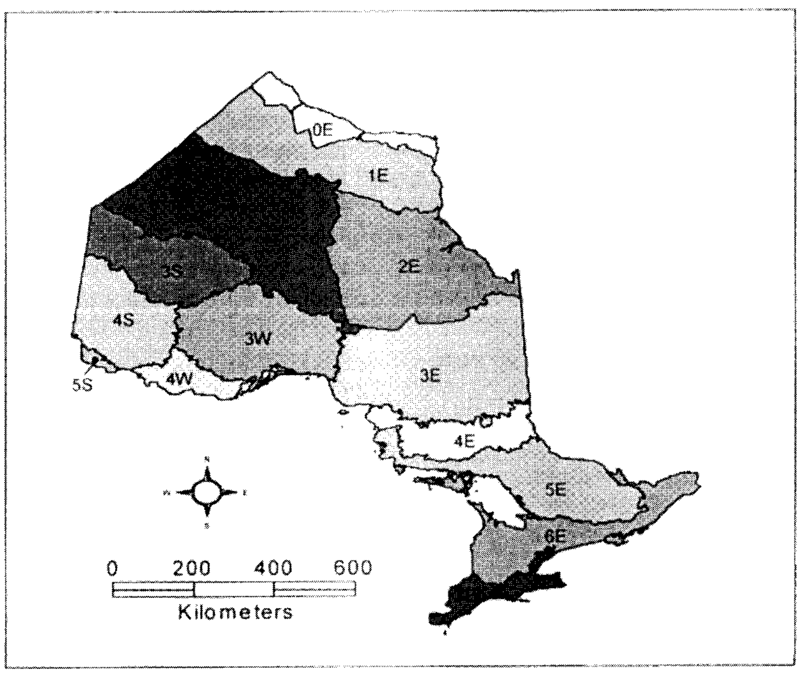


**Figure 1. Simple map of ecoregion classifications in Ontario, Canada (ELC Working Group 2000). This is the updated and improved version of Hills' site regions of Ontario (Hills 1959), which are characterized by broad climatic patterns (e.g., temperature and precipitation), soil moisture and nutrient regimes, and vegetation types.**

**Table 1. Summary statistics of tree diameter at breast height (dbh) and total height (H) for black spruce in Ontario, Canada: ecoregions, regions, and all data combined.**

| Scale | $N$ | dbh (cm) | | | | H (m) | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Mean | STD | Min | Max | Mean | STD | Min | Max |
| Ecoregion | | | | | | | | | |
| 3E | 5,661 | 11.45 | 5.97 | 0.70 | 35.10 | 10.24 | 4.78 | 1.30 | 27.30 |
| 3S | 620 | 12.19 | 6.29 | 2.50 | 36.50 | 11.06 | 5.01 | 2.25 | 26.80 |
| 3W | 2,791 | 10.87 | 6.55 | 1.42 | 33.10 | 9.64 | 5.43 | 1.67 | 25.60 |
| 4E | 432 | 10.13 | 6.28 | 2.50 | 28.40 | 9.38 | 5.00 | 1.61 | 26.07 |
| 4S | 1,240 | 11.13 | 6.19 | 2.50 | 35.40 | 10.28 | 5.07 | 2.09 | 22.85 |
| 4W | 696 | 11.67 | 5.94 | 2.50 | 34.70 | 10.63 | 4.81 | 2.10 | 25.00 |
| 5E | 172 | 10.14 | 6.82 | 2.50 | 27.90 | 8.98 | 5.21 | 1.81 | 21.30 |
| Region | | | | | | | | | |
| Boreal | 11,008 | 11.32 | 6.17 | 0.70 | 36.50 | 10.15 | 5.01 | 1.30 | 27.30 |
| Central | 604 | 10.13 | 6.43 | 2.50 | 28.40 | 9.27 | 5.06 | 1.61 | 26.07 |
| Province | | | | | | | | | |
| Overall | 11,612 | 11.26 | 6.19 | 0.70 | 36.50 | 10.11 | 5.01 | 1.30 | 27.30 |

NOTE: $N$—sample size (number of trees); STD, standard deviation; Min, minimum; Max, maximum.

boreal and central regions, and all data combined (overall) in Table 1.

## Methods

The Chapman-Richards growth function was chosen to model the relationship between H and dbh across the ecoregions for black spruce trees based on its well-known flexibility with biologically interpretable coefficients (Pienaar and Turnbull 1973). In addition, the Chapman-Richards function is considered one of the best nonlinear functions in describing height-diameter relationships for various species in the forestry literature (Huang et al. 1992, Garman et al. 1995, Zhang et al. 1996, Zhang 1997, Fang and Bailey 1998) as well as for major tree species in Ontario (e.g., Peng 1999, Peng et al. 2001a). The Chapman-Richards function can be expressed as

$$H = 1.3 + a(1 - e^{-b \cdot dbh})^{c} \qquad (1)$$

where H is total tree height (m), dbh is tree diameter at breast height (cm), and $a$, $b$, and $c$ are asymptote, scale, and shape parameters, respectively. The Chapman-Richards function was fit to: (1) the overall data ($N$ = 11,612); (2) the boreal region data ($N$ = 1008); (3) the central region data ($N$ = 604); and (4) each of the seven ecoregions separately. The PROC NLIN procedure in the Statistical Analysis System (SAS Institute, Inc. 1999) was used to estimate the model parameters and statistics. Three model parameters ($a$, $b$, and $c$), and model mean squared error (MSE) are shown in Table 2 for the 10 different models.

