

Adjustment of the age–height relationship for uneven-aged black spruce stands

Hakim Ouzennou, David Pothier, and Frédéric Raulier

Abstract: Site index (SI) is commonly used in natural stands, even when their diameter distribution deviates from that of the monospecific, even-aged, fully stocked stands used to develop basic age–height relationships. Since deviations from basic age–height trajectories can be reflected in deviations of stand diameter distribution from a bell shape, we incorporated different diameter diversity indices into an age–height equation to help improve height predictions and determine which index is best related to stand dominant height. This procedure was performed using black spruce (*Picea mariana* (Mill.) BSP) stands from a large network of permanent sample plots established across the province of Quebec, Canada. The age–height model that minimized the Akaike’s information criterion used the Shannon evenness index (E_{Sh}) as an equation modifier accounting for the diameter diversity variable. The model showed that for stands established on relatively poor sites (SI = 9), no substantial differences in dominant height were found between two contrasting E_{Sh} values. For SI = 15, however, the larger E_{Sh} value increased the dominant height by as much as 1 m at 80 years. These results suggest that introduction of E_{Sh} into an age–height model can improve calculation of site index, particularly in regions characterized by the presence of numerous uneven-aged stands.

Résumé : L’indice de qualité de station (IQS) est souvent estimé pour des peuplements naturels, même si leur distribution de diamètres s’éloigne de celle des peuplements mono-spécifiques, de structure équiennne, et de densité optimale qui sont utilisés pour mettre au point les relations âge–hauteur de référence. Puisque des déviations aux trajectoires âge–hauteur de référence peuvent se refléter dans des déviations de la distribution des diamètres des peuplements par rapport à une courbe normale, nous avons soumis différents indices de diversité diamétrale à une équation âge–hauteur dans le but d’améliorer la prédiction de la hauteur et de déterminer l’indice le mieux relié à la hauteur dominante des peuplements. Cette procédure a été appliquée à des peuplements d’épinette noire (*Picea mariana* (Mill.) BSP) à l’aide d’un vaste réseau de placettes échantillons permanentes établies dans la province de Québec, au Canada. Le modèle âge–hauteur qui a minimisé le « Akaike’s information criterion » utilisait l’indice de régularité de Shannon (E_{Sh}) comme modificateur d’équation relié à la diversité diamétrale. Dans le cas des peuplements établis sur des stations relativement pauvres (IQS = 9), ce modèle n’a pas produit de différences substantielles de hauteur dominante entre deux valeurs contrastées de E_{Sh} . Cependant, pour une valeur d’IQS égale à 15, la plus forte valeur de E_{Sh} a produit une augmentation de la hauteur dominante de 1 m à 80 ans. Ces résultats indiquent que l’introduction de E_{Sh} dans un modèle âge–hauteur peut améliorer l’estimation de l’IQS, particulièrement pour régions caractérisées par la présence de nombreux peuplements de structure inéquiennne.

Introduction

Site index is widely used to assess the potential productivity of forest stands for its ease of computation from common forest inventory data, for its efficacy in predicting wood volume, and for its ease of integration into forest growth and yield models. Site index seems to have appeared around the end of the 19th century with the first normal yield tables produced for even-aged and fully stocked stands (Assmann 1970). Accordingly, trees suitable for estimating site index are generally defined as free-growing, uninjured, dominant trees that are found in even-aged, well-stocked stands not affected by recent disturbances (Carmean and Lenthall 1989). While tree plantations and many natural stands composed of pioneer species correspond to these criteria, a large proportion of natural stands deviate from this definition. Nonetheless, site index continues to be used in the absence of other effective variables. This is the case with second-

growth stands originating from advance regeneration, stands partially disturbed by climatic events or insect outbreaks, old-growth stands, etc. As such stands cover a large part of the forested land of Quebec, Canada, certain concerns arise. On the one hand, if site index models are developed only from the above-mentioned well-suited stands, using them with other types of stands can underestimate potential site productivity. On the other hand, if site index models integrate age–height data from stands of all structures, they could be associated with large prediction errors that would affect the accuracy of the merchantable volume projection at the landscape level, and might even produce substantial bias at the local scale.

In stands deviating from an even-aged structure, trees of all crown classes may have undergone a suppression period during which height growth was reduced compared with that of a free-growing tree of an equivalent age. If a dominant tree selected for site index estimation has been suppressed,

Received 23 November 2007. Accepted 20 March 2008. Published on the NRC Research Press Web site at cjfr.nrc.ca on 13 June 2008.

H. Ouzennou, D. Pothier,¹ and F. Raulier. Centre d’étude de la forêt, Département des sciences du bois et de la forêt, Pavillon Abitibi-Price, 2405 rue de la Terrasse, Université Laval, Québec, QC G1V 0A6, Canada.

¹Corresponding author (e-mail: david.pothier@sbf.ulaval.ca).

the resulting site index will have a lower value than that estimated with free-to-grow dominant trees. In other words, the site index will be underestimated. Different methods have been proposed to circumvent this problem, such as correcting tree age (Pothier et al. 1995; Hamel et al. 2004), predicting site index from permanent biophysical site characteristics (Ung et al. 2001; Hamel et al. 2004), or developing different complementary approaches for site index estimation, each of which is applied to a particular succession stage (Nigh 1998). However, while these methods can be used to successfully estimate site index, they require supplementary data not commonly available from the large-scale forest inventories used in timber supply calculations. In contrast, supplementary data are not required for diameter–height relationships that have been proposed as replacements for age–height relationships in mixed or uneven-aged stands (Huang and Titus 1993), but the underlying hypotheses of this approach have been invalidated and cannot be considered as a reliable alternative to site index (Wang 1998).

Since uneven-aged or, more generally, irregular stands are expected to follow a different age–height trajectory than even-aged stands, introducing a variable representing stand diameter distribution into the age–height model may improve the predictive ability of the model. Indeed, diameter distributions of even-aged and irregular stands are quite different and can thus be used to detect possible deviations from age–height trajectories of free-growing trees. According to McCarthy and Weetman (2007), the diameter distribution of a typical boreal stand established after a major disturbance evolves from a truncated reverse-J shape at young ages to a bell shape around maturity, and then to reverse-J to bi-modal shapes when the stand is over-mature or is affected by secondary disturbances such as insect defoliation. Such a pattern of change in diameter distribution is expected to be similar for all site qualities and stand densities, but the rate of change would be faster in more fertile sites (Boucher et al. 2006), and this should lead to a positive correlation between diameter diversity and site quality.

