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

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ARTICLE INFO

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.

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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 (m²/ha)
N4	57	50–80	Young	Some trees did not reach the canopy; trees diameters are relatively small	4220 ± 1180	37 ± 7
N59	76					
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 and diameters; thick organic matter layer	1730 ± 655	27 ± 9
POP1	173					
N50	226					

We measured only canopy gaps: they were defined as the vertical projection of a canopy opening caused by the mortality of one or more mature trees (Kneeshaw and Bergeron, 1998). Due to the narrow conical crown of black spruce there are few differences in size between canopy gap, the area directly under the canopy opening, and the expanded gap, which includes the canopy gap plus the adjacent area extending to the stems of surrounding trees (Runkle, 1982; Pham et al., 2004). Also, regeneration present inside the gap had to be lower than two-thirds of the canopy height of the surrounding trees (Pham et al., 2004). Openings without gap makers were measured and we added them to the gap fraction to calculate total canopy openness.

For each gap encountered along a transect, gap area was estimated using the formula for an ellipse, measuring the longest axis and the largest perpendicular axis (Runkle, 1981). Two ellipses were used to estimate gap area when gaps had an "L" shape. Gap size could not be measured in stands older than 140 years because stand density was low and gaps were interconnected. In these sites, only gap fraction and canopy openness were calculated. Basal area was measured at two random locations in each transect with a factor 2 prism, while stand density was measured three times per stand in 10 m × 10 m quadrat.

In each gap, we collected data on all dead trees which contribute to gap creation (gap makers). Gap makers had a DBH superior to 5 cm and a height at least two-thirds of the average canopy height. We distinguished different modes of mortality for each gap maker: standing dead, snapped crown (defined as trees standing dead with a fallen crown), uprooted and broken (at the base or at a height greater than 1.5 m above the ground). The mode of mortality, the number of gap makers, gap maker species, the orientation of the log for stems broken at the base or for uprooted trees were noted.

Tree regeneration was also sampled in all gaps. When the gap area was less than 7 m^2, regeneration was sampled in the entire gap. When the gap area was greater than 7 m^2, we sampled regeneration (gap fillers) in a 2 m wide transect oriented north–south. Every gap filler was grouped by species, by 15 cm height classes (0–15; 15–30; …; 195–210; >210), and by mode of reproduction (layer or seedling). Furthermore, we noted whether gap fillers were free of tree competition which means being at least 50 cm from another gap filler (Kneeshaw and Bergeron, 1998) and if they were growing in Sphagnum patches. Regeneration density was also calculated under canopy cover in two randomly determined locations per transect to compare regeneration in gaps and under forest cover.

In each gap, we counted the number of living and dead saplings [trees higher than 1 m (Runkle, 1981) and having a DBH smaller than 5 cm]. In stands older than 140 years, where gaps were interconnected, gap makers and saplings were sampled in a 4 m wide transect oriented north–south and tree recruitment in a 2 m wide transect, along the same transects used to calculate gap fraction. Sphagnum cover was evaluated in all gaps and in a 2 m wide transect inside gaps in the old-growth stands.

For each stand, six gaps were randomly chosen in which to measure light transmission and to estimate ericaceous cover. Light was determined using hemispherical photographs taken during conditions of diffuse skylight using a fisheye lens mounted on a Nikon Coolpix 4500 digital camera. The camera was always located in the middle of the gap (or at equal distance from the southern and northern edge of the opening), at 30 cm above the ground, in a horizontal position and oriented to magnetic north. Photographs were then analysed with the software Gap Light Analyser (version 2.0). The cover of understorey species was estimated in five 20 cm × 20 cm plots inside the six randomly chosen gaps per stand. The understorey was largely dominated by ericaceous species. All the ericaceous species covers were combined for the analysis of their impact on regeneration density.