The differences in height-diameter relationships among different ecoregions were examined with the nonlinear extra sum of squares method (Bates and Watts 1988; Neter et al. 1996). The method requires the fitting of full and reduced models. The full model corresponds to different sets of parameters for each of the ecoregions involved, while the reduced model corresponds to the same set of parameters for all ecoregions. This method has been recently used to compare the differences of ecoregion-based taper equations (Huang 1994; Huang et al. 1999), single tree volume equations (Pillsbury et al. 1995), and ecoregion-based individual tree height-diameter models in Alberta (Huang 1999; Huang et al. 2000).

An indicator (dummy) variable approach was used to facilitate hypothesis tests (Bates and Watts 1988, Huang et al. 2000) as follows.

*Test on the Overall Model*

To exam the sufficiency of the overall model for the seven ecoregions, the following full model was fitted:

$$H = 1.3 + \left(a + \sum_{i=1}^{6} a_i z_i\right)\left[1 - e^{-(b+\sum_{i=1}^{6} b_i z_i)dbh}\right]^{(c+\sum_{i=1}^{6} c_i z_i)} \qquad (2)$$

The six indicator variables ($z_1 - z_6$) were defined as:

If ecoregion = 3E, $z_1 = 1$, all other $Z_i = 0$;
If ecoregion = 3S, $z_2 = 1$, all other $Z_i = 0$;
If ecoregion = 3W, $z_3 = 1$, all other $Z_i = 0$;
If ecoregion = 4E, $z_4 = 1$, all other $Z_i = 0$;
If ecoregion = 4S, $z_5 = 1$, all other $Z_i = 0$;
If ecoregion = 4W, $z_6 = 1$, all other $Z_i = 0$ and
If ecoregion = 5E, all other $Z_i = 0$.

**Table 2. Estimated coefficients (*a,b,c*) of Chapman-Richards function for black spruce by ecoregion, region, and all data combined.**

| Scale | $N$ | $a$ | $b$ | $c$ | MSE |
|---|---|---|---|---|---|
| Ecoregion | | | | | |
| 3E | 5,661 | 22.1206 | 0.0727 | 1.4820 | 2.9173 |
| 3S | 620 | 28.3605 | 0.0512 | 1.3305 | 2.5308 |
| 3W | 2,791 | 26.8566 | 0.0592 | 1.5016 | 3.2276 |
| 4E | 432 | 22.5901 | 0.0712 | 1.4320 | 2.0839 |
| 4S | 1,240 | 21.1688 | 0.0825 | 1.5335 | 2.9894 |
| 4W | 696 | 37.1555 | 0.0307 | 1.1242 | 3.3965 |
| 5E | 172 | 18.6390 | 0.1013 | 1.7248 | 2.2114 |
| Region | | | | | |
| Boreal | 11,008 | 24.5403 | 0.0613 | 1.4352 | 3.0679 |
| Central | 604 | 20.9289 | 0.0817 | 1.5259 | 2.1407 |
| Province | | | | | |
| Overall | 11,612 | 24.3815 | 0.0637 | 1.4354 | 3.0224 |

NOTE: $N$—sample size (number of trees); MSE—model mean squared error.

The full model (Equation 2) has 21 parameters to be estimated, and an error sum of squares *SSE(F)* with degrees of freedom $df_F = N - 21$, where $N$ is the total number of observations in the overall data (i.e., $N$ = 11,612). The reduced model for this test takes the form of Equation 1 with three parameters, and has an error sum of squares *SSE(R)* with degrees of freedom $df_R = N - 3$. The null and alternative hypotheses are

$$H_0: a_1 = a_2 = a_3 = a_4 = a_5 = a_6 = b_1 = b_2 = b_3 = b_4 = b_5 = b_6 = c_1 = c_2 = c_3 = c_4 = c_5 = c_6 = 0,$$

and

$H_a$: at least one parameter is not equal to 0.

Rejecting the null hypothesis would indicate that separate models are required for the seven ecoregions, and failing to reject the $H_0$ would indicate that the overall model from all data combined is sufficient for each ecoregion.

*Test on the Boreal Region Against the Central Region*

To compare the height-diameter relationship between the boreal and central regions, the following full model was used:

$$H = 1.3 + (a + a_1 z_1)[1 - e^{-(b+b_1 z_1)dbh}]^{(c+c_1 z_1)} \quad (3)$$

Only one indicator variable was defined as: if the boreal region, $z_1 = 1$, otherwise, $z_1 = 0$. The full model (Equation 3) has six parameters to be estimated, and an error sum of squares *SSE(F)* with the degrees of freedom $df_F = N - 6$, where $N$ is the total number of observations in the combined data of the boreal and central regions ($N$ = 11,612). The reduced model, again, takes the form of Equation 1 with three parameters and has an error sum of squares *SSE(R)* with the degrees of freedom $df_R = N - 3$. The null and alternative hypotheses are:

$H_0$: $a_1 = b_1 = c_1 = 0$ and

$H_a$: at least one parameter is not equal 0.

Rejecting the null hypothesis would indicate a significant difference in height-diameter relationships between boreal and central regions.

