Juvenile growth of black spruce (*Picea mariana* [Mill.] BSP) stands established during endemic and epidemic attacks by spruce budworm (*Choristoneura fumiferana* [Clemens]) in the boreal forest of Quebec, Canada

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ABSTRACT

In the boreal forest of Quebec, 80% of harvested black spruce (*Picea mariana* [Mill.] BSP) stands regenerate naturally. In the remaining 20%, forest regeneration is ensured by planting seedlings and these plantations are expected to increase future forest yields. However, predictions of future yields using the information from very young plantations in this ecosystem may have low accuracy. To compare juvenile growth in plantations versus naturally regenerated stands, and also to evaluate the impacts of spruce budworm *Choristoneura fumiferana* (Clemens) defoliation periods during the juvenile phase, annual height and volume growth were calculated from measurements on nine black spruce stands. The nine sites consisted of two plantations and seven post-fire, naturally regenerated stands. Of the seven naturally regenerated sites, four were epidemic and 3 endemic. The term "epidemic" refers to stands regenerated during known spruce budworm defoliation periods. The term "endemic" refers to stands regenerated during periods without severe defoliation. For height and volume growth, 5 different methods were used and compared. The annual height and volume growth of all black spruce showed a sigmoid trend, characterized by low values in the first years after germination, followed by an exponential acceleration and finally oscillation around a horizontal asymptote. The black spruce stands established during endemic periods were more productive than those established during epidemic periods, but plantations were the most productive.

Key words: black spruce, juvenile growth, plantation, post-fire stands, spruce budworm outbreak, volume, yield

RÉSUMÉ

Dans la forêt boréale du Québec, 80% des peuplements récoltés d'épinette noire (*Picea mariana* [Mill.] BSP) se régénèrent naturellement. La régénération du 20% restant est assurée par des plantations qui devraient augmenter le rendement futur des forêts. Le jeune âge (< 20 ans) des plantations dans cet écosystème limite cependant la portée des prédictions futures. Afin d'évaluer la croissance juvénile et l'impact possible de la tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* (Clemens)) (TBE) durant la phase juvénile de croissance, les accroissements en hauteur et en volume ont été calculés dans neuf peuplements d'épinette noire. Cinq méthodes différentes de calcul ont été comparées. Les neuf sites consistaient en deux plantations et sept peuplements régénérés naturellement après feu. De ces 7 peuplements régénérés naturellement, quatre étaient épidémiques et trois endémiques. Le terme « épidémique » fait référence aux peuplements régénérés durant des périodes connues de défoliation par la TBE. Le terme « endémique » fait référence aux peuplements régénérés durant des périodes sans défoliation par la TBE. La croissance annuelle en hauteur et en volume de toutes les épinettes présente une tendance sigmoïde, caractérisée par des valeurs faibles dans les premières années après la germination, suivie ensuite par une accélération exponentielle et enfin une phase de stagnation. Les peuplements d'épinette noire qui se sont régénérés en périodes endémiques ont été plus productifs que ceux en périodes épidémiques, mais restaient inférieurs au volume des plantations.

Mots-clés : épinette noire, croissance juvénile, plantation, peuplements après feu, épidémie de tordeuse des bourgeons de l'épinette, volume, rendement

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Introduction

Black spruce (*Picea mariana* [Mill.] BSP) is the main tree species in the boreal forest of eastern Canada (Rowe 1972, Farrar 1995). It can grow in climatic conditions characterized as cold with a moisture regime varying from humid to dry subhumid. It usually grows in wet organic soils, but also in other soil types from deep humus through clay, sands, coarse till, boulder pavements

and shallow soil mantles over bedrock (Viereck and Johnston 1990). Black spruce most commonly grows as pure stands, but when it is associated with other tree species, these will be mainly balsam fir (*Abies balsamea* (Mill.)), jack pine (*Pinus banksiana* Lamb.) and white birch (*Betula papyrifera* Marsh.). Black spruce is classed as shade-tolerant, but is considered less tolerant than balsam fir.