2.2. Dendrochronology

We took samples of gap makers and gap fillers in four gaps per stand. Gaps were chosen randomly among those that had at least three saplings (when possible) with the goal of studying the impact of mature tree death on the growth of saplings. All dead trees and a maximum of three saplings (or gap fillers close to 1 m high) inside these gaps had disks taken at the bottom of their stems. For a few dead trees which had rotten bases, disks were taken in the best part of the first three meters of the trunk. Disks were sanded and rings counted and measured along two radii using a Velmex Uni Slide measuring table (0.001 mm resolution). When the samples were not too rotten, the radii were perpendicular; when they were affected by decomposition, the radii followed a path through the best part of the disks. Trees were then cross-dated with event years and verified by comparing reference chronologies with the computer programs COFECHA (Holmes, 1999) and TSAP (Rinn, 1996). Reference chronologies originated from previous studies in the region (M. Simard, unpublished data; Hofgaard et al., 1999). Rings were counted on 120 cookies and 105 of them were successfully cross-dated.

A disk was also taken at the base of 101 saplings (95 black spruce and 6 balsam fir; mean height of 2.73 m). Disks were sanded and measured. We used the IMPACT micro-program (from the Dendrochronology Program Library) to compare mean annual radial increment before and after an impact or disturbance, i.e. the opening of the canopy, which is thought to cause a change in growth (Holmes, 1999). We define a growth release as a growth change in a tree-ring series exceeding 200% and lasting for at least 5 years. We chose a criterion of 200% because growth rates are very low thus making the method very sensitive to changes in ring width (Fraver and White, 2005). We limited our temporal comparison to 5 years before and after the year of tree death in order to use all the gap makers that died before 2000. Using 10 years as done in other studies (Nowacki and Abrams, 1997; Black and Abrams, 2003; Fraver and White, 2005) would have reduced the sample size of dead trees by one third, since many of the trees died too recently to have been included given these more conservative formulas for growth release.

2.3. Data analysis

Linear regressions were used to test the relationship between canopy openness and gap fraction as a function of stand age. We compared regeneration density in gaps vs. under forest canopy using a Kruskal–Wallis test since data were not normally distributed. Relationships between regeneration density in gaps and environmental variables (stand age, canopy openness, light transmission, Sphagnum cover, ericaceous cover, basal area, stand density and gap maker density) were evaluated using a principal component analysis (PCA). All statistical analyses were conducted using the JMP computer program (version 5.1) or with Canoco for Windows (version 4.52). The critical value of ρ for all tests was 0.05.

3. Results

3.1. Gap and stand characteristics

Gap fraction increased with stand age (slope = 0.2789, Prob > |t| = <0.0001, R^2 = 0.6747) and reached a maximum of 77% in the oldest site. Canopy openness, which includes both gaps and openings without gap makers, also increased with stand age (slope = 0.2973, Prob > |t| = <0.0001, R^2 = 0.7801) (Fig. 1) and was on average 8% greater than gap fraction. Stand density decreased from 4220 stems/ha in the youngest stands to 1730 stems/ha in old-growth stands. Stand basal area, on the other hand, reached a maximum (41 m^2/ha) in mature stands (80–110 years) and then,
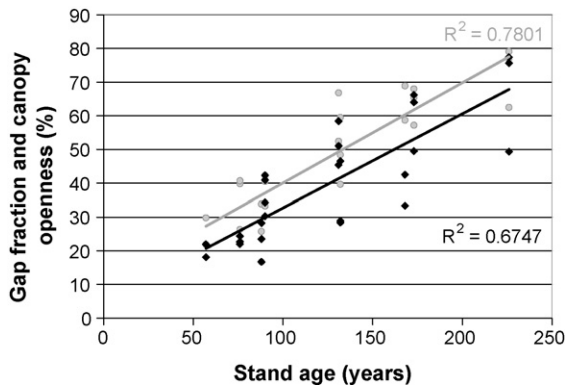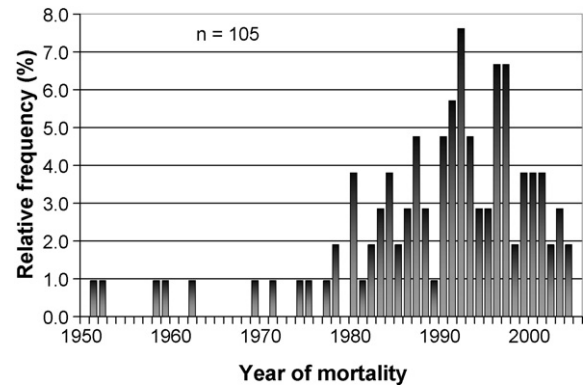
Fig. 1. Gap fraction in black and percentage of canopy openness in grey (including gaps and openings without gap makers) as a function of stand age.

also decreased with stand age until 27 m²/ha in the old-growth stands (Table 1). Gaps were generally small (Fig. 2): 80% were less than 30 m² in area. There were more small gaps in young stands (mean of 11.9 m²) and the larger gaps, including the biggest one (207.75 m²), were found in the 110–140 years old stands (mean of 32. 9 m²).