To be of practical use, the diameter distribution variable introduced into the age–height model must be computable from measurements taken during large-scale forest inventories. For example, stand diameter diversity, as computed by the Shannon index, has been successfully introduced into the age–height relationships of black spruce (*Picea mariana* (Mill.) BSP) stands, although its effect has not been discussed extensively (Ung et al. 2001; Raulier et al. 2003). The objectives of this study are thus to determine the stand diameter distribution variable that best explains the residual variation of the age–height relationship of black spruce stands and to develop a reliable age–height model that would be applicable over a broad range of stand structures. To achieve these objectives, we chose to use information from sequential medium-term (~10 years) measurements of permanent sample plots (PSPs), because they can take into account the possible changes in tree dominance (Elfving and Kiviste 1997; Raulier et al. 2003; García 2005). Moreover, compared with stem analyses, PSPs normally cover a narrower range of ages, but are fully compatible with forest inventories

used in timber supply calculations and reproduce the bias related to a constant plot size when estimating properties of a fixed number of trees per hectare (Zeide and Zakrzewski 1993).

Material and methods

Sampled stands and data collection

The stands sampled for this study were selected from a network of permanent sample plots established by the ministère des Ressources naturelles et de la Faune du Québec (MRNFQ) from 1970 on. PSP selection was based on a stand composition criterion to limit the scope of the study to black spruce stands, which were defined as stands in which black spruce made up at least 75% of merchantable basal area during the first measurement period. As well, we only retained PSPs that had been measured at least twice and that included at least two dominant or co-dominant black spruce trees whose age and total height were measured. Moreover, these PSPs had to include at least four trees with a diameter at breast height (1.3 m, DBH) larger than 9 cm to estimate the stand dominant height (the four largest trees in a 400 m² plot correspond to the 100 largest trees per hectare). Using these criteria, 1390 PSPs were selected to represent a large range of growing conditions and stand characteristics. These PSPs were repeatedly inventoried over periods ranging from 4 to 33 years. These 1390 PSPs were then randomly divided into two groups. One group was used to calibrate the model (715 PSPs), while the other evaluated its performance (675 PSPs). The main characteristics of these two groups of PSPs are summarized in Table 1. According to Vanclay (1994), evaluating model performance with an independent data set better reveals its overall quality than does cross-validation.

Between 1970 and 2005, the selected PSPs were inventoried two to five times during snow-free periods. The inventory consisted in measuring the DBH (± 1 mm) of each tree larger than 9.0 cm within a 400 m² circular plot and in determining the age and the height (± 0.1 m) of 2–13 dominant or co-dominant trees. Moreover, the number of saplings (trees with DBH larger than 1.0 cm but smaller than 9.1 cm) per 2 cm diameter class was determined for each species in a 40 m² subplot located in the central part of the 400 m² plot. The tree species most commonly found with black spruce in these PSPs were balsam fir (*Abies balsamea* (L.) Mill.), jack pine (*Pinus banksiana* Lamb.), white birch (*Betula papyrifera* Marsh.), and trembling aspen (*Populus tremuloides* Michx.).

Dominant height and stand age

The age–height model used in this study is based on dominant height and stand age. Dominant height (H_d) is here defined as the mean height of the 100 largest trees per hectare (Pardé and Bouchon 1988), which corresponds to the four largest trees per plot. Since the height of the four largest trees per plot was not systematically measured, we estimated H_d according to an equation proposed by Bégin and Raulier (1995) and parameterized by Pothier and Savard (1998):

Table 1. Stand characteristics determined at the first measurement period of the permanent sample plots (PSPs) for the calibration and the evaluation data sets.

Characteristic	Calibration				Evaluation			
	\bar{x}	s	Min.	Max.	\bar{x}	s	Min.	Max.
No. of PSPs	715				675			
Measured twice	298				300			
Measured three times	334				312			
Measured four times	81				62			
Measured five times	2				1			
Age at 1 m (years)	97	40	16	227	97	39	16	218
Dominant height (m)	12.8	3.0	6.1	22.9	12.7	2.8	6.3	21.5
Mean quadratic diameter (cm)	8.5	2.7	3.4	19.0	8.6	2.7	3.5	20.2
Time interval between two measurements (years)	10.7	3.3	4	24	10.7	3.2	4	24

Note: The following symbols were used in the table: \bar{x} , mean; s , standard deviation; min., minimum value; and max., maximum value.

$$[1] \quad H_d = 1.3 + \left[\frac{\bar{D}_4}{\left(\frac{\bar{D}}{\bar{H}-1.3}\right) + \beta_0(\bar{D}_4 - \bar{D})} \right]$$

where H_d is dominant height (m), \bar{D}_4 is the mean DBH (cm) of the four largest trees per plot, \bar{D} is the mean DBH (cm) of the trees sampled for height measurements, \bar{H} is the mean height (m) of the trees sampled for height measurements, and β_0 is the value ($\beta_0 = 0.03490$) of a parameter calculated from a very large plot sample (nearly 28 000 temporary sample plots located throughout the range of black spruce range in Quebec, Canada).

Stand age was defined as the age of the dominant trees determined at 1 m above ground level to remove a portion of the possibly erratic growth occurring during the juvenile stage (Carmean 1975). As it is only since 1990 that tree age in our PSPs was measured at 1 m, previous age measurements (determined from 0.15 to 1.37 m above ground level) were corrected according to a method proposed by Pothier and Savard (1998). First, a temporary site index was calculated for each plot measurement using the following equation:

$$[2] \quad SI_{temp} = \beta_1 H_d^{\beta_2} [1 - \exp(-\beta_3 \bar{A})]^{\beta_4 H_d^{-\beta_5}}$$

where SI_{temp} is the temporary site index (m at 50 years), H_d is dominant height (m), \bar{A} is the mean age (years) of the sampled dominant and co-dominant black spruce trees measured at any height between 0.15 and 1.37 m, and β_1 to β_5 are regression parameters calculated from the same large sample as for eq. 1 ($\beta_1 = 0.9604$, $\beta_2 = 0.9412$, $\beta_3 = 0.03379$, $\beta_4 = -0.6970$, and $\beta_5 = -0.1046$). This temporary site index was then used to calculate the number of years necessary for a black spruce tree to reach a height of 1 m according to another equation parameterized by Pothier and Savard (1998):

$$[3] \quad Y = \beta_6 SI_{temp}^{\beta_7}$$

where Y is the number of years necessary to reach 1 m, SI_{temp} is the temporary site index (m at 50 years), and $\beta_6 = 310.0$ and $\beta_7 = -1.751$ as calculated from the same sample as eqs. 1 and 2. Equations 2 and 3 were used solely to cor-

rect the age of trees measured at a height other than 1 m. For example, if the age of a tree was measured at 15 cm above ground level, the corresponding age at 1 m was equal to the age at 15 cm minus $(1 - 0.15)$ times Y .