Forest industries favour this species because the wood has high mechanical resistance and fibres are easy to bleach (Singh 1987, Harris 1993, Hatton and Johal 1996, Zhang *et al.* 1996, Ahmed *et al.* 2005, Alteyrac *et al.* 2006). Advance growth, consisting of young seedlings as well as layers around the harvested trees, is protected during the harvesting process. The use of existing overstory trees as a natural shelterwood system is widely applied in eastern Canada, because of the prevalence of over-mature stands that have had an opportunity to accumulate advance regeneration (Groot *et al.* 2005). This management policy of favouring existing understorey regeneration, as practised in Quebec, ensures approximately 80% of stands are successfully regenerated following harvest. In addition, the protection of advance regeneration allows for the renewal of the genetic pool, while preserving the biodiversity of the dominant shade-tolerant tree species such as black spruce. Planting black spruce is considered whenever natural restocking in the understorey following harvest is insufficient and also after fire episodes with insufficient natural regeneration. Around 20% of harvested black spruce stands in the boreal forest of Quebec need to be planted to ensure sufficient stocking (MRN 2002), accounting for more than 60 million seedlings planted annually in the last few years (Parent and Fortin 2006).

Currently, there are two types of seedlings produced for the boreal forest of Quebec: container grown or bare-root

stock. In the last 20 years, seedlings have been produced mostly in small rigid walled containers (Halter *et al.* 1993, Lindström and Rune 1999, Thiffault *et al.* 2003). Since the use of seedlings grown in small, rigid-walled containers is relatively recent, they are only found in young plantations. This type of seedling production is expected to increase forest yields in the future because of seed selection and competition control after plantation in the forest (OIFQ 1996).

Measures of site productivity are needed in order to estimate growth and yield of naturally regenerated stands and plantations. For even-aged stands dominated by a single species in North America, site productivity is determined by estimating site index, which is the average height of dominant and co-dominant trees in a forest stand at a reference age (Clutter *et al.* 1983). To determine the site index, a height-age equation has to be developed based on height and age data obtained from suitable trees. This process usually excludes very young trees (Monserud 1988, Wykoff 1990). For very young trees, growth intercept methods have been developed to estimate site index using measurements of height growth and age to estimate the site index (e.g., Nigh 1999).

As well as measures of site productivity, accurately characterizing juvenile growth is needed as the first step in quantifying the long-term yield for different forest types. Yield estimates in young plantations and in naturally regenerated stands are generally not very accurate (Popovich 1974). While older plantations in the southern regions of Quebec provide better estimates, in the boreal forest of Quebec, the low number of plantations older than 20 years leads to a decrease in the precision of existing yield curves (Prégent *et al.* 1996). Growth of juvenile trees in young plantations may not reflect long-term growth and yield.

The uncertainty about the impact of natural disturbances on plantation growth is another factor to consider when predicting yields. It is well known that the boreal forest is frequently affected by fire and insect outbreaks (MacLean *et al.* 1984, Cogbill 1985, Baskerville 1986). In northeastern North America, spruce budworm (*Choristoneura fumiferana* [Clem.]) periodically defoliated both balsam fir and black spruce (Blais 1965, Hardy *et al.* 1983, Krause and Morin 1999). Spruce budworm outbreaks caused significant reductions in radial increments in black spruce, even possibly triggering increased tree mortality during severe defoliation periods (Raske and Sutton 1986, Lussier *et al.* 2002). A reduction of height growth during a defoliation period in young balsam fir was reported by Ghent (1958), Piene and Little (1990) and Piene and MacLean (1999). There is currently little information available about the potential negative impact of spruce budworm outbreaks on black spruce plantations during the seedling stage. To the best of our knowledge, only one study noted that seedling height growth of black spruce seemed to be affected during spruce budworm outbreaks (Fournier 1997).

The objective of this research project was to accurately reconstruct annual and cumulative height and volume growth of black spruce trees in plantations and in naturally regenerated post-fire black spruce stands in the boreal forest of Quebec. The results could then be used to describe the juvenile phase of tree growth and to compare volume growth between study sites. Some of the naturally regenerated stands were initiated during spruce budworm outbreaks (epidemic periods) and others during periods of no defoliation (endemic periods). This allowed the investigation of the

impact of this defoliator on black spruce development in the juvenile phase. In addition, the study investigated the precision and usefulness of 5 different calculation methods used to predict growth performance.

