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La dynamique et la croissance de jeunes peuplements d'épinettes noires (*Picea mariana* (Mill.) B.S.P.), entre les 51ième et 52ième degrés de latitude nord au Québec

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« To My Dear Mother and Father»

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ABSTRACT

In Quebec, although the growth and dynamics of black spruce [*Picea mariana* (Mill.) BSP] stands situated north of the 52nd parallel and south of the 51st parallel have been considered in several studies, no study, however, has yet considered the growth and dynamics of black spruce stands situated between the 51st and the 52nd parallels, north of closed black spruce-moss forests. In this study, we compared age structures, diameter, height and volume growth of black spruce regenerated naturally after fire in three young stands located on mesic sites between latitude 51° and latitude 52°, taken from a stratified random sampling.

The three study stands were established following a fire roughly around 1900, 1920, and 1925 on the C6S1, C7S1 and TO1, respectively. The age structures of the three studied sites were similar and showed a period of establishment ranging from 15 to 20 years.

We performed stem analysis on 10 living dominant black spruce trees of each study sites. Dendrochronological techniques were used on sampled stem-sections of black spruce to construct age and growth pattern. Mean height, diameter and volume growth curves were constructed for the sample trees. We also compared growth of dominant black spruce trees in the two most northern studied stands to those of two black spruce stands located in the middle of black spruce-moss forest between the 49th and the 51st parallels.

There was no significant difference in DBH and total height of black spruce trees between the three studied stands at the time they were sampled for detailed stem analysis. Also, total height, diameter and volume did not differ significantly between the three studied stands at the age of 70, the last common age between the sampled trees. Our results support the hypothesis that the juvenile growth of black spruce is very slow. Black spruces had a similar diameter, height and volume growth patterns across the three studied stands. No difference in overall average 5-year diameter and volume growth rates was found between the three studied stands, nor between the two areas. There was also no significant difference in overall average 5-year height growth rates between the three studied stands. In contrast, a significant difference in overall average 5-year height growth rates was found between the two areas. Significant differences were also found for the initial post-fire years of growth in diameter, height and volume between the studied stands as well as between the two areas.

Slenderness (height/DBH) in the two southern black spruce stands was higher than those located between 51st and the 52nd parallels because of a higher stem density. However, since this study was carried out in a few study sites, it is suggested to put forward more researches with incorporation of a greater number of study sites from the study area as well as from the middle of Quebec's boreal forest.

The results indicated that the mean annual diameter growth rates of saplings of all the studied stands differed slightly from each other. In all studied site, the dominant black spruce trees had a higher growth rate than the black spruce saplings and the two groups presented a similar year-to-year growth variation. Thus, under these closed even-aged stands, saplings grew much more slowly than overstory even if they were of even age and would not reach 5 cm in diameter before the age of 60, on the average.

Furthermore, it would notably be interesting to compare growth of understory black spruce trees from our three even-aged stands with those growing in similar stands located in the lower latitudes of Quebec's Boreal Forest.

RÉSUMÉ

Au Québec, bien que la croissance et la dynamique des peuplements d'épinettes noires [*Picea mariana* (Mill.) BSP] situés au nord du 52^{ième} parallèle et au sud du 51^{ième} parallèle aient souvent été étudiées, aucune étude n'a toutefois encore porté sur les peuplements situés entre les latitudes 51° N et 52° N, soit au nord de la pessière à mousse fermée. Dans cette étude, nous avons comparé les structures d'âge et la croissance en diamètre, en hauteur et en volume des épinettes noires régénérées naturellement après feu dans trois jeunes peuplements situés sur des sites mésiques entre les 51^{ième} et 52^{ième} parallèles, issus d'un échantillonnage stratifié.

Les trois peuplements à l'étude se sont établis suite à un feu ayant eu lieu autour de 1900, 1920 et 1925 dans les sites C6S1, C7S1 et TO1, respectivement. La structure d'âge des trois sites étudiés était équienne et a montré une période d'établissement s'étendant sur 15 à 20 ans.

Nous avons aussi procédé à une analyse de tige sur les 10 épinettes noires dominantes vivantes de chaque site d'étude. L'analyse dendrochronologique des sections de tige prélevées sur ces épinettes noires a permis de déterminer leur âge et de construire des courbes moyennes de croissance en hauteur, en diamètre et en volume. Nous avons aussi comparé la croissance des épinettes noires dominantes des peuplements étudiés à celle de deux peuplements situés entre les 49^{ième} et 51^{ième} parallèles soit au cœur de la pessière à mousse.

Il n'y avait aucune différence significative dans le DHP et la hauteur totale des épinettes noires entre les trois peuplements étudiés à l'époque où ils ont été échantillonnés pour l'analyse détaillée de la tige. Également, la hauteur, le diamètre et le volume total n'ont pas différé de manière significative entre les peuplements à 70 ans, soit le dernier âge commun entre les arbres échantillonnés. Notre résultat supporte l'hypothèse que la croissance juvénile des épinettes noires est très lente. Les épinettes noires ont un modèle de croissance en diamètre, en hauteur et en volume semblable pour les trois peuplements étudiés. Dans l'ensemble, aucune différence dans les taux de croissance en diamètre et en volume moyens sur 5 - ans n'a été trouvées entre les trois peuplements étudiés, ni entre les deux secteurs. Il n'y avait également aucune différence significative dans les taux de croissance en hauteur moyens sur 5-ans entre les trois peuplements étudiés. Par contre, une différence significative dans les taux d'accroissement en hauteur moyens sur 5-ans a été trouvée entre les deux secteurs. Aussi, des différences significatives ont été trouvées pour les premières années suivant le feu au niveau de l'accroissement en diamètre, en hauteur et en volume entre les peuplements étudiés de même qu'entre les deux secteurs. En raison d'une densité de tige plus élevée, le coefficient de défilement (Hauteur/DHP) dans les deux peuplements d'épinettes noires au sud était plus haut que ceux situés entre les $51^{ième}$ et $52^{ième}$ parallèles.

Les résultats ont indiqué que les taux de croissance annuels moyens en diamètre des gaules de tous les peuplements étudiés ont différé légèrement les uns des autres. Également, les épinettes noires dominantes de chaque site ont eu un taux de croissance plus élevé que les gaules de la même espèce bien que les deux groupes présentent une variation de croissance semblable d'année en année. Ainsi, sous ces peuplements équiennes fermés, les gaules se sont développées beaucoup plus lentement même si elles ont le même âge que les arbres de l'étage dominant et n'atteindront pas 5 cm de diamètre avant l'âge de 60 ans.

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CHAPTER I

INTRODUCTION

1.1 Introduction

In Quebec, the majority of the forests located between the 49th and the 52nd parallels (latitude) consist of closed black spruce (*Picea mariana* (Mill.) BSP)-moss forests (Gagnon 1995; Bergeron 1996, Saucier *et al.* 1998). Moving towards the north, approximately to the 52nd parallel, the forest landscapes seem fairly uniform, since the forest canopy is dominated extensively by black spruce. This species often grows in pure stands but is also accompanied occasionally by other species, such as the balsam fir (*Abies balsamea* (L.) Mill), (Ministère des Ressources naturelles 2003).

North of the 52nd parallel, several studies have been related to black spruce in the spruce-lichens forest (Taiga), and the forest tundra (Sirois and Payette 1991; Payette *et al.* 2000). The dynamics of the natural forests (Greene *et al.* 1999; Gagnon and Morin 2001; Lussier *et al.* 2002a), and their growth (Doucet 1988; Fantin and Morin 2002), are two important aspects that have been studied in the forests located between the 49th and the 51st parallels in Quebec. Beyond the northern limit of this zone (circa 51°-51°30'), the northern limit of the ascribable forests can be found. Following the classification that has been used in the report of the committee on the northern limit of the ascribable forests (Ministère des Ressources Naturelles 2000); this area is classified as the northern area of management.

Black spruce has great economic importance in the eastern Canadian forest industry (Doucet 1990). Parent (1994) reported that black spruce dominates more than 70% of the forest stock of Quebec's boreal forest. Despite its economic importance, the northern parts of the closed spruce-moss forests located between the 51st and the 52nd parallels have received very little attention. The distance to the factories and the presumed low potential of regeneration and growth are the principal reasons for the little commercial interest in this area.

All researchers acknowledge the fact that there is little information available on the dynamics and growth of trees in these forests. The knowledge about the annual and cumulative diameter, height and volume growth of black spruce trees under natural conditions is particularly poor. Closed spruce-moss forests cover a large proportion of the landscape in this area; therefore it is essential to carry out research in this area in order to make the best possible management decisions. One of the recommendations of the final report of the committee on the northern limit of the ascribable forests (Ministère des Ressources naturelles 2000) was to put forward some research in the northern area of the boreal forest, in order to specify certain criterion and indicators. We undertook this study of black spruce dynamics, to fill these information gaps.

Black spruce is well suited for rapid regeneration after fires and frequently dominates the post-fire originating cohort forest (St-Pierre *et al.* 1992; Sirois 1995). Black spruce generally regenerates itself quickly within three years after a fire, provided that there are enough seeds and seedbeds (St-Pierre *et al.* 1992) according to a cyclic mechanism which is very well known (Heinselman 1981a; Gagnon and Morin 2001).

Post-fire stands of black spruce are also generally even-aged, with the exception that there can be a lack of regeneration and the creation of an open stand like spruce-lichen woodland if seeds are missing, due to repeated disturbances or if there isn't enough seed-beds available (Riverin and Gagnon 1996; Payette *et al.* 2000; Gagnon and Morin 2001). The known cases of disturbance are successive fires (Gagnon and Morin 2001), and severe epidemic of the spruce budworm (*Choristoneura fumiferana* (Clem.)), followed by a fire (Payette *et al.* 2000).

Black spruce is a species very well adapted to grow in the boreal forest. It is recognized that the best conditions for its growth are cool and moist temperatures (Brooks *et al.* 1998). Dendroclimatologic studies have compared the growth of black spruce located at the southern limit and the northern limit of the closed boreal forest. These studies show that generally, precipitations have a positive influence on the growth of the conifer species in the boreal forest (Hofgaard *et al.* 1999; Deslauriers *et al.* 2003b). The influence of the temperature is more difficult to establish because the results are often contradictory (Dang and Lieffers 1989; D'Arrigo *et al.* 1992; Brooks *et al.* 1998; Hofgaard *et al.* 1999).

In Quebec, tree ring analyses were used to reconstruct the dynamic and stand history of the boreal forest located south of the 51st parallel (Morin 1994), but the same technique has not been applied to the boreal forest north of the 51st parallel because of inaccessibility. Age and stand structure of trees can provide critical insight into the role of small scale processes and the influence of past major disturbances (Stewart 1986a; Duncan

1993; Frelich and Graumlich 1994). In the study reported here, tree ring analyses were used to reveal stand history and growth dynamics of black spruce, as well as to estimate diameter, height and volume growth of the trees.

This present work was part of a larger project on the dynamics and growth of the boreal black spruce forest. It includes three study sites out of the 24 study sites located between the 51^{st} and the 52^{nd} parallels.

1.2 Study objectives and hypothesis

The objectives of the present study were to: i) determine the dynamics of young (<120 yrs) black spruce stands on mesic sites located between the 51^{st} and the 52^{nd} parallels; ii) evaluate the quantity and distribution of the understory regeneration in the natural stands; iii) measure radial, height and volume growth of the dominant trees by stem analysis, and iv) to compare dynamics and growth of black spruce growing in the study area to those on the mesic sites present in the middle of the boreal forest (circa 49°-51°).

In order to better understand black spruce dynamics of older stands across the study area, it is important to know first the dynamics of black spruce in younger stands in the area. Therefore, dynamics and growth of black spruce in younger stands of the 24 study sites were considered in this project.

The purpose of this study was to test the three current hypotheses about the dynamics and growth of black spruce in young fire-origin stands located between latitudes 51° and 52°. We hypothesized that i) dynamics of the study stands would be governed by fires and the majority of the stands age structures should be naturally even-aged and show a fast regeneration of the stands after fire; ii) the juvenile growth of black spruce should be very slow, as was reported for black spruce growing in the middle of the boreal forest in Quebec (Fantin *et al.* 2002), and iii) similar patterns of growth in height, diameter and volume to those in the middle of Quebec's boreal forest should be observed.

CHAPTER II

MATERIALS AND METHODS

2.1 Study area

This study was conducted in three study sites located between the 51st and the 52nd parallels, east of Mistassini Lake, about 337 km north of Chicoutimi (Québec); an area located in black spruce-moss sub-domains east 6 (C6S1) and west 6 (TO1 & C7S1) of the bioclimatic domain 6 (Saucier *et al.* 1998). This area is generally dominated by black spruce and jack pine (*Pinus banksiana*) stands. The geographical locations of these study sites are: (51°00′43.2″N, 73°00′08.9″E), (51°20′23.1″N, 70°06′01.8″E), and (51°27′01.4″N, 71°24′21.9″E), for TO1, C6S1 and C7S1 respectively (Fig. 2.1).

2.2 Climate description

Climatic data directly applicable to this study area was unavailable, due to the absence of meteorological stations in the area. Therefore, climatic data were obtained from the nearest meteorological station (Bonnard) 30 km south of the study area. The climate is cold and snowy with long winters and short growing seasons. The length of the growing season (number of days with an average temperature over 4 °C) is approximately 120 days. The snow cover lasts from about the middle of October to the end of May with much of the precipitation falling as snow and accumulating to form a deep snow cover that typically does not fully melt until June. The annual mean temperature is –1.8 °C and the annual mean precipitation is about 946.4 mm (Environment Canada 1971-2000).

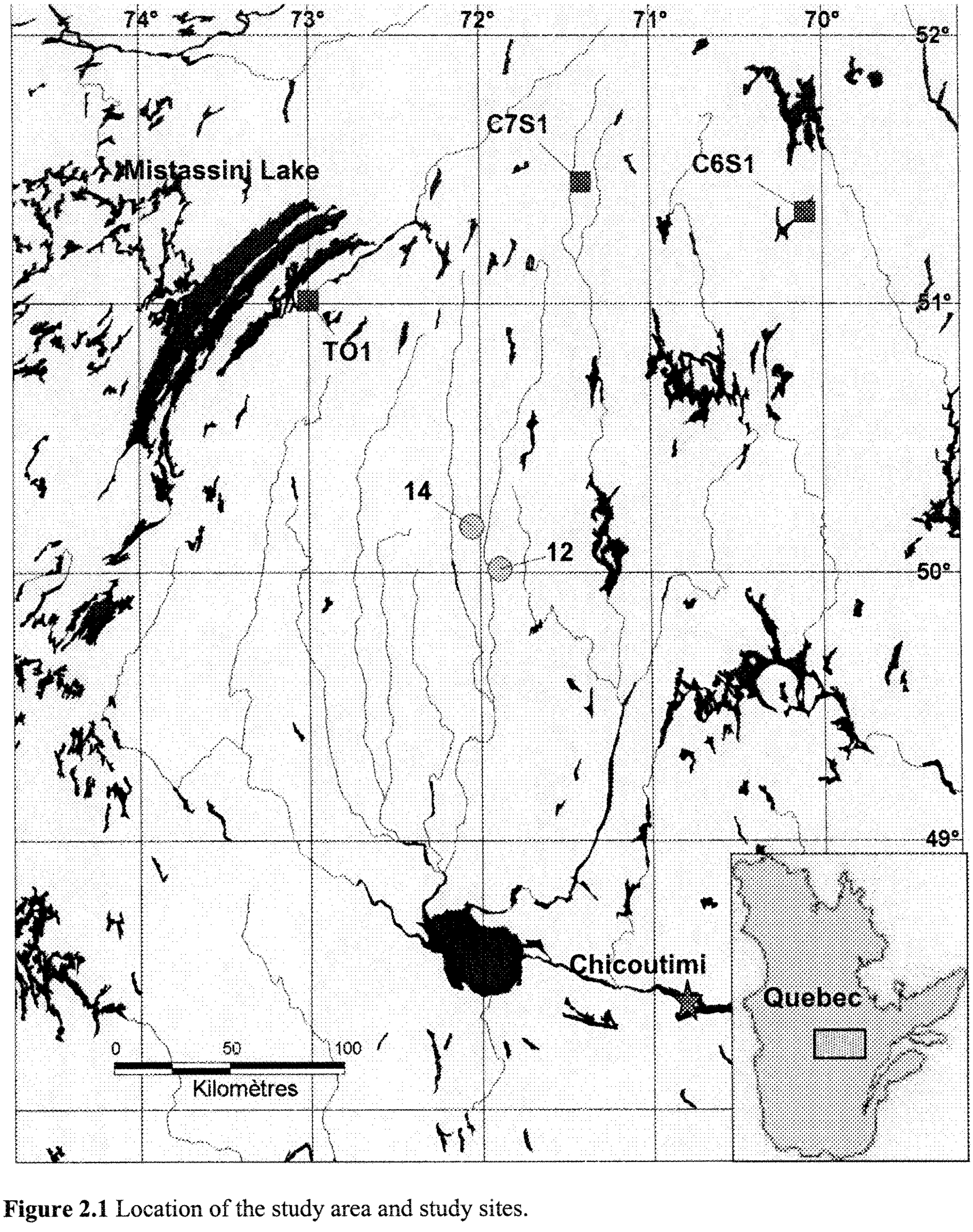

Figure 2.1 Location of the study area and study sites.

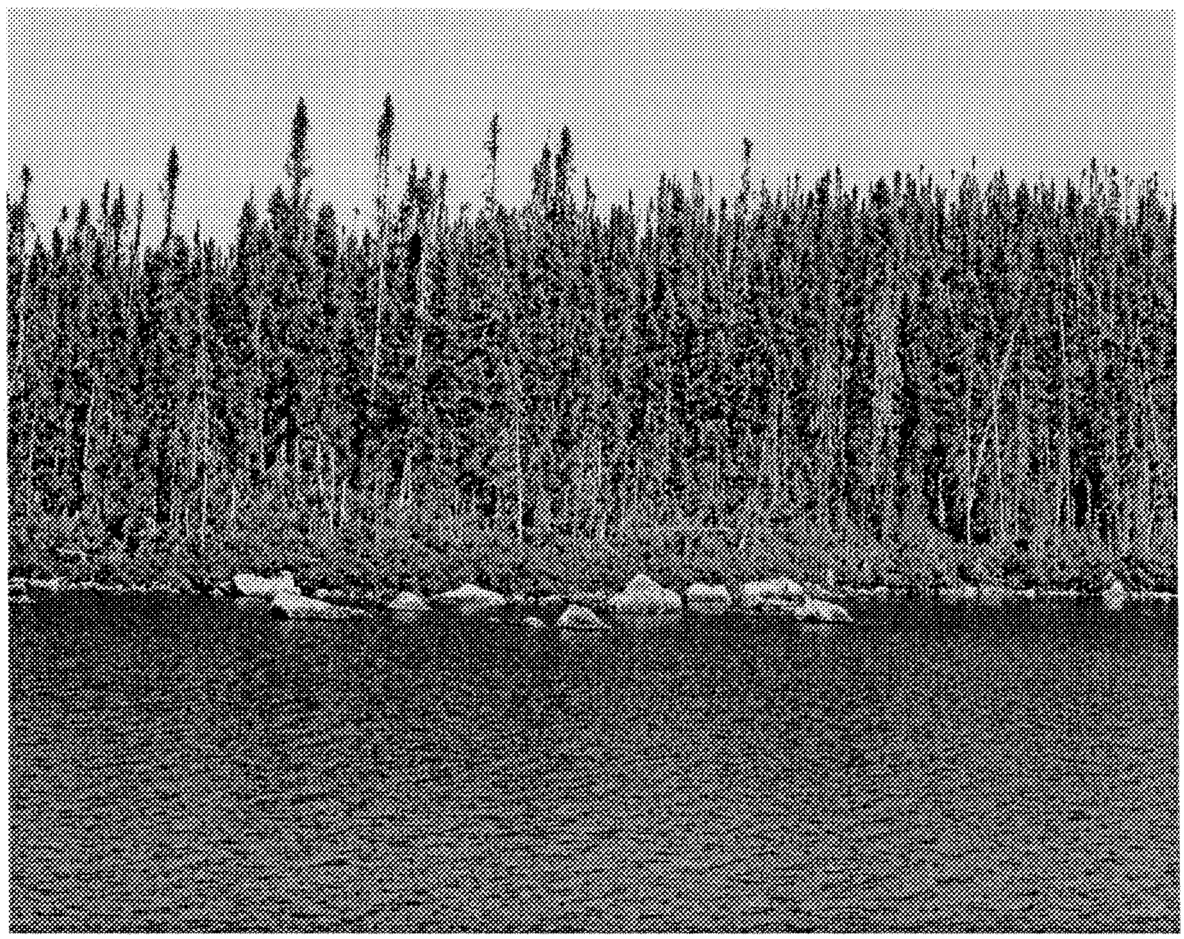

Figure 2.2 General view of overstory and understory of a dense black spruce fire-origin stand in a boreal forest located between the 51st and the 52nd parallels, in northern Quebec.