*Test on the Differences Among the Seven Ecoregions*

To test the pairwise differences among the seven ecoregions, a total of 21 ecoregion pairs were formulated. The 21 testing pairs required 21 full models that take the form of Equation 3, and 21 reduced models that take the form of Equation 1. For example, to test the difference between ecoregion 3E against 3S, one indicator variable can be defined as if ecoregion = 3E, $z_1 = 1$ and if ecoregion = 3S, $z_1 = 0$. Similarly, the full model (Equation 3) has six parameters to be estimated, and an error sum of squares *SSE(F)* with the degrees of freedom $df_F = N - 6$, where $N$ is the total number of observations in the combined data of ecoregions 3E and 3S. The reduced model takes the form of Equation 1 with three parameters and has an error sum of squares *SSE(R)* with the degrees of freedom $df_R = N - 3$. The null and alternative hypotheses are:

$H_0$: $a_1 = b_1 = c_1 = 0$ and

$H_a$: at least one parameter is not equal 0.

Rejecting the null hypothesis would indicate a significant difference in height-diameter relationships between ecoregion 3E and 3S.

**Table 3. Results of model comparisons (*F*-tests of the regional differences) for black spruce at ecoregional, regional, and provincial scales.**

| | Full model | | Reduced model | | | | |
|---|---|---|---|---|---|---|---|
| Model comparison | $df_F$ | *SSE(F)* | $df_R$ | *SSE(R)* | *N* | *F*-value | *P*-value |
| Overall | 11,591 | 34385.61 | 11,609 | 35086.94 | 11,612 | 13.13 | <0.0001 |
| Boreal-Central | 11,606 | 35048.79 | 11,609 | 35086.94 | 11,612 | 4.21 | 0.0055 |
| 3E-3S | 6,275 | 18067.59 | 6,278 | 18207.43 | 6,281 | 16.19 | <0.0001 |
| 3E-3W | 8,446 | 25504.76 | 8,449 | 25839.32 | 8,452 | 36.93 | <0.0001 |
| 3E-4E | 6,087 | 17400.09 | 6,090 | 17429.51 | 6,093 | 3.439 | 0.0163 |
| 3E-4S | 6,895 | 20203.96 | 6,898 | 20334.52 | 6,901 | 14.85 | <0.0001 |
| 3E-4W | 6,351 | 18859.91 | 6,354 | 18976.99 | 6,357 | 13.14 | <0.0001 |
| 3E-5E | 5,827 | 16879.84 | 5,830 | 16890.79 | 5,833 | 1.26 | 0.2860 |
| 3S-3W | 3,405 | 10560.14 | 3,408 | 10617.03 | 3,411 | 6.11 | 0.0004 |
| 3S-4E | 1,046 | 2455.47 | 1,049 | 2479.06 | 1,052 | 3.35 | 0.0185 |
| 3S-4S | 1,854 | 5259.34 | 1,857 | 5324.78 | 1,860 | 7.69 | <0.0001 |
| 3S-4W | 1,310 | 3915.29 | 1,313 | 3930.13 | 1,316 | 1.66 | 0.1748 |
| 3S-5E | 786 | 1935.22 | 789 | 1998.51 | 792 | 8.57 | <0.0001 |
| 3W-4E | 3,217 | 9892.63 | 3,220 | 9983.25 | 3,223 | 9.82 | <0.0001 |
| 3W-4S | 4,025 | 12696.50 | 4,028 | 12946.31 | 4,031 | 26.40 | <0.0001 |
| 3W-4W | 3,481 | 11352.45 | 3,484 | 11444.89 | 3,487 | 9.45 | <0.0001 |
| 3W-5E | 2,957 | 9372.38 | 2,960 | 9439.59 | 2,963 | 7.07 | <0.0001 |
| 4E-4S | 1,666 | 4591.83 | 1,669 | 4595.15 | 1,672 | 0.40 | 0.7520 |
| 4E-4W | 1,122 | 3247.78 | 1,125 | 3276.56 | 1,128 | 3.31 | 0.0194 |
| 4E-5E | 598 | 1267.71 | 601 | 1286.54 | 604 | 2.96 | 0.0317 |
| 4S-4W | 1,930 | 6051.65 | 1,933 | 6137.83 | 1,936 | 9.16 | <0.0001 |
| 4S-5E | 1,406 | 4071.58 | 1,409 | 4095.20 | 1,412 | 2.72 | 0.0433 |
| 4W-5E | 862 | 2727.53 | 865 | 2792.03 | 868 | 6.80 | 0.0002 |

NOTE: *N*, sample size; *SSE(F)*, error sum of squares of the full model; $df_F$, degrees of freedom of *SSE(F)*; *SSE(R)*, error sum of squares of reduced model; $df_R$, degrees of freedom of *SSE(R)*.

*Testing and Comparison Statistics*

The appropriate test statistic for the above tests is an $F$-test

$$F = \frac{SSE(R) - SSE(F)}{df_R - df_F} \div \frac{SSE(F)}{df_F} \quad (4)$$

with $df_1 = df_R - df_F$, and $df_2 = df_F$. Test results for the 23 tests (overall model test, boreal versus central region, and 21 pairwise tests between the seven ecoregions) are presented in the Table 3. Generally, the $F$-test is significant if the $P$ value for the test is less than 0.05.