Diameter distribution variables

Among the numerous diameter diversity variables developed by various authors, we selected six indices (Table 2), which were computed using data from the periodic measurements of each PSP and then incorporated as explanatory variables into the age–height regression model. The calculation of these indices used the number of live trees by 2 cm DBH classes, and included saplings as well as merchantable trees. The first five of these six indices have already been described and tested by Lexerød and Eid (2006) in a study aiming at evaluating different diameter diversity indices for forest management planning.

The Shannon index is commonly used in forest research to represent tree size diversity (Lexerød and Eid 2006). This index takes a zero value when all the trees are in the same diameter class and the maximum value $\ln(S)$ when the basal area is evenly distributed among all diameter classes. In our PSP sample, 16 diameter classes (S) were required to include all the trees, and this number was thus used as S . By dividing the Shannon index by $\ln(S)$, we obtained a standardized index known as the Shannon evenness index that always takes a value between 0 and 1 (Table 2).

The Simpson index corresponds to the probability that two randomly selected trees belong to the same diameter class (Lexerød and Eid 2006). Counterintuitively, at maximum diversity, the Simpson index value equals 0, while at minimum diversity, it equals 1. Hence, the reciprocal of the Simpson index value is often used to obtain an index value that increases with greater diversity (Table 2). The McIntosh index is a measure of dominance that is independent of the number of diameter classes (Lexerød and Eid 2006). Its calculation is based on both stand basal area and the summation of the basal area of each diameter class. This index can be standardized by taking into account the number of diameter classes, in which case it becomes an evenness index ranging between 0 and 1 (Table 2).

The Gini coefficient is a measure of heterogeneity, which

Table 2. Diameter diversity indices used in this study.

Index	Formula
Shannon evenness index	$E_{Sh} = \frac{-\sum_{i=1}^S p_i \ln(p_i)}{\ln(S)}$
Simpson index	$D_{Si} = 1 - \sum_{i=1}^S p_i^2$
McIntosh evenness index	$E_{MI} = \frac{BA - \sqrt{\sum_{i=1}^S ba_i^2}}{BA - \frac{BA}{\sqrt{S}}}$
Gini coefficient	$GC = \frac{\sum_{j=1}^n (2j - n - 1)ba_j}{\sum_{j=1}^n ba_j(n - 1)}$
Berger–Parker index	$D_{BP} = 1 - \frac{ba_{max}}{BA}$
Shape parameter “c” of the Weibull function	$F_d = 1 - \exp(-(DBH/b)^c)$

Note: p_i is the proportion of basal area in diameter class i , S is the number of diameter classes; BA is stand basal area ($m^2 \cdot ha^{-1}$), ba_i is the basal area in the diameter class i ($m^2 \cdot ha^{-1}$), ba_j is the basal area of the tree with rank j ($m^2 \cdot ha^{-1}$), j is the rank of a tree in ascending order from 1 to n , n is the total number of trees, ba_{max} is the basal area in the diameter class with the largest basal area ($m^2 \cdot ha^{-1}$), F_d is the Weibull function fitted with the cumulated frequencies of tree diameter (DBH), and b and c are the scale and the shape parameter of the Weibull function, respectively.

requires ranking all trees by diameter in ascending order. The Gini coefficient is a measure of the deviation from perfect equality and has a minimum value of zero, when all trees have exactly the same diameter, and a maximum theoretical value of one, when only one tree has a diameter in an infinite population (Lexerød and Eid 2006). The Berger–Parker index is independent of the number of diameter classes and expresses the proportional importance of the diameter class with the largest basal area in a stand (Lexerød and Eid 2006). The reciprocal form of this index is normally used to produce a zero value when all trees are in the same diameter class and a theoretical value of one when the basal area of each diameter class is exactly the same (Table 2).

The sixth and last diameter distribution variable corresponds to the shape parameter “c” of the Weibull diameter distribution model (Bailey and Dell 1973). To calculate this parameter, the Weibull function was fitted to the cumulated frequency of tree diameters in each PSP measurement with the NLIN procedure of the SAS system. The value of this shape parameter indicates different diameter distributions that can be grouped into four large classes: when $c \leq 1$, the diameter distribution corresponds to a reverse-J shape; when $1 < c < 3.6$, the diameter distribution is mound shaped and positively skewed; when c is close to 3.6, the diameter distribution is approximately normal; and when $c > 3.6$, the diameter distribution becomes progressively more negatively skewed (Bailey and Dell 1973).

Dominant height modelling

The age–height model used in this study is based on the broadly used Chapman–Richards model, which was formulated as a difference equation:

$$[4] \quad H_{d,i(j+1)} = 1 + (H_{d,ij} - 1) \left[\frac{1 - \exp(-\beta_8 A_{c,i(j+1)})}{1 - \exp(-\beta_8 A_{c,ij})} \right]^{\beta_9} + \varepsilon_{i(j+1)}$$

When this model was fitted with dominant height trajectories of individual PSPs, Raulier et al. (2003) found that parameters β_8 and β_9 were strongly correlated. Consequently, they reparameterized their equation by relating β_9 as a function of β_8 and by expanding parameter β_8 as a function of various independent variables that correlated with the residuals of previous incomplete models. Following the same methodology and after many trials, the final version of the model included three modifiers of β_9 that took into account the variation of the asymptotic height ($f_{\tilde{h}_{max}}$), the number of years between two measurements ($f_{\Delta t}$), and the diameter diversity index (f_{DD}).

$$[5] \quad \beta_9 = b_8 \beta_8$$

$$[6] \quad \beta_8 = b_9 f_{\tilde{h}_{max}} f_{\Delta t} f_{DD}$$

where

$$f_x = 1 + c_x \left(\frac{x - \bar{x}}{\bar{x}} \right)$$

$$\tilde{h}_{max} = 1 + \frac{H_{d,ij} - 1}{[1 - \exp(-b_9 A_{c,ij})]^{b_9 b_8}}$$

where $H_{d,i(j+1)}$ and $A_{c,i(j+1)}$ are the dominant height (m) and

the age at 1 m, respectively, of the $(j + 1)$ th measurement of the plot i , $H_{d,ij}$ and $A_{c,ij}$ are the dominant height (m) and the age at 1 m, respectively, of the j th measurement of the plot i , β_8 , β_9 , b_8 , b_9 , and c_x are parameters to estimate, \tilde{h}_{\max} is an approximation of the asymptotic height of eq. 4 using the mean expected value of β_9 , f_x are modifiers of the parameter β_9 , which were expressed as centered values around the mean of each considered variable x (with x corresponding to \tilde{h}_{\max} , Δt , or DD), and $\varepsilon_{i(j+1)}$ is the error term. The modifiers retained in the model were all associated with parameters significantly different from 0 at $\alpha \leq 0.05$.