2.3 Sites selection

A stratified random sampling based on the age and density class of the stands was used to select 24 black spruce stands that were on mesic sites. In order to verify them, a field survey was necessary in 2003. All young black spruce stands which were found during the field survey were selected for this present work. The three young black spruce stands were selected on mesic sites to provide a representative sample of the study area because it is on these sites that the majority of black spruce stands in this area are located. Mesic sites should therefore be representative of the total area when considering the aspects of dynamics and growth of black spruce stands.

2.3.1 Sector accessible by the road

Many fires occurred during the summer of 2002, in the study area. The majority of those burned areas were located north of the 51st parallel, east of Mistassini Lake. The roads in those burned areas gave us access to some sample plots which did not burn. The TO1 stand with characteristics similar to those of the two other study stands was selected for sampling in this sector.

2.3.2 Sector non-accessible by the road

A major problem for realizing this study was accessibility. The maps available from the Ministère des Ressources Naturelles du Québec (MRN) were 1/50 000 and 1/20 000 scale for this sector. They were less precise for the northern part of the area, but a field survey of all sites in 2003 allowed us to acquire more information on the cover types of these forests, species communities, origin, density, stands height, disturbances, age class and slope class. The locations of the C7S1 and C6S1 sites were determined on these maps. The sites used for getting samples had to be near a lake that had at least 1 km in length for easy access via hydroplane (Fig. 2.2).

2.4 Sampling design

In each stand, a 200 to 400 m^2 rectangular plot was placed in a homogeneous and representative site to include at least 50 black spruce trees. This surface is usually sufficient for black spruce, based on what has been done before (DesRochers and Gagnon 1997; Gagnon and Morin 2001; Deslauriers *et al.* 2003b). In C7S1 and TO1 stands, a 10m × 20m plot, and at C6S1 stand, a 20m × 20m plot, were delimited.

Percentage stocking and density of trees, saplings and seedlings were determined for each study plot based on a technique that is used by the Ministère des Ressources Naturelles du Québec. Two parallel transect lines 10 meters apart were established starting from the center of each plot and circular 4 m^2 sub-plots were spaced at 5 m intervals along each line [(300 m for sites (C6S1 & C7S1)) and (500 m for site (TO-1))].

In addition, at each study site, the ground vegetation (plants with a maximum height of 1 m) was described in five sub-plots of 1 m^2 with four distributed in the corners and one in the middle of the plot. A mean coverage for all the species in each study site was calculated by combining the five sub-plots. Vegetation was recorded according to the relevés method (Mueller-Dombois and Ellenberg 1974).

2.5 Data collection

The sites were scheduled to be clear-cut in the summer of 2004. Field work was carried out as part of a larger research project from early to mid July, 2004. In order to test the first hypothesis concerning the stand dynamics after fire, it was necessary to examine age structure of each stands. In each plot, cross-sections were collected from the base of all standing trees and saplings (DBH > 1 cm) of all species, alive or dead. They were inventoried, and their species were identified, and then measured for diameter at breast height with a dbh measuring tape, prior to felling. The regeneration method (by layering or seeds) of saplings was determined visually in the field. After felling a tree or sapling, we measured its total height and a stem cross-section about 2 cm thick was taken as close as possible to the ground level. Ground level sections provided a considerable advantage over increment cores for our work because they gave a ring count closer to the germination point. The age distributions of tree population (DBH > 1 cm) were examined using histograms.

In order to test the second hypothesis concerning the growth of black spruce tree in the study area, we felled 10 black spruce trees with the largest diameters at breast height in each plot, for a total of 30 sample trees (3 plots × 10 trees per plot). They were considered the dominant trees in our study (MRNF). They had no signs of crown damage due to insects, animals, disease, or unusual conditions. We used prominent forking as the primary indicator of past damage. We marked and measured diameter at breast height (DBH) prior to felling and cut each stem close to ground level. After felling a dominant tree, we measured its total height as well as the distance from the base to the first live branch.

Finally, stem cross-sections were taken at 0, 0.3, 0.6, 1.0, 1.3 m (breast height) and at every meter starting from 2 m to the top of the trees. Sections were taken from both sides of forked stems.

Stem cross-sections were placed inside a greenhouse on horizontal platforms in order to ease the drying process. Then, the cross-sections were sanded with progressively finer grades of sandpaper (up to 400 grit) until xylem cells were clearly visible under a binocular microscope (40-100×). After the sanding process, cross-sections were dated by counting annual growth rings from the bark to the pith along two diameters at right angles with a binocular microscope (40-100×), or by using the WinDENDRO™ software (version, 2003a). Then, following the usual technique, tree-ring widths of each cross-section were measured from the pith to the bark along the counted rays using the WinDENDRO™ software or the Henson (Morin and Laprise 1990). Data from WinDENDRO™ software were organized into worksheets to create the graphs by using SigmaPlot software version 6.0. The out prints of the tree ring curves and ring-sequences were firstly compared and cross-dated visually using the pattern of wide and narrow rings to determine as accurately as possible the germination date of the living and dead stems. Then, the computer program COFECHA (Holmes 1983) was run in order to verify cross-dating among the ring measurement series and to indicate possible dating or measurement problems and corrections were made when necessary. Cross-dating was conducted between sections within a tree, and among sections between trees, separately. It was also run to check cross-dating among chronologies between the sites within the study area.

Tree ring curves of all samples were corrected, including missing rings that are not uncommon in black spruce, especially in condition of suppression (Black and Bliss 1980; Carleton 1982, 1985), and excluding false rings. Therefore, we were able to assign the true year of formation for every ring of each sample. From the resulting corrected curves, mean curves for every individual and in a second step, mean curves for each stands, and finally mean curves for all study stands across the investigation area were constructed for further analysis. Then, the computer program WinStem ™ (version, 2003d) was run to conduct the stem analysis of each dominant tree. It allowed us to visualize the data produced by the WinDENDRO file. It produced the mean radii, diameter and area for all stem disks as well as the tree height and volume as a function of age by using the method of Carmean (1972).

2.6 Comparison of black spruce growth in diameter, height and volume between the study stands and areas

Comparison of black spruce growth in diameter, height and volume between the study stands were made first by statistical analyses on growth data and then by graphical interpretation of the growth curves. The growth curves of sampled trees from each study stand as well as area were represented by a mean growth curve, since no marked difference between the obtained growth curves of trees in each study stand or area [between the 51^{st} and the 52^{nd} parallels (hereafter referred to as *northern area*), and between the 49^{th} and the 51^{st} parallels (hereafter referred to as *southern area*)], was observed. In addition, diameter, height and volume growth histories were summarized by study stands and areas.

2.7 Statistical analysis

2.7.1 Data from field measurements

Data from field measurements on trees (DBH > 9 cm) were subjected to one-way analysis of variance (ANOVA). They were analysed, with the stand as the independent variable and either the total height, DBH, clear length or live-crown ratio (defined here as the ratio between the height from the base to the live foliage and the total height) as the dependent variables. For significant effects, Tukey Kramer HSD tests were used to identify significantly different means among dependent variables within research plots.

To perform statistical analysis of saplings in this study, DBH and height data of saplings among research plots at all three study sites were analysed using JMP software, with a two-way analysis of variance (ANOVA), with interaction between the effects, site and regeneration method (sexually by seed or asexually by layering). There were two factors: randomly selected sites and fixed regeneration method. For significant effects, Tukey Kramer HSD tests were used to identify significantly different means among diameter at breast height and height treatments within research plots, and the Student's t test was used to identify significant differences among research plots means within diameter at breast height and height treatments. The Student's t test was also used to test whether the difference of the means is significantly different from a hypothesized value of zero.

2.7.2 Data from laboratory measurements

One-way analysis of variance was performed to analyse total height, diameter (under bark) and volume of the dominant black spruce trees from the three study sites, at age 70, the latest common age for the three stands.

Repeated measures analysis of variance (ANOVAR) was used to compare cumulative diameter growth (under bark), diameter growth rate, cumulative height growth, height growth rate, cumulative volume growth and volume growth rate of dominant black spruce trees between the stands and the areas. As response variables for the experiment, these six growth parameters were separately averaged for consecutive 5-year periods. Five-year means were used in this study in order to consider short-term growth differences in diameter, height and volume of black spruce trees between the study stands and the areas. The sphericity assumption was rejected for the comparison and adjusted F values were used for hypothesis testing of the within subject effects. The probability of Greenhouse-Geisser ($P_{G\text{-}G}$) is considered to be more conservative than the Huynh-Feldt ($P_{H\text{-}F}$) (Fernandez 1991; Scheiner and Gurevitch 1993). Data from the same sequential 5-year growth periods were analysed separately with a univariate ANOVA at each time point. It was performed to determine from which 5-year period of growth the independent variables (stand and area) were significantly different.

Linear and quadratic orthogonal polynomial contrasts were used to examine trends in diameter, height and volume growth rates across time. Data related to years over 70 for stands located between the 51st and the 52nd parallels, and over 65 for comparing the northern and southern areas were omitted from our analysis because the last common 5-year period between the study-stands and between the areas were 65 to 70 and 61 to 65, respectively. Linear and quadratic model forms adequately described the patterns of the diameter, height and volume growth rates observed for this range of data.

Repeated measure analysis of variance was also used to compare average 5-year diameter growth rate of black spruce saplings between the study stands. Statistical significance for all tests was set at the $P < 0.05$ level. All statistical analysis was performed using JMP IN software version 5.1. (SAS Institute Inc., Cary, North Carolina, USA).

CHAPTER III

RESULTS

3.1 Dynamics and growth of black spruce trees in three study stands

3.1.1 Site descriptions

The first study site (TO1) was located about 6 km east of Mistassini Lake at an altitude of 420 m above sea level. The slope form of the study plot was regular and averaged 8%. The second study site (C6S1) was located about 122 km northeast of the first one, at an altitude of 530 m above sea level. The study plot had a flat topography and the slope form was regular. The third study site (C7S1) was located about 92 km east of the second site and about 55 km west of the Manicouagan Reservoir, at an altitude of 530 m above sea level. The slope form of the study plot was regular and averaged 8%. Site characteristics are summarized in table 3.2.

Situated in the east of the study area, the oldest stand (C6S1) consisted of almost single-species spruce stand and exhibited the lowest upper-canopy density (833 tree/ha), and the lowest basal area (10 m^2/ha), as compared with the two other study stands. The TO1 stand was located in the west of the study area and had the highest upper-canopy density (3500 tree/ha). The C7S1 stand had the highest basal area (23 m^2/ha) but the density of trees per hectare (1042 tree/ha) was low (Tables; 3.1 & 3.3).

The studied stands were almost similar with respect to mean dominant height and diameter, at the time of establishment of the study (Table 3.1). In C6S1 stand, the average dominant height was 10.7 m with a range of 0.26 m. Stand C7S1 was as uniform, the respective values being 10.33 m and 0.3 m. In the third stand (TO1), the average dominant height was 9.36 m, with a range of 0.2 m. In TO1, C6S1 and C7S1 stands, the amounts of seedlings per hectare were evaluated to be approximately 16500, 12083 and 6250 stem/ha, respectively. As well, the sapling density of TO1, C6S1 and C7S1 stands were evaluated to be approximately 3000, 1667 and 2708 stem/ha, respectively. The percent stocking for dominant black spruce trees tallied on C6S1, C7S1 and TO1 study-plots were approximately 31.67, 28.33 and 68, respectively (Table 3.3).

Young black spruce study stands in the study area have three well recognizable strata: i) a tree canopy layer usually dominated by black spruce (*Picea mariana* (Mill.) BSP), ii) an understorey community often dominated by Labrador-tea (*Ledum groenlandicum*), Early low Blueberry (*Vaccinium angustifolia*), Velvetleaf blueberry (*Vaccinium myrtilloides*), Sheep laurel (*Kalmia angustifolia* L.) and a few herbs and iii) ground cover often dominated by Schreber's moss (*Pleurozium schreberi* (*Calliergon schreberi*)), Plume moss (*Ptilium cristacastrensis*) and Sphagnum *sp.* in C6S1 and TO1 stands and by Coral lichen (*Cladina stellaris*), Reindeer lichen (*Cladina rangiferina*) and Schreber's moss (*Pleurozium schreberi* (*Calliergon schreberi*)) in C7S1 stand.

Table 3.1 Dendrometric characteristics of the study stands.

	Southern area		Northern area		
	12	14	C6S1	C7S1	TO1
Average age (yr)	66	69	99.05 (0.46)	79.04 (5.19)	73.88 (0.30)
Maximum age (yr)	68	72	107	81	77
Average DBH (cm)	12.4	11.2	13.38 (0.48)	12.75 (0.39)	11.49 (0.30)
Average height (m)	14.1	12.2	10.70 (0.26)	10.33 (0.30)	9.36 (0.20)
Stem number ha^{-1}	1417	2050	833	1041	3500
Basal area (m^2 ha^{-1})	18	20	10	23	21
Black spruce %	93%	98%	99%	99%	99%
Date of establishment	1927	1923	1900	1920	1925

Note: Values are mean with standard errors in parentheses.

Table 3.2 A summary information about study sites characteristics.

Site	TO1	C6S1	C7S1
Latitude	51°00'43.2"	51°20'23.1"	51°27'01.4"
Longitude	73°00'08.9"	70°06'01.8"	71°24'21.9"
Altitude	420 m.a.s.l	530 m.a.s.l	530 m.a.s.l
Cartographical species group*	EEA470	EED470	EEC4VIN
Size of study plot	10m × 20m	20m × 20m	10m × 20m
Slope of study plot	8%	0%	8%
Exposition of study plot	61°	285°	90°
Slope form of study plot	Regular	Regular	Regular

* The notations are used by the MRNF (Normes d'inventaire forestier 1984).

Table 3.3 The percent stocking values and density for each commercial species tallied on the study plots at the time of sampling.

	C6S1		C7S1		TO1	
Commercial tree	Stocking %	Density (No. stem/ha)	Stocking %	Density (No. stem/ha)	Stocking %	Density (No. stem/ha)
Black spruce:						
Seedling	76.67	12083.33	53.33	6250	88	16500
Sapling	43.33	1666.67	43.33	2708.33	49	3000
Tree	31.67	833.33	28.33	1041.67	68	3500
Balsam fir:						
Seedling	0	0	0	0	5	125
Sapling	0	0	0	0	7	250
Tree	0	0	0	0	0	0
Jack pine:						
Seedling	0	0	0	0	2	0
Sapling	0	0	1.67	208.33	4	0
Tree	5	0	1.67	0	2	0

3.1.2 Age structure

Tree age of black spruce was determined at ground level for all trees over 1 cm in DBH. Age data from section-cuts (at ground levels) of sample trees indicated that all study stands originated after a major fire disturbance roughly around 1900, 1920 and 1925 in the C6S1, C7S1 and TO1 sites, respectively. However, the oldest documented trees on the C6S1, C7S1 and TO1 stands were 107, 81 and 77-years-old, respectively (Table 3.1). This is the minimum age estimate for the time of fire disturbance. Because of missing rings located under ground surface, cross-dating below the adventitious roots of black spruce may add 3-19 years to the age estimate compared with the age at ground level (DesRochers *et al.* 1997). The true year of germination might therefore be at least a few years older since black spruce at the seedling stage require some years for growing to the height of ground level.

Figure 3.1 shows the overall age class distribution of the standing sampled stems (living + dead). In general, individuals in each stand displayed a single-cohort even-age structure due to the short period of time of the stands' establishment. The age distribution diagrams show that black spruce trees established intensively during a short period of time, ranging from 15 to 20 years. All stands show a peak in recruitment just a decade after fire. Moreover, the age distribution diagram shows a little difference in age structure between the populations of spruce and jack pine in the C7S1 sample plot. Black spruce is continuously present in all age classes, while jack pine is absent in younger age classes.

