Temporal variability of aging error and its potential effects on black spruce site productivity estimations

William Marchand *, Annie DesRochers

Institut de Recherche sur les Forêts, Université du Québec en Abitibi-Témiscamingue, 341 Principale Nord, Amos, QC J9T 2L8, Canada

ABSTRACT

As a black spruce (*Picea mariana* (Mill.) BSP) tree expands its adventitious rooting system, its root collar is amalgamated into the stump. Total tree age determined by ring counts at ground level or 1 m height on the stem is thus underestimated. This age underestimation would increase with stand age because of the continuous growth of adventitious roots and the sinking of the stem under its own weight. Tree age underestimation could lead to productivity overestimation. The goal of this study was to evaluate the effect of stand age on aging error of trees and productivity estimation. Three trees within each of fifteen non-paludified and naturally regenerated black spruce stands aged 37–204 years were excavated to harvest the stump and locate the root collar. Stump sections were cross-dated down to the root collar to obtain trees' total biological age which was then compared to a ring count done at 1 m height. Height and volume growth curves obtained by stem analysis were compared with those derived from Pothier and Savard's (1998) models. Age difference between total biological age and age at 1 m (aging error) ranged 9–58 years and significantly increased with stand age. Site indices (SI; height of trees at 50 years of age) were significantly over-estimated by using age at 1 m, and the overestimation significantly increased with stand age and aging error. The use of age at 1 m lead to poor modeling of height- and volume-growth trajectories, as early height and volume-growth obtained through stem analysis was slower than predicted and stand senescence also occurred later. Due to their period of horizontal growth, seedlings don't accumulate any height during the first years. Additionally, early tree growth of our oldest trees seems to have been slower than early growth of our younger trees, probably because of less favorable growing conditions. Despite large differences between volume and height growth trajectories, predicted volumes from theoretical SI calculations were not significantly different from observed values using stem analysis, at the time of sampling. Predictive models should nevertheless be adjusted by using total biological age or time since the last fire, to consider the first years of slow growth and to obtain more accurate productivity estimations.

© 2016 Elsevier B.V. All rights reserved.

Résumé

L'épinette noire (*Picea mariana* (Mill.) BSP) développe continuellement ses racines adventives. Le collet de l'arbre se retrouve englobé à l'intérieur de la souche et localisé sous la surface du sol. Un âge déterminé par un décompte de cernes au niveau du sol ou à 1 m de hauteur sur la tige est donc sous-estimé. Cette sous-estimation de l'âge devrait augmenter avec l'âge du peuplement par la croissance continue des racines adventives et l'enfouissement progressif de la base de la tige sous son propre poids. Or, une sous-estimation de l'âge des arbres devrait entrainer une surestimation de leur productivité. Le but de cette étude était d'évaluer l'effet de l'âge du peuplement sur l'erreur d'estimation de l'âge et l'estimation de la productivité. Trois arbres de quinze peuplements âgés de 37 à 204 ans, non paludifiés et régénérés naturellement après feu ont été excavés et leur souche récoltée. Les sections de souche ont été inter-datées jusqu'au collet et l'âge total a été comparé à un décompte de cernes à 1 m de hauteur. Les courbes de hauteur et volume obtenues par analyse de tiges ont été comparées à celles dérivées des modèles de Pothier et Savard (1998). La différence entre l'âge réel et celui à 1 m variait de 9 à 58 ans et augmentait avec l'âge du peuplement. Les indices de qualité de station (IQS; hauteur à un âge de 50 ans) étaient

---

* Corresponding author.
E-mail addresses: William.Marchand@uqat.ca (W. Marchand), Annie.Desrochers@uqat.ca (A. DesRochers).

significativement surestimés quand l'âge à 1 m était utilisé, et la surestimation augmentait avec l'erreur d'âge et l'âge du peuplement. L'utilisation de l'âge à 1 m a induit une mauvaise modélisation des trajectoires de croissance en hauteur et volume. La croissance juvénile réelle en hauteur et volume était plus lente que celle prédite avec l'âge à 1 m. Les années de croissance englobées dans la souche font que les semis n'accumulent aucune hauteur pendant les premières années de vie. La sénescence des peuplements semblait également survenir plus tardivement. De plus, la croissance juvénile des arbres les plus vieux était plus lente que celle des arbres plus jeunes, possiblement à cause de conditions de croissance moins favorables. Bien que les valeurs prédites de volumes ne différaient pas significativement des valeurs observées par analyse de tige, les modèles de croissance devraient être ajustés en utilisant l'âge total des arbres ou le temps depuis le dernier feu, afin de considérer les premières années de croissance et obtenir une meilleure estimation de la productivité.

1. Introduction

Black spruce (*Picea mariana* Mill. BSP) is an important species of the boreal forests of eastern Canada because of its abundance (Rowe, 1972) and commercial-important fibre quality characteristics (Singh, 1987; Burton et al., 2003). The reproductive ecology of black spruce is highly dependent on natural disturbances, particularly wildfires; semi-serotinous cones maintain an aerial seedbank that allows a quick re-establishment of the population after stand-replacing fires (Gagnon and Morin, 2001). Accumulation of organic material on the forest floor (Fenton et al., 2005; Fenton and Bergeron, 2007) slows tree growth, but black spruce has physiological adaptations to these conditions (Islam et al., 2003); trees progressively produce shallow adventitious roots that replace in time the initial root system, ensuring trees better nutrient supply and an efficient anchoring system (Krause and Morin, 2005; Tarroux et al., 2014). These adventitious roots, the accumulation of organic matter and sinking of trees under their own weight burry the base of stems and explain why the root collar (i.e. the root/shoot interface) is located below ground level (Telewski and Lynch, 1991; DesRochers and Gagnon, 1997; Parent and Morin, 2002). Radial growth ceases in the buried part of the stem (reversed taper; DesRochers and Gagnon, 1997; Matison and Brümelis, 2008; Wilmking et al., 2012), and outer rings are missing on stem sections below adventitious roots (Peters et al., 2002). At the same time, growth rings corresponding to the first years after germination are located belowground close to the root collar, and do not appear higher up the stem (DesRochers and Gagnon, 1997). Thus, there are missing rings both at (or above) ground level and at the root collar: at no position on the stem do ring counts accurately represent the total biological age of a tree, which needs cross-dating to be determined. DesRochers and Gagnon (1997) found age differences up to 19 years between the age at ground level and the total biological age of trees. Similar studies, working on other species (balsam fir *Abies balsamea*: Parent et al. (2000), white spruce *Picea glauca*: Gutsell and Johnson (2002), Peters et al. (2002), Norway spruce *Picea abies*: Niklasson (2002)) found similar discrepancies.

Despite inaccurate aging of trees from a single ring count along the stem, it remains the common practice in forestry to use the age determined at the stump-soil interface as representative of a tree's total biological age. Erroneous age determination may however cause misinterpretations of stand dynamics. For example, it appears that mature black spruce stands regenerate within a period of time occurring 5–25 years after fire (Sirois and Payette, 1989; Lieffers et al., 1996; Bergeron, 2000; Côté et al., 2014). This is in contradiction with results from young stands, showing a regeneration period occurring within the first five years after fire (St-Pierre et al., 1992; Landhaüsser and Wein, 1993; Duchesne and Sirois, 1995; Côté et al., 2014). Some authors (Gagnon and Morin, 1992; Gagnon et al., 1992) suggested that the gap between fire occurrence and tree establishment observed in other studies was due to this age underestimation from ground level ring counts. Because of the continuous development of roots and forest floor, 'regeneration lag' or age underestimation of trees may increase with stand age.

Many studies have tried to build predictive models of the number of years that trees require to reach a determined height, on the basis of physical and environmental parameters. Most of these equations take into account dendrometric measures of a tree such as coring height, height and diameter at breast height (DBH) (Henry and Swan, 1974; Loewenstein et al., 2000; Wong and Lertzman, 2001; Fraver et al., 2011; Trotsiuk et al., 2012). Some models have tried to integrate environmental variables such as soil parameters, slope or elevation (Matthes et al., 2008; Rohner et al., 2013a,b). However, according to Wong and Lertzman (2001), these models are only valid at the studied stand scale and for a narrow range of environmental conditions. They do not allow, for example, an effective correction of the age at 1 m height used in the calculation of annual allowable cut (AAC) of commercial species of Quebec's public forests (Pothier and Savard, 1998). For black spruce, it is assumed that a maximum of 7 years is necessary for a tree to reach 1 m height (Pothier and Savard, 1998). This value does not consider the variation in the distance between the ground surface and the root collar through time, induced by the development of adventitious roots, the sinking of trees under their own weight, or a period of horizontal growth as is often observed for black spruce (DesRochers and Gagnon, 1997). Dendrochronological studies have shown that about twenty annual growth rings were missing from ground level sections compared with ring counts down to the root collar (DesRochers and Gagnon, 1997; Gutsell and Johnson, 2002; Niklasson, 2002; Peters et al., 2002). According to Garet et al. (2012), the age of 80% of commercial forest stands is underestimated. Garet et al. (2012) and Fourrier et al. (2013) argued that time since the last fire would better represent stand age (and age of trees) than the age taken at 1 m height.

The goal of this study was to evaluate the extent of age underestimation that is made with 1 m height ring counts in relation to age of stands, and to evaluate the associated productivity overestimation of black spruce stands. Fifteen stands originating from fires that occurred 37–204 years prior were investigated. We hypothesized that age underestimation and stand productivity overestimation would increase with stand age, as correctly estimated.

