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The role of gaps and tree regeneration in the transition from dense to open black spruce stands

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ABSTRACT

Black spruce forests growing on clay soils in northwestern Quebec change structure from dense even-aged stands to open uneven-aged stands such that almost all forests older than 200 years have an open canopy. These forests become unproductive over time because they are prone to paludification. The main goal of our study was to document the transition between dense and open stands in terms of gap dynamics, with a focus on tree regeneration. Our objective was to determine whether forests remain open due to a lack of regeneration, a lack of growth or both. Nine stands along a 50–250-year-old time since fire gradient were sampled with the line intersect sampling method. Gap fraction increased with stand age and reached a maximum of 77% in the oldest site. In old-growth stands, gaps were interconnected due to the low density of these forests. Most of the gap makers were found with broken stems. Regeneration was dominated by black spruce layers and was relatively abundant (1.71 stems/m^2). However, the majority of gap fillers were smaller than 1 m in height in stands of all ages. Instead of a lack of regeneration, the opening of the forests is due to a lack of growth associated with cold and wet organic deposits. Partial harvesting could be implemented on the most productive sites, while management techniques including soil disturbances will be required on low productivity sites to recreate good growth conditions.

1. Introduction

Studies of gap dynamics in tropical and temperate ecosystems have shown the importance of gaps in tree recruitment and in forest succession (Brokaw, 1985; Canham, 1989; Runkle, 1981). Variations in gap size influence species composition, growth rates and the height distribution of the regeneration layer (Brokaw, 1985). In boreal forests, the impact of gap formation on regeneration is less clear than in temperate and tropical forests; gaps do not necessarily lead to compositional change (Liu and Hytteborn, 1991). In high latitude mixed-species stands, direct light only reaches the forest floor in the very largest gaps due to the low sun angle (Kneeshaw and Bergeron, 1999). These few large gaps are required for the maintenance of early successional and shade-intolerant species, such as aspen, while frequent smaller gaps promote the transition towards dominance of shade-tolerant species, such as fir (Leemans, 1991; Kneeshaw and Bergeron, 1998). In coniferous stands dominated by late-successional and shade-tolerant individuals, self-replacement is common (Leemans, 1991; Kneeshaw and Gauthier, 2003) and forest development is thus more related to structural changes (Harper et al., 2003).

Since the end of the Little Ice Age (~1850), fire frequency and burned areas have decreased considerably in the eastern boreal forest of Canada (Bergeron et al., 2001). It has been suggested that the global warming occurring since 1850 may have created a moister climate which is less prone to large forest fires (Bergeron et al., 2001). Therefore, a greater number of stands escape fire for periods long enough to reach the old-growth stage. The death of the post-fire cohort of trees creates gaps and thus space for understorey stems to grow to the canopy and eventually, these second cohort trees replace those from the first one (Oliver and Larson, 1990; Kneeshaw and Gauthier, 2003). This transition remains incomplete in black spruce (*Picea mariana*) stands growing on the Clay Belt, a physiographic area of northwestern Quebec and northeastern Ontario, covered by clay soils. After a high severity fire, trees rapidly establish on mineral soil to form dense even-aged stands dominated by tall stems, which evolve to an open uneven-aged stands dominated by smaller trees (Lecomte et al., 2006).

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Stand break up begins about 100 years after fire and almost all forests older than 200 years can be characterised as having open canopies (Harper et al., 2002; Boudreault et al., 2002; Lecomte et al., 2006). Natural disturbances may play an important role in the transition between dense and open forests. Secondary disturbances such as windthrow and, to a lesser extent, spruce budworm outbreaks affect stands aged between 100 and 300 years (Harper et al., 2002). Once initiated, stand break up generally proceeds rapidly and some stands may lose up to half their volume in a decade (Arnup et al., 1988; Smith et al., 1987).

The opening of black spruce stands suggests either a lack of regeneration or a lack of growth of the second cohort trees (or both). Forests growing on poorly drained soils of the Clay Belt are prone to paludification, which reduces productivity. During forest succession, the soil organic layer increases (Simard et al., 2007) and *Sphagnum* species invade the bryophyte layer (Fenton and Bergeron, 2006) leading to waterlogged conditions (Lavoie et al., 2005). Paludification is also associated with a reduction in soil temperature and nutrient availability (Simard et al., 2007) which may restrict tree germination and tree growth. Ericaceous competition and allelopathy have also been identified as potential causes of conifer regeneration failure (Mallik, 2003).

