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Growth and productivity of black spruce in even- and uneven-aged stands at the limit of the closed boreal forest

Sergio Rossi *, Marie-Josée Tremblay, Hubert Morin, Germain Savard

Département des Sciences Fondamentales, Université du Québec à Chicoutimi, 555 Boulevard de l'Université, Chicoutimi (QC) G7H2B1, Canada

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ABSTRACT

The increasing commercial interest and advancing exploitation of new remote territories of the boreal forest require deeper knowledge of the productivity of these ecosystems. Canadian boreal forests are commonly assumed to be evenly aged, but recent studies show that frequent small-scale disturbances can lead to uneven-aged class distributions. However, how age distribution affects tree growth and stand productivity at high latitudes remains an unanswered question. Dynamics of tree growth in even- and uneven-aged stands at the limit of the closed black spruce (*Picea mariana*) forest in Quebec (Canada) were assessed on 18 plots with ages ranging from 77 to 340 years. Height, diameter and age of all trees were measured. Stem analysis was performed on the 10 dominant trees of each plot by measuring tree-ring widths on discs collected each meter from the stem, and the growth dynamics in height, diameter and volume were estimated according to tree age. Although growth followed a sigmoid pattern with similar shapes and asymptotes in even- and uneven-aged stands, trees in the latter showed curves more flattened and with increases delayed in time. Growth rates in even-aged plots were at least twice those of uneven-aged plots. The vigorous growth rates occurred earlier in trees of even-aged plots with a culmination of the mean annual increment in height, diameter and volume estimated at 40–80 years, 90–110 years earlier than in uneven-aged plots. Stand volume ranged between 30 and 238 m^3 ha^{-1} with 75% of stands showing values lower than 120 m^3 ha^{-1} and higher volumes occurring at greater dominant heights and stand densities. Results demonstrated the different growth dynamics of black spruce in single- and multi-cohort stands and suggested the need for information on the stand structure when estimating the effective or potential growth performance for forest management of this species.

1. Introduction

The boreal forest represents the widest reservoir of wood of the northern hemisphere. In these environments, forest exploitation has moved from south to north towards the remoter territories and new forested regions. Because of long forest rotations, Canada has repeatedly extended the area involved in forest management, relocating its boundaries northwards to maintain adequate production to meet the demand for timber (Ministère des Ressources Naturelles, 2000). In Quebec, these boundaries have crossed the 50th parallel, approaching the northern limit of the closed forest of black spruce (*Picea mariana*). Although this species has been extensively studied within its major managed area (Johnson, 1992; Paquin and Doucet, 1992; Lussier et al., 2002), north of the 50th parallel the studied stands become increasingly rare because of their inaccessibility and presumed low growth and regeneration potential (Perron, 2003; Ministère des Ressources Naturelles, 2000). This lack of study sites has led to a shortage of information on the real productivity of the forest at high latitudes. However, the increasing commercial interest in the northern forests requires deeper knowledge of these biotopes that have an evident ecological importance but basically still unknown economic potential.

Natural forests of black spruce originate from fire, which kills the previously established trees creating even-aged stands from the aerial seed banks released by the semi-serotinous cones (Lieffers, 1986; St-Pierre and Gagnon, 1992; Charron and Greene, 2002; Bouchard et al., 2008). In the absence of other intense disturbances that could again kill the whole stand or in cases where the fire interval exceeds tree lifespan, the stand is affected by secondary disturbances: approximately 120–200 years after a fire, the death and/or falling of larger trees begins to open up gaps in the canopy (De Grandpré et al., 2000; Harper et al., 2003). Within these gaps, dead trees are gradually replaced by other individuals from a new cohort that modifies the stand creating a multi-aged structure (Pham et al., 2004; Harper et al., 2006). This multi-aged structure represents 70% of the stands in the eastern Quebec (Boucher et al., 2003) and is expected to represent an important

* Corresponding author. Tel.: +1 418 545 5011x2330; fax: +1 418 545 5012.
E-mail address: sergio.rossi@uqac.ca (S. Rossi).

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proportion of the forests of high latitudes. If and how age structure within a stand affects tree growth and stand productivity of these ecosystems remains a crucial but unanswered question.

In the past, the boreal forest was erroneously assumed to be a mere mosaic of even-aged stands, frequently reinitiated by major disturbances. This induced a widespread use of clear-cutting to emulate the conditions created by nature. However, in the last decade the previously overlooked small-scale events have been clearly demonstrated (Kneeshaw and Gauthier, 2003) and, as a result, the gap dynamics in the conifer-dominated populations of North America has begun to be taken into account in ecosystem-based forest management (Bergeron et al., 2002; Bergeron, 2004; Brassard and Chen, 2006). Although the age-related changes in forest structure have been analyzed for the Canadian boreal forest (cf. McCarthy, 2001), to our knowledge there is still a lack of growth models of black spruce at high latitudes.

The ecosystem-based forest management is in part substituting the traditional practices of clear-cutting to maintain functioning of the boreal forests (Bergeron et al., 2002). The new practices should attempt to more closely simulate the natural processes and disturbances occurring in these environments. However, conservation, restoration, and management require knowledge on features and dynamics of the stands in natural, pristine areas (Kneeshaw and Gauthier, 2003). The aim of this study was to assess changes in growth during stand development at both tree and stand level by investigating (i) dynamics of tree growth and (ii) stand volume in even- and uneven-aged stands of black spruce at the limit of the closed boreal forest in Quebec, Canada.