2. Methods

2.1. Study sites

Study sites were located between 48°07′N 76°56′W and 49°76′N 79°30′W in the boreal forest of western Quebec (Canada), within the western balsam fir-paper birch (*Abies balsamea–Betula*

papyrifera)/western spruce–moss bioclimatic domains (Grondin, 1996) (Fig. 1). Pure (62–100% of the total stem number) black spruce stands of different ages were randomly chosen to obtain an age gradient, for a total of fifteen studied stands ranging from young to mature stands. To select stands, age estimates were done using fire maps and increment cores collected from jack pine (*Pinus banksiana*) and trembling aspen (*Populus tremuloides*) trees growing in immediate proximity to the sampled stands, from which a count of the growth rings was performed. These species were chosen because of their fast initial growth and lack of adventitious roots (Burns and Honkala, 1990; Lauzon et al., 2006). Fire origin was confirmed at each site by the presence of charcoal and the lack of visible anthropogenic indicators (cut stumps). Soils were characterized by glacial deposits (till) and fine clay particles, with good to moderate drainage. In order to dissociate the effects of organic matter accumulation and age of stands, only sites with thin organic layers (≤25 cm) were chosen. Study sites were located close to roads (0–50 m), to facilitate access and transport of samples, and were separated from each other by a minimal distance of 500 m. Stands were dominated by black spruce, with a few stems of balsam fir, aspen, paper birch, tamarack (*Larix laricina*) and jack pine. Characteristics of the studied stands are compiled in Table 1. From 1971 to 2010, precipitation records from Amos, Berry and Val d'Or meteorological stations, the three closest stations to our study sites, averaged 917 mm annually (667 mm as rainfall, 257 mm as snowfall). Mean annual temperature was 0.9 °C, maximum 6.9 °C and minimum −5 °C (Environnement Canada, 2011).

2.2. Field measurements and sample collection

Sampling was done in summers of 2014 and 2015. A circular 400-m² sample plot was delineated within each of the studied stands. Plots were sampled according to the Quebec Ministry of Natural Resources norms for temporary sample plots (MRNF, 2011). Organic layer thickness was measured in the center of the plot and at the four cardinal points with a soil auger, and averaged for the plot. Diameter at breast height (DBH) and species were recorded for each tree of commercial size (DBH >9 cm) or, for the younger stands, trees with DBH >5 cm, and a number was randomly assigned to each of them when measured. Three trees per plot were selected: (i) the tree closest to the center of the plot among the three biggest trees based on their DBH, (ii) the tree corresponding to the median tree within the tree number list, (iii) the tree with the DBH nearest to the average DBH of the plot. Ground level height was marked on each stem before they were felled by cutting the main lateral roots with a chainsaw. Cross-sections were collected at 0 m, 0.4 m, 1 m and then at regular heights above ground level on the remaining stem, following the method of Chhin et al. (2010). Tree stumps were excavated and cut into 2 cm transverse sections using a portable sawmill.

2.3. Dendrochronological analysis

All cross-sections were air-dried for several weeks, then sanded with sequentially finer grades of sand paper up to 120 grit. To increase visibility of growth rings, a ray on the surface of each section was cut with a razor blade and white chalk was applied before growth rings were observed under a binocular microscope. To evaluate the total biological age of each tree, all stump sections were cross-dated down to the location of the root collar, where the spindle-shaped vascular system of the root replaces the circular-shaped pith cells cluster of the stem (Esau, 1967; DesRochers and Gagnon, 1997). If the early stem grew horizontally, cross-sections were sawn again in the transversal axis. Cross-dating was
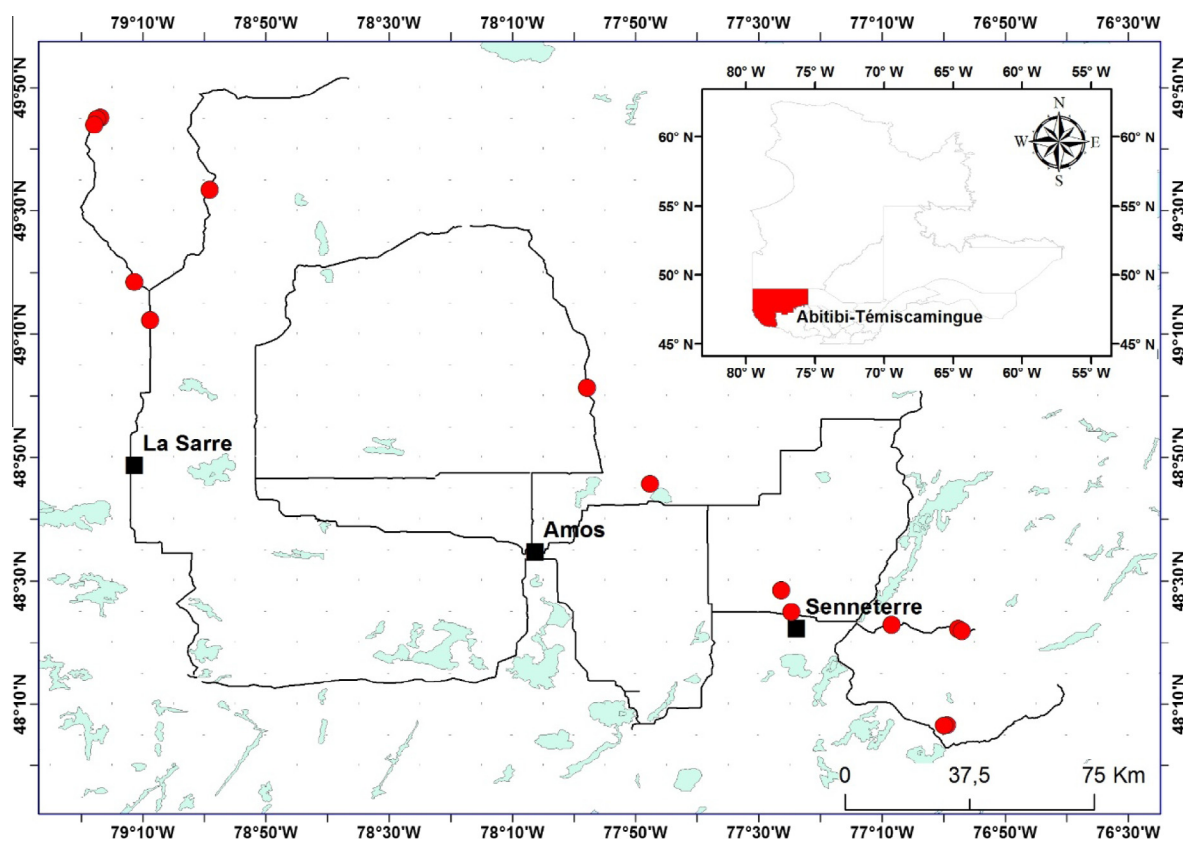

Fig. 1. Map of the study area. Circles represent studied stands.

Table 1
Stand characteristics.

Stand	Lat.	Long.	Stand age	% stem	% BA	Mean OLT (cm)	Mean tree height (m)	Mean DBH (cm)	Density (trees ha^{-1})	SI$_{theo}$ (m)
1	49.75	−79.29	37	79	65	11.6	6.85	6.91	3700	15.89
2	49.73	−79.29	37	62	36	4.8	8.02	8.46	1800	18.35
3	49.75	−79.28	38	79	78	11.6	7.41	7.56	2400	15.28
4	48.11	−77.00	61	86	65	5.6	10.61	12.41	1100	15.09
5	48.11	−76.99	62	96	93	12.4	10.27	11.69	2400	14.82
6	48.37	−76.96	70	75	69	6.8	13.31	13.63	1700	18.26
7	48.36	−76.95	87	100	100	14.8	12.34	13.95	1500	15.94
8	48.42	−77.41	97	97	92	17.6	14.41	14.91	2200	16.96
9	48.38	−77.14	100	76	70	16.0	15.29	17.75	1100	17.62
10	48.48	−77.44	101	88	89	13.2	11.36	12.32	1800	16.48
11	49.31	−79.19	104	94	92	14.0	11.31	12.32	1800	13.30
12	48.76	−77.79	112	76	73	22.4	14.64	14.09	2600	16.66
13	49.21	−79.15	182	90	93	22.8	12.43	14.94	1700	14.16
14	49.02	−77.96	191	90	92	15.8	13.14	16.01	1500	15.23
15	49.56	−78.99	204	94	95	25.0	11.47	13.63	1200	11.70

Note: Lat = latitude, Long = longitude, OLT = organic layer thickness of the stand, % stem is the percentage of spruce based on stem number, % BA is the percentage of spruce based on basal area, DBH = Diameter at breast height (1.3 m), density was obtained by multiplying the number of trees of a plot by 25 and was rounded to the nearest hundred. SI$_{theo}$ are values of site indices (height at 50 years) evaluated according to Pothier and Savard (1998) models.

performed using the skeleton plot method (Swetnam et al., 1985). Frost marks, compression wood, false rings, traumatic resin ducts and narrow or wide rings were used as pointer-years. Stem sections were digitalised (Epson 10000XL A3 optical scanner, resolution of 1200 dpi). A total of 12 cross-sections per tree was analysed, at heights corresponding to 0 m (ground level), 0.3 m, 1 m and every 10% of the remaining height on the stem (Fig. 2). Annual diameter and height increments were measured using the Windendro™ software (Regent Instruments Inc., 2009) along two paths, avoiding areas of the cross-section with compression wood or unusually thin rings. Data was then analysed with Winstem stem analysis program (Regent Instruments Inc., 2009) in order to obtain tree height (m) and volume (dm^3) temporal developmental trajectories.
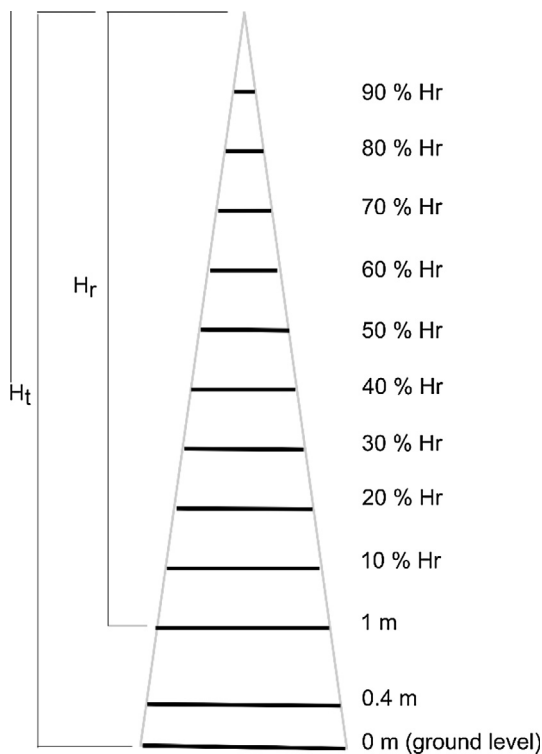
Fig. 2. Position of the collected cross-sections on the stem. H_t is the total height of the tree; H_r is the residual height above 1 m ($H_r = H_t - 1$ m). Based on Chhin et al. (2010).