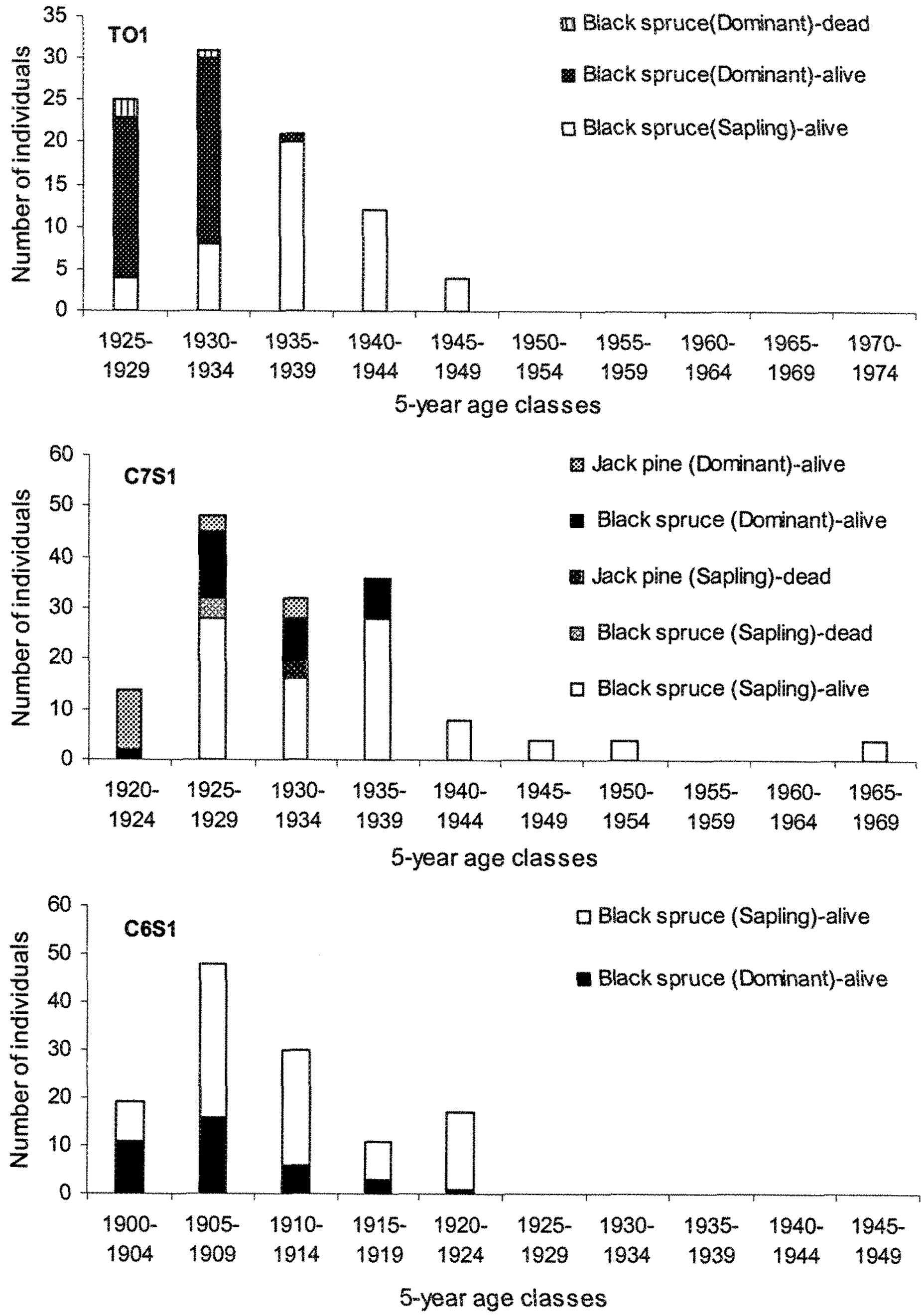

Figure 3.1 Age-class distributions of all individuals with DBH > 1 cm, (as divided into dominant trees with DBH ≥9 cm and saplings with 9 cm > DBH > 1 cm) located in a sampling area of 400 m^2 in plot C6S1 and 200 m^2 in plots C7S1 and TO1.

3.1.3 Diameter and diameter growth of dominant black spruce trees

The study stands were almost homogeneous with respect to mean diameter at breast height, at the time of establishment of the study (Table 3.4). Black spruces trees in the C6S1 stand, which were larger in diameter, had significantly shorter clear length (Table 3.4). No significant difference in DBH of sample trees were found between the stands at the time they were harvested for detailed stem analysis (P = 0.0766), or at age 70 (P = 0.2465), the last common age between the sample trees (Tables; 3.4 & 3.5).

Diameter growth curves of the 30 sampled dominant black spruce stems showed a similar diameter growth pattern across the studied area (Fig. 3.2). Every diameter growth curve from the studied sites presented a more or less short period of suppression (slow growth) in the early growth of the black spruce, followed by a marked release (fast growth) almost synchronous between the trees of a given site (Fig. 3.2). It is recognized that black spruce even-aged stand has a stylized sigmoid shaped growth curve in a boreal forest. This is confirmed by our results as shown in figure 3.2. Radial growth of black spruce growing in the studied area declines as the tree gets older (Fig. 3.3). The growth curves indicate that in the two most northern study-stands (C7S1 & C6S1), gradual decline on radial growth of black spruce trees occurred approximately 10 to 15 years later than for those growing in stand TO1. On the average, black spruce in these young stands across the studied area attained their maximum point of annual diameter 22 years following the stand establishment (Fig. 3.5).

There was no significant difference in overall average 5-year diameter growth rates of dominant black spruce trees between the stands (P = 0.5107). There was however, a highly significant difference between the average 5-year diameter growth rates over time ($P < 0.0001$). In addition, the interaction between stand and time was significantly different ($P < 0.0001$). There was a significant negative linear relationship and a significant quadratic trend in the average 5-years diameter growth rates over time ($P < 0.0001$), indicating a general decrease in the average 5-year diameter growth rates with increasing time. As well, the linear relationship and quadratic trend were also significantly different between the stands (Table 3.6a).

In univariate analysis of variance, difference in the average 5-years diameter growth rates of dominant black spruce trees were statistically significant between the stands for each of the following 5-years periods: 1-5, 6-10, 11-15, 36-40, 41-45, 46-50, 51-55, 56-60 and 61-65 years (Table 3.6b). Average 5-year diameter growth rates of the dominant black spruce trees in the TO1 stand were always lower than in the C6S1-C7S1 stands, with the exception of the first 15 years after establishment. However, the growth differences were minimal from age 16 to age 35 after establishment (Fig. 3.4a).

There was no significant difference in overall average 5-year cumulative diameter growth of dominant black spruce trees between stands (P = 0.6987). The interaction between stand and time was significantly different (P = 0.04, Table 3.7a). In univariate analysis of variance, significant difference in the average cumulative diameter growth of dominant black spruce trees were found between the stands for each of the following 5-year periods: 1-5, 6-10, 11-15, 16-20, and 21-25 years (Table 3.7b). Dominant black spruce trees in the C6S1 stand had a cumulative diameter growth almost similar to those in the C7S1 stand, whereas the cumulative diameter growth of dominant black spruce trees in TO1 stand was higher for the first 45 years after establishment (Fig. 3.4b). Diameter growth was similar across the studied stands during the 70 years documented in this study, allowing us to develop the following single equation for black spruce growing in young even-aged fire-origin stands:

[1] Diameter under bark (mm) = -3.149212 + 2.7829751 Age $R^2 = 0.986$

This equation has been created in Microsoft Excel using the regression analysis tool on the mean diameter growth data of the three study stands.

Table 3.4 Characteristics (average) of the 10 sampled dominant black spruce trees growing in each study stands at the time they were harvested for detailed stem analysis.

Stand	DBH (cm)	Height (cm)	Clear length (m)	Live crown ratio* (%)
TO1 (Age 74)	14.17 [a]	10.92 [a]	7.35 [a]	67 [a]
C7S1 (Age 76)	15.23 [a]	12.00 [a]	6.98 [ab]	58 [ab]
C6S1 (Age 99)	16.35 [a]	12.01 [a]	4.97 [b]	43 [b]
F value	0.0766	0.1769	0.0211	0.0112

* Live crown ratio = (height to base of live foliage/total height) × 100.

NOTE: Differences are significant ($P < 0.05$) between values designated by different letters (Tukey Kramer HSD tests). Letters also indicate ranking of means: a > b.

Table 3.5 One-way analysis of variance of dominant black spruce trees at age 70, for stand difference in total height, dbh and volume.

Source	df	MS	F Ratio	$P > F$
DBH (under bark)	2	453.56	1.4757	0.2465 *ns*
Height	2	5.5100	3.0024	0.0665 *ns*
Volume	2	1237.3	2.1713	0.1335 *ns*

Levels of statistical significance are denoted with $ns = p > 0.05$.

Table 3.6 Results of repeated measure analysis of variance (ANOVAR) (**a**), and of the univariate analysis of variance for each consecutive 5-year period (**b**), of dominant black spruce trees for stand differences in diameter growth rates.

(a) ANOVAR					
				Adjusted $P > F$	
Source	df	F	$P > F$	G-G	H-F
Between subject					
Stand	2	0.6890	0.5107		
Within subject					
Time	13	52.449	0.0001	0.0001	0.0001
Linear	1	34.250	0.0001		
Quadratic	1	200.04	0.0001		
Time× Stand	26	8.2347	0.0001	0.0001	0.0001
Linear	2	9.5596	0.0007		
Quadratic	2	20.566	0.0001		

(b) Univariate ANOVA for each consecutive 5-year period of growth.

Source	Time (year)	df	F	$P > F$
Stand	1-5	2	23.921	0.0001
Stand	6-10	2	27.382	0.0001
Stand	11-15	2	5.9777	0.0071
Stand	16-20	2	1.1017	0.3468
Stand	21-25	2	1.2200	0.3099
Stand	26-30	2	2.0422	0.1493
Stand	31-35	2	3.1658	0.0582
Stand	36-40	2	8.7423	0.0012
Stand	41-45	2	12.267	0.0002
Stand	46-50	2	9.8623	0.0006
Stand	51-55	2	6.5687	0.0047
Stand	56-60	2	5.7826	0.0081
Stand	61-65	2	4.7541	0.0170
Stand	66-70	2	2.6746	0.0871

Note: Adjusted $P > F$ probabilities are for Greenhouse-Geisser (G-G) and Huynh-Feldt (H-F) adjusted F tests.

Table 3.7 Results of repeated measure analysis of variance (ANOVAR) (**a**), and of the univariate analysis of variance for each consecutive 5-year period (**b**), of dominant black spruce trees for stand differences in cumulative diameter growth.

(a) ANOVAR

Source	df	F	$P > F$	Adjusted $P > F$ G-G	Adjusted $P > F$ H-F
Between subject					
Stand	2	0.3634	0.6987		
Within subject					
Time	13	608.97	0.0001	0.0001	0.0001
Time × Stand	26	3.0353	0.0001	0.0474	0.0412

(b) Univariate ANOVA for each consecutive 5-year period of growth.

Source	Time (year)	df	F	$P > F$
Stand	1-5	2	27.494	0.0001
Stand	6-10	2	32.907	0.0001
Stand	11-15	2	25.453	0.0001
Stand	16-20	2	12.644	0.0001
Stand	21-25	2	5.7136	0.0085
Stand	26-30	2	2.4870	0.1020
Stand	31-35	2	1.0634	0.3593
Stand	36-40	2	0.3587	0.7028
Stand	41-45	2	0.1063	0.8995
Stand	46-50	2	0.0159	0.9842
Stand	51-55	2	0.0450	0.9561
Stand	56-60	2	0.1463	0.8646
Stand	61-65	2	0.2814	0.7569
Stand	66-70	2	0.4076	0.6693

Note: Adjusted $P > F$ probabilities are for Greenhouse-Geisser (G-G) and Huynh-Feldt (H-F) adjusted F tests.

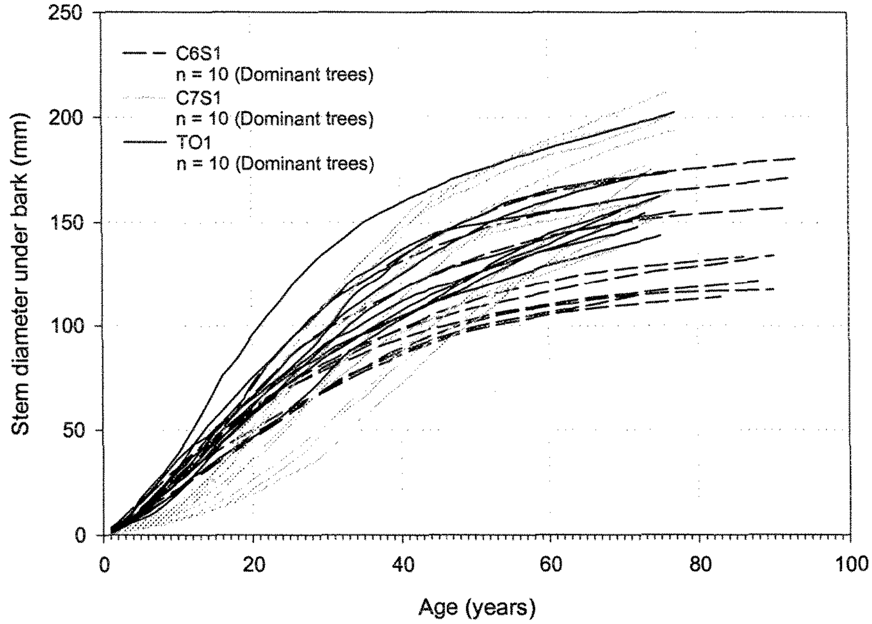

Figure 3.2 Diameter growth curves for the 30 sampled dominant black spruce trees in the study area. Note the slow growth of the black spruce during the initial establishment phase of 10 years.

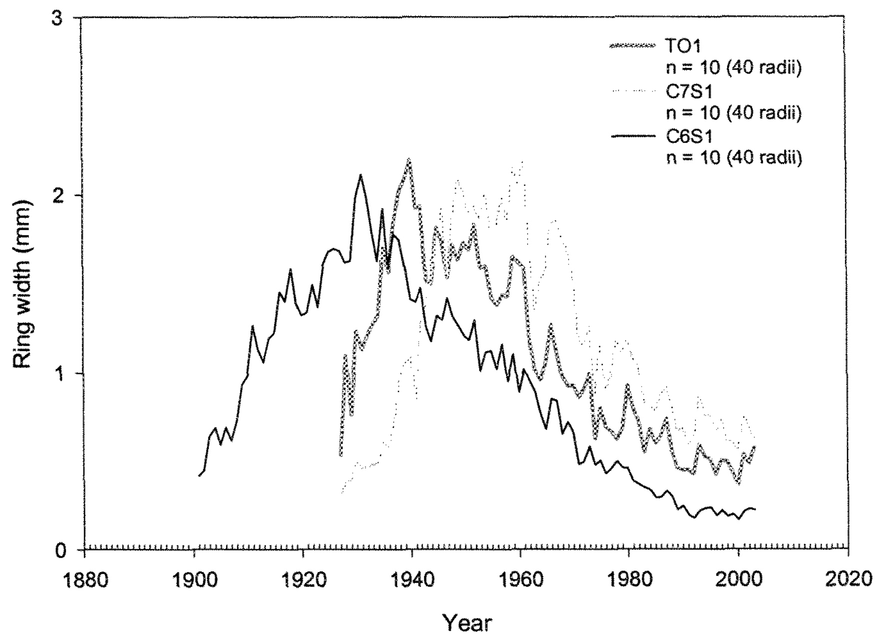

Figure 3.3 Mean growth curves from three black spruce stands located between the 51st and the 52nd parallels in northern Quebec.

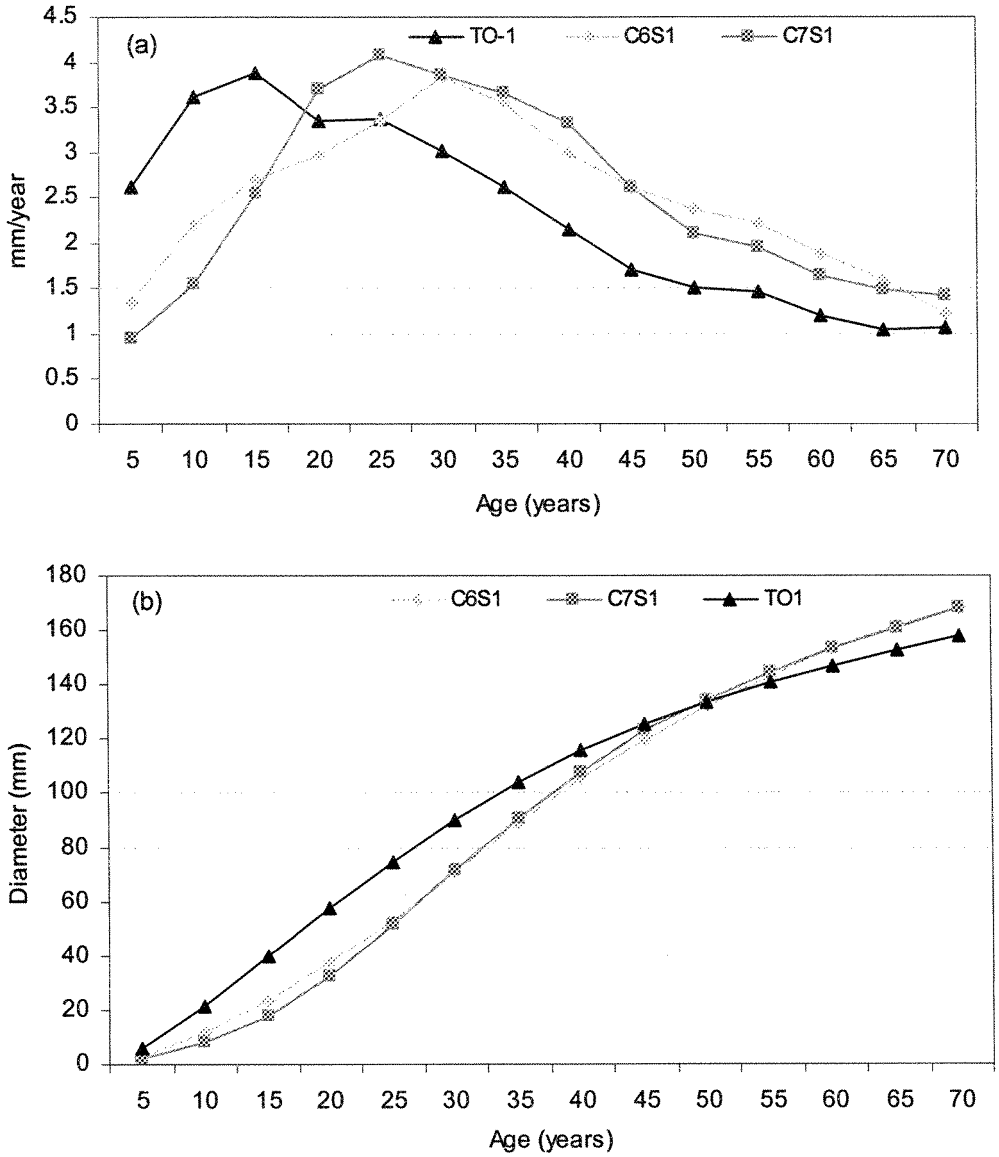

Figure 3.4 Mean diameter growth rates (a), and cumulative diameter growth (b) of the 10 sampled dominant black spruce trees per stands.

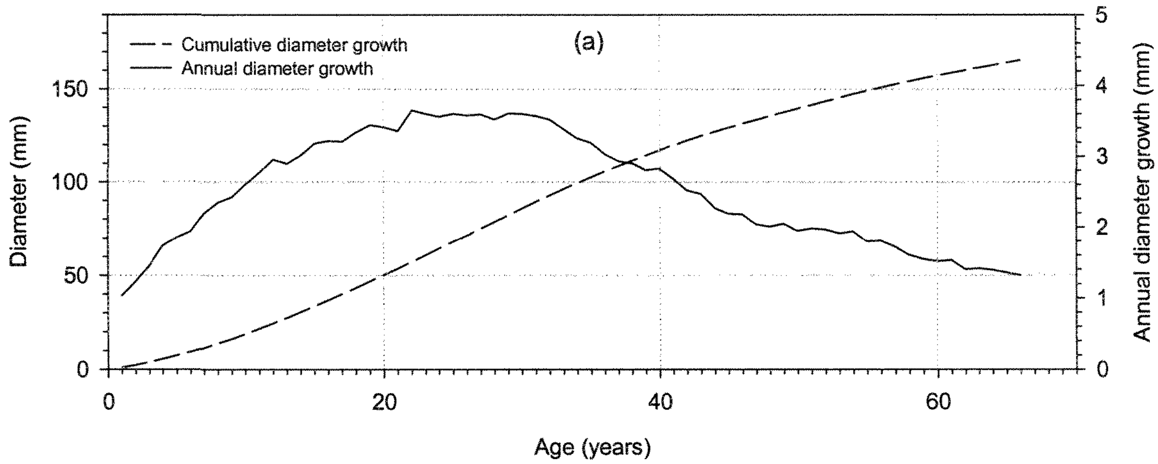

Figure 3.5 Graphical comparison of the cumulative and annual mean diameter growth curves of dominant black spruce trees (n = 30), in the study area, over a 66-year period following the stand establishment.