To understand the consequences of "applying" a height-diameter model in different ecoregions, the overall model, boreal regional model, and central regional model were used to predict total tree heights for each ecoregion, and ecoregion models were used to predict tree height in each of the other six ecoregions. Mean ($\bar{e}$) and the standard deviation ($S_e$) of prediction error were computed as follows:

$$\bar{e} = \frac{\sum_{i=1}^{m} (H_i - \hat{H}_i)}{m} \quad (5)$$

$$S_e = \sqrt{\frac{\sum_{i=1}^{m} (e_i - \bar{e}_i)^2}{m - 1}} \quad (6)$$

where $e_i$ is the difference between the observed ($H_i$), and predicted ($\hat{H}_i$) height, $i = 1, 2, \ldots, m$, and $m$ is the number of observations in the relevant ecoregion. The prediction bias is defined as

$$\text{Bias}(\%) = \frac{\bar{e}}{\bar{H}} \times 100 \quad (7)$$

where $\bar{H}$ is the mean of observed tree heights. A $t$-test was used to test the null hypothesis that mean prediction error = 0:

$$t = \frac{\bar{e}}{S_e / \sqrt{m}} \quad (8)$$

To investigate the quality of prediction by the overall and (boreal or central) regional models applied to each ecoregion across tree sizes, the prediction errors ($m$) from the three models were averaged for 5-cm diameter intervals if there were at least three trees in a diameter class.

## Results

Table 4 shows the prediction errors and associated tests when the overall model is applied to each of the seven ecoregions. Table 5 provides the prediction errors and as-

**Table 4. Prediction errors of the overall model applied to each ecoregion in Ontario.**

| Ecoregion | $N$ | $\bar{H}$ (m) | $\hat{H}$ (m) | $\bar{e}$ | $S_e$ | Bias (%) | $t$ | $P$-value |
|---|---|---|---|---|---|---|---|---|
| 3E | 5,661 | 10.2234 | 10.3017 | –0.0783 | 1.7141 | –0.7662 | –3.4383 | 0.0006 |
| 3S | 620 | 11.0551 | 10.8229 | 0.2322 | 1.6027 | 2.1003 | 3.6075 | 0.0003 |
| 3W | 2,791 | 9.6375 | 9.7319 | –0.0945 | 1.8168 | –0.9798 | –2.7457 | 0.0061 |
| 4E | 432 | 9.3772 | 9.1901 | 0.1871 | 1.4479 | 1.9951 | 2.6856 | 0.0075 |
| 4S | 1,240 | 10.2752 | 10.0194 | 0.2559 | 1.7381 | 2.4900 | 5.1835 | 0.0001 |
| 4W | 696 | 10.6286 | 10.4669 | 0.1617 | 1.8582 | 1.5215 | 2.2959 | 0.0220 |
| 5E | 172 | 8.9837 | 9.1035 | –0.1198 | 1.5321 | –1.3332 | –1.0253 | 0.3067 |

NOTE: $N$, sample size; $\bar{H}$, average of observed tree height; $\hat{H}$, average of predicted tree height from the model; $\bar{e}$, average of prediction error; $S_e$, standard deviation of prediction error.

**Table 5. Prediction errors of the regional model applied to each ecoregion in Ontario.**

| Ecoregion | $N$ | $\bar{H}$ (m) | $\hat{H}$ (m) | $\bar{e}$ | $S_e$ | Bias (%) | $t$ | $P$-value |
|---|---|---|---|---|---|---|---|---|
| Boreal regional model applied to | | | | | | | | |
| 3E | 5,661 | 10.2234 | 10.0558 | 0.1676 | 1.7135 | 1.6395 | 7.3599 | <0.0001 |
| 3S | 620 | 11.0551 | 10.5697 | 0.4855 | 1.6083 | 4.3914 | 7.5162 | <0.0001 |
| 3W | 2,791 | 9.6375 | 9.5020 | 0.1355 | 1.8237 | 1.4057 | 3.9245 | <0.0001 |
| 4E | 432 | 9.3772 | 8.9687 | 0.4085 | 1.4521 | 4.3562 | 5.8472 | <0.0001 |
| 4S | 1,240 | 10.2752 | 9.7816 | 0.4937 | 1.7429 | 4.8044 | 9.9737 | <0.0001 |
| 4W | 696 | 10.6286 | 10.2164 | 0.4122 | 1.8570 | 3.8783 | 5.8559 | <0.0001 |
| 5E | 172 | 8.9837 | 8.8906 | 0.0931 | 1.5287 | 1.0367 | 0.7989 | 0.4254 |
| Central regional model applied to | | | | | | | | |
| 3E | 5,661 | 10.2234 | 10.4254 | –0.2020 | 1.7100 | –1.9760 | –8.8882 | 0 |
| 3S | 620 | 11.0551 | 10.9264 | 0.1288 | 1.6621 | 1.1648 | 1.9291 | 0.0541 |
| 3W | 2,791 | 9.6375 | 9.8319 | –0.1944 | 1.8703 | –2.01756 | –5.4924 | <0.0001 |
| 4E | 432 | 9.3772 | 9.3069 | 0.0703 | 1.4436 | 0.7501 | 1.0128 | 0.31174 |
| 4S | 1,240 | 10.2752 | 10.1319 | 0.1433 | 1.7289 | 1.3949 | 2.9193 | 0.0036 |
| 4W | 696 | 10.6286 | 10.5950 | 0.0336 | 1.8951 | 0.3161 | 0.4677 | 0.6402 |
| 5E | 172 | 8.9837 | 9.1843 | –0.2006 | 1.4894 | –2.2327 | –1.7661 | 0.0792 |

NOTE: $N$, sample size; $\bar{H}$, average of observed tree height; $\hat{H}$, average of predicted tree height from the model; $\bar{e}$, average of prediction error; $S_e$, standard deviation of prediction error.