2.4. Data analyses

2.4.1. Effect of stand age on aging error

Stand age was considered as the age of the oldest tree in the plot. Aging error was calculated by substracting the age found at 1 m height (considered as the standard method for determining the age of a tree) to the cross-dated age at root collar (total biological age); this was measured for each of the sampled trees ($N = 45$). A relative density index (RDI) was calculated based on the equation from Pothier and Savard (1998) (Eq. (1)), a site occupancy measure which then allowed the calculation of productivity parameters. Although it was parameterized for trees >1 cm, we used this equation with our data (i.e. trees >9 cm), and it could lead to approximations.

$$\text{RDI} = N\left(\frac{D_q}{10^{b1}}\right)^{\frac{1}{b2}} \tag{1}$$

where RDI is the Relative Density Index, N is the number of stems per hectare, D_q is the mean quadratic diameter, $b1$ and $b2$ are species-specific coefficients available in Pothier and Savard (1998).

Tree merchantable volume (m^3) was estimated using the equation developed by Fortin et al. (2007), which takes into account species-specific regional effects. Volumes of all trees of the plot were summed and the resulting value was converted in m^3 ha^{-1}. Since height of trees was not measured for every tree within plots, it was estimated using the equation from Fortin et al. (2009), which takes into account the regional variability of growing conditions by including average annual temperatures and coefficients related to ecological subdivisions and drainage conditions of the studied area.

A regression analysis was used to evaluate the effect of stand age on aging error. All statistical analyses were performed in R v. 3.1.1 (R Core Team, 2014). A probability level of $\alpha = 0.05$ was chosen to denote statistical significance. The response variable was square-root of aging error, and explanatory variables were: age at 1 m, height and DBH of selected trees, stand age, average height and DBH of the studied plot, mean organic layer thickness (OLT), RDI and merchantable volume. Interactions between explanatory variables were included at first, and then removed if not significant. We calculated pairwise correlations between all explanatory variables. We put covariates which presented a high degree of correlation into separate models. Linear mixed models were fitted using the lme function of the nlme package (Pinheiro et al., 2015) with plot as a random effect to account for unmeasured environmental variability and for the lack of independence in the plot level covariates (Hurlbert, 1984). Normality and homogeneity

of *Pearson's* residuals were visually checked, and aging error was square-root transformed to improve homogeneity. Alternate models were compared based on Akaike's Information Criterion adjusted for small sample size (AICc) using the aictab function of the AICcmodavg package (Mazerolle, 2015). Models with the lowest ΔAICc values were considered to have the greatest predictive power. Effect of the explanatory variables was highlighted with the multi-model inference approach (Burnham and Anderson, 2002) based on the values of model-average estimates and 95% unconditional confidence intervals. Predictive values of aging error were obtained from the fitted models using the modavgpred function of the AICcmodavg package (Mazerolle, 2015).

2.4.2. Effect of aging error on the estimation of productivity

Site index (SI) is a numerical index of growth potential. It is a parameter of height-age equations used to model height of the larger trees of a stand (the dominant height, $H_d(A)$) through time. Permanent (PSP) or temporary (TSP) sample plot protocols specify how the larger trees of a stand are defined and sampled. SI is defined as the dominant height at an age of 50 years measured at 1 m height ($H_d(50)$). Pothier and Savard (1998) have defined an equation of $H_d(A)$ based on TSP measurements. Because our sample protocol followed the TSP protocol, we calculated H_d using their Eq. (2), and used this value and Eq. (3) to obtain theoretical values of SI (SI$_{theo}$)

$$H_d = 1.3 + \frac{D_4}{\left(\frac{D}{H-1.3}\right) + a(D_4 - D)} \tag{2}$$

where H_d is the dominant height (m), D_4 is the average DBH of the four largest trees in the plot (cm), D is the average DBH of the sampled trees (cm), H is the average height of the three selected trees (m), and a is the regression coefficient for black spruce given in Pothier and Savard (1998).

$$SI = aH_d^b(1 - e^{-cA})^{dH_d^e} \tag{3}$$

where SI is the site index (m at 50 years), A is the averaged actual age at 1 m of sampled trees (years), a, b, c, d, e are regression coefficients for black spruce given in Pothier and Savard (1998).

We used SI$_{theo}$ values into Eq. (4) to build height-age curves and to estimate $H_d(A)$ for later use in our volume calculations.

$$H_d(A) = a + bSI^c(1 - e^{d\,A})^{eSI^f} \tag{4}$$

where $H_d(A)$ is the dominant height (m) of a stand at age A, A is the age at 1 m height (years) varying from 1 to 220 years, and a, b, c, d, e, f are coefficients for black spruce given in Pothier and Savard (1998).

We used the stem analysis data of the three selected trees per plot (the same trees that were used to calculate H_d) to reconstruct the observed trajectory of $H_d(A)$. Because these relationships were approximately linear in the vicinity of $A = 50$, we have extrapolated $H_d(50)$ for young stands using simple linear models. We obtained SI$_{obs}$ ($H_d(50)$) using the observed or extrapolated $H_d(A)$ curves.

SI$_{theo}$ and SI$_{obs}$ were compared for each plot using a paired t-test. SI difference was defined as the difference between SI$_{theo}$ and SI$_{obs}$. To evaluate the effect of stand age on SI$_{diff}$, aging error and other explanatory variables (mean age at 1 m, RDI, mean height, mean DBH, mean OLT, merchantable volume), linear models were constructed with SI$_{diff}$ as the response variable. Statistical approach was similar to that described for aging error, using multiple linear regression models instead of mixed models, because all variables were measured at the plot level.

Relative density index (RDI(A)), quadratic diameter ($D_q(A)$), basal area ($G(A)$) and volume ($V(A)$) were calculated using Eqs. (5)–(8). Two volume estimates were obtained from Eq. (8):

$V_{theo}(A)$ using the height estimate produced by Eq. (4) using the theoretical site index value (SI$_{theo}$); and $V_{obs}(A)$ using the height estimate derived from Eq. (4) based on observed site index (SI$_{obs}$).

Both SI$_{obs}$ and SI$_{theo}$ were used to build volume–age curves for each stand, using equations of Pothier and Savard (1998) (Eq. (5)). We used the senescence index of Pothier and Savard (1998) which simulates stand senescence by a gradual decline in the volume values.

$$RDI(A) = \exp(a + b\,RDI(100))A^{-1} \tag{5}$$

where RDI(A) is the relative density index at an age A, RDI(100) is the value of RDI for a 100 year old stand as given in Pothier and Savard (1998), and a and b are species-specific coefficients given in Pothier and Savard (1998).

$$D_q(A) = a\,b^{H_d(A)}A^c RDI(A)^d \tag{6}$$

where $D_q(A)$ is the quadratic diameter (cm) of the stand at an age A, and a, b, c and d, are species-specific coefficients given in Pothier and Savard (1998).

$$G(A) = a\,H_d(A)^b c^{H_d(A)}A^d RDI(A)^e \exp\left(\frac{f}{A_c}\right) \tag{7}$$

where $G(A)$ is the basal area (m^2 ha^{-1}) of a stand at an age A, and a, b, c, d, e and f, are species-specific coefficients given in Pothier and Savard (1998).

$$V(A) = a\,H_d(A)^b G(A)^c D_q(A)^d \tag{8}$$

where $V(A)$ is the merchantable volume of the stand (m^3 ha^{-1}) at an age A, and a, b, c and d are species specific coefficients given in Pothier and Savard (1998).

We calculated an average volume per tree V_{indiv} based on stem analysis values. For comparison purposes, this value was converted to represent a volume per hectare, using the same density as Pothier and Savard (1998) models, derived from relative density index and quadratic diameter (Eq. (9)).

$$V_{stem}(A) = V_{indiv}(A)\,RDI(A)\left[\frac{D_q(A)}{10^a}\right]^{\frac{-1}{b}} \tag{9}$$

where $V_{stem}(A)$ is the observed volume (m^3 ha^{-1}) at an age A, $V_{indiv}(A)$. is the average volume of a tree based on stem analysis values (m^3) at an age A, corresponding to an arithmetic average of the three values of individual volumes given by each selected tree of a stand, for each year of life, RDI(A) and $D_q(A)$ are relative density index and quadratic diameter (cm) of the stand at an age A and derived from Eq. (6) and SI$_{theo}$, and a and b are coefficients for black spruce given in Pothier and Savard (1998).

V_{theo}, V_{obs} and V_{stem} were values of volumes derived from SI$_{theo}$, SI$_{obs}$ and stem analysis at the current stand age. These values were compared using a paired t-test. Volume difference (ΔV) was calculated as the difference between V_{theo} and V_{obs}. To assess the effect of aging error on ΔV, stand age, SI differences and other explanatory variables (mean age at 1 m, RDI, mean height, mean DBH, mean OLT), linear models were constructed employing the volume difference as the response variable.

3. Results and discussion

3.1. Effect of stand age on aging error

Age at root collar ranged 33–204 years while the age at 1 m ranged 17–177 years. Ages measured at 1 m and at root collar differed from 9 to 58 years (mean ± sd: 24.04 ± 12.07), while ages at ground level (0 m) and at root collar differed from 1 to 31 years (mean ± sd: 11.4 ± 7.96). About 40% (27) of our trees, mostly the

oldest trees, had their root collar missing from the stump wood, thus having the entire initial root system replaced by adventitious roots. Since radial growth stops in buried stem sections (Fayle, 1968) if the root collar is not included within the stump wood, it is often lost to decay. One could argue that these trees could have originated from layering, or from seeds germinated after the establishment of the initial cohort. For these trees, the year corresponding to the last observed growth ring was used as the total biological age even though trees were most likely older. The large unexplained variation of aging error for the oldest stands (Fig. 3) probably comes from the uncertainty about the true biological age of trees. We could not find non-paludified stands aged 120–180 years (Table 1) within the time frame and distance constraints of this study.