3.1.3 Diameter and diameter growth of black spruce saplings (1cm< dbh <9cm)

The two-way analysis of variance for dbh and height showed that one of the main effects (regeneration method) was significant, but the other main effect (site) and the two-way interaction site-regeneration method were not significant (Table 3.8). A Tukey multiple comparisons test revealed that the mean diameter at breast height for the saplings regenerated by seeds was significantly larger than those regenerated by layering process. However, the mean diameter at breast height of saplings in C6S1 stand (BA=10 m^2/ha) was not significantly larger than that of the two other study stands (C7S1; BA= 23 m^2/ha, TO-1; BA = 21 m^2/ha), (Table 3.9). In addition, the average height for the saplings regenerated by seeds was significantly taller than that of the saplings regenerated by layering process (Table 3.9).

There was a significant difference in overall average 5-year diameter growth rates of black spruce saplings between the stands ($P = 0.0306$). There was also a highly significant difference between average growth rates over time ($P < 0.0001$). As well, the interaction between stand and time was also significantly different ($P < 0.0001$, Table 3.10a). In univariate analysis of variance, difference in average diameter growth rates of black spruce saplings were statistically significant between the stands for each of the following 5-year periods: 1-5, 6-10, 11-15, 36-40, 41-45, 46-50, 51-55, 56-60 and 61-65 years (Table 3.10b). Average 5-year diameter growth rates in the C7S1 stand were always lower than in the C6S1 and TO1 stands, with the exception of the 41-45 years period after establishment. However, the growth differences were minimal from age 16 to age 35 after establishment (Fig. 3.6).

The growth pattern of the dominant trees and saplings in terms of the changes in diameter was considered separately in the three study sites (Figs. 3.7). We were interested to know if the growth pattern of the dominant and suppressed trees is affected by the site. Figure 3.8 shows a similar year-to-year variation in diameter growth of dominant trees and saplings growing in each stand.

In order to present the tree long-term growth data for each study site at the time of sampling, the cumulative annual diameter growth curves of all measured individuals were graphed for each stand separately (Fig. 3.7). Although the trees in these even-aged stands regenerate at about the same time and are almost similar in age, they did not grow at the same rate. As can be seen from the figure 3.7, the mean cumulative diameter growth curve of saplings in all study stands differed slightly from each other. This was due to the smaller stem number in C6S1 stand. However, in these closed even-aged stands, black spruce saplings grew much more slowly than dominant black spruce trees and would not reach 5cm in diameter before the age of 60, on the average. The difference in size is due to the difference in growth rates between these dominant and suppressed trees and does not directly reflect the difference in time of establishment.

Table 3.8 Two-way analysis of variance in diameter at breast height and height for saplings growing in three study sites.

Source of variation	df	F value and level of significant	
		DBH	Height
Main effects			
Site	2	0.5663 ns	1.2876 ns
Regeneration method	1	12.6504**	7.0305*
2-way interaction			
Site×Regeneration method	2	0.0490 ns	0.0445 ns

Levels of statistical significance are denoted with stars (* for $p < 0.05$, ** for $p < 0.01$) and ns (for $p > 0.05$).

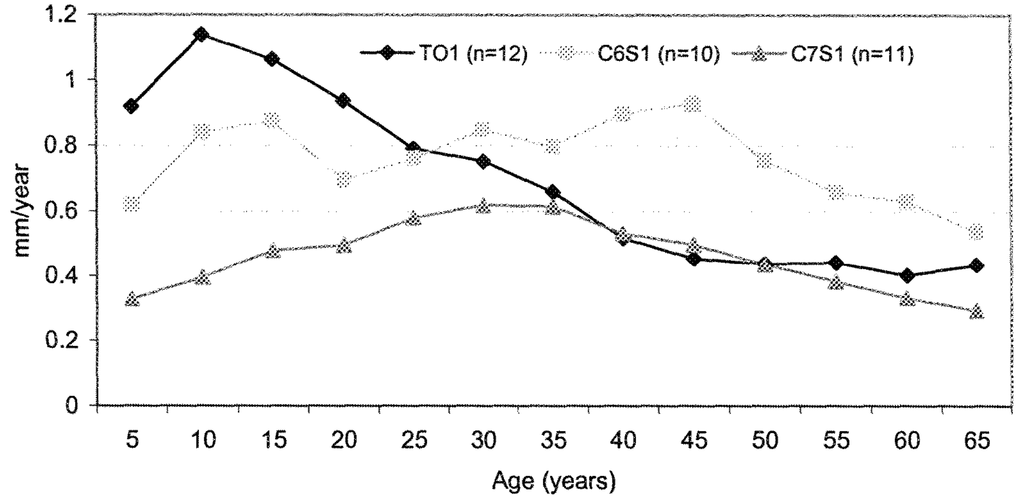

Figure 3.6 Mean diameter growth rates of black spruce saplings per stand.

Table 3.9 Characteristics (average) of black spruce saplings regenerated by seed and layering, growing in the understory of three study stands at the time they were harvested.

Regeneration method	DBH (cm)	Height (m)	Age (year)
Layering	2.75 (1.02)	3.02 (1.41)	70.21 (10.31)
Seed	5.53 (2.47)	5.48 (2.45)	76.64 (14.61)

Note: Values are means with standard errors in parentheses.

Table 3.10 Results of repeated measure analysis of variance (ANOVAR) (**a**), and of univariate analysis of variance for each consecutive 5-year period (**b**) of black spruce saplings for stand differences in diameter growth rates.

(a) ANOVAR

Source	df	F	$P > F$	Adjusted $P > F$ G-G	Adjusted $P > F$ H-F
Between subject					
Stand	2	3.9271	0.0306		
Within subject					
Time	12	7.0868	0.0001	0.0001	0.0001
Time × Stand	24	5.6169	0.0001	0.0001	0.0001

(b) Univariate ANOVA for each consecutive 5-year period of growth.

Source	Time (year)	df	F	$P > F$
Stand	1-5	2	13.668	0.0001
Stand	6-10	2	12.121	0.0001
Stand	11-15	2	4.8898	0.0145
Stand	16-20	2	2.4293	0.1052
Stand	21-25	2	0.7879	0.4640
Stand	26-30	2	1.0216	0.3722
Stand	31-35	2	0.9424	0.4009
Stand	36-40	2	5.1954	0.0115
Stand	41-45	2	10.511	0.0003
Stand	46-50	2	5.0134	0.0132
Stand	51-55	2	3.8100	0.0335
Stand	56-60	2	5.7837	0.0075
Stand	61-65	2	3.6013	0.0396

Note: Adjusted $P > F$ probabilities are for Greenhouse-Geisser (G-G) and Huynh-Feldt (H-F) adjusted F tests.

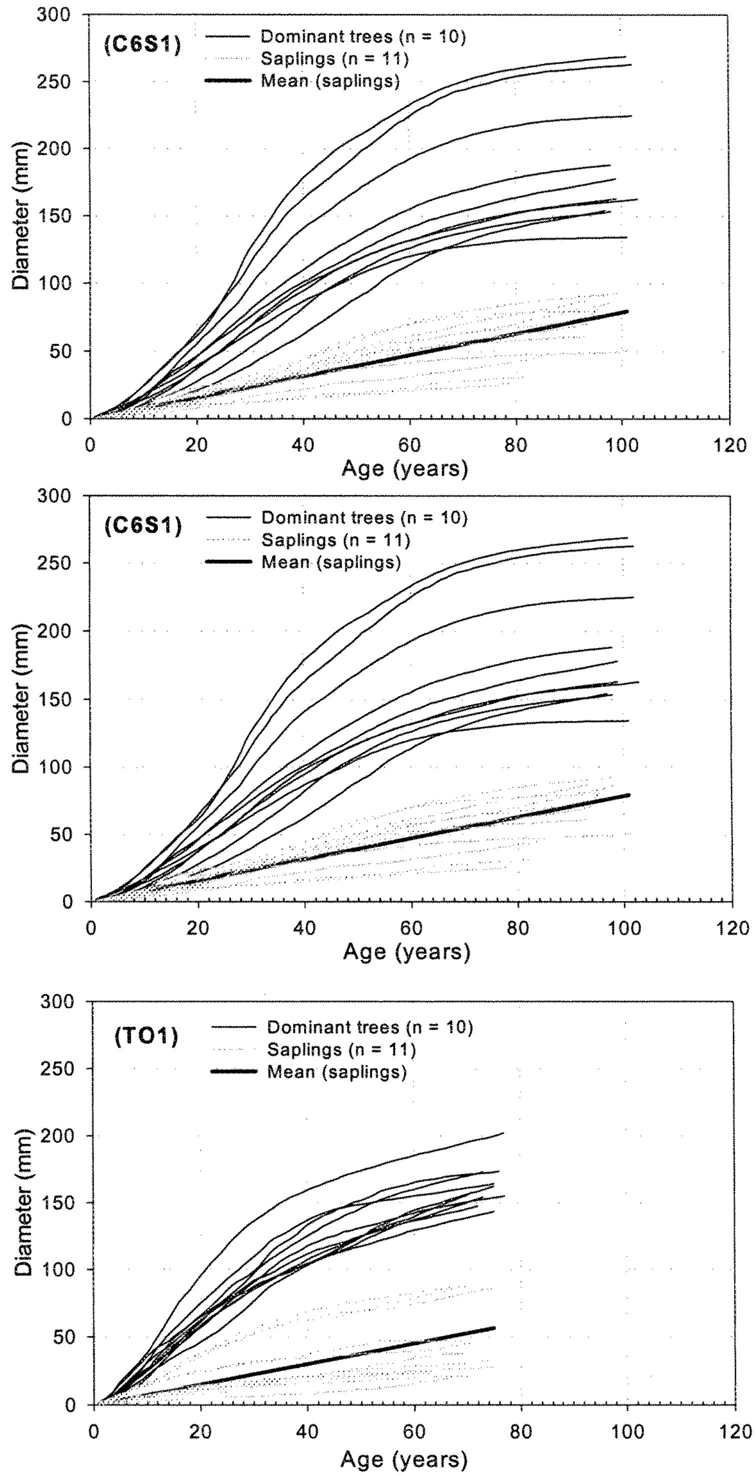

Figure 3.7 Cumulative growth curves (obtained from tree-ring analysis) of stem diameter for the individual dominant (DBH ≥ 9cm) and saplings (9cm > DBH > 1cm) black spruce.

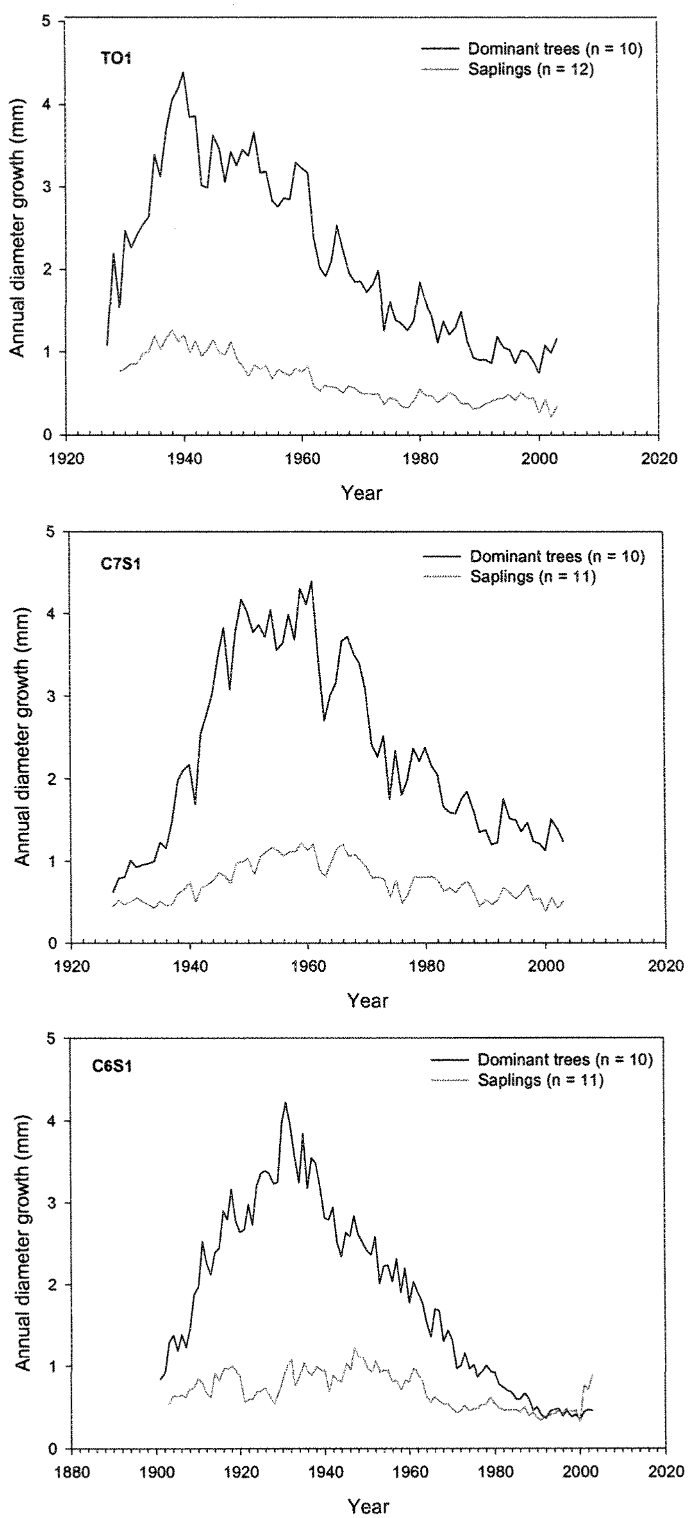

Figure 3.8 Mean annual growth curves (obtained from tree-ring analysis) of stem diameter for the dominant black spruce trees (DBH $\geq$ 9cm), and black spruce saplings (9cm > DBH > 1cm).

3.1.4 Height and height growth of dominant black spruce trees

The study stands were almost homogeneous with respect to average dominant height at the time of establishment of the study (Table 3.1). In stand C6S1, the average dominant height was 10.7 m; with a range of 0.26 m. Stand C7S1 was as uniform, the respective values being 10.33 m and 0.3 m. As well, in stand TO1 the average dominant height was 9.36 m; with a range of 0.2 m. The sampled dominant trees had the greatest clear length in the youngest stand, averaging approximately 7.35 m in the 74 year-old stand (Table 3.4). The live-crown ratio for main canopy stems differed significantly between the youngest and oldest stands, but did not differ significantly between the TO1 and C7S1 stands, or between the C7S1 and C6S1 stands. As black spruce trees become older and taller, there is a marked reduction in live crown ratio (Table 3.4). The average crown ratio of dominant trees was 67 % in stand TO1, 58 % in stand C7S1 and 43 % in stand C6S1. However the live-crown ratio for main canopy stems averaged 56 % across the three sites (Table 3.4).

There was no significant difference in total height of sampled dominant trees between study stands at the time they were harvested for detailed stem analysis (P = 0.1769), or at age 70 (P = 0.0665, Tables 3.2 & 3.3). Height growth curves of the 30 sampled dominant black spruce stems showed a similar height growth pattern across the study stands (Fig. 3.9). Every height growth curve from the study sites presented a more or less short period of suppression in the early growth of the black spruce, followed by a marked synchronous release between the trees of a given site.

There was no significant difference in overall average 5-year height growth rates of dominant black spruce trees between the stands ($P = 0.0722$). The interaction between stand and time was significantly different ($P < 0.0001$). There was a significant negative linear relationship and quadratic trend in height growth over time ($P < 0.0001$), indicating a general decrease in height growth rate with increasing time. As well, the linear relationship and quadratic trend were also significantly different between the stands ($P < 0.0001$, Table 3.11a).

In univariate analysis of variance, significant differences in the average 5-year height growth rate of dominant black spruce trees were found between the stands for each of the following periods: 1-5, 6-10, 11-15, 31-35, 36-40, 41-45, 46-50, 51-55, 56-60 and 61-65 years (Table 3.11b). Average 5-year height growth rates on the TO1 stand were almost always lower than in the C6S1-C7S1 stands, with the exception of the first 20 years after establishment. However, the growth differences were minimal during the 16 to 30 years period after establishment (Fig. 3.11a). On the average, black spruce attained their maximum point of annual height growth approximately 26 years after the stand establishment. (Fig. 3.10).

There was no significant difference in overall average 5-year cumulative height growth of dominant black spruce trees between the stands ($P = 0.1121$). The interaction between stand and time was significantly different ($P < 0.0001$, Table 3.12a). In univariate analysis of variance, significant differences in the average 5-year cumulative height growth of dominant black spruce trees were found between the stands for each of the following periods: 1-5, 6-10, 11-15, 16-20, 21-25, 26-30 years (Table 3.12b). Average 5-year cumulative height growth of dominant black spruce trees in the TO1 stand was always higher than in the C6S1 and C7S1 stands, until age 50. However, the growth differences were minimal after age 30 (Fig. 3.11b). Height growth was similar across the study stands during the 70 years documented in this study, allowing us to develop the following single equation for black spruce growing in young even-aged fire-origin stands:

[2] $$\text{Height (m)} = -0.680259 + 0.1745251 \text{ Age} \qquad R^2 = 0.99$$

This equation has been created in Microsoft Excel using the regression analysis tool on the mean height growth data of the three study stands.

Table 3.11 Results of repeated measure analysis of variance (ANOVAR) (**a**) and of univariate analysis of variance for each consecutive 5-year period (**b**) of dominant black spruce trees for stand differences in height growth rates.

(a) ANOVAR.

Source	df	F	$P > F$	Adjusted $P > F$ G-G	Adjusted $P > F$ H-F
Between subject					
Stand	2	2.9015	0.0722		
Within subject					
Time	13	45.368	0.0001	0.0001	0.0001
Linear	1	26.190	0.0001		
Quadratic	1	318.19	0.0001		
Time× Stand	26	6.1843	0.0001	0.0001	0.0001
Linear	2	10.561	0.0004		
Quadratic	2	20.587	0.0001		

(b) Univariate ANOVA for each consecutive 5-year period of growth.

Source	Time (Year)	df	F	$P > F$
Stand	1-5	2	31.933	0.0001
Stand	6-10	2	11.146	0.0003
Stand	11-15	2	3.8826	0.0330
Stand	16-20	2	2.6450	0.0893
Stand	21-25	2	1.7001	0.2016
Stand	26-30	2	2.1482	0.1362
Stand	31-35	2	8.9667	0.0010
Stand	36-40	2	15.038	0.0001
Stand	41-45	2	11.092	0.0003
Stand	46-50	2	6.4832	0.0050
Stand	51-55	2	5.2622	0.0118
Stand	56-60	2	6.6412	0.0045
Stand	61-65	2	4.9449	0.0148
Stand	66-70	2	3.3621	0.0500

Note: Adjusted $P > F$ probabilities are for Greenhouse-Geisser (G-G) and Huynh-Feldt (H-F) adjusted F tests.