3.2. Gap makers

Gaps were created by the mortality of 4–5 mature trees (on average). The majority of gaps (95%) had less than 10 gap makers and 13% resulted from the mortality of only one mature tree. Gap makers were mostly found broken (69%): 47% were snapped at their base and 22% were broken at a height greater than 1.5 m above the ground (Fig. 3). The logs of trees broken at their base and

Fig. 2. Gap size frequency for stands younger than 140 years.

Fig. 3. Observed type of mortality of gap makers: broken, uprooted, standing dead and snapped crown; for all stands pooled.

**Fig. 4.** Relative frequency of stems by year of death of gap makers; for all stands pooled.

those of infrequently uprooted stems (7%) were oriented in many different directions. Downed wood (76%) was more prevalent than snags (24%) (which includes all gap makers standing dead (17%) and gap makers standing dead with their crown snapped (7%)).

Mortality occurred from 1951 to 2004 with 48% of trees dying in the 1990s and 75% between 1980 and 1999; small peaks in mortality occurred in 1991 (5.7%), 1992 (7.6%), 1996 and 1997 (6.7% each) (Fig. 4). The frequency of trees that died before the eighties should probably be higher than 11%, but 15 trees of the 120 sampled were too decayed to establish the year of their death. Also, the number of gap makers was very low in old-growth stands (0.14 stems/m²) probably because some trees died long ago and the organic matter rapidly covered the downed wood (Table 2).

3.3. Gap maker–gap filler comparisons

Gap makers were mostly black spruce (91%) with some jack pine (7%), trembling aspen (1%) and balsam fir (1%). Gap makers were replaced 99% by black spruce and 1% by balsam fir. There were generally more saplings than gap makers in gaps, except in the mature 80–110 year old stands (Table 2). In these forests, the number of gap makers per area was the highest (0.61 stems/m²), and the number of saplings and the mean regeneration density were the lowest (0.08 stems/m² and 0.58 stems/m², respectively). In young and mature forests, an average of 0.86 stems/m² and 0.31 stems/m² of saplings were dead (i.e. an average of 6 and 4 dead saplings per gap, respectively). In the other stands (over-mature and old-growth), the number of dead saplings decreased to 0.07 stems/m² and 0.06 stems/m² (Table 2).

Many saplings are as old as the gap makers, particularly in stands where time since fire is less than 110 years. In fact, in young and mature stands, the mean age of gap makers (54 years) was similar to the current mean age of saplings (53 years) (Fig. 5a). The age established for each sample represents a minimum estimate as some rings may have been located below the current soil level (Desrochers and Gagnon, 1997) since the organic soil layer rises through the thickening of the moss layer (Boily and Doucet, 1993).
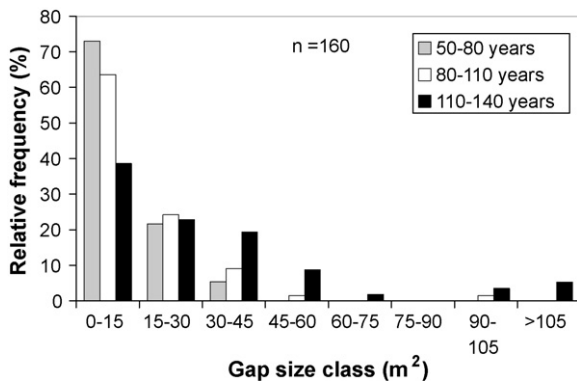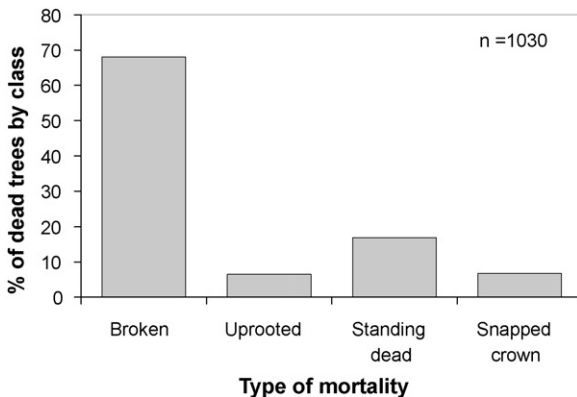
Table 2
Densities of gap makers, saplings, dead saplings and regeneration by stand age class.