Materials and Methods

The trees under investigation were part of two black spruce plantations and seven black spruce natural post-fire stands (Table 1). All study sites were located in the boreal forest of Quebec, between latitudes 49° and 50° north and longitudes 70° and 72° west in the ecological region of west and east balsam fir–white birch domain and the west spruce–moss domain (Table 1) (MRN 2003). The black spruce plantations were established 1986 and 1990. Post-fire stand germination dates ranged from 1920 to 1983. All black spruce stands were growing on mesic sites. Ground cover in the older naturally regenerated post-fire stands was mostly characterized by mosses (*Pleurozium schreberi* (BSG) Mitt. and *Sphagnum* sp.), lichens (*Cladonia rangiferina* and *C. stellaris*) and shrubs (*Kalmia angustifolia* and *Ledum groenlandicum*). Sparse populations of *Chiogenes hispidula*, *Rubus idaeus* L., *Vaccinium angustifolia*, *V. myrtilloides* and other *Vaccinium* species were also noted. In the planted stands, *Salix*, *Prunus*, *Alnus* and *Cornus* species were present in small proportions. Common

boreal herbaceous species such as *Cornus canadensis* L., *Maianthemum canadense* Desp and *Coptis groenlandica* (Oeder) Fern. were also identified.

The seven natural post-fire stands were labelled as either epidemic or endemic, depending on the conditions under which they regenerated. Epidemic stands regenerated during spruce budworm defoliation periods. Endemic stand regenerated during periods without severe defoliation (Table 1). This classification was based on known historic spruce budworm outbreak periods reported by Morin and Laprise (1990) and by Krause and Morin (1999). The seven post-fire stands were dominated mostly by black spruce accompanied by other species, with the exception of post-fire stand ChiNF71 where jack pine was more abundant (Table 2). Post-fire stands regenerated in epidemic periods are rare; therefore, we took advantage of unpublished data for stand GirF54 (Morin and Fantin unpublished manuscript).

Soil samples showed all the stands were growing on podzols (Table 2). There were slight differences in terms of pH and nitrate-nitrogen concentrations. However, two post-fire stands, ChiF70 and ChiNF71, showed higher concentrations of calcium-magnesium, potassium and phosphorus.

Stand density on the study sites, based on the count of merchantable plus non-merchantable stems, ranged from

Table 1. Descriptive statistics of the black spruce study site

Site	Stand origin	GPS coordinates	Ecological region	Year of origin	Year of sampling	Outbreak influence
BwF20	fire	49°21'37"N – 71°57'04"W	West balsam fir – white birch domain	1920	2005	endemic
SimF22	fire	48°12'56"N – 71°14'35"W	West balsam fir – white birch domain	1922	2005	endemic
GirF54	fire	49°16'59"N – 72°35'15"W	West balsam fir – white birch domain	1954	1999	epidemic
MyrF56	fire	47°52'02"N – 70°46'34"W	East balsam fir – white birch domain	1956	2004	epidemic
ChiF70	fire	49°52'56"N – 74°19'58"W	West spruce – moss domain	1970	2004	epidemic
ChiNF71	fire	50°00'23"N – 74°12'54"W	West spruce – moss domain	1971	2004	epidemic
DesF83	fire	49°26'06"N – 73°15'19"W	West spruce – moss domain	1983	2004	endemic
MvPL86	plantation	48°53'01"N – 70°33'17"W	East balsam fir – white birch domain	1986	2002	endemic
LauPL90	plantation	48°14'19"N – 71°21'16"W	West balsam fir – white birch domain	1990	2005	endemic

Table 2. Dendrometric statistics of the study sites

Site	Stems/ha ^a	Stand ^b composition	Soil type	pH values by soil layer				Mean values, tree level		
				humus	Ae	B	n	age ± std (years)	dsh (cm)	height (m)
BwF20	3275	BS	podzol	3.2	4	4.6	15	80 ± 2	24.6 ± 4.7	16.8 ± 1.4
SimF22	3000	BS – BF	podzol	3.4	3.5	–	15	78 ± 4	26.2 ± 6.3	15.8 ± 2.6
GirF54	2050	BS – JP	podzol	n/a	n/a	n/a	10	42 ± 2	14.5 ± 2.3	8.1 ± 0.9
MyrF56	1100	BS – JP	podzol	3.6	3.8	–	15	36 ± 5	15.1 ± 2.5	7.4 ± 1.2
ChiF70	1000	BS – PB – TA	podzol	3.8	4	4.9	14	29 ± 2	9.6 ± 1.2	4.8 ± 0.6
ChiNF71	1200	JP – BS	podzol	5	4.7	4.5	15	31 ± 1	9.3 ± 0.7	5.3 ± 1.0
DesF83	4480	BS	podzol – organic	3.8	4.3	4.5	15	18 ± 0	6.7 ± 2.3	2.9 ± 0.6
MvPL86	3000	BS	podzol	4.4	4.8	5	15	17 ± 0	9.4 ± 2.0	3.9 ± 1.0
LauPL90	3100	BS	podzol	4.3	4.2	5.3	15	17 ± 0	9.5 ± 1.7	4.9 ± 0.8