Table 3.12 Results of repeated measure analysis of variance (ANOVAR) (**a**) and of univariate analysis of variance for each consecutive 5-year period (**b**) of dominant black spruce trees for stand differences in cumulative height growth.

(a) ANOVAR

Source	df	F	$P > F$	Adjusted $P > F$ G-G	Adjusted $P > F$ H-F
Between subject					
Stand	2	2.3756	0.1121		
Within subject					
Time	13	1254.4	0.0001	0.0001	0.0001
Time × Stand	26	6.1359	0.0001	0.0009	0.0005

(b) Univariate ANOVA for each consecutive 5-year period of growth.

Source	Time (year)	df	F	$P > F$
Stand	1-5	2	33.6202	0.0001
Stand	6-10	2	25.8763	0.0001
Stand	11-15	2	14.2513	0.0001
Stand	16-20	2	8.2838	0.0016
Stand	21-25	2	5.8548	0.0077
Stand	26-30	2	4.4303	0.0217
Stand	31-35	2	2.9997	0.0666
Stand	36-40	2	2.1181	0.1398
Stand	41-45	2	1.6784	0.2056
Stand	46-50	2	1.8176	0.1817
Stand	51-55	2	2.0662	0.1462
Stand	56-60	2	2.3394	0.1156
Stand	61-65	2	2.6100	0.0920
Stand	66-70	2	2.8750	0.0738

Note: Adjusted $P > F$ probabilities are for Greenhouse-Geisser (G-G) and Huynh-Feldt (H-F) adjusted F tests.

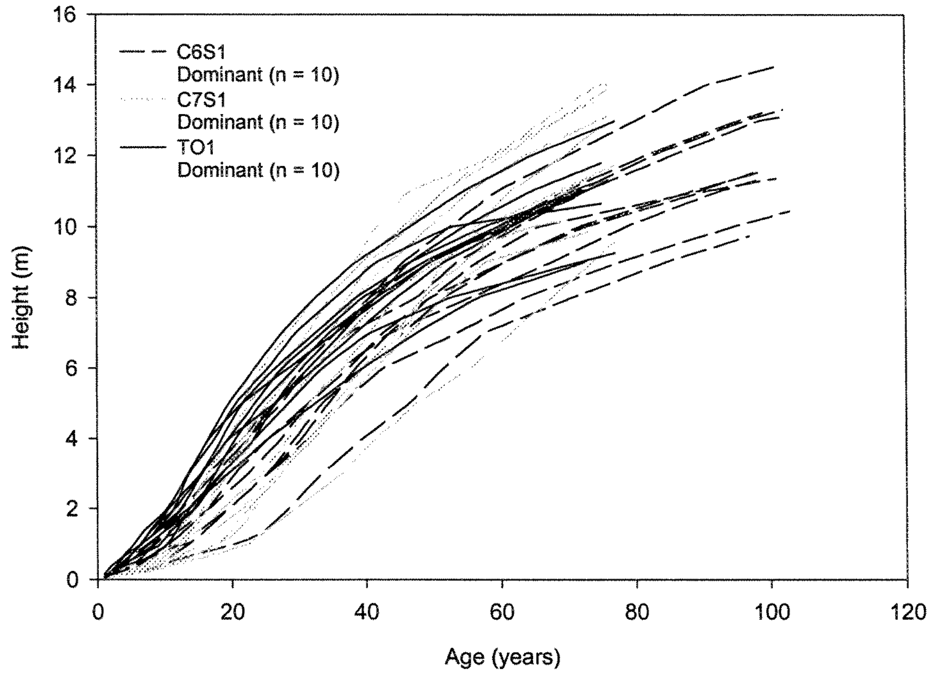

Figure 3.9 Height growth curves for the 30 sampled dominant black spruce trees in the study area. Note the slow growth of the black spruce during the initial establishment phase of 10 years.

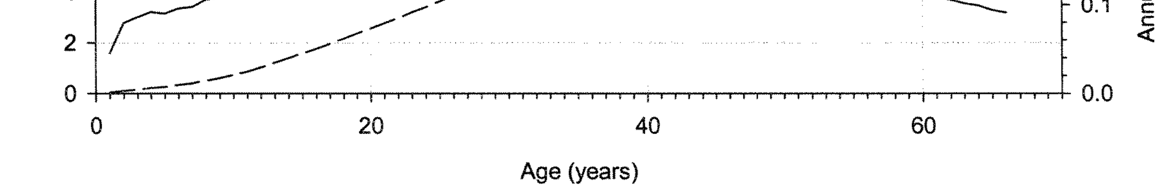

Figure 3.10 Graphical comparison of the cumulative and annual mean height growth curves of dominant black spruce trees (n = 30), in the study area, over a 66-year period following the stand establishment.

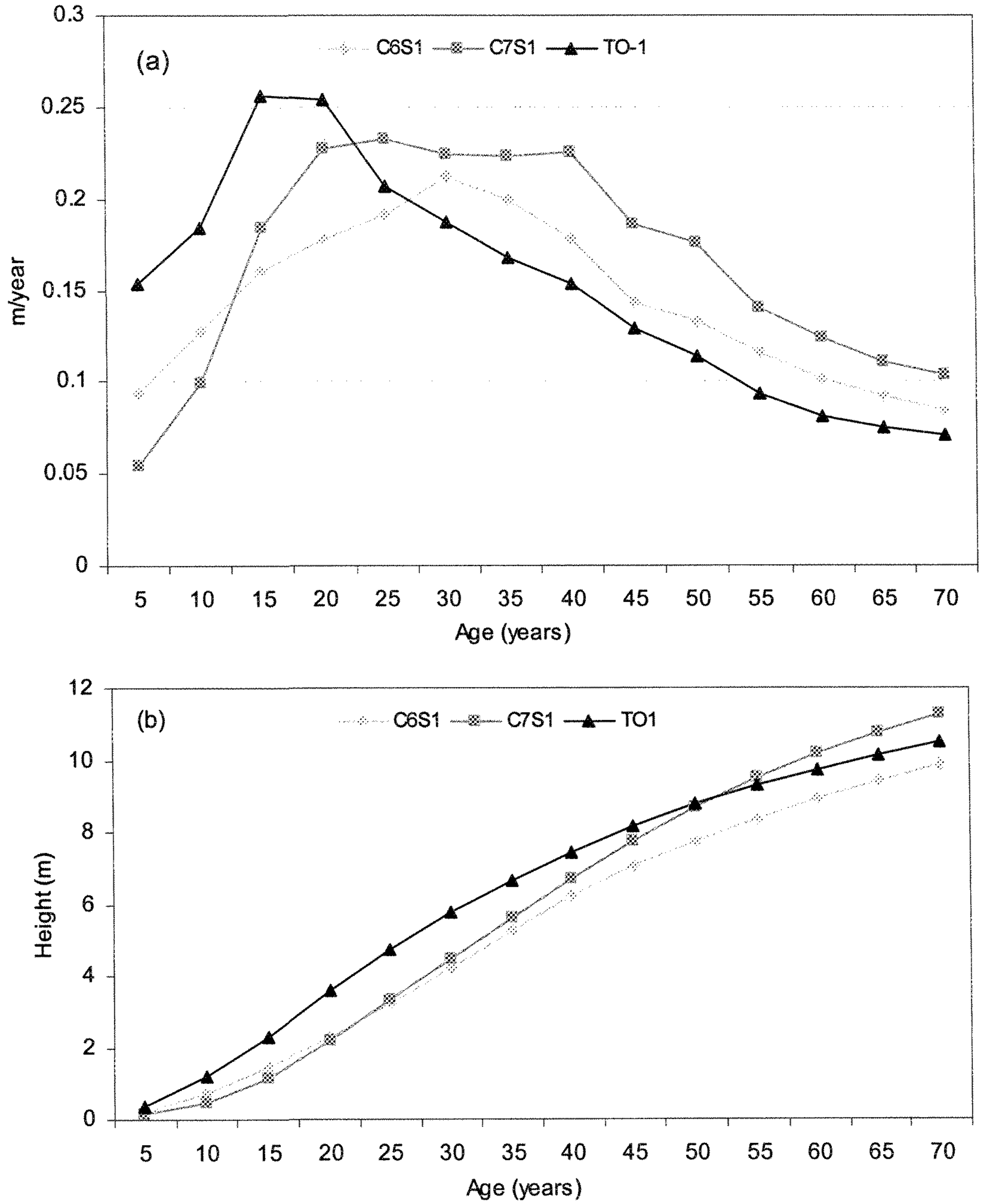

Figure 3.11 Mean height growth rates (a) and cumulative height growth (b) of the 10 sampled dominant black spruce trees per stand.

3.1.5 Volume and volume growth of dominant black spruce trees

Total volume was not significantly different ($P = 0.1335$) between the stands at age 70 (Table 3.5). There was no significant difference in overall average 5-year volume growth rates of dominant black spruce trees between the stands ($P = 0.1339$). However, the interaction between stand and time was significantly different ($P < 0.001$, Table 3.13a). Polynomial contrasts revealed a significant negative linear relationship and quadratic trend in volume growth over time ($P < 0.0001$, Table 3.13a), indicating a general decrease in volume growth rate with increasing time. As well, there was a significant negative linear relationship between the stands ($P < 0.0001$).

In univariate analysis of variance, significant differences in the average 5-year volume growth rates of dominant black spruce trees were found between the stands for each of the following periods: 1-5, 6-10, 11-15, 16-20, 41-45, 46-50, 51-55, 56-60, 61-65 and 66-70 years (Table 3.13b). Average 5-year volume growth rates in the TO1 stand were almost always lower than in the C6S1 and C7S1 stands, from the age 35 after establishment. However, the growth differences were minimal during the 21 to 40 year period after establishment (Fig. 3.12a). On the average, black spruce attained their maximum point of annual volume growth approximately 54 years after the stand establishment (Fig. 3.13).

There was no significant difference in overall average 5-year cumulative volume growth of dominant black spruce trees between the stands ($P = 0.4190$). The interaction between stand and time was not significantly different (P = 0.12, Table 3.14a). In univariate ANOVA, significant differences in the average 5-year cumulative volume growth of dominant black spruce trees were found between the stands for each of the following periods: 1-5, 6-10, 11-15, 16-20 and 21-25 years (Table 3.14b). Volume growth was similar across the study stands during the 70 years documented in this study, allowing us to develop the following single equation for black spruce growing in the young even aged stands:

[3] $$\text{Volume under bark } (dm^3) = -13.04851 + 0.6991446 \text{ Age} + 0.0104998 (\text{Age}-33.5)^2$$

$R^2 = 0.99$

This equation has been created in Microsoft Excel using the regression analysis tool on the mean volume growth data of the three study stands.

Table 3.13 Results of repeated measure analysis of variance (ANOVAR) (**a**) and of univariate analysis of variance for each consecutive 5-year period (**b**) of dominant black spruce trees for stand differences in volume growth rates.

(a) ANOVAR

Source	df	F	*P* > *F*	Adjusted *P* > *F* G-G	Adjusted *P* > *F* H-F
Between subject					
Stand	2	2.1684	0.1339		
Within subject					
Time	13	101.21	0.0001	0.0001	0.0001
Linear	1	291.31	0.0001		
Quadratic	1	43.523	0.0001		
Time × Stand	26	5.0272	0.0001	0.0010	0.0004
Linear	2	12.899	0.0001		
Quadratic	2	0.4981	0.6132		

(b) Univariate ANOVA for each consecutive 5-year period of growth.

Source	Time (year)	df	F Ratio	*P* > *F*
Stand	1-5	2	13.080	0.0001
Stand	6-10	2	24.192	0.0001
Stand	11-15	2	12.533	0.0001
Stand	16-20	2	7.1170	0.0033
Stand	21-25	2	2.7660	0.0808
Stand	26-30	2	0.5719	0.5712
Stand	31-35	2	0.7803	0.4683
Stand	36-40	2	1.9504	0.1617
Stand	41-45	2	4.0390	0.0292
Stand	46-50	2	5.5667	0.0095
Stand	51-55	2	6.6625	0.0044
Stand	56-60	2	6.1517	0.0063
Stand	61-65	2	6.3179	0.0056
Stand	66-70	2	7.9793	0.0019

Note: Adjusted *P* >*F* probabilities are for Greenhouse-Geisser (G-G) and Huynh-Feldt (H-F) adjusted *F* tests.

Table 3.14 Results of repeated measure analysis of variance (ANOVAR) (**a**) and of univariate analysis of variance for each consecutive 5-year period (**b**) of dominant black spruce trees for stand differences in cumulative volume growth.

(a) ANOVAR					
				Adjusted $P > F$	
Source	df	F	$P > F$	G-G	H-F
Between subject					
Stand	2	0.8985	0.4190		
Within subject					
Time	13	194.19	0.0001	0.0001	0.0001
Time × Stand	26	2.1841	0.0009	0.1263	0.1208

(b) Univariate ANOVA for each consecutive 5-year period of growth.

Source	Time (year)	df	F	$P > F$
Stand	1-5	2	17.955	0.0001
Stand	6-10	2	24.481	0.0001
Stand	11-15	2	16.611	0.0001
Stand	16-20	2	11.013	0.0003
Stand	21-25	2	6.5880	0.0047
Stand	26-30	2	3.3151	0.0516
Stand	31-35	2	1.5993	0.2206
Stand	36-40	2	0.9473	0.4003
Stand	41-45	2	0.9093	0.4148
Stand	46-50	2	0.9301	0.4068
Stand	51-55	2	1.1218	0.3404
Stand	56-60	2	1.3411	0.2784
Stand	61-65	2	1.5778	0.2249
Stand	66-70	2	1.9894	0.1563

Note: Adjusted $P > F$ probabilities are for Greenhouse-Geisser (G-G) and Huynh-Feldt (H-F) adjusted F tests.

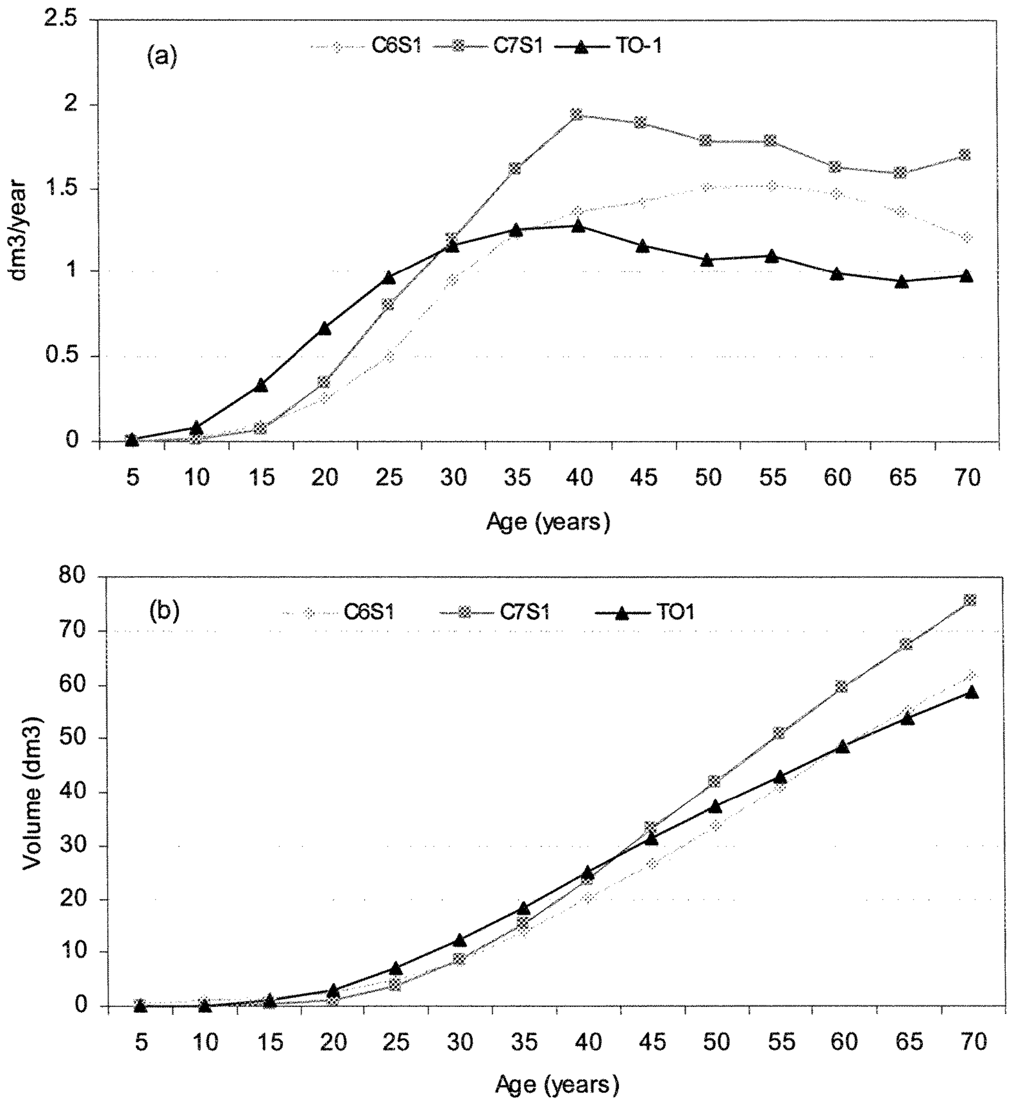

Figure 3.12 Mean volume growth rates (a) and cumulative volume growth (b) of the 10 sampled dominant black spruce trees per study stands.

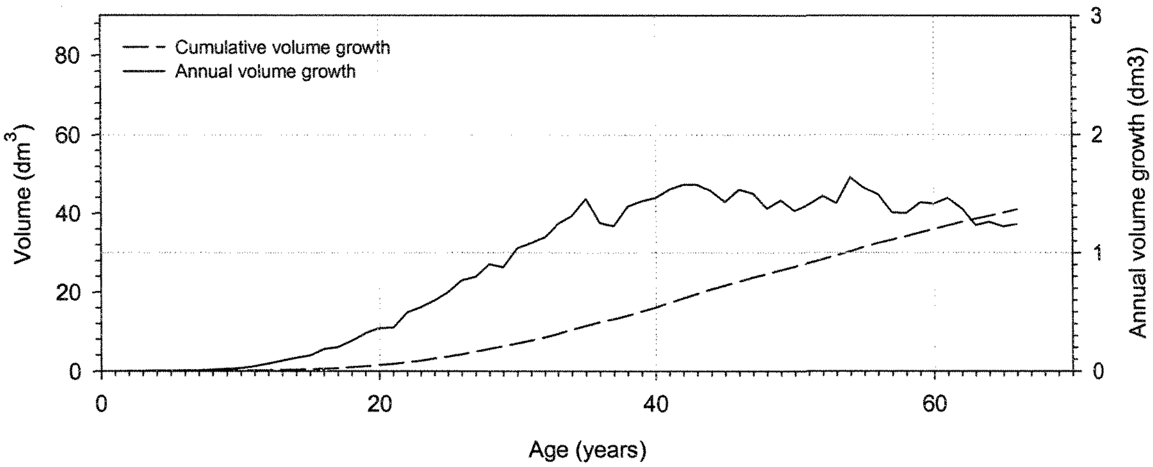

Figure 3.13 Graphical comparison of the cumulative and annual mean volume growth curves of dominant black spruce trees (n = 30), in the study area, over a 66-year period following the stand establishment.