Stand age (years)	Gap maker density (stems/m²)	Sapling density (stems/m²)	Dead sapling density (stems/m²)	Regeneration density (stems/m²)
Young (50–80)	0.40	0.74	0.86	1.77
Mature (80–110)	0.61	0.08	0.31	0.58
Over-mature (110–140)	0.22	0.48	0.07	2.28
Old-growth (>140)	0.14	0.38	0.06	2.36
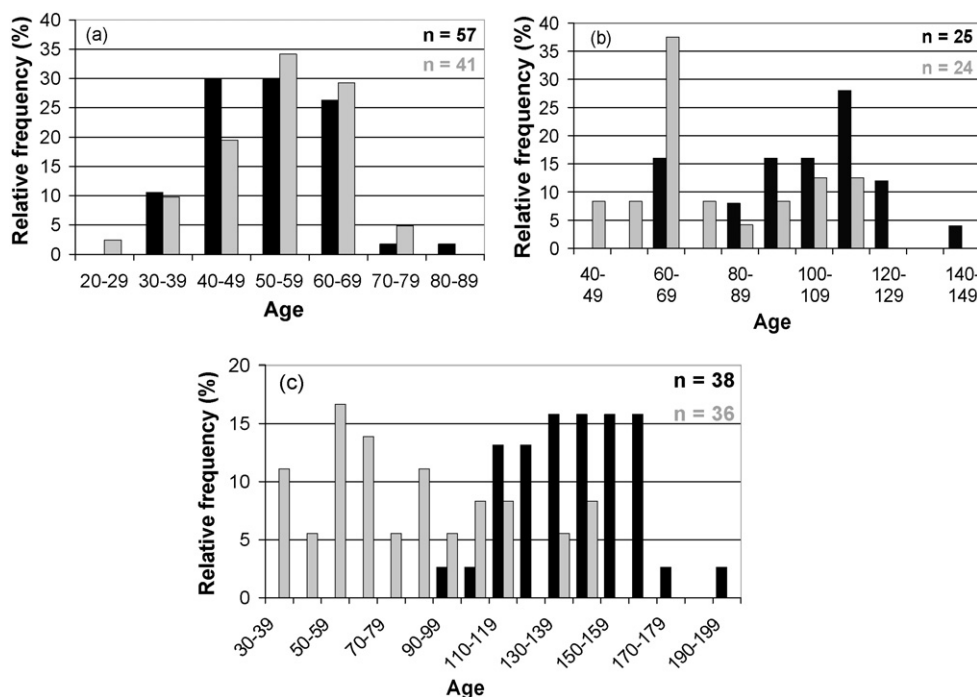
Fig. 5. Age at time of death for gap makers (in black) and current age of saplings (in gray) (a) in stands younger than 110 years; (b) in stands 110–140 years old; (c) in stands older than 140 years.

Saplings younger than gap makers became more frequent in stands older than 110 years, although 27% of saplings sampled exceed 100 years. In stands 110–140 years old, the mean age of gap makers (101 years) was higher than the mean age of saplings (76 years) (Fig. 5b). Finally, in old-growth stands (>140 years), there were a lot of saplings aged between 30 and 89 years old, but the mean sapling age remained relatively high (80 years) (Fig. 5c). Mortality occurred mainly when trees were between 110 and 169 years old, with a mean gap maker age of 140 years (Fig. 5c).