A three-step procedure was used to estimate parameters of eq. 4 to facilitate the convergence of parameter estimation. The first step helped in estimating the mean expected values of parameters β_8 and β_9 without accounting for possible modifiers of β_8 (eq. 6). This step was performed using the SAS NLIN procedure and resulted in initial, provisional estimates of parameters β_8 and β_9 . These provisional estimates were used to calculate \tilde{h}_{\max} for each measurement of each plot. A second step was then used to estimate simultaneously all the parameters of eqs. 4, 5, and 6 with the same procedure, still ignoring the correlation among the measurements of each plot. Finally, a third step estimated the final values of the parameters of eqs. 4, 5, and 6 with PROC NLMIXED, with starting values obtained in step two. This procedure uses a random parameter approach to consider a random plot effect that is different from and independent of the residual random effect. Hence, once the plot effect is taken into account, the model residuals (eq. 4) are independently distributed (Biging 1985; Lappi and Bailey 1988; Lappi and Malinen 1994). Moreover, a weight $w = 1/n$, where n is the number of plots per combination of site index and age classes, was used to counteract the bias caused by random sampling of the plots, which produces an unequal representation of the plots among these classes (Smith 1984; Verbyla and Fisher 1989). The site index value (dominant height at 50 years) used in the weighing procedure was estimated for each measurement of each plot of the calibration data set by using the age ($A_{c,ij}$) and dominant height ($H_{d,ij}$) of each measurement, by fixing $A_{c,i(j+1)}$ at 50 years, and by using parameters β_8 and β_9 estimated during step two.

Evaluation of model performance

The six diameter diversity variables were incorporated in turn as modifiers into the age–height model (eq. 4), in each case accompanied by the same two other modifiers (asymptotic height and time interval between two measurements). Consequently, we had to compare six models that differed solely in the diameter distribution variable that was introduced as a modifier. The best model among these six was determined using Akaike’s information criterion (AIC), which was transformed into Akaike’s weight, as this can be directly interpreted as the probability that a model is suitable (Buckland et al. 1997). According to these authors, Akaike’s weight can be calculated as:

$$[7] \quad w_k = \frac{\exp[-0.5(\text{AIC}_k - \text{AIC}_{\min})]}{\sum_{i=1}^6 \exp[-0.5(\text{AIC}_i - \text{AIC}_{\min})]}$$

where w_k is the Akaike’s weight of the model k , AIC_k is the

AIC value of the model k , and AIC_{\min} is the minimal AIC value among the six models. Analyses of residuals were also performed on each model to detect any deviations from normality and homoscedasticity using the SAS UNIVARIATE procedure.

Finally, model performance was evaluated with the 712 PSPs that were not used for calibration. As many of these PSPs had more than two measurement intervals, we were able to evaluate the model for each of these measurement intervals and for the entire period of time covered by the measurements. The model was evaluated using two statistics: the bias, that is, the average of the differences between the observed and the predicted dominant height, and the root mean square error of prediction (RMSEP), that is, the square-root of the sum of the squared differences between the observed and the predicted dominant height.

Results

The six diameter diversity indices introduced in eq. 4 resulted in different fits to the age–height model (Table 3). According to Akaike’s weight, the best model was that incorporating the Shannon evenness index as the modifier accounting for the diameter diversity variable. The model that incorporated the Gini coefficient could be considered as a good alternative, but its slightly lower fit statistics (Table 3) and its more complex computational method (Table 2) made this index less attractive than the Shannon evenness index. Therefore, further modelling development focused on the adjustment and the predictive potential of the age–height model with the Shannon evenness index as an explanatory variable.

Table 3 shows the values of each parameter of the model that uses the Shannon evenness index, as well as the mean values used in the calculation of modifiers. The residuals of the model are well distributed around the zero value (results not shown), which suggests that the model is unbiased and statistically appropriate. The negative sign of the parameters associated with the Shannon evenness index and the time interval between two measurements indicates that both variables have a positive impact on the prediction of dominant height. Hence, for a given mean stand age, an increase in stand diameter diversity is associated with larger height growth of dominant trees. Similarly, for a given projection period, dominant height predictions using fewer (i.e., longer) intervals produce higher values than those using more (i.e., shorter) intervals. On the other hand, since \tilde{h}_{\max} is estimated from solely $H_{d,ij}$ and $A_{c,ij}$, all stands characterized by a given age and dominant height correspond to only one \tilde{h}_{\max} value. Consequently, the role of the positive parameter value associated with \tilde{h}_{\max} in eq. 4 is only to constrain the long-term dominant height projection to a plateau value determined by $A_{c,ij}$, $H_{d,ij}$, and the other modifiers.

The evaluation data set allowed us to compute some statistics related to model performance. Hence, the model’s overall bias is 0.08 m, while the RMSEP is 0.86 m for a mean projection period of 10.7 years (Table 4). When these two statistics are computed by class of Shannon evenness index value, the bias remains low for all classes, while the RMSEP tends to increase with increasing index value (Table 4). These biases, computed from eq. 4, are 50%

Table 3. Estimated parameters, mean values of modifiers, and fitting statistics of the age–height model (eq. 4) that were calculated using six different diameter diversity indices.

Parameter	Diameter diversity index introduced in eq. 4					
	E_{Sh}	D_{Si}	E_{MI}	GC	D_{BP}	c
b_1	45.294 (2.180)	44.645 (2.726)	44.867 (2.726)	42.144 (1.876)	44.732 (2.018)	43.733 (2.711)
b_2	0.07645 (0.00698)	0.07204 (0.00744)	0.07053 (0.00652)	0.02294 (0.00257)	0.07146 (0.00718)	0.01705 (0.00264)
$c_{\bar{h}_{max}}$	1.5140 (0.1121)	1.5141 (0.1168)	1.4688 (0.0936)	0.8649 (0.3586)	1.5254 (0.1148)	-0.5115 (0.8538)
$c_{\Delta t}$	-0.6077 (0.0962)	-0.5777 (0.1111)	-0.4424 (0.1306)	1.7566 (0.1711)	-0.6283 (0.1058)	1.7043 (0.1755)
c_{DD}	-2.4961 (0.2366)	-6.6613 (1.0355)	-2.9752 (0.6339)	0.8588 (0.3163)	-4.4678 (0.5412)	-0.2441 (0.1007)
Mean value						
\bar{h}_{max}	18.0	18.0	18.0	18.0	18.0	18.0
$\bar{\Delta t}$	10.7	10.7	10.7	10.7	10.7	10.7
\bar{DD}	0.68	0.83	0.78	0.56	0.74	1.38
Statistic						
R^2	0.913	0.913	0.899	0.907	0.913	0.912
AIC	3423.6	3450.8	3653.9	3438.4	3445.7	3472.1
w_k	0.9994	<0.0001	<0.0001	0.0006	<0.0001	<0.0001

Note: \bar{h}_{max} is the mean proxy of the asymptotic height; $\bar{\Delta t}$ is the mean number of years between two measurements; \bar{DD} is the mean value of the diameter diversity index as calculated from the calibration data set; R^2 is the coefficient of determination; and w_k is the Akaike's weight of each model.

lower than those computed from the application of the age–height relationship of Pothier and Savard (1998), which does not take into account stand diameter diversity (Table 4).