**Table 6. Prediction errors of the ecoregional models applied to each ecoregion in Ontario.**

| Ecoregion | $N$ | $\bar{H}$ (m) | $\hat{H}$ (m) | $\bar{e}$ | $S_e$ | Bias (%) | $t$ | $P$-value |
|---|---|---|---|---|---|---|---|---|
| 3E model applied to | | | | | | | | |
| 3E | 5,661 | 10.2234 | 10.2318 | −0.0084 | 1.7077 | −0.0823 | −0.3708 | 0.7108 |
| 3S | 620 | 11.0551 | 10.7354 | 0.3197 | 1.6374 | 2.89226 | 4.8621 | <0.0001 |
| 3W | 2,791 | 9.6375 | 9.6577 | −0.0202 | 1.8503 | −0.2098 | −0.5774 | 0.5637 |
| 4E | 432 | 9.3772 | 9.1318 | 0.2454 | 1.4439 | 2.6168 | 3.5324 | 0.0005 |
| 4S | 1,240 | 10.2752 | 9.9480 | 0.3272 | 1.7324 | 3.1846 | 6.6513 | <0.0001 |
| 4W | 696 | 10.6286 | 10.3965 | 0.2321 | 1.8768 | 2.1837 | 3.2625 | 0.0012 |
| 5E | 172 | 8.9837 | 9.0288 | −0.0451 | 1.5001 | −0.5019 | −0.3942 | 0.6939 |
| 3S model applied to | | | | | | | | |
| 3E | 5,661 | 10.2234 | 10.5256 | −0.3022 | 1.7344 | −2.9561 | −13.1099 | <0.0001 |
| 3S | 620 | 11.0551 | 11.0683 | −0.0131 | 1.5882 | −0.1188 | −0.2058 | 0.8370 |
| 3W | 2,791 | 9.6375 | 9.9635 | −0.3261 | 1.8008 | −3.3836 | −9.5667 | <0.0001 |
| 4E | 432 | 9.3772 | 9.4035 | −0.0263 | 1.4669 | −0.2803 | −0.3724 | 0.7098 |
| 4S | 1,240 | 10.2752 | 10.2435 | 0.0318 | 1.7577 | 0.3090 | 0.6361 | 0.5248 |
| 4W | 696 | 10.6286 | 10.6941 | −0.0655 | 1.8510 | −0.6165 | −0.9340 | 0.3507 |
| 5E | 172 | 8.9837 | 9.3330 | −0.3493 | 1.5842 | −3.8880 | −2.8917 | 0.0043 |
| 3W model applied to | | | | | | | | |
| 3E | 5,661 | 10.2234 | 10.2012 | 0.0222 | 1.7512 | 0.2173 | 0.9546 | 0.3398 |
| 3S | 620 | 11.0551 | 10.7479 | 0.3072 | 1.5928 | 2.7790 | 4.8027 | <0.0001 |
| 3W | 2,791 | 9.6375 | 9.6284 | 0.0090 | 1.7959 | 0.0936 | 0.2652 | 0.7909 |
| 4E | 432 | 9.3772 | 9.0626 | 0.3146 | 1.4883 | 3.3548 | 4.3934 | <0.0001 |
| 4S | 1,240 | 10.2752 | 9.9203 | 0.3549 | 1.7698 | 3.4542 | 7.0619 | <0.0001 |
| 4W | 696 | 10.6286 | 10.3648 | 0.2639 | 1.8644 | 2.4826 | 3.7338 | 0.0002 |
| 5E | 172 | 8.9837 | 8.9989 | −0.0152 | 1.6125 | −0.1693 | −0.1237 | 0.9017 |
| 4E model applied to | | | | | | | | |
| 3E | 5,661 | 10.2234 | 10.5001 | −0.2767 | 1.7080 | −2.7070 | −12.1914 | <0.0001 |
| 3S | 620 | 11.0551 | 11.0104 | 0.0448 | 1.6308 | 0.4052 | 0.6839 | 0.4943 |
