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Interactions of multiple disturbances in shaping boreal forest dynamics: a spatially explicit analysis using multi-temporal lidar data and high-resolution imagery

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Summary

1. Mixed-wood boreal forests are often considered to undergo directional succession from shade-intolerant to shade-tolerant species. It is thus expected that overstorey gaps should lead to the recruitment of shade-tolerant conifers into the canopy in all stand development stages and that the recruitment of shade-intolerant hardwoods would be minimal except in the largest gaps.

2. We analysed short-term gap dynamics over a large 6-km^2 spatial area of mixed-wood boreal forest across a gradient of stands in different developmental stages with different times of origin since fire (expressed as stand 'age') that were affected differentially by the last spruce budworm (SBW) outbreak. Structural measurements of the canopy from lidar data were combined with spectral classification of broad species groups to characterize the gap disturbance regime and to evaluate the effect of gap openings on forest dynamics.

3. Estimated annual gap opening rates increased from 0.16% for 84-year-old stands to 0.88% for 248-year-old stands. Trees on gap peripheries in all stands were more vulnerable to mortality than interior canopy trees.

4. Due to recovery from the last SBW outbreak 16 years previously, gap closure rates were higher than opening rates, ranging from 0.44% to 2.05% annually, but did not show any relationship with stand age. There was, however, a continuing legacy of the last SBW outbreak in old-conifer stands in terms of a continued high mortality of conifers. In all stands, the majority of the openings were filled from below, although a smaller but significant proportion filled from lateral growth of gap edge trees.

5. *Synthesis*. The forest response to moderate- to small-scale disturbances in old-growth boreal forest counters the earlier assumption that the transition from one forest state to the next is slow and directional with time since the last fire. Overall, a small 6% increase in hardwoods was observed over 5 years, largely due to regeneration in-filling of hardwoods in gaps instead of successional transition to more shade-tolerant conifers. Gaps are vital for hardwood maintenance while transition to softwoods can occur without perceived gap-formation as overstorey trees die, releasing understorey trees.

Key-words: boreal forests, canopy composition, canopy gap opening and closure, canopy turn over times, high-resolution images, lidar, natural disturbance, spruce budworm legacy effect, succession

Introduction

Forest dynamics are generated by a complex set of interactions between multiple disturbance events occurring at different moments in stand development. At the landscape scale, the composition of boreal forests has been directly linked to time since fire such that forests are dominated by late-successional

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species when intervals between fires are long and by pioneer species when intervals between fires are short (Liu 1990; Flannigan & Bergeron 1998). When fires are infrequent, insect disturbances modify forest dynamics and some authors suggest that insects, such as the spruce budworm (SBW), accelerate succession or maintain shade-tolerant species (Baskerville 1975; MacLean 1988) while others suggest that they aid in maintaining shade-intolerant, non-host species (Ghent, Fraser & Thomas 1957; Bouchard, Kneeshaw & Bergeron 2006). When fires and outbreaks interact, forest development patterns may thus be altered and not follow a directional pattern (Bergeron & Dansereau 1993).

Similar patterns of convergent and divergent succession have also been observed for gaps (Runkle 1981; Frelich & Reich 1995; Kneeshaw & Bergeron 1998). However, the role of gaps in influencing forest composition and structure, although important in tropical and temperate forests where they ensure that certain tree species attain canopy status (Denslow & Spies 1990; Runkle 1998), is ambiguous in boreal systems. It has been suggested that large gaps favour intolerant hardwoods while smaller gaps lead to the recruitment of shade-tolerant conifers (Kneeshaw & Bergeron 1998). However, in other boreal forests gaps were found to have limited influence on understorey tree establishment and in determining species composition (Webb & Scanga 2001; Hill, Mallik & Chen 2005; de Romer, Kneeshaw & Bergeron 2007). The complexity of interactions between gaps and other disturbances may also render generalization about the influence of gaps on successional dynamics difficult.

Structural stand development may also be linked to gap size. Random small openings in the canopy due to single treefalls have been shown to be closed rapidly by adjacent vegetation in the initial stages of development while larger openings due to insect infestation, wind-throw or multiple gap makers in the old-growth stage are filled through advance regeneration (Tyrrell & Crow 1994; Oliver & Larson 1996; Yamamoto & Nishimura 1999). There are also questions as to the distance gap effects may extend into the understorey with some research suggesting that distance effects should be important in high-latitude forests (Canham *et al.* 1990; Ban *et al.* 1998). Trees on gap edges may also be more vulnerable to disturbances, such that gaps may expand over time. Although this phenomenon has not been directly measured in boreal forests, the influence of gap edge is equivocal in other ecosystems. For example, the presence of gaps did not influence gap edge tree mortality rates in hardwood temperate forests (Runkle & Yetter 1997; Runkle 1998), but gap expansions were more frequent in wind-prone sub-alpine forests (Worrall, Lee & Harrington 2005).

Investigations on disturbance regimes and forest dynamics are often based on a small number of transects, small plots in a limited number of stands, or coarse-scale analysis at the landscape level. These techniques provide useful results on replacement patterns and composition or structural changes, yet are spatially constrained to sites deemed representative. Large-area studies at fine scales of forest dynamics, such as possible with lidar (light detection and ranging) and high-resolution images, are needed to account for spatial heterogeneity within a forest, and thus to provide greater confidence in the rate at which change is occurring.