To determine site index, age–height relationships are often used for long-term projections when the observed stand age differs greatly from the reference age (50 years). Since our model includes the Shannon evenness index, we thus verified whether this index was stable over time or not. We found that this index changed over time, so we modelled the pattern of change of the Shannon evenness index over time with a difference equation into which we incorporated several explanatory variables. The following linear model was chosen because of its simplicity and its predictive ability:

$$[8] \quad E_{Sh,i(j+1)} = \alpha_0 + \alpha_1 E_{Sh,ij} + \alpha_2 A_{c,ij} + \alpha_3 H_{d,ij}$$

where $E_{Sh,i(j+1)}$ is the Shannon evenness index of the $(j+1)$ th measurement of the plot i , where $E_{Sh,i(j+1)}$, $A_{c,ij}$, and $H_{d,ij}$ are the Shannon evenness index, the age at 1 m, and the dominant height, respectively, of the j th measurement of the plot i , and α_0 to α_3 are parameters to estimate. This model was fitted using the SAS MIXED procedure within which we used a power covariance structure (SP(POW)), with time interval between two consecutive inventories as a power, to take into account the irregular time intervals between repeated measurements of each PSP (Moser 2004). The residuals of this model are well distributed around the zero value (results not shown), while the parameter values and the related statistics are indicated in Table 5. The time interval between two PSP measurements ($A_{c,i(j+1)} - A_{c,ij}$) was incorporated into this model but failed to explain a significant part of the variation of $E_{Sh,i(j+1)}$ when the other variables were already in the model. This likely means that the variation in the time interval between two successive measurements in our PSP network is not large enough to induce significant changes in E_{Sh} .

The long-term projection model of stand dominant height, composed of eq. 8 integrated into eq. 4, was then validated with the PSPs that were not used in the calibration procedure. This evaluation data set allowed us to estimate stand dominant height for different projection periods in the case of PSPs measured more than twice. For these PSPs, we used only the information from the first measurement to estimate the stand dominant height and the Shannon evenness index at the year of the second measurement, and these estimates were then used to calculate the same variables at the third measurement, and so on. We calculated the modelling error, which was expected to increase with increasing projection period, from the observed values of each measurement. While a slight increase in RMSEP was observed over the projection period (from 0.80 m below 15 years to 1.15 m over 25 years), the calculated bias and RMSEP were lower than 1% and 10%, respectively, of the average observed H_d for every 5-year class of the projection period (from 5 to 30 years). These results from the long-term stand dominant height model can be appreciated in Fig. 1, which shows a rather stable residual distribution around zero for the entire range of projection length.

Equations 4 and 8 were used to graph long-term projections of stand dominant height for two site indices and two base Shannon evenness indices representative of our data set

Table 4. Bias and root mean square error of prediction (RMSEP) for dominant height as computed from eq. 4 and from Pothier and Savard (1998) with the evaluation data set for five classes of Shannon evenness index values (the mean projection length was 10.7 years).

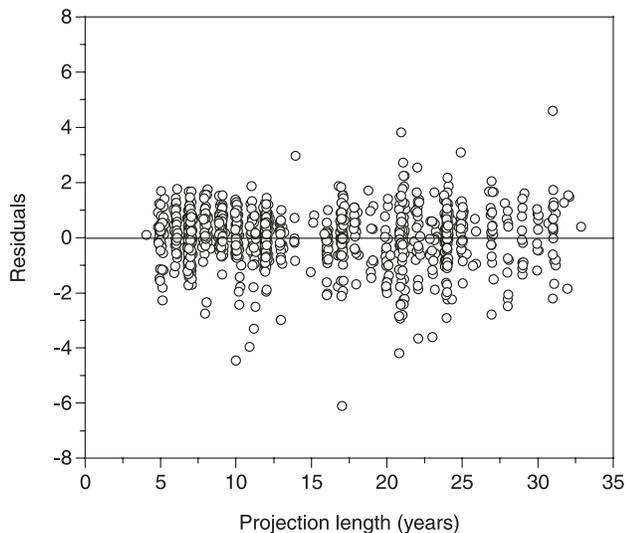
	Class of Shannon evenness index value					Total
	$E_{Sh} < 0.5$	$0.5 < E_{Sh} \leq 0.6$	$0.6 < E_{Sh} \leq 0.7$	$0.7 < E_{Sh} \leq 0.8$	$E_{Sh} \geq 0.8$	
Equation 4						
Bias (m)	-0.035	0.066	0.186	0.014	-0.026	0.084
RMSEP (m)	0.836	0.757	0.784	0.909	1.094	0.859
Pothier and Savard 1998						
Bias (m)	0.035	0.163	0.214	0.100	0.159	0.155
RMSEP (m)	0.850	0.753	0.802	0.932	1.096	0.875
No. of observations	31	126	446	426	85	1114

Table 5. Estimated parameters and standard errors (in brackets) for the model predicting the Shannon evenness index (eq. 8).

Variable	Value
α_0	0.1454 (0.0100)
α_1	0.7914 (0.0182)
α_2	-0.00015 (0.00003)
α_3	0.00194 (0.00055)
N	1199
R^2	0.738
RMSEP	0.0457

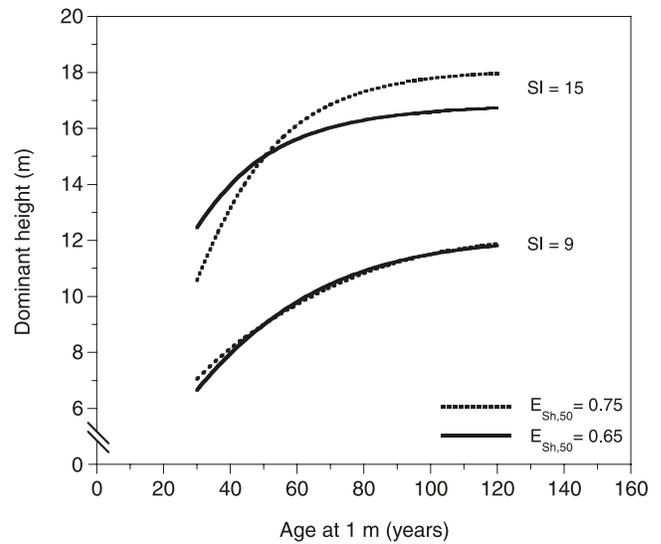
Note: α_0 to α_3 refer to the parameters of eq. 8; N , number of observations; R^2 , coefficient of determination; and RMSEP, root mean square error of prediction.