Our observed aging error values are similar to what was found in DesRochers and Gagnon (1997), Parisien et al. (2005) and Vasiliauskas and Chen (2002). The value of 7 years considered by Pothier and Savard (1998) as the time necessary for a tree to reach 1 m in poor sites is thus much lower than what we observed for trees growing on good sites (SI_{theo} values >15 m, Carmean et al. (2006)), and does not consider the significant increase of aging error with stand age. Parisien et al. (2005), working on trees <1.5 m of mature fire-originating black spruce stands, also showed a difference between the number of bud scars (considered as the total biological age) and ring counts at ground level more marked in older stands. Working on mesic sites over a smaller range of ages (time since fire 53–85 years), Vasiliauskas and Chen (2002) also found a positive correlation between time to reach breast height and time since last fire (equivalent to stand age).

The difference between age at ground level or at 1 m height and age at root collar is due to the below ground position of the root collar hiding initial growth rings (DesRochers and Gagnon, 1997). Horizontal growth of the stem, frequently observed on black spruce seedlings (DesRochers and Gagnon, 1997; Parent et al., 2000), and difficult growing conditions in boreal environments (Van Bogaert et al., 2015) contribute to the slow initial height growth of seedlings. One might argue that this slow and/or horizontal initial growth is required for trees to install their adventitious root system (Tarroux et al., 2014), whose development is stimulated by a moist substrate. As a consequence, growth rings are missing even from sections taken at ground level (DesRochers and Gagnon, 1997) which is often mistaken for the root collar.
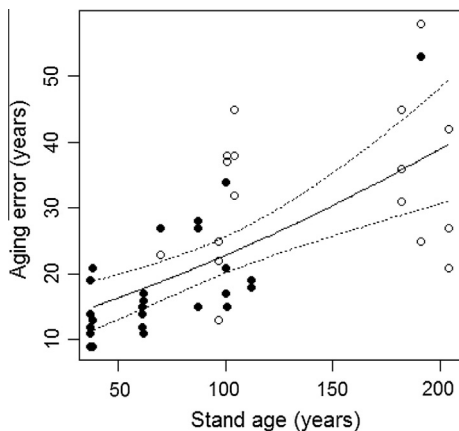
Trees of the plot were on average 12.5% shorter and 11.6% thinner than sampled trees. The merchantable volume of studied stands ranged 13–265 m^3 ha^{-1} and the average relative density index (RDI) ranged 0.23–0.95. Organic layer thickness (OLT) presented slight differences between plots, ranging 4.8–25 cm, with an average of 14.29 ± 5.9 cm. Organic layer was thinner in younger stands (9.3 cm on average for stands younger than 50 years) than in older ones (17.95 cm on average for stands older than 75 years). We selected non-paludified stands in order to discriminate the effect of stand age from that of organic matter accumulation. Even if organic layer thickness was slightly greater for our older stands (above 150 years), it remained relatively low. Organic layer could contribute to hide initial growth years; in highly paludified stands, it could be expected that the maximum difference between the age at 1 m and at root collar would be greater than 58 years, the thicker OLT hiding even more growth rings under the soil level. Unpublished data from our laboratory show that aging error can reach more than 100 years for trees growing in paludified sites (OLT >75 cm).

Aging error increased with stand age from an average of 13 ± 4.2 years for younger stands (<50 years) to an average of 38 ± 12.8 years for stands older than 150 years (Fig. 3). Stand age

Table 2

Model selection based on the Akaike Information Criterion (AICc). Response variable is root-square of aging error. Models were fitted with the lme function. Akaike Information Criterion corrected for small sample sizes (AICc), AICc scores (ΔAICc) and Akaike's weight (ωi) values are given for each candidate model.

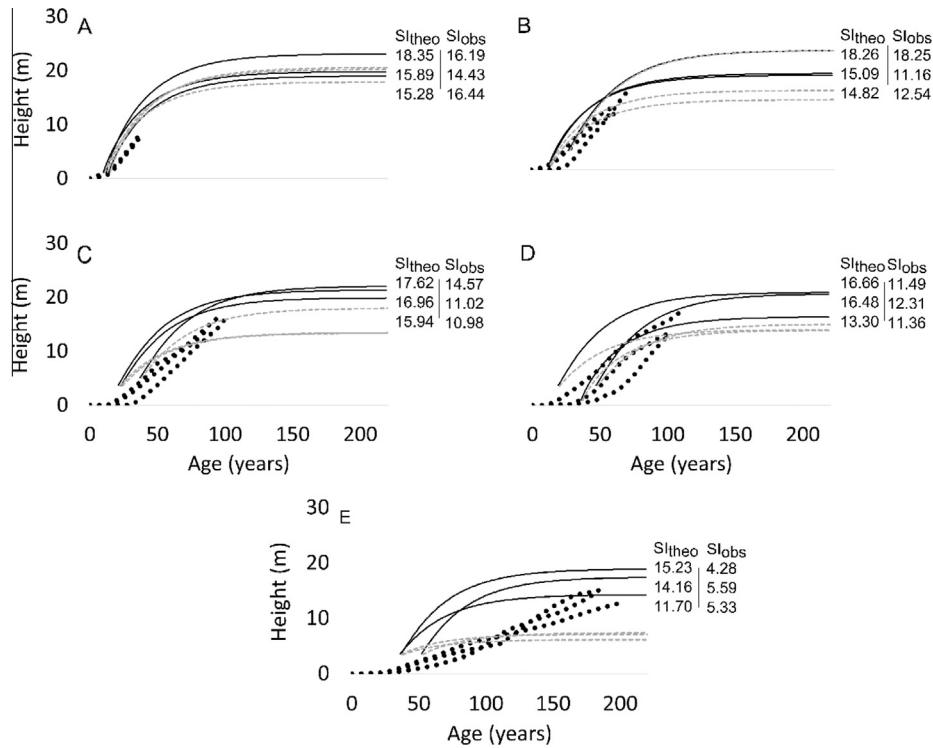| Explanatory variables	AICc	ΔAICc	ωi
Stand age	119.88	0.00	0.32
Stand age + mean DBH	121.54	1.66	0.14
Stand age + mean height	121.93	2.05	0.11
Stand age + merchantable volume	122.29	2.41	0.10
Stand age + RDI	122.36	2.48	0.09
Stand age + tree height	122.39	2.52	0.09
Stand age + tree DBH	122.40	2.52	0.09
Stand age + tree DBH + merchantable volume	124.96	5.08	0.03
Stand age + tree DBH + RDI	125.03	5.15	0.02
Age 1 m	131.54	11.66	0.00
Mean OLT	132.33	12.45	0.00
Age 1 m + merchantable volume	132.79	12.91	0.00
Age 1 m + RDI	133.24	13.36	0.00
Mean OLT + merchantable volume	134.03	14.15	0.00
Age 1 m + tree DBH	134.06	14.19	0.00
Mean OLT + RDI	134.48	14.60	0.00
Age 1 m + merchantable volume + tree DBH	135.40	15.52	0.00
Age 1 m + RDI + tree DBH	135.88	16.00	0.00

Note: DBH is diameter at breast height, RDI is the relative density index, OLT is the organic layer thickness.

Table 3

Multi model inference based on Akaike Information Criterion corrected for small sample sizes (AICc) for models linking root-square of aging error with explanatory variables. Model-average estimate, standard error and 95% confidence intervals are given for each explanatory variable. Values in bold are significant.

Explanatory variable	Model-average estimate	Unconditional S.E.	95% Confidence interval
Merchantable volume	0	0	0/0
RDI	0.18	0.74	−1.27/1.63
Tree height	0.01	0.04	−0.07/0.09
Tree DBH	0	0.03	−0.05/0.06
Mean OLT	0.07	0.04	−0.01/0.16
Mean height	0.05	0.07	−0.09/0.18
Mean DBH	0.01	0	0/0.02
Age 1 m	0.01	0	0/0.01
Stand age	**0.01**	**0**	**0.01/0.02**

Note: DBH is the diameter at breast height, RDI is the relative density index, OLT is the organic layer thickness.

Fig. 3. Predicted values given by the set of candidate models (continuous line) and observed values (filled circles: trees aged with root collar; open circles: trees without root collar) of aging error (difference between the total biological age of a tree and an age measured at 1 m) as a function of stand age. Dashed lines represent 95% confidence intervals.

Fig. 4. Height-growth curves for each stand. For readability, stands were grouped into 5 age classes: (A) 20–50 years, (B) 51–75 years, (C) 76–100 years, (D) 101–150 years, (E) >150 years. Dashed grey lines show height derived from SI_{obs} (value of site index from stem analysis curves) while continuous black lines show height derived from SI_{theo} (values of site index from Pothier and Savard (1998)). Dotted black lines show height derived from stem analysis. SI_{theo} and SI_{obs} values are given for each stand.

was the best predictor of aging error. Model containing stand age as the only explanatory variable presented the lowest AICc value (AICc = 119.88, ωi = 0.32). This best supported model (Error Age ∼ Stand age + (Site)) had R^2 = 0.64 (Table 2), even if about 35% of the variability remained unexplained. This model and the model without the random Site effect were similar (Anova; AICc values: 118.88 and 119.34 respectively; Chi-square: p > 0.05). This indicates that aging error varied in the same way, regardless of site. Multi-model inference showed a significant increase of aging error with stand age (estimate = 0.01; Table 3). None of the other covariates significantly contributed to explaining the variation in aging error (Table 3). Predictions based on the entire set of candidate models gave a minimum difference of 15 years and a maximum difference of 40 years between age at 1 m and age at root collar (Fig. 3, mean ± SE: 26.2 years ± 7.0).