3.4. Gap fillers

Regeneration was 95% composed of black spruce layers with the remaining 5% being composed of black spruce and balsam fir seedlings. Tree regeneration density in gaps was relatively high (1.71 stems/m^2), but not statistically different than under the forest canopy (1.34 stems/m^2) (Kruskal–Wallis test, Prob > |z| = 0.1817). Furthermore, only 10% of the gap fillers were free of competition, i.e.

at least 50 cm from the nearest individual. Regeneration density (0.58 stems/m^2) (Table 2) dropped in mature stands (80–110 years) where stand basal area (41 m^2/ha) reached a maximum (Table 1). On the other hand, regeneration density was higher in over-mature and old-growth stands (2.28 stems/m^2 and 2.36 stems/m^2, respectively) (Table 2).

Gap fillers were mainly small, 89% of them measured less than 105 cm (in stands of all ages) (Fig. 6). While the average age of saplings increased as stands aged, the average height of saplings reached 3.6 m in mature stands and then decreased as stands aged; such that the average measured height was 2.8 in over-mature stands and 2.4 m for old-growth stands (Fig. 7). Also, from a sample of 101 saplings, only 15% had a growth release of more than 200% after the death of a neighbouring gap maker. Tree regeneration density was positively correlated to stand age, light transmission, canopy openness, *Sphagnum* cover, ericaceous cover and negatively correlated to basal area, stand density and gap maker density (Fig. 8). About 35% of the gap fillers were growing in *Sphagnum* cover.
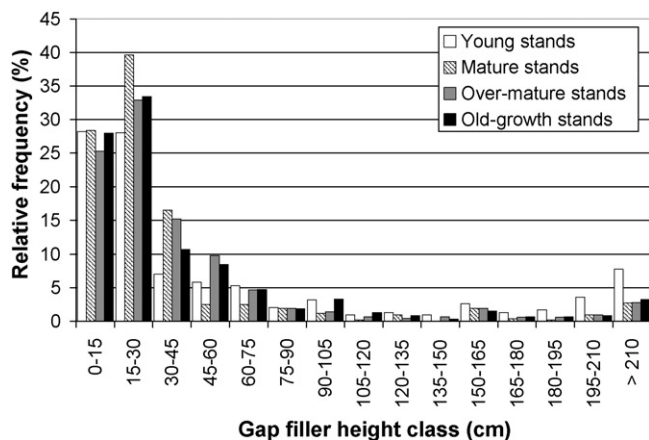
Fig. 6. Frequencies of gap filler height class (cm) in young stands (n = 528 gap fillers), in mature stands (n = 515), in over-mature stands (n = 1336) and in old-growth stands (n = 2128).
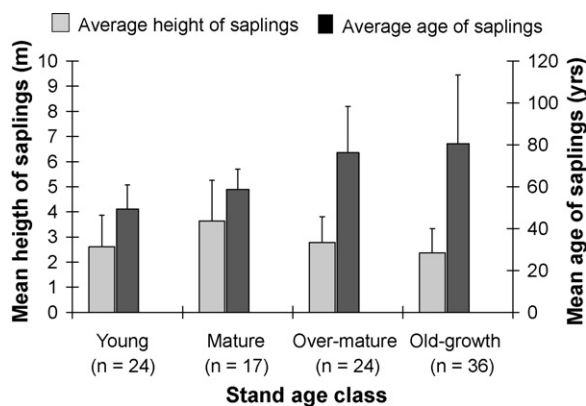
Fig. 7. Average measured height (m) and average age of saplings (years) by stand age class: young (50–80 years), mature (80–110 years), over-mature (110–140 years) and old-growth (>140 years); n = number of saplings.
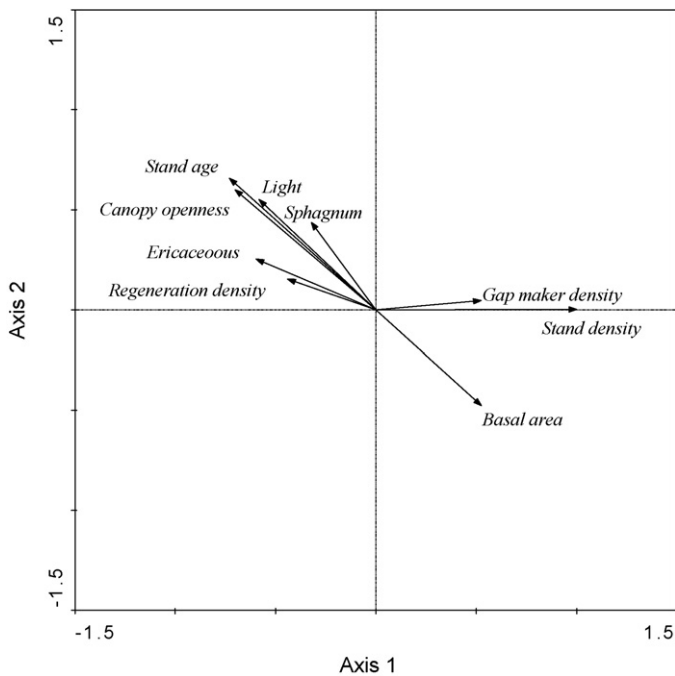
Fig. 8. Principal component analysis (PCA) of the variables Regeneration density (for each gap), Stand age, Light (light transmission in the middle of the gap), Canopy openness (canopy openness of the stand), Sphagnum (percentage of Sphagnum cover in the gap), Ericaceous (percentage of ericaceous shrub cover in the gap), Basal area (stand basal area), Stand density and Gap maker density (for each gap); axes 1 and 2.