^aAll trees, merchantable and non-merchantable

^bBS: black spruce; BF: balsam fir; JP: jack pine; PB: paper birch; TA: trembling aspen (*Populus tremuloides* Michx.); std: standard deviation; dbh: diameter outside bark at breast height; dsh: diameter outside bark at stump height; n: number of trees analyzed

1000 to 4480 stems/ha (Table 2). The lowest density was found in the post-fire stands originating in years 1956, 1970 and 1971. The mean diameter at stump height and mean tree height increased with the age of the stand. Standard deviations also increased. The site index was calculated using the method of Nigh (1997), but setting the reference height for age at 1.0 m (Mailly and Gaudreault 2005). The site index was thus obtained by calculating the top height reached at the time of sampling and the age determined at 1.0 m. Growth intercepts were calculated using the equations presented by Mailly and Gaudreault (2005) for each age₁₀₀ from one to the last year measured in given stands. Site index values in Table 2 refer to the calculation at the age of sampling.

Fifteen trees were randomly selected within each black spruce stand, with the exception of stands GirF54 and ChiF70, where only 10 and 14 trees were sampled, respectively. In order to reconstruct the annual growth of each tree accurately, it was essential to extract the whole stump to locate the root-shoot interface. If the interface was unidentifiable, the stump had to be rejected and a new tree had to be sampled to replace it. One black spruce in stand ChiF70 was rejected because the root-shoot interface was missing, but it was not replaced. Access concerns did not allow us to return to stand GirF54 for additional sampling.

Each tree was cut at soil level and the stump was excavated. For each sampled tree, the root-shoot interface was located on the stump by identifying the anatomical changes between the pith and the central cylinder. Layered regeneration was excluded from this analysis. Second, locations of all bud scars along the stem were recorded, from the top of the tree downwards to the root-shoot interface. The location of the bud scars was used in one approach to reconstruct the height development over time. In the lower parts of the stem, especially close to the stump, the count of annual tree-rings in transverse sections was essential to offset the difficulty of locating the oldest bud scars. The oldest stands (BwF20, SimF22, GirF54) were excluded from this analysis due to the difficulty of locating bud scars formed during the first years after germination. The average annual height growth was calculated from the cambial age of each tree for each stand studied. The average annual height growth is thus given from beginning of germination (without looking to calendar years). Values were averaged for each site.

Radial growth was measured at 50-cm intervals along the stem, starting from the root-shoot interface up to the top of the tree. Transverse sections were cut, dried and the surface gradually sanded (80 to 400 grit). Ring widths were measured along two radii with an accuracy of 0.01 mm using a manual Henson or a semiautomatic Win-Dendro tree-ring measuring device (Guay *et al.* 1992). The two radii were then averaged to obtain a ring width for each ring and each section (stem analysis data). The tree-ring measurements were cross-dated on a light table and afterwards verified with the COFECHA program (Holmes 1983) and dates were corrected if necessary to minimise the introduction of errors in the volume calculations by year.

Annual height and volume growth and yield

In order to calculate annual growth and yield of height and volume, first the trees were reconstructed at each age for the entire measurement period. As noted, the cambial age of each

tree was used to compare the juvenile growth of trees at the same stage of development. Two methods were used to reconstruct the trees: the Carmean (1972) method and the bud scar method. For both methods, the radius for each year and the top and bottom of each section were obtained by summing the ring widths up to that year. Then, for the Carmean method, the height was estimated at each age, using the annual ring width measurements taken every 50 cm over the tree stem along with stem lengths. In this way, the radii and the lengths were reconstructed for each tree at each age, with the top section of the reconstructed trees having lengths of ≤50 cm (Fig. 1). For the bud scar method, a similar approach was used, except that the ring width measurements along the stem were combined with the exact position of the bud scars in estimating height. The Carmean method was selected because it is the most precise among the widely used methods to estimate annual heights from stem analysis data. The bud scar method is much more laborious, but is more precise, especially in the first years of tree establishment when height growth rate is slow. The formula used in both these calculations is:

$$[1] \quad V = \frac{1}{3} \pi h (a^2 + ab + b^2)$$

where V: volume of a 50 cm segment;
h: length of a segment;
a: radius at the top of a segment; and
b: radius at the bottom of a segment.