Fig. 1. Residuals ($H_{d,i(j+1)} - \hat{H}_{d,i(j+1)}$) of the entire model of dominant height projection using E_{Sh} as a modifier (eqs. 4 and 8) as a function of the projection period as determined from the two to five measurements of PSPs of the evaluation data set (1114 observations in 675 PSPs).



(Fig. 2). For poor site index (SI = 9 m at 50 years), no substantial differences in dominant height can be observed from 30 to 120 years between stands characterized by contrasting Shannon evenness indices representative of the observed

Fig. 2. Relationship between stand age and dominant height for black spruce stands with different site indices (SI, m at 50 years) and Shannon evenness indices at 50 years ($E_{Sh,50}$).

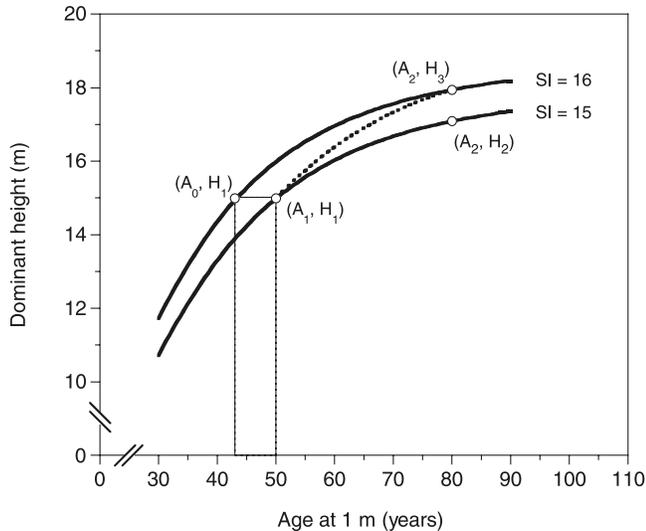


values (Fig. 2). However, for SI = 15 m, the larger Shannon evenness index resulted in differences greater than 1 m for stand ages below 35 and above 80 years (Fig. 2). The impact of introducing the Shannon evenness index in the age–height relationship thus seems to vary with site quality, the more fertile sites gaining more precision as compared with less fertile ones.

Discussion

Several diameter diversity indices were tested to determine their capacity to help predict stand dominant height in eq. 4. According to Lexerød and Eid (2006), two of these indices are a measure of evenness (E_{Sh} and E_{MI}), two others are a measure of dominance (D_{Si} and D_{BP}), one is influenced by the diameter range (GC), and the last one reflects the shape of the diameter distribution (parameter “c” of the Weibull function). The index that best explained dominant height variation when all other variables were incorporated into the model was the Shannon evenness index (E_{Sh}), as it minimized AIC (Table 3). The worst performing index was the other evenness index (E_{MI} , Table 3), which has a computational method based on basal area values rather than the

Fig. 3. Relationship between stand age and dominant height for black spruce stands with different site indices (SI, m at 50 years) but having the same Shannon evenness indices at 50 years ($E_{Sh,50} = 0.730$). The dotted line between (A_1, H_1) and (A_2, H_3) represents the dominant height trajectory of a black spruce stand with SI = 15 and $E_{Sh,50} = 0.805$.



proportion of basal area of each diameter class as in E_{Sh} (Table 2). The shape parameter “ c ” of the Weibull function was initially expected to perform well because of the flexibility of this function in fitting a variety of shapes and degrees of skewness (Liu et al. 2002; Zhang et al. 2003). However, this index was unable to discriminate old, multi-aged, true reverse-J stands from young single-cohort stands as already observed by McCarthy and Weetman (2007). Indeed, these authors found that the diameter distribution of balsam fir stands as old as 40 years is characterized by a reverse-J shape with an effective truncation of the largest diameter classes. Consequently, for these young even-aged stands, the shape parameter “ c ” of the Weibull function takes a low value — characterized by a reverse-J shaped diameter distribution — instead of a larger value corresponding to a bell-shaped diameter distribution with free-growing dominant trees.

The mathematical relationships among the variables in eq. 4 imply that a negative sign for the parameters associated with the Shannon evenness index and the time interval between two measurements results in a positive impact on the prediction of H_d . High E_{Sh} values correspond to a frequency distribution spread over several diameter classes that characterizes irregular old-growth stands and, to a lesser extent, even-aged, mature or overmature stands (McCarthy and Weetman 2007). Consequently, high E_{Sh} values tend to represent stands within which mortality of dominant trees began to occur, so that age–height relationships of trees selected for site index estimation likely deviate from that of free-growing trees. This can help explain the smaller bias associated with eq. 4 for large E_{Sh} values as compared with the prediction of H_d from the equation of Pothier and Savard (1998) (Table 4), which does not take into account stand diameter diversity when predicting dominant height. Whereas eq. 4 tends to reduce the bias associated with the prediction of H_d for all classes of E_{Sh} , the magnitude of this bias reduc-

tion is greater for E_{Sh} values larger than 0.7, which correspond to 46% of the observations in the evaluation data set. This increase in accuracy at predicting dominant height contributes to reducing the overall bias of the model as compared with that of Pothier and Savard (1998), while the RMSEPs of both models were similar (Table 4). For both models, the RMSEP tends to increase with increasing E_{Sh} values, indicating that the dominant height of stands with a large diameter range is difficult to predict. This is likely because many processes can result in a given diameter diversity but varying dominant height. For example, irregular diameter structures can be produced by senescence of dominant trees (Hatcher 1963; Harper et al. 2003), insect epidemics (Pham et al. 2004; Bouchard et al. 2006; McCarthy and Weetman 2007), pathogens, windthrow, snow loading, and ice damage (McCarthy 2001), all of which are expected to differently affect the pattern of change in H_d , because they are associated with different rates of tree degradation and mortality and produce different intensities and spatial patterns of mortality.

The parameter significantly different from zero associated with the time interval between two measurements (Table 3) primarily means that eq. 4 can only be used with the average time interval of the calibration data set so as to avoid introducing a prediction bias. Hence, for long-term projections of stand dominant height, eq. 4 should be used to estimate H_d by 10-year steps that involve using these estimations as starting values for subsequent 10-year projections. This iterative procedure means that our model is not path invariant, which is a sought-after property leading to identical predictions for different combinations of projection lengths (Clutter et al. 1983). However, our model produced prediction errors that were very similar over different projection lengths (Fig. 1), which suggests that lack of path invariance is not a major concern.