4. Discussion

4.1. Gap and stand characteristics

In black spruce stands of northwestern Quebec, gap fraction increases with time since fire and may reach almost 80% in the oldest stands. These results are consistent with the work of Harper et al. (2002, 2006) in the same region. However, the gap fraction of our old-growth stands is greater than those reported in old-growth boreal forests in southeastern (Kneeshaw and Bergeron, 1998) and northeastern (Pham et al., 2004) Quebec, and sub-boreal forests in British Columbia (Bartemucci et al., 2002). Canopy openness and gap fraction coincide with a drop in stand density and basal area to 1730 stems/ha and 27 m^2/ha in the old-growth stands.

Gaps generally expand over time (Liu and Hytteborn, 1991). In our study, they were on average 2.8 times larger in over-mature stands than in young stands. Nonetheless, even in over-mature stands, gaps are relatively small (mean of 33 m^2) compared to those found in other boreal or subalpine forests where average gap size usually varies between 41 m^2 and 141 m^2 (McCarthy, 2001). Gaps are small because of the conical and narrow crown of black spruce (McCarthy, 2001), the main gap maker species, and the limited number of individuals creating a gap (average of 4 to 5 per gap). As with other studies (Pham et al., 2004; Liu and Hytteborn, 1991), the majority of gaps contain less than 10 gap makers. However, the old-growth stands (>140 years) would probably contain larger gaps if we had been able to delimit them, but due to the low density of these forests, the wide tree spacing and the uneven-aged structure, openings were interconnected.

4.2. Gap makers

Gaps are created continuously along the gradient of time since fire. In young and mature forests, gaps are created by self-thinning and density-dependent mortality (Franklin et al., 2002). Stand density and gap maker density are at their maximum in these stands, mortality of saplings is high and tree mortality occurs before trees reach senescence (mostly between 40 and 69 years old, Fig. 5a). Stand break up begins in mature stands (80–110 years) where the number of gap makers is the highest and regeneration density, the lowest. During the mature stage, causes of mortality begin to be non-competitive and secondary disturbances (insects, diseases and wind) become more important causes of mortality (Franklin et al., 2002).

Black spruce trees growing on poorly drained organic soils and producing adventitious roots in peat have been identified as being more susceptible to windthrow (Smith et al., 1987; Lieffers and Rothwell, 1987). A study in the Clay Belt region showed that windthrow affects more than 16% of the area occupied by the 100–250-year-old stands (Harper et al., 2002). Most of our gap makers were found broken, but only 7% of gap makers were uprooted and no dominant direction of fallen logs was observed. Further research is needed to clarify the impact of wind on tree mortality in boreal stands.

It has been shown that the spruce budworm (Choristoneura fumiferana) has a negligible impact in stands of northwestern Quebec, compared to forests further south and east (Gray et al., 2000; Lecomte et al., 2006). However, the high proportion of gap makers (75%) that died between 1980 and 1999 may be partially due to the last spruce budworm outbreak (1970–1987; Morin et al., 1993). In northwestern Quebec, black spruce stands lost between 1.23 and 32.97% of their volume because of the last spruce budworm outbreak (Morin et al., 2008). Trees may have died during the outbreak or have been weakened and subsequently died years after the outbreak ended. Mortality is often caused by the accumulation of multiple factors (Manion, 1981; Kuuluvainen, 1994).