The greater difference between age at 1 m and total biological age of the trees in older stands could be explained by the continuous development of adventitious roots throughout their life (DesRochers and Gagnon, 1997; Krause and Morin, 2005), the progressive sinking of trees under their own weight, or growing conditions that were less favorable to tree growth in the past (Arseneault and Payette, 1997), as our data show that it took seedlings longer to reach 1 m height in the oldest stands (Fig. 4). This difference between growth rates of old vs young trees was also observed by Fantin and Morin (2002) and Gagné (2000). Older trees germinated during the Little Ice Age (1570–1880) which was colder and drier (Scott et al., 1988). Lavoie and Payette (1992) linked this period with a sustained decline in spruce growth, followed by warmer temperatures during the 20th century. Increasing atmospheric CO_2 concentration, as well as increasing temperatures and precipitations (Bradley et al., 1987; Houghton et al., 1990), have favored photosynthetic rates and lengthened plants' growing seasons (Lamarche et al., 1984; Jacoby and D'Arrigo, 1997; Bronson et al., 2009). Girardin et al. (2012)

Table 4

Model selection based on the Akaike Information Criterion corrected for small sample sizes (AICc). Response variable is the difference between site index from Pothier and Savard (1998) (SI_{theo}) and from stem analysis (SI_{obs}). Akaike Information Criterion corrected for small sample sizes (AICc), AICc scores (ΔAICc) and Akaike's weight (ωi) values are given for each candidate model.

Explanatory variables	AICc	ΔAICc	ωi
Age 1 m	66.27	0.00	0.26
Stand age	66.64	0.37	0.22
Age 1 m + merchantable volume	68.49	2.22	0.09
Age 1 m + RDI	68.62	2.35	0.08
Age 1 m + mean DBH	68.63	2.36	0.08
Stand age + RDI	69.15	2.89	0.06
Stand age + merchantable volume	69.25	2.98	0.06
Age 1 m + mean height	69.46	3.19	0.05
Stand age + mean DBH	69.91	3.64	0.04
Stand age + mean height	70.18	3.91	0.04
Age 1 m + RDI + mean DBH	73.01	6.74	0.01
Age 1 m + RDI + mean height	73.15	6.88	0.01
Age difference	76.80	10.53	0.00
Age difference + merchantable volume	78.08	11.81	0.00
Age difference + RDI	78.21	11.94	0.00
Age difference + mean OLT + RDI + mean OLT:age difference	78.71	12.44	0.00
Age difference + merchantable volume + mean OLT + age difference:mean OLT	79.07	12.80	0.00
Age difference + mean DBH + mean OLT	80.21	13.94	0.00
Age difference + merchantable volume + mean OLT	80.76	14.49	0.00
Age difference + RDI + mean OLT	80.94	14.67	0.00
Age difference + mean DBH + mean OLT + age difference:mean OLT	81.14	14.87	0.00
Age difference + mean OLT + mean height	81.19	14.92	0.00
Age difference + mean OLT + mean height + age difference:mean OLT	81.99	15.73	0.00

Note: DBH is the diameter at breast height, RDI is the relative density index, OLT is the organic layer thickness, age difference is the difference between the age at 1 m and at root collar (aging error).

Table 5
Multi model inference based on Akaike Information Criterion corrected for small sample sizes (AICc) for models linking SI difference (difference between SI derived from Pothier and Savard (1998) and from stem analysis curves) with explanatory variables. Estimate, standard error and 95% confidence intervals are given for each explanatory variable. Values in bold are significant at $p < 0.05$.

Explanatory variable	Model-average estimate	Unconditional S.E.	95% Confidence interval
Merchantable volume	0.01	0.01	−0.01/0.02
RDI	2.50	2.53	−2.46/7.45
Mean OLT	0.17	0.13	−0.08/0.42
Mean Height	0.12	0.26	−0.39/0.62
Mean DBH	0.19	0.21	−0.23/0.60
Age 1 m	**0.06**	**0.03**	**0.03/0.08**
Age difference	**0.16**	**0.07**	**0.02/0.31**
Stand age	**0.05**	**0.01**	**0.03/0.07**

Note: DBH is the diameter at breast height, RDI is the relative density index, OLT is the organic layer thickness, age difference is the difference between the age at 1 m and at root collar (aging error).

observed a positive response in mature black spruce stands with these improved growth conditions, while over-mature stands were negatively impacted. Despite the lack of studies concerning juvenile stands, it could be expected that they also respond favorably to climate warming, making recently regenerated trees reach 1 m height faster than in the past.

Because of the large difference between age at 1 m and the real age of trees, mature trees appeared to have established a long time after fire (Sirois and Payette, 1989; Lieffers et al., 1996; Côté et al., 2014), or to have originated from layering. This increase in aging error with time means that one has to increasingly adjust correction factors applied to ages not measured at 1 m, e.g. ages measured during the first two Quebec's national forest inventories (1970–1983 and 1981–1994) which were taken at 0.3 m or 1.3 m on the stem and had to be adjusted (Pothier and Savard, 1998). Because black spruce regenerates rapidly after fire (St-Pierre et al., 1992), time since the last fire should be highly representative of stand age and, if available, could be used in the place of total biological age (Garet et al., 2009, 2012; Fourrier et al., 2013). However, for fire cycles longer than their lifespan, trees may die due to secondary disturbances, and time since the last fire could overestimate the average total biological age of trees growing in over-mature stands (Garet et al., 2009, 2012).

3.2. Effect of aging error on the estimation of productivity

Theoretical SIs overestimated SI_{obs} by 4.0 ± 3.2 m. Our stands presented SI_{theo} values varying between 11.7 m and 18.4 m

(mean ± SE = 15.75 ± 1.87 m; Fig. 4). Stem analysis curves, however, gave SI_{obs} values between 4.3 m and 18.3 m (mean ± SE = 11.7 ± 4.1 m, Fig. 4). Paired *t*-test showed significant differences between theoretical (i.e. derived from the equation of Pothier and Savard) and observed (i.e. taken on our stem analysis curves as the height reached at a 1 m age of 50 years) SI values ($p < 0.005$).

Model selection showed that age at 1 m was the best predictor of the difference between the two SI values. Model containing only age at 1 m as explanatory variable presented the lowest AICc value (AICc = 66.27, ωi = 0.26, Table 4). This model had a R^2 of 0.68 which could be considered high because the model remained simple (no multiple interactions were added). The model including stand age was also well supported (AICc = 66.64, ωi = 0.22, Table 4). Multi-model inference revealed that the difference between SI_{theo} and SI_{obs} was significantly greater when stand age, age at 1 m and aging error increased (Table 5, Fig. 5). The more missing years there were on the 1 m section, the more SI_{obs} was overestimated.

It is known that height-age curves, as those used in the province of Quebec (Pothier and Savard, 1998) tend to be less precise for estimating site indices in young stands (Nigh, 1995). Growth intercept models have been proposed to provide more reliable SI estimates for juvenile stands (Mailly and Gaudreault, 2005; Nigh and Klinka, 2001). But, as for height-age curves, they are based on an age measured at 1 m height or at DBH. Mailly and Gaudreault (2005) assumed that their growth intercept models have a precision of 2 m, which increases with age of the selected trees. For stands <20 years, these models tend to underestimate SI. When we compared our SI_{theo} and SI_{obs} values with values obtained following the growth intercept method used by Mailly and Gaudreault (2005), SI values obtained from the growth intercept

Table 6
Values of SI according to different methods of calculation, for young stands (average 1 m age <50 years): SI_{gr} were obtained from Mailly and Gaudreault (2005) growth intercept model, SI_{theo} were obtained with Pothier and Savard (1998) height-age models, and SI_{obs} were derived from our stem analysis values.

Site	Age (1 m)	SI_{gr}	SI_{theo}	SI_{obs}
1	25.33	12.91	15.89	14.43
2	23	14.53	18.35	16.19
3	21	14.65	15.28	16.44
4	47	11.45	15.09	11.16
5	46.33	13.17	14.82	12.54
6	42	17.26	18.26	18.25
10	44.33	13.98	16.48	12.31
Mean	33.25	13.99	16.31	14.47

Note: Age (1 m) is the average age at 1 m height of the 3 sampled trees per stand.
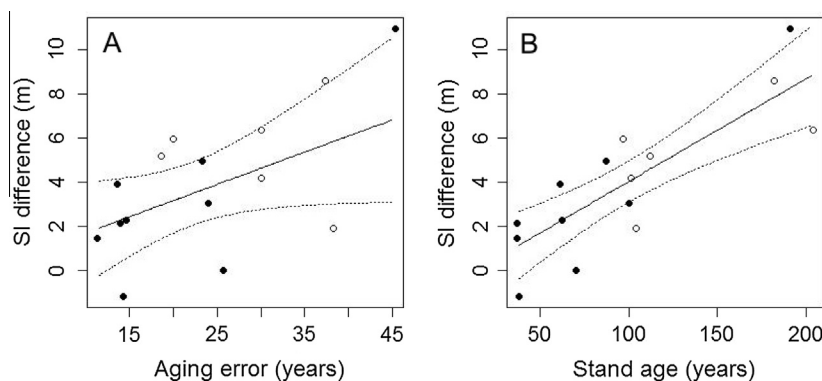
Fig. 5. Predicted (continuous lines) and observed values (filled circles: stands aged from trees with root collar; open circles: stands aged from trees without root collar) of SI difference (difference between SI derived from Pothier and Savard (1998) and from stem analysis curves) based on the entire set of candidate models, as a function of (A) aging error; (B) stand age. Dashed lines represent 95% confidence intervals.
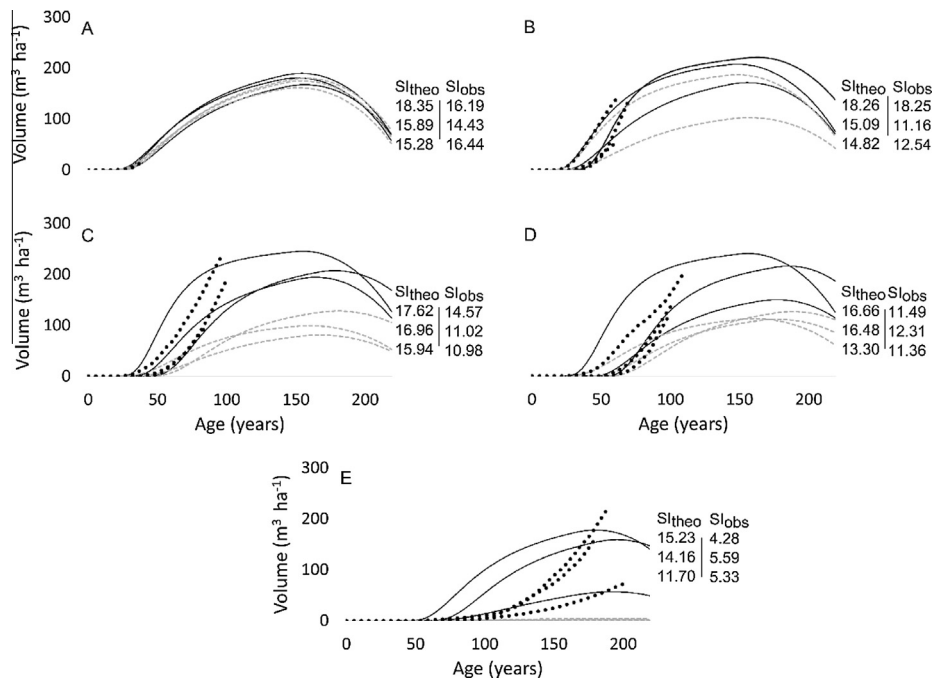
Fig. 6. Volume–age curves according to Pothier and Savard (1998) model. For readability, stands were grouped into 5 age classes: (A) 20–50 years, (B) 51–75 years, (C) 76–100 years, (D) 101–150 years, (E) >150 years. Dashed grey lines show volume derived from site index obtained with stem analysis (SI_{obs}), while continuous black lines show volume derived from site index calculated with Pothier and Savard (1998) models (SI_{theo}). Dotted black lines show volumes derived from stem analysis. SI_{theo} and SI_{obs} are given for each stand.