By itself, eq. 4 must be used only for estimating H_d during one 10-year period. For longer projection periods, we have to take into account the pattern of change of E_{Sh} over time, i.e., integrate eq. 8 into eq. 4. Combining these two equations enabled us to estimate H_d for projection periods varying from 5 to 35 years, including up to four successive estimations of H_d and E_{Sh} (the maximum number of measurements for a PSP in the evaluation data set was five). The H_d prediction errors were remarkably stable (Fig. 1) along this range of projection lengths, especially if we consider the increasing risk of height growth alteration with increasing projection length. This suggests that the model is reliable and flexible, as it can generate reasonable estimates for relatively long projection periods and for a territory as large as the commercial black spruce range in the province of Quebec, which covers roughly 650 000 km².

Long-term projections of the model (eqs. 4 and 8) produced dominant height patterns that differed when two E_{Sh} values at 50 years were applied to two distinct site indices (Fig. 2). For black spruce stands established on relatively poor sites (SI = 9), stand diameter diversity seemed to have very little influence on the pattern of change of dominant height. On these sites, open stands with large diameter diversity often originate from limited regeneration establishment resulting from inadequate seedbed conditions or a reduced seed pool caused by insect herbivory (Payette et al.

2000). Moreover, the slow development of trees on these poor sites generally increases their longevity because of a lack of resources (Robichaud and Methven 1993). Consequently, dominant trees sampled for site index determination were likely free to grow since their origin, and this situation reduces the possible shifts in social status. This could explain why the dominant height of these stands was not affected by the diameter structure and followed a general H_d trajectory close to that of even-aged stands.

On the other hand, an increase in stand diameter diversity on more fertile sites ($SI = 15$) is associated with larger H_d estimation after 50 years (Fig. 2). According to Bergeron et al. (1999) and Bouchard et al. (2008), such stands generally originate from forest fires that promote black spruce regeneration in an even-aged structure. This stand structure is conserved until natural mortality occurs among dominant trees, at which time mortality-induced gaps can be filled by black spruce regeneration, generally through layering (De Grandpré et al. 2000; McCarthy 2001; Pham et al. 2004). As this process progresses, stand diameter structure becomes more diversified with a diversification rate that increases with higher site qualities (Boucher et al. 2006). This is supported by our results, since E_{Sh} was found to increase faster in tall stands (eq. 8 and Table 5). Consequently, stands with large diameter diversity are more likely to be found on fertile sites that have been spared catastrophic disturbances over a long period of time. Once time since fire stretches beyond average black spruce longevity, trees sampled for site index determination are increasingly likely to belong to a tree cohort that developed under the canopy of a preceding cohort. Thus, the height development of these trees has a greater likelihood of deviating from that of a free-growing tree, and this situation should result in a different age–height relationship. The role of E_{Sh} in the age–height relationship can thus be seen as an index of departure from the normal age–height relationship that adjusts stand dominant height for a given determined age.

The introduction of E_{Sh} into the age–height relationship of these black spruce stands can also be seen as an age correction substituting years of normal growth for years of suppression of dominant trees (cf. Pothier et al. 1995; Hamel et al. 2004). This analogous effect is illustrated in Fig. 3, in which the point (A_1, H_1) represents the initial state of a given stand, and the point (A_2, H_3) corresponds to its state after a 30-year period when the initial value of E_{Sh} was 0.805. If the initial value of E_{Sh} was 0.730, the dominant height of this stand would have reached the point (A_2, H_2) 30 years later (Fig. 3). Hence, the difference between H_3 and H_2 corresponds to an adjustment of dominant height caused by introducing a higher E_{Sh} value into the age–height relationship. This H_d adjustment could have also been produced by correcting the stand age to remove about 7 years of suppression ($A_1 - A_0$), but by using a E_{Sh} value of 0.730 instead of 0.805. With this correction of age, the site index would have been calculated as 16 m at 50 years (instead of 15), and the dominant height at 80 years would have reached 17.9 m (A_2, H_3) . In this example, taking stand diameter diversity into account has thus the same effect as increasing the site index value from 15 to 16 because of an age correction. However, we believe that it is easier to use E_{Sh} than to correct age for years of suppression, because

stand diameter diversity can be easily calculated from standard forest inventories, while age correction requires supplementary data collection (increment core) and analyses to determine the number of years during which suppression occurred.

Conclusion

The introduction of a diameter diversity index into an age–height relationship helps to improve predictions of the dominant height of black spruce stands, especially for those established on good quality sites that are subject to more rapid changes in diameter structure. We thus recommend using such an equation to enhance predictions of dominant height, a key variable in systems of equations used for sustained yield calculations. These improved predictions of dominant height are particularly important in regions characterized by a long fire return interval, because they are composed of numerous uneven-aged stands for which determination of site index is problematic. Moreover, use of a diameter diversity index could also be explored as a means to improve site index determination in stands known to be problematic in this regard, such as mixedwoods or those composed of uneven-aged tolerant hardwoods. However, improvement of age–height relationships likely requires a calibration data set covering a rather large range of E_{Sh} , which could hardly become available for stand types subjected to uneven-aged management for a long time.

References

- Assmann, E. 1970. The principles of forest yield study. Pergamon Press, Oxford, UK.
- Bailey, R.L., and Dell, T.R. 1973. Quantifying diameter distributions with the Weibull function. *For. Sci.* **19**: 97–104.
- Bégin, J., and Raulier, F. 1995. Comparaison de différentes approches, modèles et tailles d'échantillons pour l'établissement de relations hauteur-diamètre locales. *Can. J. For. Res.* **25**: 1303–1312.
- Bergeron, Y., Harvey, B., Leduc, A., and Gauthier, S. 1999. Stratégies d'aménagement forestier qui s'inspirent de la dynamique des perturbations naturelles: considérations à l'échelle du peuplement et de la forêt. *For. Chron.* **75**: 55–61.
- Biging, G.S. 1985. Improved estimates of site index curves using a varying-parameter model. *For. Sci.* **31**: 248–259.
- Bouchard, M., Kneeshaw, D., and Bergeron, Y. 2006. Forest dynamics after successive spruce budworm outbreaks in mixedwood forests. *Ecology*, **87**: 2319–2329. doi:10.1890/0012-9658(2006)87[2319:FDASSB]2.0.CO;2. PMID:16995632.
- Bouchard, M., Pothier, D., and Gauthier, S. 2008. Fire return intervals and tree species succession in the North Shore region of eastern Quebec. *Can. J. For. Res.* **38**: 1621–1633.
- Boucher, D., Gauthier, S., and De Grandpré, L. 2006. Structural changes in coniferous stands along a chronosequence and a productivity gradient in the northeastern boreal forest of Quebec. *Ecoscience*, **13**: 172–180. doi:10.2980/i1195-6860-13-2-172.1.
- Buckland, S.T., Burnham, K.P., and Augustin, N.H. 1997. Model selection: an integral part of inference. *Biometrics*, **53**: 603–618. doi:10.2307/2533961.
- Carmean, W.H. 1975. Forest site quality evaluation in the United States. *Adv. Agron.* **27**: 209–267.
- Carmean, W.H., and Lenthall, D.J. 1989. Height–growth and site index curves for jack pine in north central Ontario. *Can. J. For. Res.* **19**: 215–224.