| 3W | 2,791 | 9.6375 | 9.9184 | −0.2809 | 1.8451 | −2.9148 | −8.0432 | <0.0001 |
| 4E | 432 | 9.3772 | 9.3857 | −0.0085 | 1.4402 | −0.0906 | −0.1226 | 0.9025 |
| 4S | 1,240 | 10.2752 | 10.2106 | 0.0646 | 1.7300 | 0.6288 | 1.3151 | 0.1887 |
| 4W | 696 | 10.6286 | 10.6693 | −0.0407 | 1.8745 | −0.3831 | −0.5731 | 0.5668 |
| 5E | 172 | 8.9837 | 9.2776 | −0.2939 | 1.5035 | −3.2712 | −2.5634 | 0.0112 |
| 4S model applied to | | | | | | | | |
| 3E | 5,661 | 10.2234 | 10.5725 | −0.3491 | 1.7122 | −3.4146 | −15.3404 | <0.0001 |
| 3S | 620 | 11.0551 | 11.0812 | −0.0261 | 1.6520 | −0.2357 | −0.3928 | 0.6946 |
| 3W | 2,791 | 9.6375 | 9.9681 | −0.3307 | 1.8597 | −3.4310 | −9.3933 | <0.0001 |
| 4E | 432 | 9.3772 | 9.4348 | −0.0576 | 1.4426 | −0.6145 | −0.8302 | 0.4069 |
| 4S | 1,240 | 10.2752 | 10.2737 | 0.0015 | 1.7276 | 0.0145 | 0.0304 | 0.9757 |
| 4W | 696 | 10.6286 | 10.7450 | −0.1164 | 1.8927 | −1.0949 | −1.6221 | 0.1052 |
| 5E | 172 | 8.9837 | 9.3091 | −0.3254 | 1.4971 | −3.6219 | −2.8504 | 0.0049 |
| 4W model applied to | | | | | | | | |
| 3E | 5,661 | 10.2234 | 10.4863 | −0.2629 | 1.7364 | −2.5719 | −11.3933 | <0.0001 |
| 3S | 620 | 11.055 | 11.0812 | −0.0261 | 1.6520 | −0.2357 | −0.3928 | 0.6946 |
| 3W | 2,791 | 9.6374 | 9.9729 | −0.3355 | 1.8202 | −3.4809 | −9.7368 | <0.0001 |
| 4E | 432 | 9.3772 | 9.4263 | −0.0491 | 1.4727 | −0.5232 | −0.6924 | 0.4890 |
| 4S | 1,240 | 10.2752 | 10.2200 | 0.0552 | 1.7748 | 0.5370 | 1.0948 | 0.2738 |
| 4W | 696 | 10.6286 | 10.6525 | −0.0239 | 1.8402 | −0.2251 | −0.3430 | 0.7317 |
| 5E | 172 | 8.9837 | 9.3752 | −0.3915 | 1.5836 | −4.3576 | −3.2420 | 0.0014 |
| 5E model applied to | | | | | | | | |
| 3E | 5,661 | 10.2234 | 10.2465 | −0.0231 | 1.7252 | −0.2257 | −1.0063 | 0.3143 |
| 3S | 620 | 11.0551 | 10.7313 | 0.3239 | 1.7363 | 2.9295 | 4.6445 | <0.0001 |
| 3W | 2,791 | 9.6375 | 9.6347 | 0.0027 | 1.9300 | 0.0281 | 0.074 | 0.9410 |
| 4E | 432 | 9.3772 | 9.1244 | 0.2529 | 1.4632 | 2.6965 | 3.5918 | 0.0004 |
| 4S | 1,240 | 10.2752 | 9.9464 | 0.3288 | 1.7380 | 3.1997 | 6.6614 | <0.0001 |
| 4W | 696 | 10.6286 | 10.4172 | 0.2114 | 1.9430 | 1.9890 | 2.8705 | 0.0042 |
| 5E | 172 | 8.9837 | 8.9761 | 0.0076 | 1.4783 | 0.0850 | 0.0677 | 0.9461 |