The main goal of our study was to document the transition between dense and open stands in terms of gap dynamics, with a focus on tree regeneration. This knowledge is critical if foresters are to reproduce this transition with partial harvesting. Specifically, our goals were to verify that gap fraction and gap size increase systematically with stand age along a 50–250-year time since fire gradient. Tree mortality was studied to establish whether forests open suddenly or gradually, and whether tree mortality is due to secondary disturbances such as windthrow and insect outbreaks. We hypothesized that gap fraction would gradually increase with time since fire due to gap expansion caused by the asynchronous death of gap makers. We also asked whether forests remain open due to a lack of regeneration, due to the slow growth of the second cohort trees or both.

1.1. Study area

The study area is located in the eastern boreal forest of Canada, in northwestern Quebec (49°00′N to 50°00′N; 78°30′W to 79°20′W). At this latitude, the bioclimatic domain is the black spruce (*P.* mariana) feathermoss forest (Robitaille and Saucier, 1998). The climate is cold and wet, the average annual temperatures recorded at the closest weather stations are 0.7 °C and −0.7 °C and the average annual precipitation varies between 890 mm and 906 mm [means calculated for the period 1971–2000 from La Sarre 48°46′N, 79°13′W and Matagami 49°46′N, 77°49′W, respectively] (Environment Canada, 2004). The region is part of the Clay Belt of western Quebec and northeastern Ontario, a major physiographic area created by deposits left by the glacial Lakes Barlow and Ojibway (Vincent and Hardy, 1977). The topography is relatively flat and soils are dominated by clay and organic deposits. Fire is the most important disturbance; however the fire cycle increased from 135 years between 1850 and 1920 to 398 years after 1920 (Bergeron et al., 2004). Harvesting is common throughout most of the territory. Our sampling took place during the summers 2005 and 2006.

2. Methods

2.1. Sampling

Nine black spruce stands were sampled along a 50–250-year time since fire gradient which includes the stand break up period. All stands originated from high severity fires suggesting that they were initially dense and even-aged (Lecomte et al., 2006; Simard et al., 2007). Stands were dominated by black spruce (*P. mariana*). Jack pine (*Pinus banksiana*) was co-dominant and present only in the youngest and mature stands (50–80 and 80–110 years), trembling aspen (*Populus tremuloïdes*) occurred in mature stands while balsam fir (*Abies balsamea*) was uncommon. The ground layer was covered mainly by *Pleurozium schreberi* and others feathermosses with some patches of *Sphagnum* species. Ericaceous shrubs dominated by Labrador tea (*Rhododendron groenlandicum*, formerly *Ledum groenlandicum*) and *Vaccinium* spp. became more abundant in old-growth forests.

Our study sites were used in previous studies where dendrochronological analysis, analysis of the forest floor, of slope and soil texture, were conducted to ensure that stands established under similar conditions (Lecomte et al., 2005, 2006; Fenton and Bergeron, 2006; Simard et al., 2007). Each stand was growing on fine-textured mineral deposits, had a gentle slope and no signs of anthropogenic disturbance (Lecomte et al., 2006; Simard et al., 2007). Paleological methods were used to estimate the initial stand conditions while stand age was determined from a stand initiation map and verified by dating a few dominant trees (see Lecomte et al., 2006 or Simard et al., 2007 for details). Our oldest dated stand was 226 years old, but may be older as the C^{14} dating of the charcoal layer indicated that the last fire occurred 369 years ago (Lecomte et al., 2005). This difference did not alter the order of stands along the gradient of time since fire. To further minimise dating errors, stands were classified into one of four age classes: young (50–80 years), mature (80–110 years), over-mature (110–140 years) and old-growth (>140 years) (Table 1).

We used the line intersect sampling method to calculate gap fraction as the ratio of transect length in gaps divided by the total transect length (Runkle, 1982; Battles et al., 1996). Stand areas were located to avoid anthropogenic disturbances (road, mineral exploration, silvicultural treatments) and unwanted landscape or forest conditions (swamp, open land, forest patches from another age). Consequently, only two to four parallel 100 m long transects, spaced 30 m from each other, were used in each stand.

Table 1
Characteristics of the nine sampled stands: site name, dendrochronological stand age, age class, stand development stage, stand characteristics, stand density and basal area (mean and standard deviation).

Site	Stand age (years)	Age class (years)	Stand development stage	Stand characteristics	Stand density (stems/ha)	Basal area (m^2/ha)
N4	57	50–80	Young	Some trees did not reach the canopy;	4220 ± 1180	37 ± 7
N59	76			trees diameters are relatively small		
S1	88	80–110	Mature	Tall trees; regular structure; dense forest	3740 ± 830	41 ± 8
N23	90					
N8	131	110–140	Over-mature	Decrease in stand density; structure begins to be irregular	2210 ± 320	30 ± 3
N75	132					
C1	168	>140	Old-growth	Irregular structure; variations in tree heights	1730 ± 655	27 ± 9
POP1	173			and diameters; thick organic matter layer		
N50	226					