method were lower than SI_{theo} but differences were not significant (Table 6; paired t test, $p > 0.1$).

Height-growth curves derived from stem analysis showed a slow early growth, followed by a linear increase with no evidence of asymptotic limits over the range of the data, fitting with observations of Van Bogaert et al. (2015), who reported an average of 25 years for black spruce trees growing north of our study area to reach 1 m height. By comparing growth potential of their stands to a height-time reference curve for young black spruce stands in northern Quebec and considering total biological age of trees (time since fire), these authors concluded that the majority of studied stands were unproductive.

Several authors developed height-growth curves showing the same pattern (Ker and Bowling, 1991; Morin and Gagnon, 1992; Larocque et al., 1996; Nigh et al., 2002; Carmean et al., 2006). In contrast, curves derived from Pothier and Savard's (1998) models were sigmoidal (Fig. 4), and do not include the slow-growing period of time between germination and the time trees reach 1 m height. Models represent a period of exponential increase followed by a plateau simulating the decrease of growth rate through time when overall stand growth decreases due to tree senescence (Pothier and Savard, 1998). Similarly, theoretical volume-growth curves didn't exhibit the same pattern than stem analysis-based volume-growth curves. Stem analysis curves show a much prolonged productive growth (Fig. 6). The early period of senescence on the theoretical curves based on 1 m ages was also observed by Garet et al. (2009). The difference we observed between theoretical and stem analysis based curves was similar to that observed by Morin and Gagnon (1992) between post-fire seed-regenerated stands and layer-origin stands after harvesting.

The use of SI_{obs} significantly lowered predicted stand volumes (Fig. 6). However, volumes calculated by stem analysis and SI_{theo} curves were similar at the time of sampling, although volume growth trajectories differed. Volumes predicted from SI_{theo} were generally higher at any given age compared to predictions from

Table 7

Model selection based on the Akaike Information Criterion corrected for small sample sizes (AICc). Response variable is the difference between volume obtained with SI values from Pothier and Savard (1998) models (V_{theo}) and volumes obtained with SI values from stem analysis curves (V_{obs}). Models were fitted with the lm function. Akaike Information Criterion corrected for small sample sizes (AICc), AICc scores (ΔAICc) and Akaike's weight (ωi) values are given for each candidate model.

Explanatory variables	AICc	ΔAICc	ωi
SI difference + RDI	140.12	0.00	0.93
SI difference + mean height	146.76	6.64	0.03
SI difference	148.60	8.48	0.01
SI difference + RDI + mean DBH + mean OLT	149.26	9.14	0.01
SI difference + mean height + mean OLT	150.81	10.69	0.00
SI difference + mean OLT	150.84	10.72	0.00
SI difference + mean DBH + mean OLT	154.01	13.89	0.00
Stand age + RDI	156.77	16.65	0.00
Age 1 m + RDI	156.82	16.70	0.00
Stand age + mean height + Stand age:mean height	159.74	19.62	0.00
Age difference + RDI	160.79	20.67	0.00
Age 1 m + RDI + mean height	161.33	21.21	0.00
Age 1 m + mean height	161.47	21.35	0.00
Age 1 m + RDI + mean DBH	161.48	21.36	0.00
Stand age	162.27	22.15	0.00
Age 1 m	162.55	22.44	0.00
Age 1 m + mean DBH	162.70	22.58	0.00
Age difference + RDI + mean OLT	163.47	23.36	0.00
Age difference + RDI + mean OLT + Age difference: mean OLT	165.50	25.38	0.00
Stand age + mean DBH + Stand age:mean DBH	165.53	25.41	0.00
Age difference + mean height + mean OLT	166.59	26.47	0.00
Age difference	166.99	26.87	0.00
Age difference + mean DBH + mean OLT	167.05	26.93	0.00
Age difference + mean height + mean OLT + Age difference:mean OLT	171.69	31.57	0.00
Age difference + mean DBH + mean OLT + Age difference:mean OLT	172.70	32.58	0.00

Note: DBH is the diameter at breast height, RDI is the relative density index, OLT is the organic layer thickness, age difference is the difference between age at 1 m and at root collar (aging error), SI difference is the difference between SI_{theo} and SI_{obs}.

Table 8
Multi model inference based on Akaike Information Criterion corrected for small sample sizes (AICc), for models linking the difference between volumes obtained with SI values from Pothier and Savard (1998) models (V_{theo}) and volumes obtained with SI values from stem analysis curves (V_{obs}) with explanatory variables. Estimate, standard error and 95% confidence intervals are given for each explanatory variable. Values in bold are significant at $p < 0.05$.

Explanatory variable	Model-average estimate	Unconditional S.E.	95% Confidence interval
SI difference	**13.47**	**1.97**	**9.61/17.32**
RDI	**100.51**	**25.93**	**49.69/151.33**
Mean OLT	0.87	1.48	−2.02/3.76
Mean height	**6.73**	**2.95**	**0.95/12.51**
Mean DBH	−2.21	3.49	−9.05/4.63
Age 1 m	**0.69**	**0.25**	**0.20/1.18**
Age difference	1.97	1.16	−0.30/4.24
Stand age	**0.55**	**0.19**	**0.18/0.93**

Note: DBH is the diameter at breast height, RDI is the relative density index, OLT is the organic layer thickness, age difference is the difference between the age at 1 m and at root collar, SI difference is the difference between SI_{theo} and SI_{obs}.

SI_{obs} (Fig. 6). V_{theo} ranged between 10.2 and 222.2 m³ ha⁻¹, while the gap with V_{obs} ranged −0.3 to 174.2 m³ ha⁻¹, which represents −2.9% to 99.2% of V_{theo}. On the other hand, V_{stem} ranged 8.5–234.5 m³ ha⁻¹. For trees from the oldest stands (Fig. 6E), SI_{obs} values were very low, much lower than the minimum SI value of 7.5 used in forestry (Johnston (1977), cited in Van Bogaert et al. (2015)). Volume–age curves calculated from these lowest SI values gave volume values close to zero. These curves were derived from SI values based on direct observations from stem analysis curves, which could explain these very low volumes: Pothier and Savard's (1998) models were not calibrated with this type of data and were, in this case, misused.

Paired t-test showed a significant difference between V_{theo} and V_{obs} ($p < 0.05$), and between V_{obs} and V_{stem} ($p < 0.05$), but no significant difference between V_{theo} and V_{stem} ($p > 0.05$). Additionally, at the time of sampling, V_{stem} calculated from our 3 sampled trees per plot was similar to volumes derived from the DBH measurements of all trees of the plot (paired t-test, $p > 0.05$). Model selection indicated that the model containing SI difference and RDI as explanatory variables was the best model to explain ΔV variability (AICc = 140.12, $\omega i = 0.93$, Table 7). This model had a great predictive power (adjusted $R^2 = 0.90$). Other candidate models were less informative (ΔAICc > 2, Table 7). Multi-model inference based on AICc revealed ΔV significantly increased with stand age, SI difference, age at 1 m, mean height and RDI (Table 8, Fig. 7).

The use of age at 1 m height as temporal variable for predictive models is preconized by some authors in order to avoid the period of erratic growth considered to occur only in some individuals which have experienced a period of suppression before becoming dominant (Pothier and Savard, 1998; Raulier et al., 2003). But, in the case of fire-originating black spruce stands, we could expect that social status of dominant or co-dominant trees is kept through time because smaller trees suffer the greatest impacts of self-thinning and disturbance (Lussier et al., 1992, 2002a,b). Additionally, fire-originated trees generally form even-aged stands and start their growth at the same time (Morin and Gagnon, 1992; Pothier et al., 1995), and we have not observed dead stems which could indicate replacement of trees due to secondary disturbances. The period of slow early growth is observed for a great majority of black spruce trees, even for fire-regenerated individuals which didn't experience suppression (Van Bogaert et al., 2015). We think that this pattern is typical of black spruce's juvenile growth, and can be non-negligible in light of the tree's lifespan. This period increases with stand age, and should be taken into account in order to obtain accurate productivity estimations over time. Because we took tree mortality into account in the calculation of V_{stem} by using the same densities than for Pothier and Savard's values (Eq. (9)), we expect that V_{stem} could adequately represent the volume trajectory of the stand. Even tough approximation was done when calculating V_{stem}, there was no difference between V_{stem} and volumes derived from the DHB of all trees from a plot, which were on average slightly smaller than the three sampled trees.