This formula is exact for a truncated cone shape. For the top segment, the length was less than or equal to 50 cm, as calculated from the estimated height, and the top radius was 0, resulting in the equation for a cone shape. The segments were then added to obtain the volume yield of the tree. This was repeated for each of the reconstruction methods, resulting in two estimates of volume yield at each age. Differences in volume yield for adjacent years resulted in annual volume growth.

In the last 3 methods, only final volume yield was calculated, and there was no annual reconstruction of trees. For the third and the fourth method, the diameter inside bark at 30% of the total stem height ($D_{0.3}$) and the stem height were used to calculate cumulative volume directly using the equation (Forslund 1982):

$$[2] \quad V = \frac{A}{(A+2)} (1-Y)^{2/(A+1)} \frac{\pi D_y^2 H C}{4}$$

where V: total stem volume (outside bark);
 D_y : inside bark diameter at a relative height
 $Y=h/H$;
h: height to the measurement position from the ground;
H: total stem height;
A: the power coefficient that determines the shape of the stem profile; and
C: the unit conversion factor

The parameter A was initially set to 1 for an assumed cone shape. For the fourth volume yields, A was set to 2 for a paraboloid shape.

Fig. 1. Bud scar versus Carmean methods for reconstruction of tree heights and radial growth over time.

Finally, for the fifth method, the volume was calculated using the formula for a cone using the basal radius and the total stem height:

$$[3] \quad V = \frac{1}{3} (\pi r^2 h)$$

where V: volume
r: radius at stem base;
h: total stem height.

The cone method was chosen to calculate the total volume of each tree analysed because of the widespread use of this assumed shape in several studies.

Statistical Analyses

To reduce the complexity in the analysis, growth and yield of height and volume measurements were averaged for all trees by stand, resulting in nine observations for each age. Differences in cumulative shoot lengths and cumulative volumes between stand types were compared using a repeated measures analysis of variance (ANOVA) in a split-plot design to trends over time and differences in stand types. Statistical analyses were done using the SAS JMP software package with the GLM procedure and the EMS option (SAS Institute Inc. 2003). Main plots consisted of stand types: plantation, endemic and epidemic. The repeated-measures factor, time, had 13 levels (years 1 to 13) for height and for volume yields. In order to produce a balanced analysis, we kept only the first 13 years, even though some plots were measured for longer

time periods. Within-plot analysis of contrasts was conducted to examine trends over these periods. Two orthogonal polynomial contrasts with time were tested (linear, quadratic) (Gumpertz and Brownie 1993). P values obtained from analysis are presented with Greenhouse-Geisser-adjusted (P_{G-G}) probabilities to correct the violations of the assumption of sphericity (Milliken and Johnson 1992, Quinn and Keough 2002). This estimate, as expressed by the epsilon statistic, is used to adjust the df for within plots/subjects tests downwards to make the tests more conservative, since non-sphericity increases the risk of Type I error (Quinn and Keough 2002). When ϵ is less than 0.75, the correction based on the Greenhouse-Geisser is better (Keselman and Keselman 1993).

Results

Annual height growth and yield

The annual height yield was reconstructed for all study sites using both the Carmean and bud scar methods, except that for the 3 oldest post-fire stands (BwF20, SimF22, GirF54), only the Carmean method was used due to the difficulty of retracing the bud scars. The annual height growth was variable on a year-to-year basis (Fig. 2A). Within all black spruce stands, the mean annual height growth increased with cambial age. The mean annual height growth was much faster in the plantations, which had heights of 30 cm already at age 9 (Fig. 2A). In the endemic post-fire stands, the mean annual heights were below 20 cm for the first 14 years, whereas in the epidemic post-fire stands, these values were below 10 cm for the first 15 years.

Height yields over time for all nine black spruce stands followed an exponential curve (Fig. 2B). Both plantations showed greater cumulative height growth than the post-fire stands. Endemic stands registered higher cumulative height values than epidemic stands. The repeated measures ANOVA indicated that there is a strong interaction between time and the main factor Stand type (St), suggesting that the annual height yield trends differ among stands ($p < 0.0001$) (Table 3; Fig. 2B).

There were significant linear effects in the component of the regression for interactions $T \times PL$ vs $T \times END$ ($p = 0.0011$), $T \times PL$ vs $T \times EPI$ ($p < 0.0001$) and for $T \times END$ vs $T \times EPI$ ($p = 0.0016$) (Table 3). There is a strong effect in the curvature of the regression, as indicated by the quadratic interactions, $T \times PL$ vs $T \times END$ ($p = 0.0037$) and $T \times PL$ vs $T \times EPI$ ($p = 0.0009$). The quadratic contrasts with time indicate no significant interactions for $T \times END$ vs $T \times EPI$ ($p = 0.1877$). The significant interactions indicate that the lines are not parallel.