3.2 Growth of black spruce trees growing in the stands located between the 49th and the 51st parallels

Two closed pure black spruce stands located in the middle of boreal forest (between the 49th and the 51st parallels) in equivalent mesic sites with similar dendrometric characteristics to our three study stands were selected from the Laboratoire d'écologie végétale de l'UQAC data bank, in order to test the third hypothesis: comparing growth of dominant black spruce trees in diameter, height and volume to those in the study area (Table 3.1). The existing growth data of the 10 largest black spruce trees (5 trees per plot) in the southern area were analysed in the same way as in the northern area.

ANOVAR revealed that there was no significant difference in overall average 5-year diameter growth rates of dominant black spruce trees between the two southern stands (P = 0.6670). In addition, the interaction among stand and time was not significantly different (P = 0.34, Table 3.15a). There was a significant difference in overall average 5-year height growth rates of dominant black spruce trees between the two stands (P = 0.005). The interaction among stand and time was not significantly different (P = 0. 07, Table 3.15b). There was no significant difference in overall average 5-year volume growth rates of dominant black spruce between the two stands (P = 0.2394). As well, the interaction among stand and time was not significantly different (P = 0.28, Table 3.15c).

Table 3.15 Repeated measure analysis of variance results of dominant trees for stand differences in diameter (a), height (b), and volume (c) growth rates in the southern area.

ANOVAR					
				Adjusted $P > F$	
Source	df	F	$P > F$	G-G	H-F
a- *Diameter (mm/Yr)*					
Stand	1	0.1995	0.6670		
Time	12	22.263	0.0001	0.0001	0.0001
Time × Stand	12	1.1506	0.3299	0.3397	0.3479
b- *Height (m/Yr)*					
Stand	1	14.626	0.0051		
Time	12	18.768	0.0001	0.0001	0.0001
Time × Stand	12	2.5049	0.0066	0.0722	0.0243
c- *Volume (dm3/Yr)*					
Stand	1	1.6159	0.2394		
Time	12	67.675	0.0001	0.0001	0.0001
Time × Stand	12	1.3696	0.1939	0.2825	0.2763

Note: Adjusted $P > F$ probabilities are for Greenhouse-Geisser (G-G) and Huynh-Feldt (H-F) adjusted F tests.

3.3 Comparison of black spruce cumulative and annual growth in diameter, height and volume between the two areas

As stated earlier, we have pooled together the stem analysis data by area to make the following growth analysis since there was not much difference between the stands. Cumulative and annual growth in diameter, height and volume of the 10 largest dominant black spruce trees (5 tree per stand) growing in the two most northern study stands (C7S1 and C6S1) were compared to the 10 largest dominant black spruce trees (5 trees per stand) from the two black spruce stands (12 and 14) located between the 49^{th} and the 51^{st} parallels. Mean diameter, height and volume growth curves were constructed separately for black spruce growing in the northern forest area and the southern forest area. We were interested to know whether growth of dominant black spruce trees in the young even-aged black spruce stands located between the 51^{st} and the 52^{nd} parallels were similar to those in the young even-aged black spruce stands located between the 49^{th} and the 51^{st} parallels in northern Quebec.

3.3.1 Diameter and diameter growth

There was no significant difference in overall average 5-year diameter growth rates of dominant black spruce trees between the two areas (P = 0.3916). The interaction between area and time was significantly different (P = 0.0019, Table 3.16a). In univariate analysis of variance, significant differences in the average 5-year diameter growth rates of dominant black spruce trees were found between the two areas for each of the following periods: 1-5, 6-10, 11-15, 26-30, 31-35, 36-40, 41-45 and 46-50 years (Table 3.16b).

Average 5-year diameter growth rates of dominant black spruce trees in the southern area were always higher than in the northern area during the first 20 years following stand establishment (Fig. 3.14a). However, the growth differences were minimal through 16 to 35 and 51 to 65 years after establishment. On the average, dominant black spruce trees in the northern and southern areas attained their maximum point of annual diameter growth at approximately the same time since establishment (at age 23) (Fig.3.15).

There was no significant difference in overall average 5-year cumulative diameter growth of dominant black spruce trees between the two areas ($P = 0.8918$). The interaction between area and time was not significantly different ($P = 0.078$, Table 3.17a). Cumulative diameter growth patterns of dominant black spruce trees in both areas were fairly similar over the 65 year period documented in this study, as indicated by the similar stylized sigmoid shaped growth curves (Fig. 3.15). Looking at the mean cumulative growth curves of diameter over age for dominant black spruce trees would indicate a juvenile period of slow diameter growth for about a decade in both areas (Fig. 3.15).

In univariate analysis of variance, significant differences in the average 5-year cumulative diameter growth of dominant black spruce trees were found between the two areas for each of the following periods: 6-10, 11-15 and 16-20 years (Table 3.17b). Average 5-year cumulative diameter growth of dominant black spruce trees in the southern area was always higher than in the northern area until age 40 following stand establishment (Fig. 3.14b). However, the growth differences were minimal after age 20 following stand establishment.

Table 3.16 Results of repeated measure analysis of variance (ANOVAR) (**a**) and of univariate analysis of variance for each consecutive 5-year period (**b**) of dominant black spruce trees for area differences in diameter growth rates.

(a) ANOVAR

Source	df	F	$P > F$	Adjusted $P > F$ G-G	Adjusted $P > F$ H-F
Between subject					
Area	1	0.7706	0.3916		
Within subject					
Time	12	45.094	0.0001	0.0001	0.0001
Time × Area	12	6.4356	0.0001	0.0019	0.0007

(b) Univariate ANOVA for each consecutive 5-year period of growth.

Source	Time (year)	df	F	$P > F$
Area	1-5	1	16.863	0.0007
Area	6-10	1	8.0900	0.0108
Area	11-15	1	6.7154	0.0184
Area	16-20	1	0.9590	0.3404
Area	21-25	1	0.2880	0.5981
Area	26-30	1	4.9881	0.0385
Area	31-35	1	8.8700	0.0081
Area	36-40	1	14.544	0.0013
Area	41-45	1	7.1220	0.0157
Area	46-50	1	6.5777	0.0195
Area	51-55	1	3.0343	0.0989
Area	56-60	1	0.5573	0.4650
Area	61-65	1	0.1956	0.6636

Note: Adjusted $P > F$ probabilities are for Greenhouse-Geisser (G-G) and Huynh-Feldt (H-F) adjusted F tests.

Table 3.17 Results of repeated measure analysis of variance (ANOVAR) (**a**) and of univariate analysis of variance for each consecutive 5-year period (**b**) of dominant black spruce trees for area differences in cumulative diameter growth.

(a) ANOVAR

Source	df	F	$P > F$	Adjusted $P > F$	
				G-G	H-F
Between subject					
Area	1	0.0190	0.8918		
Within subject					
Time	12	596.09	0.0001	0.0001	0.0001
Time × Area	12	3.0802	0.0005	0.0779	0.0713

(b) Univariate ANOVA for each consecutive 5-year period of growth.

Source	Time (year)	df	F	$P > F$
Area	1-5	1	3.3700	0.0830
Area	6-10	1	9.8832	0.0056
Area	11-15	1	8.0413	0.0110
Area	16-20	1	6.3120	0.0217
Area	21-25	1	3.7686	0.0680
Area	26-30	1	1.2460	0.2790
Area	31-35	1	0.1447	0.7081
Area	36-40	1	0.0007	0.9797
Area	41-45	1	0.0918	0.7654
Area	46-50	1	0.2605	0.6160
Area	51-55	1	0.5964	0.4500
Area	56-60	1	0.7737	0.3907
Area	61-65	1	0.7968	0.3838

Note: Adjusted $P > F$ probabilities are for Greenhouse-Geisser (G-G) and Huynh-Feldt (H-F) adjusted F tests.

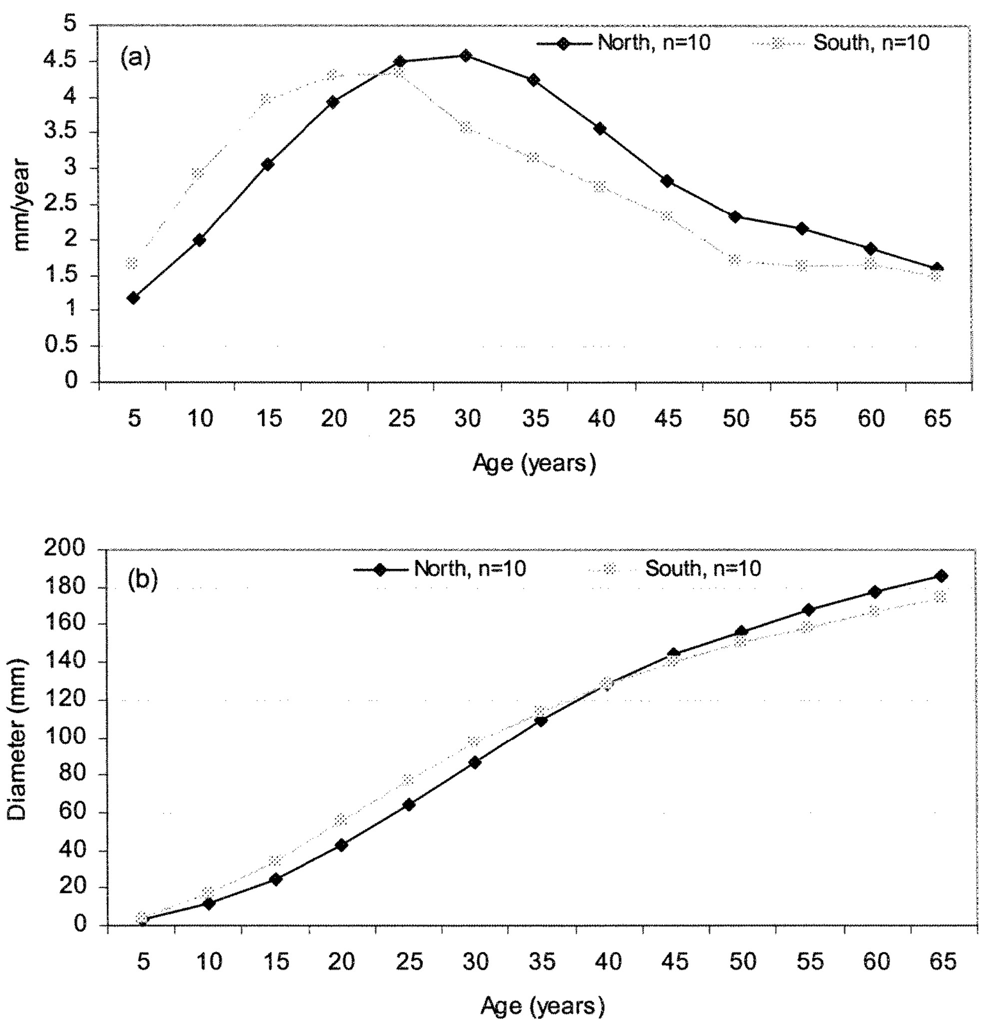

Figure 3.14 Mean diameter growth rates (a) and cumulative diameter growth (b) of the 10 biggest dominant black spruce trees per study area. Study areas are as follows: South (between the 49^{th} and the 51^{st} parallels); North (between the 51^{st} and the 52^{nd} parallels).

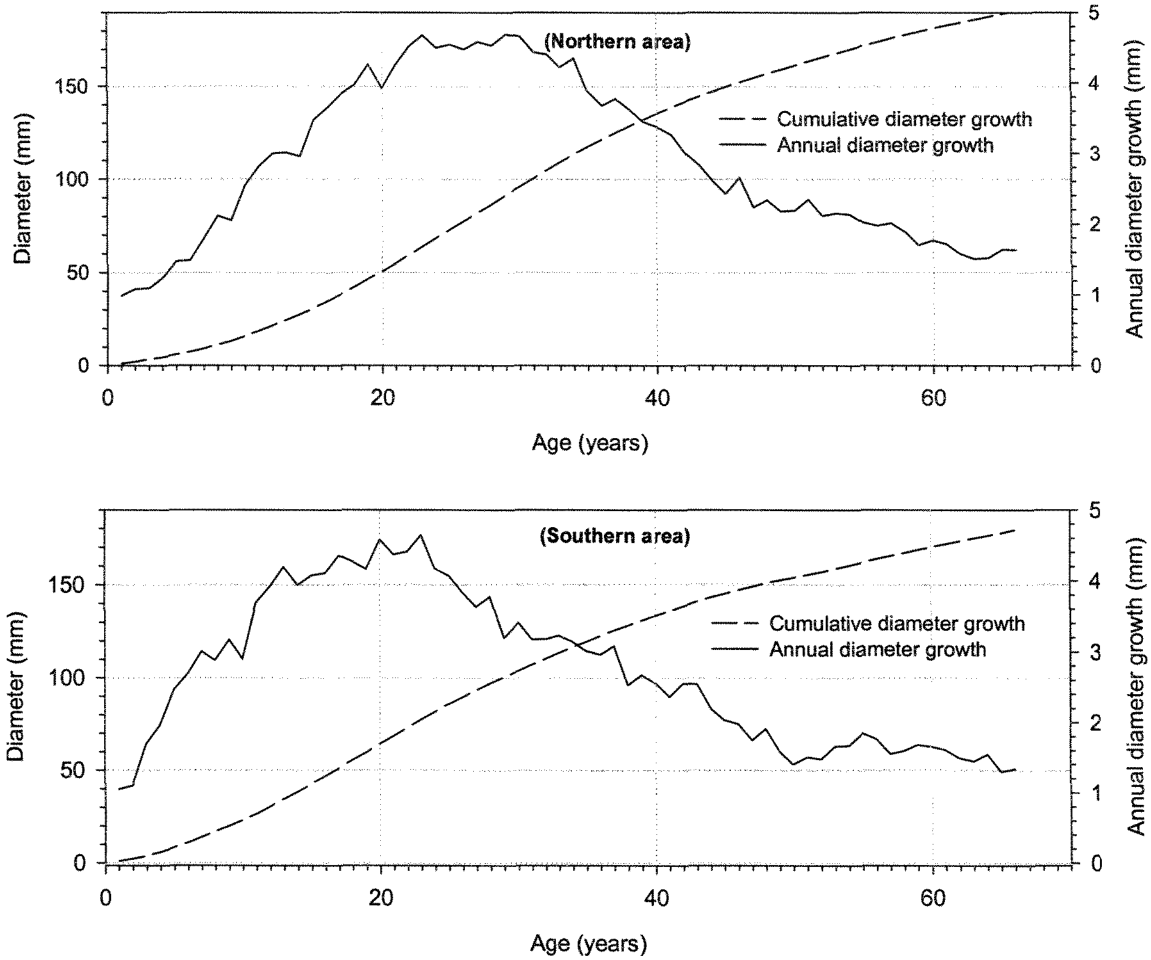

Figure 3.15 Graphical comparison of the cumulative and annual mean diameter growth curves of dominant black spruce trees (n =10), in the northern area (located between the 51st and the 52nd parallels) and the southern area (between the 49th and the 51st parallels, Quebec), over a 66-year period, following the stand establishment.

3.3.2 Height and height growth

There was a significant difference (*P* = 0.0190) in overall average 5-year height growth rates of dominant black spruce trees between the two areas (Table 3.18a). The interaction between area and time was not significantly different (*P* = 0.0511). The significant differences in the average 5-year height growth rates of dominant black spruce trees were found only for the following periods: 1-5, 6-10 and 11-15 years between the two areas (Table 3.18b). On the average, dominant black spruce trees in the northern and southern areas attained their maximum point of annual height growth at approximately the same age since establishment (at age 18), (Figs.3.17). Average 5-year height growth rates of dominant black spruce trees in the southern area were always higher than in the northern area, with the exception of the 45 to 50 year period following stand establishment (Fig. 3.16a). However, the growth differences were minimal from age 16 after establishment.

There was a significant difference (*P* = 0.0072) in the average 5-year cumulative height growth of dominant black spruce trees between the two areas (Table 3.19a). The interaction between area and time was not significantly different (*P* = 0.0967). The significant difference in the average 5-year cumulative height growth of dominant black spruce trees was found between the two areas for all consecutive 5-year periods (Table 3.19b). Average 5-year cumulative height growth of dominant black spruce trees in the southern area was always higher than in the northern area over the 65-year period following stand establishment (Fig. 3.16b). Looking at the cumulative growth curves of height over age for dominant black spruce trees would indicate a juvenile period of about a decade in both areas (fig.3.17).

Table 3.18 Results of repeated measure analysis of variance (ANOVAR) (**a**) and of univariate analysis of variance for each consecutive 5-year period (**b**) of dominant black spruce trees for area differences in height growth rates.

(**a**) ANOVAR						
					Adjusted $P > F$	
Source		df	F	$P > F$	G-G	H-F
Between subject						
Area		1	6.6365	0.0190		
Within subject						
Time		12	30.479	0.0001	0.0001	0.0001
Time × Area		12	2.4788	0.0047	0.0511	0.0310
(**b**) Univariate ANOVA for each consecutive 5-year period of growth.						
Source	Time (year)	df	F	$P > F$		
Area	1-5	1	14.330	0.0013		
Area	6-10	1	6.9201	0.0170		
Area	11-15	1	7.2127	0.0151		
Area	16-20	1	2.1949	0.1558		
Area	21-25	1	4.0741	0.0587		
Area	26-30	1	0.0435	0.3876		
Area	31-35	1	0.0824	0.7773		
Area	36-40	1	0.4184	0.5259		
Area	41-45	1	0.3016	0.5897		
Area	46-50	1	1.5398	0.2306		
Area	51-55	1	0.0002	0.9523		
Area	56-60	1	2.7056	0.1173		
Area	61-65	1	3.0379	0.0984		

Note: Adjusted $P > F$ probabilities are for Greenhouse-Geisser (G-G) and Huynh-Feldt (H-F) adjusted F tests.

Table 3.19 Results of repeated measure analysis of variance (ANOVAR) **(a)** and of univariate analysis of variance for each consecutive 5-year period **(b)** of dominant black spruce trees for area differences in cumulative height growth.