2. Materials and methods

2.1. Study area

The study was conducted between Lac Mistassini and Manicouagan Reservoir, at the limit of the closed boreal forest in Quebec, Canada. The region has a gently rolling topography with hills reaching 500–700 m a.s.l. on thick and undifferentiated glacial till deposits. This area is part of the black spruce-feather moss bioclimatic domain (Robitaille and Saucier, 1998), with a potential vegetation composed mainly of black spruce and balsam fir (*Abies balsamea*). The closest meteorological station is located in Bonnard (50°43′N, 71°03′W, 506 m a.s.l.), 75 km from the study area. The climate is continental, with cool, short summers and long, cold winters with a 30-year mean annual temperature of −1.8 °C and total precipitation of 946 mm. About 300 cm of snow covers the ground from October to May, only disappearing completely in June. The sum of the mean temperatures exceeding 5 °C is 970.9 °C day.

2.2. Methods

Eighteen natural stands were selected from the inventory maps at the scale 1:50 000 (Quebec Ministry of Natural Resources) according to a stratified random selection. Stands were divided according to their reported forest age and density and samples were selected from each stratum independently in order to obtain as wide as possible a range of stand ages and densities. In each selected stand, sample plots were established that were at least twice the area of the larger gaps (cf. McCarthy, 2001) and sampled during 2003–2005 (Table 1). Because tree density varied among stands, plot sizes varied from 200 to 400 m^2 so that all plots included at least 24 sampled trees (Rossi et al., in press). As the area was inaccessible by road, stand selection was based on the proximity of a lake at least 1 km in length to permit access by floatplane. Because of their remote location and the absence of evidence of human impact, the stands were considered to have developed under the influence of natural disturbances.

In each plot, height and diameter at breast height (DBH) were measured on all living trees with a diameter at breast height (DBH) larger than 9-cm and 2-cm-thick discs were collected from the stem base. Discs were also collected along the stem of 10 dominant black spruce [*Picea mariana* (Mill.) B.S.P.] trees at sampling heights of 0.3, 0.6, 1 and 1.3 m from the collar. Above 1.3 m, discs were collected at intervals of 1 m for the remaining length of the stem. The dominant trees had upright stem, elevated DBH and heights similar to those of the bigger trees of the stand. Trees with polycormic stems, evident damage due to parasites and reduced or partially dead crowns were excluded from the selection of the dominant trees. However, in 11 trees (6% of the total), the last 2–3 m from the top was polycormic; in this case, only the longer and upright stem was used for measurements. Discs were air-dried and sanded with progressively finer grade sandpaper. Tree-ring widths were measured to the nearest 0.01 mm using a Henson measuring system along two to four paths, according to the uniformity of the tree rings on the disc. All ring width series were corrected by cross-dating performed both visually and using the COFECHA computer program (Holmes, 1983). Measurements were averaged for each disc and tree ring.

Table 1
Location, structure and characteristics of the 18 selected plots at the limit of the closed boreal forest in Quebec, Canada. The number of trees within plot is reported in parentheses.

Stand	Latitude	Longitude	Altitude (m)	Plot size (m)	Sampling year	Stand structure	Number of trees in the plot		Dominant height (m)	Mean DBH (cm)	Stand density (trees ha^{-1})	Stand basal area ($m^2\ ha^{-1}$)
							Black spruce	Other species				
1	51°00′	73°00′	420	10 × 20	2003	Even-aged	42		11.00	11.49	2100	22.41
2	51°27′	71°24′	541	10 × 20	2004	Even-aged	29	17	13.02	12.76	2300	30.67
3	51°20′	70°06′	539	20 × 20	2004	Even-aged	38		13.24	13.39	950	14.01
4	51°31′	70°26′	601	10 × 20	2005	Even-aged	74	1	12.73	12.82	3750	49.41
5	51°42′	71°09′	615	20 × 20	2004	Even-aged	48		14.70	14.41	1200	20.75
6	51°06′	71°57′	570	20 × 20	2004	Even-aged	77	4	15.10	14.18	2025	33.83
7	51°20′	70°47′	540	20 × 20	2005	Even-aged	45		12.25	11.41	1125	11.76
8	51°13′	71°47′	534	20 × 20	2005	Even-aged	33		12.68	13.22	825	12.14
9	51°02′	72°36′	520	20 × 20	2003	Uneven-aged	46	5	14.48	12.41	1275	16.23
10	51°00′	72°40′	480	10 × 20	2003	Uneven-aged	44	3	16.93	15.64	2350	47.06
11	51°00′	71°11′	531	10 × 20	2005	Uneven-aged	34		17.22	14.51	1700	30.4
12	51°09′	71°04′	546	20 × 20	2004	Uneven-aged	24		16.28	13.39	600	9.5
13	51°22′	71°35′	570	20 × 20	2004	Uneven-aged	39		13.09	12.33	975	12.41
14	51°03′	72°34′	530	15 × 20	2003	Uneven-aged	48		15.77	13.51	1600	24.02
15	51°11′	71°04′	528	20 × 20	2005	Uneven-aged	57	1	14.64	13.41	1450	21.42
1	51°45′	70°33′	622	20 × 20	2004	Uneven-aged	46	5	13.15	13.88	1275	20.64
2	51°41′	70°46′	652	20 × 20	2004	Uneven-aged	40		12.06	12.66	1000	13.02
3	51°51′	70°19′	535	20 × 20	2004	Uneven-aged	30	5	9.05	11.57	875	9.45