NOTE: $N$, sample size; $\bar{H}$, average of observed tree height; $\hat{H}$, average of predicted tree height from the model; $\bar{e}$, average of prediction error; $S_e$, standard deviation of prediction error.

sociated tests when the boreal or central regional models are applied to each of the seven ecoregions. Table 6 shows the prediction errors and associated tests when the seven ecoregional models are applied to each of the seven ecoregions.

### Developing Height-Diameter Models at Three Geographical Scales

The range of average dbh was between 10–13 cm for black spruce across the seven ecoregions and average height

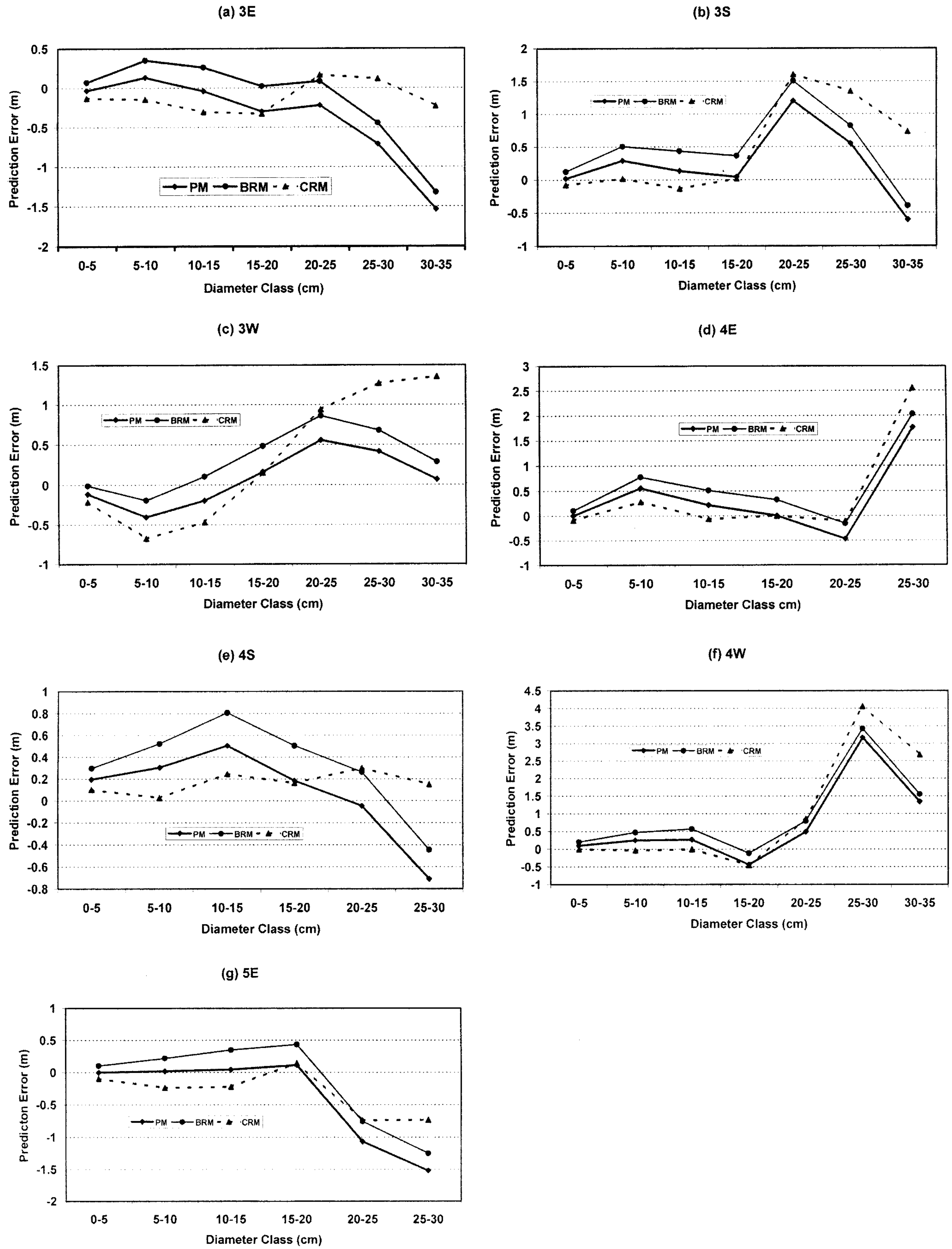


**Figure 2. Average prediction errors (*m*) across 5-cm diameter classes when the provincial (overall) model (PM: solid line with diamond), boreal region model (BRM: solid line with dot) and central region model (CRM: dotted line with triangle) are applied to predict tree total heights in each of the seven ecoregions: (a) 3E, (b) 3S, (c) 3W, (d) 4E, (f) 4W, and (g) 5E.**

**Table 7. Similarity in local environmental conditions for three paired groups.**

| Environmental conditions | Paired group 1 | | Paired group 2 | | Paired group 3 | |
|---|---|---|---|---|---|---|
| | 3E | 5E | 3S | 4W | 4E | 4S |
| 1. Historical fire occurrence[a] (number of fires) | 315 | 349 | 157 | 127 | 210 | 231 |
| 2. Mean summer rainfall[b] (mm) | 220–291 | 204–304 | 244–299 | 225–300 | 217–291 | 245–291 |
| 3. Mean length growing season[b] (days) | 167–185 | 183–219 | 162–179 | 168–188 | 171–200 | 174–188 |
| 4. Soil order[c] | | | | | | |
| Podzolic (humo-ferric podzol) | Yes | Yes | | | | |
| Brunisolic (dystric brunisol) | | | Yes | Yes | | |
| 5. Dominant drainage class[c] | | | | | | |
| Very well drained | Yes | Yes | | | | |
| Well drained | | | Yes | Yes | Yes | Yes |

[a] Li (2000).
[b] Mackey et al. (1996).
[c] Baldwin et al. (2000).

(H) ranges from 9 to 12 m (Table 1). Statistic analysis showed that mean dbh and H of sampled black spruce in boreal region were slightly higher than those in the central region (Table 1). Table 1 also suggests that the mean dbh and H for black spruce for the provincial level are very close to those in boreal region because of the large number of observations from the boreal region in the data (accounting for 95% of the black spruce).

The parameter estimates and MSE for the Chapman-Richards model for three different levels of regions are shown in Table 2. The ranges of model MSE was between 2 and 3.4, and lowest MSE value was found in 4E (MSE = 2.0839). The asymptote coefficients (coefficient $a$ in Table 2) produced for the seven ecoregions, boreal and central regions, and the province were variable. Black spruce in the boreal region has a larger asymptote coefficient than in the central region, but a similar value to province (Table 2).

### Testing Variability of Height-Diameter Relationships Among Ecoregions and Between Regions

The statistical analysis shows that height-diameter relationships between boreal and central regions are statistically significantly different, with $P$ values = 0.006 (Table 3). Although the height-diameter relationship of black spruce for 18 major pairs of ecoregion groups are statistically significant, there are still three ecoregion pairs (e.g., 3E versus 5E, 3S versus 4W, 4E versus 4S) in which $P$ values are larger than the critical value of $\alpha = 0.05$. In practice, composite height-diameter models based on the combined data from 3E and 5E, 3S and 4W, and 4E and 4S ecoregions are sufficient for tree height predictions in these three paired ecoregion groups.

### Prediction Bias of Across-Ecoregion Model Application

The above statistical tests suggest that there were significant differences for most ecoregions in the height-diameter relationships. Incorrectly "applying" a height-diameter model in these ecoregions may result in prediction biases. To evaluate the consequences, all 10 models (overall model, boreal regional model, central regional model, and seven ecoregional models) were used to predict total tree heights for a given ecoregion individually. The mean prediction error ($\bar{e}$), the prediction bias (%), and $t$-test for testing the null hypothesis that mean prediction error = 0 are were shown in Tables 4–6.