(a) ANOVAR						
					Adjusted $P > F$	
Source		df	F	$P > F$	G-G	H-F
Between subject						
Area		1	9.1865	0.0072		
Within subject						
Time		12	951.24	0.0001	0.0001	0.0001
Time × Area		12	2.6143	0.0028	0.0967	0.0878
(b) Univariate ANOVA for each consecutive 5-year period of growth.						
Source	Time (year)	df	F	$P > F$		
Area	1-5	1	9.8770	0.0056		
Area	6-10	1	9.5461	0.0063		
Area	11-15	1	7.0404	0.0162		
Area	16-20	1	8.3497	0.0098		
Area	21-25	1	8.9938	0.0077		
Area	26-30	1	10.587	0.0044		
Area	31-35	1	9.5928	0.0062		
Area	36-40	1	7.7202	0.0124		
Area	41-45	1	6.2954	0.0219		
Area	46-50	1	5.6725	0.0285		
Area	51-55	1	4.9403	0.0393		
Area	56-60	1	5.3110	0.0333		
Area	61-65	1	6.0151	0.0246		

Note: Adjusted $P > F$ probabilities are for Greenhouse-Geisser (G-G) and Huynh-Feldt (H-F) adjusted F tests.

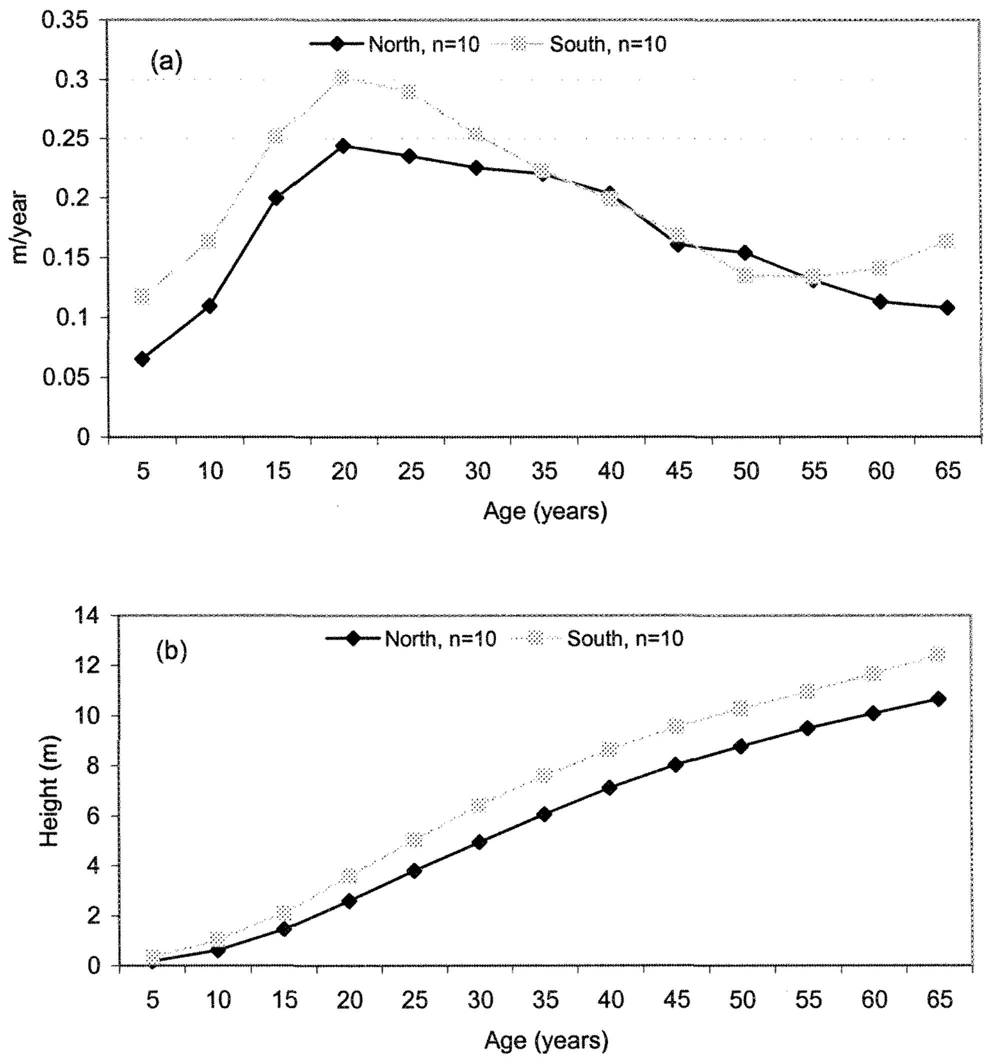

Figure 3.16 Mean height growth rates (a) and cumulative height growth (b) of the 10 biggest dominant black spruce trees per study area. Study areas are as follows: South (between the 49th and the 51st parallels); North (between the 51st and the 52nd parallels).

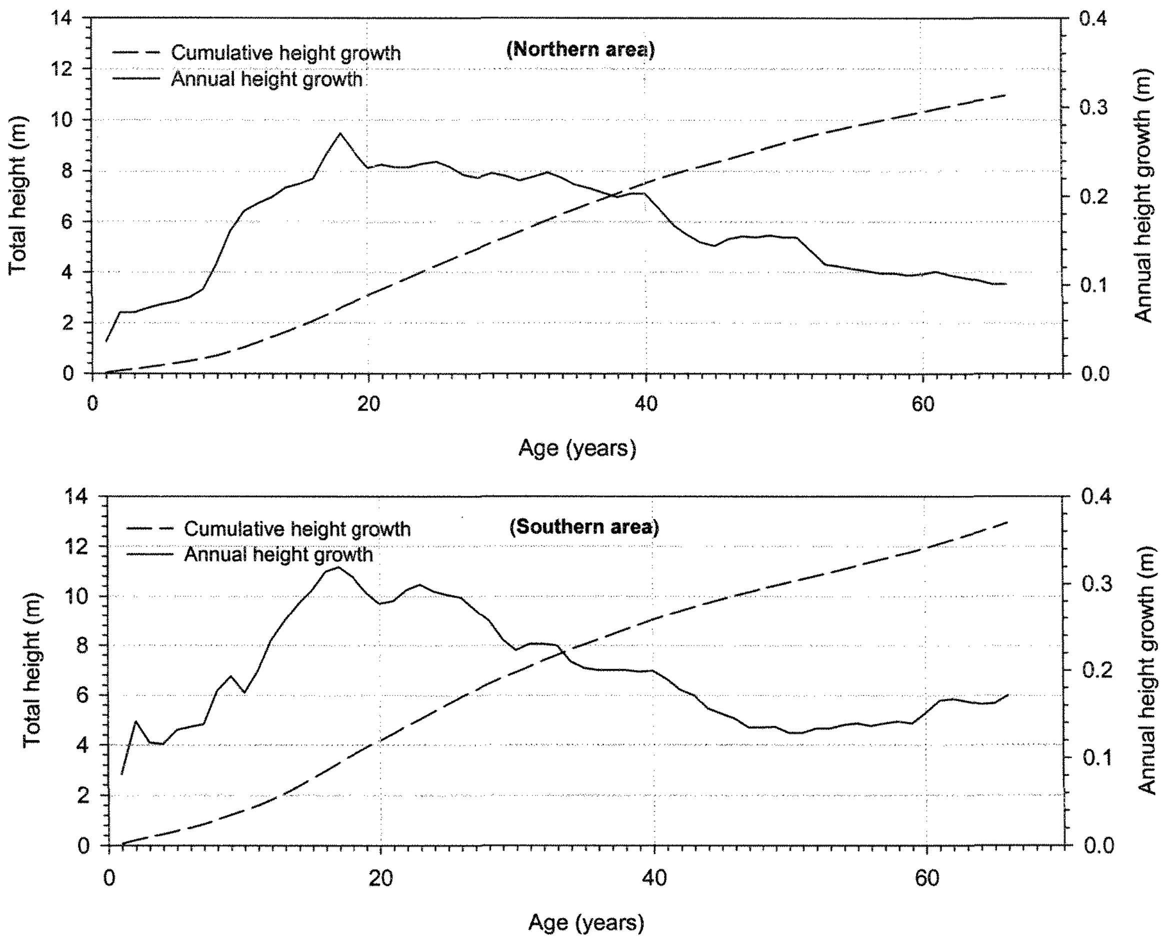

Figure 3.17 Graphical comparison of the cumulative and annual mean height growth curves of dominant black spruce trees (n =10), in the northern area (located between the 51st and the 52nd parallels) and the southern area (between the 49th and the 51st parallels, Quebec), over a 66-year period, following the stand establishment.

3.3.3 Volume and volume growth

There was no significant difference in overall average 5-year volume growth rates of dominant black spruce trees between the areas (P = 0.7840, Table 3.20a). The interaction between area and time was not significantly different (P = 0.1544). The significant differences in the average 5-year volume growth rates of dominant black spruce trees were found between the areas for each of the following periods; 1-5, 6-10 11-15, and 16-20 years (Table 3.20b). On the average, dominant black spruce trees in the northern area attained their maximum point of annual volume growth just a few years later (at age 41) than those in the southern area (at age 37), (Fig. 3.19). Average 5-year volume growth rates of dominant black spruce trees in the southern area were always higher than those in the northern area with the exception of the 51 to 55 years period following stand establishment (Fig. 3.18a). However, the growth differences were minimal from age 21.

There was no significant difference in overall average 5-year cumulative volume growth of dominant black spruce trees between the two areas (P = 0.5565). The interaction between area and time was not significantly different (P = 0.644, Table 3.21a). The significant differences in the average 5-year cumulative volume growth of dominant black spruce trees were found between the areas for each of the following periods: 1-5, 6-10, 11-15, 16-20 and 21-25 years (Table 3.21b). Average 5-year cumulative volume growth of dominant black spruce trees in the southern area were always higher than in the northern area over the 65-year period following stand establishment (Fig. 3.18b).

Table 3.20 Results of repeated measure analysis of variance (ANOVAR) (**a**) and of univariate analysis of variance for each consecutive 5-year period (**b**) of dominant black spruce trees for area differences in volume growth rates.

(a) ANOVAR

Source	df	F	*P* > *F*	Adjusted *P* > *F* G-G	Adjusted *P* > *F* H-F
Between subject					
Area	1	0.0774	0.7840		
Within subject					
Time	12	106.54	0.0001	0.0001	0.0001
Time × Area	12	1.8938	0.0364	0.1544	0.1412

(b) Univariate ANOVA for each consecutive 5-year period of growth.

Source	Time (year)	df	F	*P* > *F*
Area	1-5	1	22.367	0.0002
Area	6-10	1	10.199	0.0050
Area	11-15	1	12.137	0.0027
Area	16-20	1	11.120	0.0037
Area	21-25	1	0.2323	0.0558
Area	26-30	1	0.0269	0.4951
Area	31-35	1	0.0119	0.9144
Area	36-40	1	0.0939	0.7628
Area	41-45	1	0.2760	0.6058
Area	46-50	1	3.1328	0.0937
Area	51-55	1	1.0624	0.3163
Area	56-60	1	0.0274	0.8704
Area	61-65	1	0.1385	0.7141

Note: Adjusted *P* >*F* probabilities are for Greenhouse-Geisser (G-G) and Huynh-Feldt (H-F) adjusted *F* tests.

Table 3.21 Results of repeated measure analysis of variance (ANOVAR) (**a**) and of univariate analysis of variance for each consecutive 5-year period (**b**) of dominant black spruce trees for area differences in cumulative volume growth.

(a) ANOVAR					
				Adjusted $P > F$	
Source	df	F	$P > F$	G-G	H-F
Between subject					
Area	1	0.3591	0.5565		
Within subject					
Time	12	312.36	0.0001	0.0001	0.0001
Time × Area	12	0.2720	0.9929	0.6445	0.6635

(b) Univariate ANOVA for each consecutive 5-year period of growth.				
Source	Time (year)	df	F	$P > F$
Area	1-5	1	5.6842	0.0283
Area	6-10	1	9.1332	0.0073
Area	11-15	1	7.5873	0.0130
Area	16-20	1	7.5241	0.0134
Area	21-25	1	5.9500	0.0253
Area	26-30	1	3.2988	0.0860
Area	31-35	1	1.4030	0.2516
Area	36-40	1	0.7817	0.3883
Area	41-45	1	0.3471	0.5631
Area	46-50	1	0.1954	0.6637
Area	51-55	1	0.0261	0.8735
Area	56-60	1	0.0139	0.9075
Area	61-65	1	0.0107	0.9188

Note: Adjusted $P > F$ probabilities are for Greenhouse-Geisser (G-G) and Huynh-Feldt (H-F) adjusted F tests.

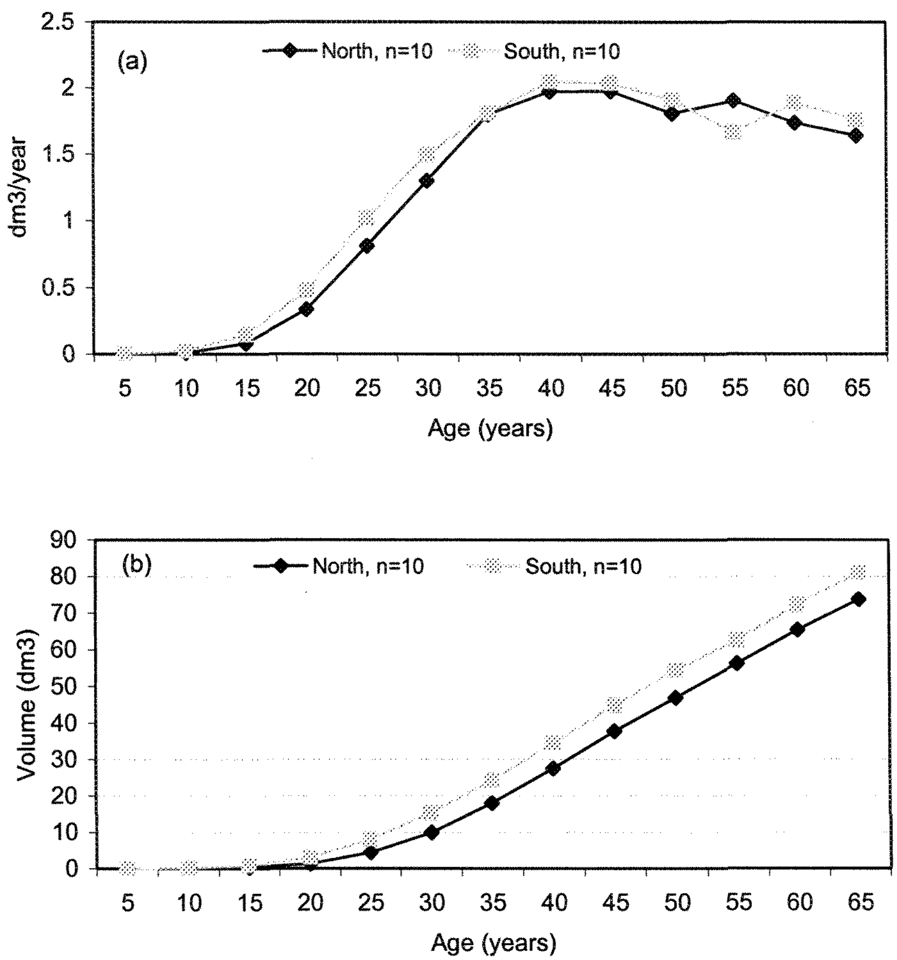

Figure 3.18 Mean volume growth rates (a), and cumulative volume growth (b) of the 10 biggest dominant black spruce trees per study area. Study areas are as follows: South (between the 49th and the 51st parallels); North (between the 51st and the 52nd parallels).

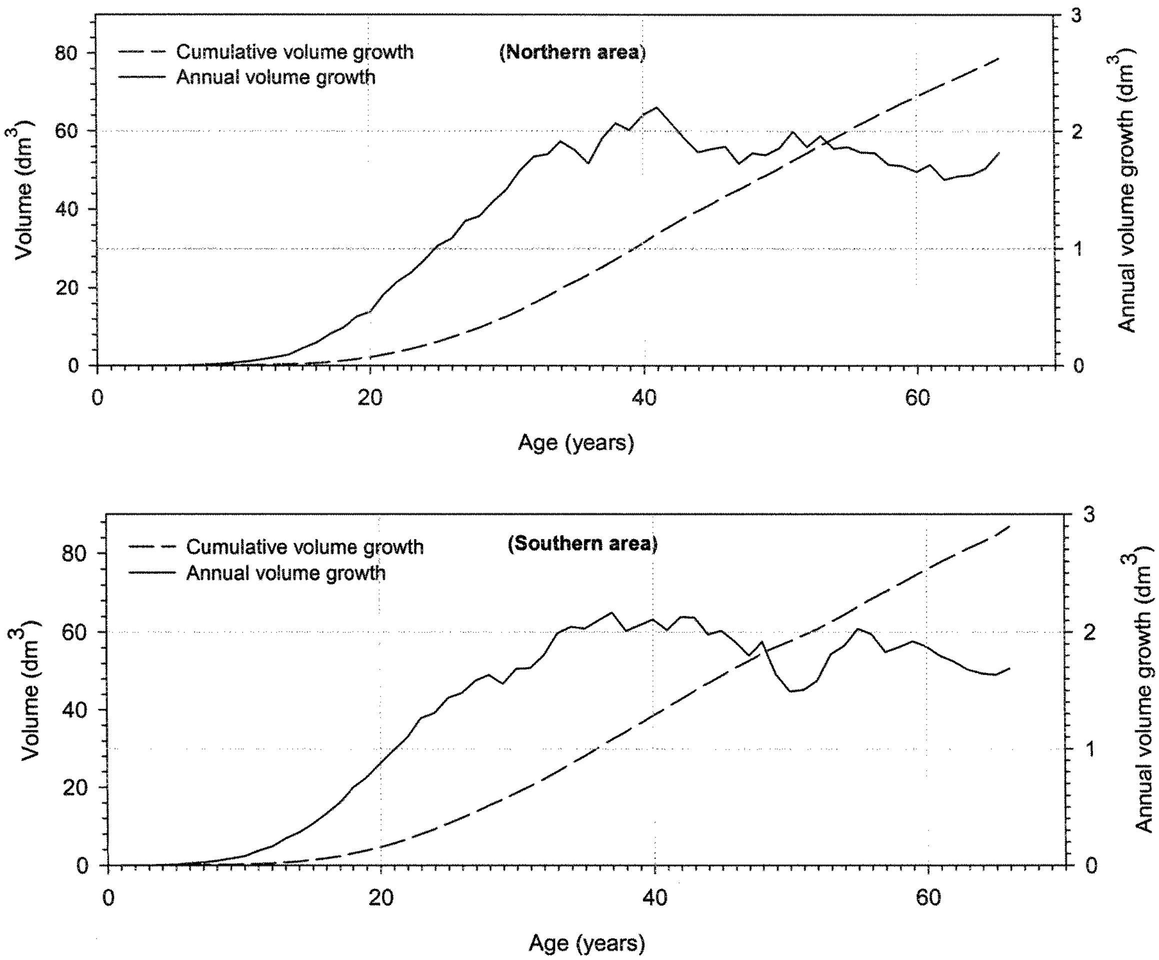

Figure 3.19 Graphical comparison of the cumulative and annual mean volume growth curves of dominant black spruce trees (n =10), in the northern area (located between the 51st and the 52nd parallels) and the southern area (between the 49th and the 51st parallels, Quebec), over a 66-year period, following the stand establishment.

CHAPTIRE IV

DISCUSSION

4.1 Age structure

The Quebec forest located between the 51^{st} and the 52^{nd} parallels belongs to a boreal forest type which is widely distributed in the Northeast of Canada and is dominated at the family level by *Pinaceae* and at the species level by black spruce, an important representative of this family. Therefore, our investigation of the young black spruce stands dynamics in the study area may be extended to many similar stands of boreal forest located between the 51^{st} and the 52^{nd} parallels in northern Quebec.