4.3. Tree regeneration

Tree recruitment in gaps is abundant (1.71 stems/m^2) and sapling density is higher than gap maker density, except in mature stands. Only 10% of gap fillers are free of tree competition because the regeneration is dense, particularly in old-growth stands (2.36 stems/m^2). Regeneration density is similar beneath the canopy or in gaps, reflecting the fact that black spruce can grow easily under a closed canopy (Pham et al., 2004). Nevertheless, regeneration density is positively associated with light transmission and canopy openness. With the evolution of light levels, Sphagnum species gradually replace the feathermosses and ericaceous shrubs, principally Labrador tea (R. groenlandicum), become more abundant (Fenton and Bergeron, 2006; Simard et al., 2007; Lecomte et al., 2005). Although ericaceous species have been found to negatively affect the establishment and growth of conifers (Mallik, 2003), regeneration density is also positively associated with the presence of ericaceous shrubs and Sphagnum species in the understorey (Fig. 8).

In young and mature stands, most of our saplings seem to be from the same cohort as gap makers as their ages are similar. Some of the post-fire cohort trees did not reach the canopy and are still suppressed because of variations in the quality of regeneration microsites following fire (Lavoie et al., 2007) and subsequent growth in environments with resources limited by larger neighbours. A second cohort of trees becomes more apparent in the old-growth stands as there are a lot of saplings aged between 30 and 89 years old. The average ages of saplings, which are frequently old, increases as stands get older (Fig. 7). Many authors have found that age is not a limiting factor for advance regeneration which usually releases after forest harvesting (Lussier et al., 1992; Boily and Doucet, 1993; Groot and Hökkä, 2000). In our study, only a few saplings (15%) are released after the death of

mature trees that creates or enlarges gaps. The lack of growth release may be an indication of poor growing conditions, but may also be an artefact of the short range of time used to detect a release through the comparison of growth rates before and after the death of a gap maker.

Regeneration is dominated by black spruce layers. Favourable seedbeds are limited in the absence of high severity fires, while vegetative reproduction may be promoted by an increase in the height of organic and *Sphagnum* layers which reach the low branches of black spruce trees. In fact, more than one out of three gap fillers are growing in *Sphagnum* cover. Growth of black spruce regeneration is influenced more by site quality than by its mode of reproduction (Boily and Doucet, 1993). Paludification, via the accumulation with time since fire of peat and a rising water table (Fenton and Bergeron, 2006; Simard et al., 2007), limits tree growth. The second cohort roots in a cold and wet organic layer while the tree cohort establishing after a high severity fire roots in fertile mineral soil (Simard et al., 2007). This could explain the drop in the average measured height of the saplings between mature and old-growth stands (Fig. 7). In old-growth stands, gap fillers are abundant, but saplings are older and smaller than in the younger stands. We conclude that the opening of black spruce forests of the Clay Belt is due to a lack of growth (related to paludification) rather than to a lack of regeneration.

5. Conclusion (management implications)

The gap dynamics of black spruce forests growing on the Clay Belt could be emulate with partial harvesting. About 40–50% of the forest could be harvested by creating artificial gaps with an average of five dominant trees removed per gap. To represent the natural distribution of gap sizes, harvested areas should vary between $15\,m^2$ and $100\,m^2$, with the majority being $30\,m^2$ in size. Nevertheless, partial harvesting may increase paludification and reduce tree growth rates (Lavoie et al., 2005). Artificially created gaps, as with natural gaps, would have difficulty in eventually closing due to the limited growth of the regeneration. Partial harvesting should be mostly done on productive sites dominated by young and mature stands to reproduce old-growth stand characteristics.

For low productivity sites dominated by over-mature and old-growth stands, it would be preferable to emulate the effect of a high severity fire by choosing management techniques disturbing the soil to recreate good growth conditions. After harvest and soil disturbance, it may be necessary to plant seedlings to promote the return of a dense and productive forest. The combination of techniques emulating natural disturbances, such as fire and gap dynamics, and preserving young and old-growth stand attributes could promote ecosystem management.

Acknowledgements

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