Use of the overall model to predict tree total height in each ecoregion resulted in significant over- or under-predictions (the $P$ values of the $t$-tests were less than 0.05 for the six ecoregions, excepting 5E). On average, the overall model underestimated (i.e., positive bias %) tree heights from 1.5 to 2.5% for ecoregions 3S, 4E, 4S, and 4W, and overestimated (i.e., negative bias %) tree heights about −0.8% in 3E, −1% in 3W, and −1.3% in 5E ecoregions. Figure 2 illustrates the mean prediction errors across 5-cm diameter classes for the seven ecoregions. Obviously, the negative biases produced by the overall model in the 3E and 5E ecoregions were due to over-estimations for large-sized trees (Figure 2, a and g). The larger positive model biases in the two boreal ecoregions (3S and 4S) come from the underestimations of trees under 25 cm dbh by the overall model (Figure 2, b and e).

Similarly, applying the boreal regional model to each ecoregion resulted in different patterns and magnitudes of prediction errors as the overall model. This model underestimated tree heights by 1–5% among the seven ecoregions, although the bias in 5E was not significant ($P > 0.05$). This was expected because the estimated parameters of the overall model were similar to those of the boreal regional model (Table 2). Therefore, the patterns of the prediction errors across the 5-cm diameter classes (Figure 2, a–g) were also very similar between the boreal regional and the overall model.

In contrast, the central regional model significantly overestimated ($P < 0.05$) tree heights for three ecoregions: 3E (−2%), 3W (−2%), and 5E (−2.2%). Figure 2 shows that the negative biases resulted from overestimations for all trees under 20 cm dbh in the three ecoregions (Figure 2, a, c, and g). For the two boreal ecoregions, the central regional model slightly underestimated tree height in the 3S (1.2%) and 4S (1.4%) ecoregions (Table 5).

When the seven ecoregion models were applied to each of the other ecoregions, they performed well only in the ecoregions for which the models were developed or for ecoregions with similar environmental conditions (e.g., climate, soil, and fire disturbance history; Table 7). Otherwise, the models produced significant prediction errors. For example, prediction bias was statistically significant in 3S (2.89%), 4E (2.62%), and 4W (2.18%) when the 3E-based ecoregion model was used to all ecoregions (Table 6). The prediction biases ranged from −4 to 0.3% for the 3S-based ecoregion model, from −0.2 to 3.5% for the 3W-based ecoregion model, from −3.2 to 0.6% for the 4E-based ecoregion model, from −3.6 to 0.01% for 4S-based ecoregion model, from −4.36 to 0.23% for 4W-based recoregion model, and from −0.23 to 3.2% for 5E-based ecoregion model, respectively (Table 6).

## Discussion

It is well-known that local environmental conditions determine tree growth and productivity. The seven ecoregions described by the updated ecoregion classification of Ontario (Figure 1) are characterized by broad climatic patterns (e.g., temperature and precipitation), soil moisture and nutrient regimes, and vegetation succession and types (Hills 1959, Hills 1960, Mackey et al. 1996, ELC Working Group 2000). Our results suggested that black spruce trees grow bigger and taller in the boreal region (including 3E, 3S, 3W, 4S and 4W) than in the central region (e.g., 4E and 5E) (Tables 1 and 2), mainly due to difference in soil moisture and organic matter, Although black spruce grow on a variety of sites and is widely distributed across boreal and central regions of Ontario, it is generally confined to wet, poorly drained lowland sites in the southern part of its range and is northward, those species usually grow better on well-drained upland sites with moist organic soils in extensive pure stands or mixed with jack pine, white spruce, balsam fir, white birch, and trembling aspen (Farrar 1995). It also important to point out that different tree species may respond to location conditions differently at different geographic scales. At recent study by Zhang et al. (2002) found that the height-diameter relationships for jack pine among the above seven ecoregions were statistically different ($P$ value $< 0.0001$). The misuse of a specific ecoregional model to other ecoregions resulted in underestimations of jack pine tree height between 1 and 15% and overestimations between 2 and 30%. This is not the same case for black spruce trees in this study. Because the height-diameter relationship of black spruce for three paired ecoregion groups (i.e., 3E versus 5E, 3S versus 4W, 4E versus 4S) were not statistically significant ($P$ value $> 0.05$) (Table 3). The similarity of height-diameter relationships for black spruce among these three paired ecoregions are probably due to similarity in fire disturbance, growing degree days, mean summer rainfall, and soil type (Table 7). For example, both 3E and 5S have similar historical fire occurrence, mean summer rainfall, and soil type. The similar soil type, mean length growing season, mean summer rainfall, and historical fire occurrence number can be also found in the 3S-4W and 4E-4S paired groups. In addition, prediction biases of black spruce resulting from height-diameter model developed at provincial, regional and ecoregion scales are much less than that of jack pine. These results support the recent finding reported by Huang (1999), Huang et al. (2001) and Zhang et al. (2002) and are an important extension of their previous works.

## Conclusions

The results presented here suggest that there are significant variations in height-diameter relationships for black spruce among different ecoregions in the boreal and central regions of Ontario. The ecoregion-based height-diameter models presented here provide more accurate predictions height than those estimated by models developed at both regional and provincial scales. The incorrect use of provincial or regional-based height-diameter models in different ecoregions as well as height-diameter models fitted from one ecoregion to different ecoregions may produce significant biases in predicted tree heights. These ecoregion-based height-diameter models provide useful tools to forest resource managers in forest management estimates and decisionmaking. Furthermore, the different tree species respond to local growth conditions (including climate, soil and disturbances) differently at different scales.

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