Annual volume growth and yield

The two estimates of annual volume yields were compared. The bud scar method using a cone frustum for each segment (Method 1) was used as the standard for comparison, as it was considered most accurate. Annual volume yields using the bud scar versus the Carmean method to obtain heights (Methods 1 and 2) were similar. Comparing all 5 volume yield estimates for the final measurement, the Carmean method had a mean overestimation of cumulative volume for the final time period of only 2% in the plantations and endemic stands (Table 4), and 3% in epidemic sites, relative to the bud scar method. The 3 other methods used to calculate cumulative volume require more simple calculations and fewer measure-

Fig. 2. Mean annual height growth (A) and yield (B) curves by stand for 15 trees per site. Solid lines refer to epidemic and endemic stands respectively. Dotted black lines refer to black spruce plantations.

Table 3. Results of repeated measures ANOVA of differences annual height and volume yields between plantation (P), endemic (END) and epidemic (EPI) stand types.

A) Between- and within-subjects analysis

Source	Annual height yield				Annual volume yield			
	DfNum ^a	DfDen	F ratio	P	DfNum ^a	DfDen	F ratio	P
Stand type (St)	Between subjects	–	–	–	Between subjects	–	–	–
	2	3	6859.3	<0.0001	2	6	161.8	<0.0001
	Within subjects	–	–	P _{G-G} ^b	Within subjects	–	–	P _{G-G} ^b
Time (T)	1.3	3.9	1623.0	<0.0001	1.3	7.6	360.8	<0.0001
Stand type (St) × T	2.6	3.9	244.2	<0.0001	2.5	7.6	193.8	<0.0001

B) Within-subjects analysis : P-values for orthogonal polynomial contrasts on time

Source	DfNum	P			DfNum	P		
T	–	–			–	–		
Linear	2	0.0002			2	<0.0001		
Quadratic	2	0.0021			2	<0.0001		
		P _{G-G} ^b				P _{G-G} ^b		
		T × PL vs T × END	T × PL vs T × EPI	T × END vs T × EPI		T × PL vs T × END	T × PL vs T × EPI	T × END vs T × EPI
St × T	–							
St × Linear	1	0.0011	<0.0001	0.0016	1	<0.0001	<0.0001	0.0594
St × Quadratic	1	0.0037	0.0009	0.1877	1	<0.0001	<0.0001	0.0658

^aDfNum: degree of freedom at numerator; DfDen: degree of freedom at denominator;

^bP_{G-G} values from univariate analysis are presented with Greenhouse-Geisser-adjusted probabilities; Bold-faced P values are significant at α = 0.05 level.

ments. The cone $1/3$ method using Forslund's taper (Method 3; A = 1) underestimated the cumulative tree volume by a mean of 10.5% and the paraboloid method using Forslund's (1982) taper model (Method 4; A = 2) underestimated it by 6% on average. The cone method (Method 5) was even less precise. On average, it overestimated the cumulative volume of the trees by 37%. The maximum overestimation for one study site was as high as 78% relative to Method 1.

Using the reconstructed trees from the bud scar or the Carmean (1972) method, the annual volume growth and yield

over time were examined for the entire measurement period. All post-fire stands produced little annual volume during the first years after germination (Fig. 3A). This first phase of development was followed by accelerated growth, which started earlier in planted sites than in the post-fire sites. This second developmental phase of annual volume can be modeled by an exponential function and lasted between 35 and 40 years. In the plantations, the annual volume increased more rapidly.

All planted and post-fire sites had an exponential curve pattern for volume yields over time (Fig. 3B). The mean annual

Table 4. Mean cumulative volume ($\text{m}^3 \times 10^{-4}$) of 15 trees by stand according to 5 different methods without bark. Differences between the calculation methods are expressed in percentage.