- Clutter, J.L., Forston, J.C., Pienaar, L.V., Brister, G.H., and Bailey, R.L. 1983. Timber management: A quantitative approach. John Wiley and Sons, New York.
- De Grandpré, L., Morissette, J., and Gauthier, S. 2000. Long-term post-fire changes in the northeastern boreal forest of Quebec. *J. Veg. Sci.* **11**: 791–800. doi:10.2307/3236549.
- Elfving, B., and Kiviste, A. 1997. Construction of site index equations for *Pinus sylvestris* L. using permanent plot data in Sweden. *For. Ecol. Manage.* **98**: 125–134. doi:10.1016/S0378-1127(97)00077-7.
- García, O. 2005. Comparing and combining stem analysis and permanent sample plot data in site index models. *For. Sci.* **51**: 277–283.
- Hamel, B., Bélanger, N., and Paré, D. 2004. Productivity of black spruce and jack pine stands in Quebec as related to climate, site biological features and soil properties. *For. Ecol. Manage.* **191**: 239–251. doi:10.1016/j.foreco.2003.12.004.
- Harper, K., Boudreault, C., DeGrandpré, L., Drapeau, P., Gauthier, S., and Bergeron, Y. 2003. Structure, composition, and diversity of old-growth black spruce boreal forest of the Clay Belt region in Quebec and Ontario. *Environ. Rev.* **11**: S79–S98. doi:10.1139/a03-013.
- Hatcher, R.J. 1963. A study of black spruce forests in northern Quebec. Canada, Department of Forestry, Forest Research Branch, Department of Forestry Publication 1018.
- Huang, S., and Titus, S.J. 1993. An index of site productivity for uneven-aged or mixed-species stands. *Can. J. For. Res.* **23**: 558–562. doi:10.1139/x93-074.
- Lappi, J., and Bailey, R.L. 1988. A height prediction model with random stand and tree parameters: an alternative to traditional site index methods. *For. Sci.* **34**: 907–927.
- Lappi, J., and Malinen, J. 1994. Random-parameter height/age models when stand parameters and stand age are correlated. *For. Sci.* **40**: 715–731.
- Lexerød, N.L., and Eid, T. 2006. An evaluation of different diameter diversity indices based on criteria related to forest management planning. *For. Ecol. Manage.* **222**: 17–28. doi:10.1016/j.foreco.2005.10.046.
- Liu, C., Zhang, L., Davis, C.J., Solomom, D.S., and Gove, J.H. 2002. A finite mixture model for characterizing the diameter distributions of mixed-species forest stands. *For. Sci.* **48**: 653–661.
- McCarthy, J. 2001. Gap dynamics of forest trees: A review with particular attention to boreal forests. *Environ. Rev.* **9**: 1–59. doi:10.1139/er-9-1-1.
- McCarthy, J.W., and Weetman, G. 2007. Stand structure and development of an insect-mediated boreal forest landscape. *For. Ecol. Manage.* **241**: 101–114. doi:10.1016/j.foreco.2006.12.030.
- Moser, E.B. 2004. Repeated measures modeling with PROC MIXED. Proceedings of the 29th SAS Users Group International Conference, 9–12 May 2004, Montreal, Que. Paper 188-29. SAS System, Cary, N.C.
- Nigh, G.D. 1998. A system for estimating height and site index of western hemlock in the interior of British Columbia. *For. Chron.* **74**: 588–596.
- Pardé, J., and Bouchon, J. 1988. *Dendrométrie*. 2nd ed. ENGREF, Nancy, France.
- Payette, S., Bhiry, N., Delwaide, A., and Simard, M. 2000. Origin of the lichen woodland at its southern range limit in eastern Canada: the catastrophic impact of insect defoliators and fire on the spruce–moss forest. *Can. J. For. Res.* **30**: 288–305. doi:10.1139/cjfr-30-2-288.
- Pham, A.T., De Grandpré, L., Gauthier, S., and Bergeron, Y. 2004. Gap dynamics and replacement patterns in gaps of the northeastern boreal forest of Quebec. *Can. J. For. Res.* **34**: 353–364. doi:10.1139/x03-265.
- Pothier, D., and Savard, F. 1998. Actualisation des tables de production pour les principales espèces forestières du Québec. Ministère des Ressources naturelles, Gouvernement du Québec, Québec.
- Pothier, D., Doucet, R., and Boily, J. 1995. The effect of advance regeneration height on future yield of black spruce stands. *Can. J. For. Res.* **25**: 536–544. doi:10.1139/x95-061.
- Raulier, F., Lambert, M.-C., Pothier, D., and Ung, C.-H. 2003. Impact of dominant tree dynamics on site index curves. *For. Ecol. Manage.* **184**: 65–78. doi:10.1016/S0378-1127(03)00149-X.
- Robichaud, E., and Methven, I.R. 1993. The effect of site quality on the timing of stand breakup, tree longevity, and the maximum attainable height of black spruce. *Can. J. For. Res.* **23**: 1514–1519. doi:10.1139/x93-191.
- Smith, V.G. 1984. Asymptotic site-index curves, fact or artifact? *For. Chron.* **60**: 150–156.
- Ung, C.-H., Bernier, P.Y., Raulier, F., Fournier, R.A., Lambert, M.-C., and Régnière, J. 2001. Biophysical site indices for shade tolerant and intolerant boreal species. *For. Sci.* **47**: 83–95.
- Vanclay, J.K. 1994. *Modelling forest growth and yield - Applications to mixed tropical forests*. CAB International, Wallington, Oxon, UK.
- Verbyla, D.L., and Fisher, R.F. 1989. An alternative approach to conventional soil–site regression modeling. *Can. J. For. Res.* **19**: 179–184.
- Wang, G.G. 1998. Is height of dominant trees at a reference diameter an adequate measure of site quality? *For. Ecol. Manage.* **112**: 49–54. doi:10.1016/S0378-1127(98)00315-6.
- Zeide, B., and Zakrzewski, W.T. 1993. Selection of site trees: the combined method and its application. *Can. J. For. Res.* **23**: 1019–1025. doi:10.1139/x93-130.
- Zhang, L., Packard, K.C., and Liu, C. 2003. A comparison of estimation methods for fitting Weibull and Johnson's S_B distributions to mixed spruce–fir stands in northeastern North America. *Can. J. For. Res.* **33**: 1340–1347. doi:10.1139/x03-054.