4. Conclusion and outlooks

This study showed that there was a significant difference between the true biological age of black spruce trees and an age taken at 1 m height on the stem, and that this difference increased with stand age, or time since the last fire. We also showed that use of age at 1 m lead to overestimation of site indices, although there was no difference between estimated and observed volumes at the time of sampling. Finally, this study showed that growth trajectories were poorly modeled: observed early growth was slower, and then increased over a longer time period compared to theoretical curves.

In the light of these results, future productivity estimation models should be adjusted with data from stands of various ages, and particularly from juvenile stands (i.e. <50 years) to accurately draw early growth trajectories. The common method of calculating site indices could lead to an overestimation of growth potential of sites.
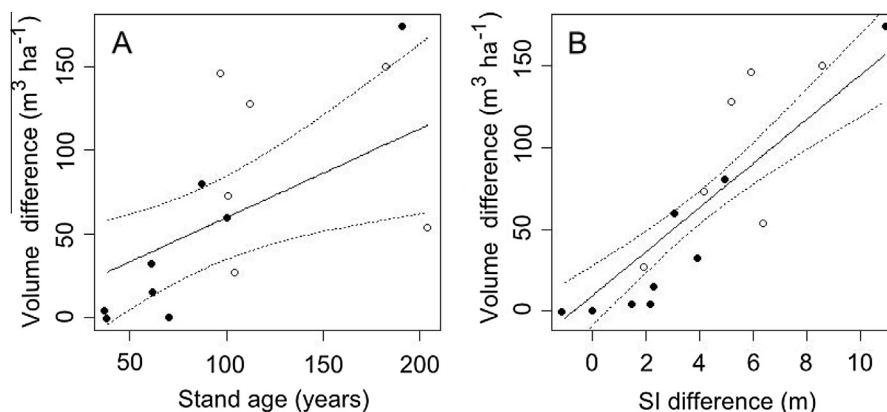
Fig. 7. Predicted (continuous lines) and observed values (filled circles: stands aged from trees with root collar; open circles: stands aged from trees without root collar) of differences between volumes obtained with SI values from Pothier and Savard (1998) models (V_{theo}) and volumes obtained with SI values from stem analysis curves (V_{obs}) based on the entire set of candidate models as a function of (A) stand age and (B) SI difference (difference between site index from Pothier and Savard (SI_{theo}) and from stem analysis (SI_{obs})). Dashed lines represent 95% confidence intervals.

Rating site indices at an age older than 50 years (e.g. at an age of 100 years, Hägglund and Lundmark (2002)) could improve the estimation of site potential by evaluating growth after the period of early slow growth. The assumption that site index of a given stand does not vary with time appears not to be respected because of temporal changes in environmental parameters. A reflection of that could be that our younger trees reached 1 m height faster than our older trees. In addition to long-term climate changes, time elapsed since the last fire can generate modifications of the forest floor properties and nutrient availability (Brais et al., 1995) as well as changes in the diametrical composition through time (Ouzennou et al., 2008) which could influence growth potential. A regression tree approach based on abiotic variables like organic layer thickness, average annual temperature or annual precipitations (McKenney and Pedlar, 2003), could give better predictions of potential growth because it would overcome inaccuracies due to age estimation. Quebec's boreal forests are managed with a rotation time of about 90 years. Since tree growth is slower than modeled, it could be hypothesized that currently harvested volumes are lower than expected. An extended forest rotation period could allow stands to reach the expected volumes.

Acknowledgements

References

Arseneault, D., Payette, S., 1997. Reconstruction of millenial forest dynamics from tree remains in a subarctic tree line peatland. Ecology 78, 1873–1883.

Bergeron, Y., 2000. Species and stand dynamics in the mixed woods of Quebec's southern boreal forest. Ecology 81, 1500–1516.

Bradley, R.S., Diaz, H.F., Eischeid, P.D., Kelly, P.M., Goodess, C.M., 1987. Precipitation fluctuations over northern hemisphere land areas since the mid-19th century. Science 237, 171–175.

Brais, S., Camiré, C., Bergeron, Y., Paré, D., 1995. Changes in nutrient availability and forest floor characteristics in relation to stand age and forest composition in the southern part of the boreal forest of northwestern Quebec. For. Ecol. Manage. 76, 181–189.

Bronson, D.R., Gower, S.T., Tanner, M., Van Herk, I., 2009. Effect of ecosystem warming on boreal black spruce burst and shoot growth. GCB Bioenergy 15, 1534–1543.

Burnham, K., Anderson, D.R., 2002. Model Selection and Multi-model Inference: A Practical Information-theoretic Approach. Springer, New York.

Burns, R.M., Honkala, B.H., 1990. Silvics of North America Vol. 1 Conifers. Agriculture Handbook, vol. 654. United States Department of Agriculture Forest Service, Washington, DC, http://www.na.fs.fed.us/pubs/silvics_manual/table_of_contents.shtm.

Burton, P.J., Messier, C., Smith, D.W., Adamowicz, W.L., 2003. Towards Sustainable Management of the Boreal Forest. NRC Research Press, Ottawa, Ontario.

Carmean, W., Hazenberg, G., Deschamps, K.C., 2006. Polymorphic site index curves for black spruce and trembling aspen in northwest Ontario. For. Chron. 82, 231–242.

Chhin, S., Hogg, E.T., Lieffers, V.J., Huang, S., 2010. Growth-climate relationships vary with height along the stem in lodgepole pine. Tree Physiol. 30, 335–345.

Côté, D., Lupi, C., Gagnon, R., Lord, D., Morin, H., 2014. Growth dynamics of successive post-fire cohorts of black spruce: is site potential reduced? For. Chron. 90, 96–104.

DesRochers, A, Gagnon, R., 1997. Is ring count at ground level a good estimation of black spruce age? Can. J. For. Res. 27, 1263–1267.

Duchesne, S., Sirois, L., 1995. First phase of post fire regeneration of subarctic conifer stands. Can. J. For. Res. 25, 307–318.

Environnement Canada, 2011. National climate archives. <https://www.ec.gc.ca/>.

Esau, K., 1967. Plant Anatomy. John Wiley & Sons, New York.

Fantin, N., Morin, H., 2002. Croissance juvénile comparée de deux générations successives de semis d'épinette noire issus de graines après feu en forêt boréale, Québec. Can. J. For. Res. 32, 1478–1490.

Fayle, D.C.F., 1968. Radial Growth in Tree Roots: Distribution-timing-anatomy. University of Toronto, Faculty of Forestry, Toronto, Ontario.

Fenton, N., Lecomte, N., Légaré, S., Bergeron, Y., 2005. Paludification in black spruce (*Picea mariana*) forests of eastern Canada: potential factors and management implications. For. Ecol. Manage. 213, 151–159.

Fenton, N., Bergeron, Y., 2007. *Sphagnum* community change after partial harvest in black spruce boreal forests. For. Ecol. Manage. 242, 24–33.

Fortin, M., Bernier, S., Saucier, J.-P., Labbé, F., 2009. Une relation hauteur-diamètre tenant compte de l'influence de la station et du climat pour 20 espèces commerciales du Québec. Gouvernement du Québec, Ministère des Ressources naturelles et de la Faune, Direction de recherche forestière, Québec.

Fortin, M., DeBlois, J., Bernier, S., Blais, G., 2007. Mise au point d'un tarif de cubage général pour les forêts québécoises: une approche pour mieux évaluer l'incertitude associée aux prévisions. For. Chron. 83, 754–765.

Fourrier, A., Pothier, D., Bouchard, M., 2013. A comparative study of long-term stand growth in eastern Canadian boreal forest: fire versus clear-cut. For. Ecol. Manage. 310, 10–18.

Fraver, S., Bradford, J.B., Palik, J., 2011. Improving tree age estimates derived from increment cores: a case study of red pine. For. Sci. 57, 164–170.

Gagné, C., 2000. Tendance à long terme de la croissance de l'épinette noire (Picea mariana (Mill.) B.S.P.) en forêt boréale québécoise (Ph.D. thesis). Université du Québec à Chicoutimi, Chicoutimi.

Gagnon, R., Morin, H., 1992. Establishment period of black spruce (*Picea mariana*) after fire. In: Bartholin, T.S., Berglund, B.E., Eckstein, D., Schweingruber, F.H. (Eds.), LUNDQUA Report 34. Lund University, Lund, pp. 112–114.

Gagnon, R., Morin, H., 2001. Les forêts d'épinette noire du Québec: dynamique, perturbations et biodiversité. Le Naturaliste Canadien 125, 26–35.

Gagnon, R., Morin, H., St-Pierre, H., Filion, J., Villeneuve, G., 1992. La régénération naturelle de l'épinette noire par graines: point de départ d'une méthode efficace d'ensemencement. In: Service de l'amélioration des arbres et Service du transfert de technologie (Ed.), Compte-rendu du Colloque sur les semences forestières, division de la recherche sur les semences, les boutures et les plants. Ministère des forêts, Sainte-Foy, Québec, pp. 171–180.

Garet, J., Pothier, D., Bouchard, M., 2009. Predicting the long-term yield trajectory of black spruce stands using time since fire. For. Ecol. Manage. 257, 2189–2197.

Garet, J., Raulier, F., Pothier, D., Cumming, S.G., 2012. Forest age class structures as indicators of sustainability in boreal forest: are we measuring them correctly ? Ecol. Indic. 23, 202–210.

Girardin, M.P., Guo, X.J., Bernier, P.Y., Raulier, F., Gauthier, S., 2012. Changes in growth of pristine boreal North American forests from 1950 to 2005 driven by landscape demographics and species traits. Biogeosciences 9, 2523–2536.

Grondin, P., 1996. Écologie forestière. In: Bédard, J., Côté, M. (Eds.), Manuel de foresterie. Presse de l'Université Laval, Sainte-Foy, Québec, pp. 133–279.

Gutsell, S.L., Johnson, E.A., 2002. Accurately ageing trees and examining their height-growth rates: implications for interpreting forest dynamics. J. Ecol. 90, 153–166.

Hägglund, B., Lundmark, J.E., 2002. Site index estimation by means of site properties – Scots pine and Norway spruce in Sweden. In: Studia Forestalia Sueica. J.G.K. Flower-Ellis, Lund, pp. 1–37.

Henry, J.D., Swan, J.M.A., 1974. Reconstructing forest history from live and dead plant material–an approach to the study of forest succession in southwest New Hampshire. Ecology 55, 772–783.