Site	species	age	1	2	3	4	5	differences %			
			bud scars	carmean	cone1/3	para- boloid	cone	1 vs 2	1 vs 3	1 vs 4	1 vs 5
BwF20	BS	80	-	1670.04			-	-	-	-	-
SimF22	BS	78	-	2146.67			-	-	-	-	-
GirF54	BS	43	-	347.56			-	-	-	-	-
MyrF56	BS	36	267.32	278.45	246.58	258.90	425.16	2%	-13%	-8%	68%
ChiNF71	BS	31	94.17	96.61	85.17	89.43	103.17	3%	-11%	-6%	13%
ChiF70	BS	29	79.00	80.89	69.84	73.33	124.75	2%	-11%	-6%	53%
DesF83	BS	18	17.59	17.98	14.92	15.66	28.17	3%	-16%	-12%	52%
LauPL90	BS	17	80.20	80.95	78.34	82.25	129.76	1%	-7%	-3%	78%
MvPL86	BS	17	64.86	65.58	58.06	60.96	74.65	2%	-8%	-3%	10%

BS: black spruce;

age: age of the oldest tree analysed

1: volume growth method including tree-ring width and shoot length

2: volume growth method including tree-ring width

3: volume growth method using the power function of a cone

4: volume growth method using the power function of a paraboloid

5: volume growth method including tree height and diameter at stump height only

Fig. 3. Mean annual volume growth (A) and yield (B) curves by stand for 15 trees per site. Solid lines refer to epidemic and endemic stands. Dotted black lines refer to black spruce plantations.

volume yield of the post-fire black spruce was low for the first 10 to 25 years, followed by an accelerating trend. However, the planted black spruce increased the volume yields earlier.

The repeated measures ANOVA tests suggested that there is a strong interaction between time and the main factor Stand type (St), meaning that the annual volume yield curves differ across stands ($p < 0.0001$) (Table 3, Fig. 3B). There were significant linear effects in the component of the regression for interactions $T \times PL$ vs $T \times END$ ($p < 0.0001$) and $T \times PL$ vs $T \times EPI$ ($p < 0.0001$). The linear contrasts with time indicate no significant interaction for $T \times END$ vs $T \times EPI$ ($p = 0.0594$). There is a strong effect in the curvature of the regression for interactions $T \times PL$ vs $T \times END$ ($p < 0.0001$) and $T \times PL$ vs $T \times EPI$ ($p < 0.0001$). Quadratic contrasts with time indicate no significant effect in interaction $T \times END$ vs $T \times EPI$ ($p = 0.0658$). The significant interactions indicate that the lines are not parallel.

Discussion

Characterization of juvenile annual and cumulative volume

In order to reconstruct the juvenile growth of trees, the identification of the root-shoot interface was essential to identify the year of germination (Telewski 1993, Desrochers and Gagnon 1997, Parent *et al.* 2000, Niklasson 2002, Krause and Morin 2005). This technique is becoming popular among dendroecologists for determining post-fire seedling recruitment (Fritts and Swetnam 1989, Motta 1998, Hellberg *et al.* 2003, Rozas 2003, Ruffner and Abrams 2003, Payette and Delwaide 2004, Rubino and McCarthy 2004) and for reconstructing stem development in time by using bud scars in measuring the annual height growth (Fantin and Morin 2002, Parent *et al.* 2002). This time-consuming step was essential in the present study to compare the juvenile growth in different stands from the time of germination and also to compare different methods of volume calculation. Annual volume growth was calcu-

lated using the reconstructed annual heights and radial growth at different stem heights, using the bud scar method as the standard for comparison to the Carmean method. Our findings clearly demonstrate that the bud scar method takes too much effort for the precision gained when compared to the Carmean (1972) method for determining heights over time, which produces comparable results with less effort.

The juvenile annual height growth pattern of black spruce can be characterized by a gradual increase of height growth before entering a more or less stagnant phase. The annual volume growth in all black spruce stands increased slowly in the first years after germination. This was followed by a period of exponential acceleration and later by a period of gradual decline. This finding is corroborated by many articles and texts on growth of organisms, including Philip (1994), who stated that the growth pattern of most living organisms follows a sigmoid pattern characterized by slow initial and terminal growth rates, with fast growth during the middle life stages, reaching a maximal final size. Generally, the early immature stage finishes when canopy closure occurs (Philip 1994). Many authors subdivide the volume yield curve into youth, maturity and senescence phases, with an exponential acceleration in the maturity phase. Volume growth is known to decline during the senescence phase, but this final phase was not found in the present study, not even in the oldest, over-70-year-old stands. Our results clearly demonstrate time trend changes depending upon the stand type. An accelerated volume yield was visible earlier in the plantations over a time span of 13 years compared to both naturally regenerated stand types. The lower stocking density in plantations offers better light availability for each tree, which increases the growth rate in black spruce (Viereck and Johnston 1990). Furthermore, the regular spacing between planted trees also favours optimal growing conditions (OIFQ 1996). Weeding is another factor that can contribute to the growth potential in plantations (OIFQ 1996).