The majority of the black spruce trees (dbh > 1cm) was established during the first 20 post-fire years and little regeneration occurred after this period. Since we used the simple ring count method in this study, the establishment period is probably shorter. Gagnon and Morin (1992) reported that by using cross-dating, the establishment period of black spruce after fire is shortened by 15 years at least. This finding supports the previous results of many studies showing that most tree regeneration generally occurs almost immediately after fire and over a short time span (LeBarron 1939; Ahlgren 1959; Hatcher 1963; MacArthur 1964; Gagnon 1973; Black and Bliss 1980; Viereck 1983; Morneau and Payette 1989; Sirois and Payette 1989; St-Pierre *et al.* 1992; Landhäusser and Wein 1993; Duchesne and Sirois 1995; Greene *et al.* 1999; Charron and Greene 2002; Gutsell and Johnson 2002). All stands show a peak in recruitment just a decade after fire. Because of these intensive periods of establishment, the stands are classified as even-aged in the three study sites. These results are in agreement with the first hypothesis that the stands age structures should be naturally even-aged and show a fast regeneration after fire. There was no evidence of a new cohort invading the study stands. This is typical of post-fire stands and they can be treated as a single cohort.

The trees were too large at the time of sampling for us to identify their origin after fire (by layering or seeds), but the slow early height growth is consistent with seeds regeneration for black spruce (Fig. 3.9). The last wild-fire disturbance usually provides a good seedbed for black spruce in the burned sites. In general, even-aged fire origin stands originate from seedlings (Archibald and Arnup 1993).

4.2 Growth of black spruce saplings in the young fire-origin stands located across the studied area

In the present study, many canopy black spruce trees were of the same age as sub-canopy black spruce trees (most of them originated from seedlings) and some sub-canopy black spruce trees were older than many canopy trees, indicating that age (at the base of stems) is not a strong indicator of canopy position (Antos and Parish 2002). Therefore, the difference in sizes is mainly due to difference in growth rates between the dominant and suppressed trees.

The finding of all reports that overstory trees grow faster than understory trees is confirmed by our results. In the 1st cohort established after fire, overstory individuals grow faster than understory ones. In the studied stands, the overstory black spruce trees with a large diameter always have a higher increment than the understory black spruce trees. As shown in figure 3.7, under these closed stands, saplings grow much more slowly than overstory trees and will not reach 5 cm in diameter before the age of 60, on the average. The figure shows the low increment rates of many understory individuals. This is the result of increasing stand cover and decreasing light from the top to the ground of these closed stands. Although no canopy replacement by understory trees has been observed in our study stands until the time they were sampled, it may be possible for these understory spruces to attain overstory status if there is mortality in the overstory as it would be in the case of gap-creating disturbances such as a budworm outbreak. In this scenario, understory trees which would have shown a slow growth during most of their lives would become dominant trees. This slow growth would be caused by the dynamics of the stand and not by edaphic or other stand conditions.

4.3 Diameter, height and volume growth of black spruce trees in young stands located across the study area.

As far as we know, this is the first study comparing the growth of black spruce in diameter, height and volume among young even-aged stands located between the 51st and the 52nd parallels in northern Quebec. By selecting the ten largest dominant black spruce trees of each study stand, we have chosen the most performing stems of each stand to research the growth of black spruce in those fire-origin stands located across the study area.

The investigation reported here suggests a consistent pattern of diameter and height development for even-aged black spruce stands with similar attributes throughout the study area. Black spruce reached the dominant position mainly by growing at a similar height rate across the study area. By age 65, black spruce in similar young even-aged stands located across the study area should be about 9 to 11 m tall, 16.42 cm in diameter at ground level and 40.13 dm^3 volume, on the average.

Both diameter and height growth curves indicated that all sampled black spruce stems followed similar diameter and height patterns that were marked by the following different growth stages: i) a juvenile period (approximately the first decade) when diameter and height growth proceeded slowly until the seedling was well established; ii) this was followed by a period of rapid growth when the rate of diameter and height growth rapidly increased, until; iii) a reduction of growth rates as the black spruce began to attain maturity and that diameter and height growth gradually tapered off. This result supports the second hypothesis that the juvenile growth of black spruce is very slow, as was reported for black spruce growing in the middle of the boreal forest in Quebec (Fantin *et al.* 2002).

Our results indicate that average 5-year diameter and height growth rates of dominant black spruce trees are significantly different during the first 15 post-fire years, fairly similar during the following 15 post-fire years and different again from the 31 to 70 post-fire years between the three study stands. Moreover, the mean volume growth rates are significantly different during the first 20 post-fire years, fairly similar during the following 20 post-fire years and different again from the 41 to 70 post-fire years between the study stands. The growth curves indicate that in the two most northern study stands (C7S1 & C6S1), gradual decline of radial growth of black spruce trees occurred 10 to 15 years later than for the spruce growing in stand TO1, possibly due to the higher density of the TO1 stand, which may be a disadvantage for the radial growth of canopy trees, since the C6S1 and C7S1 have less stand densities (Fig 3.4a).

Our results also indicate that the average 5-years cumulative height, diameter and volume growth of dominant black spruce trees are significantly different during the first 25 post-fire years and fairly similar from the 26 to 70 post-fire years between the study stands. Moreover, another important result of our study is the early differentiation of black spruce growth performance between the study stands. What would be the mechanisms responsible for the difference in growth of black spruce trees during the initial post-fire years between the three study stands?

One factor responsible for the significant difference in diameter, height and volume growth of black spruce trees between the three study stands during their initial years of growth and establishment could be associated with the presence of ericaceous understory shrubs such as Labrador tea (*Ledum groenlandicum*) (LaBarron, 1948; Inderjit and Mallik, 1995) and Sheep laurel (*Kalmia angustifolia* L.) (Mallik 1987, 2001; Inderjit and Mallik 1996). Based on our results, there was no significant difference in cover percentage of these ericaceous understory shrubs between the study sites (P = 0.8067, Table 4.1).

Therefore the significant difference in diameter, height and volume growth rates of black spruce trees during their initial years of establishment could not be related to competition and allelopathic effects of ericaceous understory shrubs present in the three study sites. However, the rate of diameter growth of black spruce trees may be affected by competition from faster growing species which overtop them during their initial years of growth and establishment after fire.

Table 4 1. Characteristics (average) of the cover percentage of the ericaceous understory shrubs (*Ledum and Kalmia)* growing in each study sites at the time of sampling.

Stand	Cover percentage (%)
TO1	30.2^{a} (7.708)
C7S1	25.2^{a} (7.708)
C6S1	23.2^{a} (7.708)
F value	0.8067

NOTE[1]: Differences are significant ($P < 0.05$) between values designated by different letters (Tukey Kramer HSD tests). Letters also indicate ranking of means: a > b.

NOTE[2]: Values are mean with standard errors in parentheses.

Depending on the year of fire disturbance, black spruce trees of similar age have germinated during different years. Therefore, the differences observed between the three study stands for black spruce height growth during the initial post-fire years may be attributed to the different environmental conditions at the time of germination and during their initial years of growth after establishment.

Black spruce is a morphologically plastic tree species adopting progressively stunted growth forms in response to increasing harsh winter conditions (Lavoie and Payette 1992). A slight difference between the altitudes of the study sites may partially explain the lower height growth rates of black spruce trees growing in the two most northern sites (both located at an altitude of 530 m above sea level) as compared to those growing in the TO1 site (located at an altitude of 420 m above sea level) during their juvenile growth.

The difference in the growth of black spruce trees in diameter, height and volume during the initial post-fire years between the three study stands may also be associated with changing snow melt timing and with soil conditions. Kirdyanov *et al.* (2003) described the importance of snow melt timing for an increase in soil temperature and growth initiation.

Precipitations have generally a positive influence on the growth of the conifer's species in the boreal forest (Hofgaard *et al.*1999; Deslauriers *et al.* 2003). Early summer precipitations have positive effects on annual growth of black spruce (Dang and Lieffers 1989; Brooks *et al.* 1998; Hofgaard *et al.* 1999). Depending on the year of fire disturbance, the variable summer precipitation during the initial post-fire years may explain the juvenile diameter growth differences of black spruce trees between the three study stands. As stated earlier, climatic data directly applicable to the study area was unavailable, due to the absence of meteorological stations in the area. It is thus difficult to verify this hypothesis at this time. Further investigation with the incorporation of environmental data analysis is required. Differences in genetic pool and natural variation may also partially explain these results.

4.4 Diameter, height and volume growth of black spruce trees in the young stands located in the northern and southern forest areas.

The study reported here suggests a similar pattern of diameter and volume development for similar young even-aged black spruce stands located in the northern and southern areas. Our results indicate that there is no difference in diameter and volume growth but there is a difference in height growth of black spruce trees between the two areas located north and south of latitude 51° in Quebec's northern boreal forest. Post-fire black spruce stands located between the 49^{th} and the 51^{st} parallels are growing significantly faster in height than the fire-origin equivalent sites located between the 51^{st} and the 52^{nd} parallels. The height of the dominant black spruce trees was higher in the southern forest area during the 65 years documented in this study (Figures; 3.16b, 3.17) which can be attributed to the higher annual growth performance during their initial years of establishment (Figures; 3.16a, 3.17) and this, even if, as trees increased in age, annual growth performance declined (until age 49) in the southern black spruce stands while it increased in the northern black spruce stands. As a result, the dominant black spruce trees in the southern area had a higher height compared with those in the northern area.

The dominant black spruce trees were thicker in the southern area during the first 40 years (Figures; 3.14b, 3.15) which can be attributed to the higher annual diameter growth performance during their initial years of establishment (Figures 3.14b, 3.15). However, as trees increased in age, annual diameter growth performance declined in the southern black spruce stands while increasing in the northern black spruce stands. A possible explanation for the increase of the annual diameter growth inequality is the relatively lower tree density of the northern stands than of the southern stands, leaving more space for individual diameter growth.

Slenderness (height/DBH) in the two southern black spruce stands was higher than in those located between the 51^{st} and the 52^{nd} parallels. The average slenderness was 85.99 and 75.37 in the two southern and northern black spruce stands, respectively. Because of the higher stem density in the two southern stands (1733 ha-1) than in the northern ones (937ha-1), the height increment should have been faster and resulted in higher slenderness value than that observed in the northern area (Côté 2004).

The dominant black spruce trees have slightly larger volume in the southern area as compared with the volume of the trees in the northern area at the same age (Figures; 3.18b, 3.19) which can be attributed to the higher annual diameter and height growth performance during their initial years of establishment (Figures; 3.18a, 3.19). However, this difference is not statistically significant.

Based on our results, diameter, height and volume growth of dominant black spruce trees were significantly different during their juvenile growth after establishment between the two forest areas. Furthermore, statistical analysis detected a significant difference in height growth of black spruce trees between the two areas. What would be the mechanisms responsible for these growth differences between the two areas?

This study suggests that conditions become increasingly less favourable for black spruce to grow in height as one goes from south toward the north of latitude 51°, in northern Quebec. Nevertheless, black spruce in those even-aged fire origin stands on the mesic sites across the study area are growing surprisingly well and reach a dominant height of 9 to 11 m in 70 years. Gamache *et al.* (2004) reported that the height growth of tree line black spruce trees generally decreased with increasing latitude. The present work also shows a general decrease in height growth of black spruce trees with increasing latitude. In contrast to stem height, diameter and volume growth of black spruce trees over time do not show the same marked differences. This suggests that the effect of latitude was more pronounced in the height growth of black spruce in these closed fire-origin stands.

In spite of the fact that the study stands sprouted following different years of fire disturbance (Table 3.1), the differences observed between the northern and southern areas for black spruce height growth may be attributed to the environmental conditions at the time of germination and during their early growth following fire. Variable summer precipitations during the initial post-fire years may also partially explain the juvenile diameter growth differences of black spruce trees between the northern and southern area. Many studies have demonstrated positive effects of early summer precipitations on annual growth of black spruce (Brooks et al. 1998; Dang and Lieffers 1989; Hofgaard et al. 1999).

Because of slight differences in altitude, harsher climatic conditions at high elevations (Gagnon 1970) may partially explain the lower height growth rates of black spruce trees growing in the two most northern sites (both located at an altitude of 530 m) as compared to those growing in the two southern sites (located at altitudes 400 and 500 m) during their juvenile growth. However, due to the absence of meteorological stations in the northern area, it is difficult to verify these hypotheses at this time. Further investigation with the incorporation of environmental data analysis is thus required.

As already pointed out, competition and allelopathic effects of ericaceous understory shrubs such as *Ledum* and *Kalmia* during the initial years of black spruce growth may also explain the early differentiation of black spruce growth performance between the two areas. LaBarron (1948) reported the inhibitory effects of *Ledum* on early growth of black spruce. Inderjit and Mallik (1996) reported a significant reduction in annual stem height, basal diameter, ring width and cumulative wood volume growth of black spruce in the *Ledum* sites compared to those located in non-*Ledum* sites. Growth inhibition in the presence of *Kalmia* has also been reported in black spruce (Mallik 1987, 2001; Inderjit and Mallik 1996). Unfortunately, in the Laboratoire d'écologie végétale de l'UQAC data bank, no data were available on understory descriptions of the two southern stands in order to compare ericaceous understory shrubs percentage covers with those in the two northern stands.

Diameter growth of black spruce from our study area as well as those in the middle of Quebec boreal forest (south of the study area) declines as the trees get older. A significant diameter growth rates difference between the northern and southern areas coincided with the end of 1975, when a spruce budworm outbreak occurred in the southern forest area (Morin and Laprise, 1990, Morin, 1994), (Fig. 4.1). The northern study stands did not show any evidence of a severe spruce budworm, but black spruce in the study area nevertheless grew slightly slower in volume than those from south of the 51^{st} parallel, on the average.

Other possible explications for the different height growth of black spruce trees between the two areas are associated with site quality and changing snowmelt timing. Oliver and Larson (1996) reported that site quality is more likely to affect tree height than diameter growth. Kirdyanov *et al.* (2003) described the importance of snowmelt timing for increasing soil temperature and growth initiation. Earlier timing of snowmelt could improve growth conditions of black spruce seedlings by increasing soil temperature during the early summer of the initial post-fire years. More research is needed to test these hypotheses.

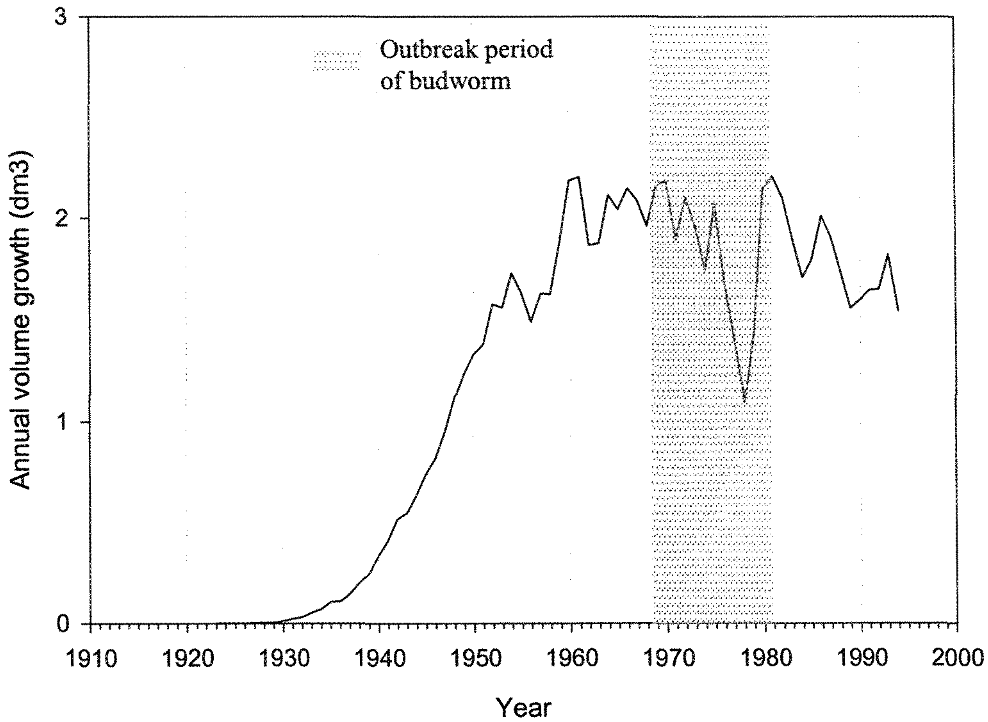

Figure 4.1 Mean annual volume growth curves of 10 sampled dominant black spruce trees growing in the two southern stands.

CHAPTER V

CONCLUSION

5.1 Conclusion

The study reported here suggests a similar pattern of diameter, height and volume development for even-aged black spruce stands with similar attributes throughout the study area. Black spruce in even-aged fire-origin stands on mesic sites grows in diameter, height and volume with rates similar across the study area. It also suggests that conditions become increasingly less favourable for black spruce to grow in height as one moves further north in Quebec. However, in contrast to stem height, diameter and volume growth of black spruce trees do not show the same marked differences over time. Slenderness (height/DBH) in the two southern black spruce stands was higher than those located between the 51^{st} and the 52^{nd} parallels because of the higher stem density.

The results from the study support the hypothesis that the dynamic of the stands would be governed by fire. The age structures are naturally even-aged and show a fast regeneration of the stands after fire. Our result also support the hypothesis that the juvenile growth of black spruce is very slow, as was reported for black spruce growing in the middle of the boreal forest in Quebec (Fantin *et al.* 2002). The same patterns of growth in height, diameter and volume related to the same environmental variables were also observed between the two areas.

As far as we know, this is the first study comparing the growth of black spruce in diameter, height and volume among young even-aged stands located between the 51^{st} and the 52^{nd} parallels in northern Quebec. For further clarification and better understanding on the dynamics and growth of young black spruce stands across the study area, the flowing points might be suggested: since this study was carried out in a few study sites, it is suggested to put forward more researches with incorporation of a greater number of study sites from the study area as well as from the middle of Quebec's boreal forest.

It is also proposed to carry out some research to determine why old black spruce stands cover a large proportion of the closed black spruce-moss forests in this area but not young black spruce stands. Furthermore, it would notably be interesting to compare growth of understory black spruce trees from our even-aged fire origin stands with those growing in similar stands located in the lower latitudes of Quebec's Boreal Forest.

Black spruce is relatively widespread throughout the study area but occurs in many different stand conditions. Future studies will be required to compare dynamics and growth of black spruce from different site conditions in the area. The presented growth and dynamics results should apply to most pure even-aged young black spruce stands in mesic sites across the study area that have similar stand attributes.

Foresters who want to plan the yield of an entire tree as well as of a forest site should be interested in our results. Forest managers could use our results to give an indication of the trends in timber quality production within young, even-aged black spruce stands across the area targeted by our study. These dynamics and growth results can apply to most young even-aged fire-origin stands with pure closed black spruce that have similar stand attributes. As well, diameter growth rate information can be used to guide thinning and harvesting decisions for these stands.

CHAPTER VI

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