Houghton, J.T., Jenkins, G.J., Ephraums, J.J., 1990. Climate Change: The IPCC Scientific Assessment. Cambridge University Press, Cambridge.

Hurlbert, S.H., 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54, 187–211.

Islam, M.A., MacDonald, S.E., Zwiazek, J.J., 2003. Responses of black spruce (*Picea mariana*) and tamarack (*Larix laricina*) to flooding and ethylene. Tree Physiol. 23, 545–552.

Jacoby, G.C., D'Arrigo, R.D., 1997. Tree rings, carbon dioxide, and climatic change. Proc. Natl. Acad. Sci. 94, 8350–8353.

Johnston, W.F., 1977. Manager's Handbook for Black Spruce in the North-Central States. USDA Forest Service, North Central Forest Experiment Station, St Paul, Minnesota.

Ker, M.F., Bowling, C., 1991. Polymorphic site index equations for four New Brunswick softwood species. Can. J. For. Res. 21, 728–732.

Krause, C., Morin, H., 2005. Adventive-root development in mature black spruce and balsam fir in the boreal forests of Quebec, Canada. Can. J. For. Res. 35, 2642–2654.

Lamarche, V.C., Graybill, D.A., Fritts, H.C., Rose, M.R., 1984. Increasing atmospheric carbon dioxide: tree ring evidence for growth enhancement in natural vegetation. Science 225, 1019–1021.

Landhäusser, S.M., Wein, W.R., 1993. Postfire vegetation recovery and tree establishment at the arctic treeline: climate-change vegetation-response hypotheses. J. Ecol. 81, 665–672.

Larocque, G.R., Parton, W.J., Archibald, D.J., 1996. Polymorphic Site Productivity Functions for Black Spruce in Relation to Different Ecological Types in Northern Ontario. Natural Ressources Canada, Canadian Forest Service, Laurentian Forestry Centre, Sainte-Foy, Quebec.

Lauzon, E., Bergeron, Y., Gauthier, S., Kneeshaw, D., 2006. Fire Cycles and Forest Management: An Alternative Approach for Management of the Canadian Boreal Forest. Sustainable Forest Management Network, Edmont, Alberta.

Lavoie, C., Payette, S., 1992. Black spruce growth forms as a record of a changing winter environment at treeline, Quebec, Canada. Arct. Alp. Res. 24, 40–49.

Lieffers, V.J., Stadt, K.J., Navratil, S., 1996. Age structure and growth of understory white spruce under aspen. Can. J. For. Res. 26, 1002–1007.

Loewenstein, E.F., Johnson, P.S., Garrett, H.E., 2000. Age and diameter structure of a managed uneven-aged oak forest. Can. J. For. Res. 30, 1060–1070.

Lussier, J.M., Morin, H., Gagnon, R., 1992. Comparaison de la croissance des marcottes d'épinette noire (*Picea mariana*) adultes après coupe à celle d'individus issus de graines après feu. Can. J. For. Res. 22, 1524–1535.

Lussier, J.-M., Morin, H., Gagnon, R., 2002a. Mortality in black spruce stands of fire or clear-cut origin. Can. J. For. Res. 32, 539–547.

Lussier, J.M., Morin, H., Gagnon, R., 2002b. Évolution de la structure diamétrale et production ligneuse des pessières noires issues de coupe et de feu. Can. J. For. Res. 32, 526–538.

Mailly, D., Gaudreault, M., 2005. Growth intercept models for black spruce, jack pine and balsam fir in Quebec. For. Chron. 81 (1), 104–113.

Matison, R., Brümelis, G., 2008. Effect of burial by sand on Scots pine (*Pinus sylvestris* L.) radial growth on seacoast wooded dunes at Cape Kolka, Latvia. Acta Univ. Latv. 745, 131–144.

Matthes, U., Kelly, P.E., Larson, D.W., 2008. Predicting the age of ancient *Thuja occidentalis* on cliffs. Can. J. For. Res. 38, 2923–2931.

Mazerolle, M.J., 2015. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R Package Version 2.0-3. <http://CRAN.R-project.org/package=AICcmodavg>.

McKenney, D.W., Pedlar, J.H., 2003. Spatial models of site index based on climate and soil properties for two boreal tree species in Ontario, Canada. For. Ecol. Manage. 175, 497–507.

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

MRNF, 2011. Normes d'inventaire forestier. Les placettes-échantillons temporaires. Ministère des Ressources Naturelles et de la Faune, Direction des Inventaires Forestiers, Québec.

Nigh, G., 1995. Variable growth intercept models for lodgepole pine in the sub-boreal biogeoclimatic zone, British Columbia. Ministry of Forests, Victoria, B.C. Research Report RR-02.

Nigh, G., Klinka, K., 2001. Growth intercept models for black spruce. Ministry of Forests, Forest Science Program, British Columbia. Extension Note EN-57.

Nigh, G., Krestov, P., Klinka, K., 2002. Height growth of black spruce in British Columbia. For. Chron. 78, 306–313.

Niklasson, M., 2002. A comparison of three age determination methods for suppressed Norway spruce: implications for age structure analysis. For. Ecol. Manage. 161, 279–288.

Ouzennou, H., Pothier, D., Raulier, F., 2008. Adjustment of the age-height relationship for uneven-aged black spruce stands. Can. J. For. Res. 38, 2003–2012.

Parent, S., Morin, H., 2002. Reply: effects of adventitious roots on age determination in balsam fir regeneration. Can. J. For. Res. 32, 1296–1300.

Parent, S., Morin, H., Messier, C., 2000. Effects of adventitious roots on age determination in balsam fir (*Abies balsamea*) regeneration. Can. J. For. Res. 30, 513–518.

Parisien, M.A., Sirois, L., Parent, S., 2005. Landscape-level variability in the age underestimation of understory black spruce in the northern boreal forest of Quebec. Can. J. For. Res. 35, 633–642.

Peters, V.S., Macdonald, S.E., Dale, M.R.T., 2002. Aging discrepancies of white spruce affect the interpretation of static age structure in boreal mixedwoods. Can. J. For. Res. 32, 1496–1501.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., 2015. R Core Team (2015). nlme: Linear and Nonlinear Mixed Effects Models. R Package Version 3.1-122. <http://CRAN.R-project.org/package=nlme>.

Pothier, D., Doucet, R., Boily, J., 1995. The effect of advance regeneration height on future yield of black spruce stands. Can. J. For. Res. 25, 536–544.

Pothier, D., Savard, F., 1998. Actualisation des tables de production pour les principales espèces forestières du Québec. Ministère des Ressources naturelles, Gouvernement du Québec, Québec.

R Core Team, 2014. R: A Language and Environment for Statistical Computing. Vienna, Austria.

Raulier, F., Lambert, M.C., Pothier, D., Ung, C.H., 2003. Impact of dominant tree dynamics on site index curves. For. Ecol. Manage. 184, 65–78.

Regent Instruments Inc., 2009. WinDendro Reference Manual, Version 2009, March 12, 2008. Régent Instruments, Québec.

Rohner, B., Bugmann, H., Bigler, C., 2013a. Estimating the age–diameter relationship of oak species in Switzerland using nonlinear mixed-effects models. Eur. J. Res. 132, 751–764.

Rohner, B., Bugmann, H., Bigler, C., 2013b. Towards non-destructive estimation of tree age. For. Ecol. Manage. 304, 286–295.

Rowe, J.S., 1972. Les régions forestières du Canada. Environnement Canada, Service canadien des forêts, Ottawa.

Scott, P.A., David, C.F.F., Bentley, C.V., Roger, I.C.H., 1988. Large-scale changes in atmospheric circulation interpreted from patterns of tree growth at Churchill, Manitoba, Canada. Arct. Alp. Res. 20, 199–211.

Singh, T., 1987. Wood density variations in thirteen Canadian tree species. Wood Fiber Sci. 19, 362–369.

Sirois, L., Payette, S., 1989. Postfire black spruce establishment in subarctic and boreal Quebec. Can. J. For. Res. 19, 1571–1580.

St-Pierre, H., Gagnon, R., Bellefleur, P., 1992. Régénération après feu de l'épinette noire (*Picea mariana*) et du Pin gris (*Pinus banksiana*) dans la forêt boréale, Québec. Can. J. For. Res. 22, 474–481.

Swetnam, T., Thompson, M., Kennedy Sutherland, E., 1985. Using Dendrochronology to Measure Radial Growth of Defoliated Trees. Agriculture Handbook, vol. 639. USDA Forest Service, Washington, DC, pp. 1–39.

Tarroux, E., DesRochers, A., Girard, J.-P., 2014. Growth and root development of black and white spruce planted after deep planting. For. Ecol. Manage. 318, 294–303.

Telewski, F.W., Lynch, A.M., 1991. Measuring growth and development of stems. In: Lassoie, J.P., Hinckley, T.M. (Eds.), Techniques and Approaches in Forest tree Ecophysiology. CRC Press, Boston, pp. 503–555.

Trotsiuk, V., Hobi, M.L., Commarmot, B., 2012. Age structure and disturbance dynamics of the relic virgin beech forest Uholka (Ukrainian Carpathians). For. Ecol. Manage. 265, 181–190.

Van Bogaert, R., Gauthier, S., Raulier, F., Saucier, J.-P., Boucher, D., Robitaille, A., Bergeron, Y., 2015. Exploring forest productivity at an early age after fire: a case study at the northern limit of commercial forests in Quebec. Can. J. For. Res. 45, 579–593.

Vasiliauskas, S., Chen, H., 2002. How long do trees take to reach breast height after fire in northeastern Ontario? Can. J. For. Res. 32, 1889–1892.

Wilmking, M., Hallinger, M., Van Bogaert, R., Kyncl, T., Babst, F., Hahne, W., Juday, G. P., de Luis, M., Novak, K., Völlm, C., 2012. Continuously missing outer rings in woody plants at their distributional margins. Dendrochronologia 30, 213–222.

Wong, C.M., Lertzman, K.P., 2001. Errors in estimating tree age: implications for studies of stand dynamics. Can. J. For. Res. 31, 1262–1271.