The impact of spruce budworm defoliation during the germination period of black spruce

During the 20th century, 3 major spruce budworm outbreaks occurred and caused black spruce growth reductions and tree mortality (Blais *et al.* 1985, Morin and Laprise 1990, Lussier *et al.* 2002). Some of the post-fire study stands germinated during these known outbreaks. The height growth in these stands was especially slower compared to the endemic sites. The impact was also visible as a slower volume gain. The impact of spruce budworm on height growth in young suppressed black spruce has been already reported by Fournier (1997). The lower volume values of the epidemic post-fire stands suggest that seedlings planted during an outbreak period may give lower yields than expected from endemic plantations because of the impact of defoliation on height growth. A larger analysis of several black spruce stands with germination during spruce budworm outbreaks is needed to confirm this hypothesis. However, epidemic stands are difficult to find, due in part to the feeding effect of spruce budworms on cones, resulting in an insufficient number of seeds (Simard and Payette 2005).

Characteristics of juvenile annual and cumulative volume and their implication for forest management

In order to manage forests in a sustainable manner, it is essential to quantify the yield of each stand precisely. Yield tables

are well established for natural and planted stands in the southern part of Quebec. In order for these tables to be reliable, trees have to be at least 25 years old. However, the young age of the plantations in the boreal forest makes the use of these tables of limited value. Instead, the stem height of dominant trees in a given year is the most common measurement used (Prégent and Vêgiard 2000). According to these authors, this parameter is suitable for predicting the long-term yield in the boreal forest. Considering the lack of other yield predictors, the stem height is still widely used. However, the annual height growth of black spruce is very slow during the first 10 years; therefore, the stem height is not an accurate predictor of the production potential of black spruce plantations. Mailly and Gaudreault (2005) introduced a new approach to evaluate the yield in planted stands using internodal growth measurements. This non-destructive method uses measurements of annual height growth and produces results comparable to the bud scar method. The drawback to the Mailly-Gaudreault method is the exclusion of juvenile growth and, consequently, the youngest trees planted. The method needs trees with a minimum height of 1.3 meters.

In the province of Quebec, a total of 332 permanent plots were established in black spruce, aged between 8 and 13 years (Prégent and Poliquin 2006). More than 100 are located in the boreal forest and allow researchers to follow the development and yield of these plantations. Based on tree height and diameter at stem base, Prégent and Poliquin predicted a low yield for the boreal black spruce plantations. The introduction of the diameter at $\frac{1}{3}$ of total stem height, combined with the use of a paraboloid power function, would be an appropriate non-destructive tool to evaluate the total volume of black spruce in the juvenile phase of growth as reported by Forslund and Paterson (1994). Our findings, based on both plantations and the seven post-fire stands, showed that the juvenile phase can be used in volume predictions. Trees showed a slow cumulative volume increase in the juvenile phase with a faster volume gain in the planted sites. At age 10, the plantations had a cumulative volume comparable to 14- to 18-year-old post-fire stands. Furthermore, this better performance seemed to increase with the age of the trees. Detailed analysis of a larger number of black spruce plantations in the boreal forest, such as those presented in this paper, combined with information about the initial stand density, which influences the amount of light available for each tree, might be necessary to predict the yield of this silvicultural practice in the future. Furthermore, complementary information should be added to reveal the different growing patterns between pure black spruce sites, as often found in plantations and mixed stands as in post-fire sites.

Conclusions

The juvenile cumulative increment of naturally regenerated and planted black spruces was characterized by a slow increase during the first year of tree establishment. This period was followed by an exponential acceleration, which started earlier in the plantations than in the post-fire sites. A reduced height and volume growth was observed in black spruce from post-fire sites regenerated during spruce budworm outbreaks. More studies are needed to evaluate the impact of spruce budworm defoliation on yield when black spruce is planted during these periods.

The annual height growth of black spruce also showed acceleration and did not follow a linear trend. Consequently,

applying a linear trend by using tree height at a given age is a very poor yield predictor for black spruce plantations. Methods, such as the one proposed by Mailly and Gaudreault (2005) might be more promising in predicting the long-term yield of boreal plantations on an annual basis. The paraboloid power function (Forslund and Paterson 1994) seems to be a good method for evaluating the total volume at a given age with few measurements. The bud scar method, though very precise, is not recommended for this task, because it is not practical due to its destructive and highly time-consuming nature. The Carmean method, while also destructive, should be favoured over other methods mentioned in this article whenever annual and cumulative volume growth of individual trees is a concern.

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