The main objective of our study was to develop an understanding of how canopy gaps affect stands previously disturbed by both the SBW and by fires at different times in the past. To attain this goal, we asked questions about (i) the rate of canopy change, (ii) the type of gap formation, and (iii) composition change in stands that vary in age (as measured by time elapsed since the last stand-initiating fire) and impact of the most recent SBW outbreak. We first hypothesized that older conifer-dominated stands should be undergoing greater closure than opening as a legacy of the SBW outbreak while younger, hardwood-dominated stands should be opening since the dominant species have attained their average longevity. Secondly, as surviving edge trees may have been weakened following SBW outbreak, we hypothesized that new gap area would be primarily due to gap expansions in conifer-dominated stands whereas random mortality would be the dominant type of gap formation in hardwood stands. Finally, earlier work suggesting directional succession (Bergeron 2000) and the presence of seedling banks of the shade-tolerant conifers lead us to expect a greater recruitment of conifers than hardwoods in all stand types.

Study site

The 6-km^2 site chosen for this study falls within the Conservation Zone (79°22′ W, 48°30′ N) of the Lake Duparquet Training and Research Forest, situated at the southern limit of the boreal forest in the balsam fir-white birch bioclimatic region of Claybelt forests in Quebec and Ontario, Canada. The region has relatively level topography (ranging from 227 to 335 m a.s.l.) interspersed with few small hills. The regional climate is described as subpolar, subhumid, continental with 0.8 °C mean annual temperature, 857 mm of average precipitation and a 160-day growing season (Environment Canada 1993). The frost-free period lasts 64 days on average, but occasional frost episodes may occur anytime during the growing season. Sixty-three percent of the study site is covered by forest and nearly 29% is floodplains. Surface deposits are largely clay, till soils or rocky outcrops.

This part of the boreal forest is largely dominated by mixed-wood stands which originated from different fires between 1760 and 1944 (Danserau & Bergeron 1993). Canopy height varies between 20 and 25 m. Balsam fir (*Abies balsamea* L. [Mill.]) is the dominant species in the older forests whereas trembling aspen (*Populus tremuloides* [Michx]) dominates the younger forests (Bergeron 2000). These species grow in association with white spruce (*Picea glauca* [Moench] Voss), black spruce (*Picea mariana* [Mill] B.S.P.) and white birch (*Betula papyrifera* [Marsh.]). Eastern white cedar (*Thuja occidentalis* L.) is also a late-successional associate of balsam fir on mesic sites and is abundant on shore lines and on rich organic sites. All of the hardwood species found in the study area are shade-intolerant while the studied softwood species are shade-tolerant (Kneeshaw *et al.* 2006).

The main disturbances in this area are forest fires and SBW outbreaks (Morin, Laprise & Bergeron 1993). There has been a considerable decrease in the frequency and extent of fires since 1850 (Bergeron & Archambault 1993). Three major SBW epidemics were recorded for the 20th century by Morin, Laprise & Bergeron (1993), with the 1972–87 outbreak resulting in the death of most adult fir trees. Defoliation due to forest tent caterpillar outbreaks in 1950 and 2001 has also been documented as causing a decrease in hardwood species. Although part of the forest was selectively cut, much of the study forest is relatively undisturbed and remains unaffected by human activities (Bescond 2002).

Materials and methods

LIDAR AND GAP DYNAMICS

Multi-temporal lidar surfaces were used to characterize gap dynamics while broad species compositions were derived from the high-resolution images. Owing to its ability to directly measure the 3-D distribution of plant canopies as well as subcanopy topography with unprecedented accuracy and consistency, lidar, in recent decades, has emerged as a superior tool for estimating vegetation height, cover and detailed canopy structure of the forest (Lefsky *et al.* 2002; St-Onge, Treitz & Wulder 2003). Comparing canopy height models (CHM, a raster surface representing canopy height) over time, a few recent studies have validated the ability of lidar to detect treefalls of varying sizes (Vepakomma, St-Onge & Kneeshaw 2008) and estimation of height growth (St-Onge & Vepakomma 2004; Yu *et al.* 2004). In this study, we investigated boreal forest dynamics using a combination of lidar and high-resolution multi-spectral imagery over a period of 5 years between 1998 and 2003.

LIDAR DATA AND CANOPY SURFACES

The study site was surveyed on 28 June 1998 and 14–16 August 2003. The data specifications and acquisition details are provided in Table 1. For this study, only the first returns classified as vegetation (vegetation returns) and the last returns classified as ground (ground returns) by the provider were considered. Both lidar datasets were assessed for accuracy in measuring tree height in two different studies (Coops *et al.* 2004; Véga & St-Onge 2008). Clearly identifiable hardwood and softwood trees, 36 (for 1998) and 77 (for 2003) with a height range of 5.6–33.1 m, were field-measured for maximum tree height. The relationship between field-measured maximum tree height and maximum lidar height for the delineated crowns was found to be strong ($r^2 = 0.88$ for 1998 and 0.86 for 2003) with an RMSE of 1.8 and 1.85 m, respectively. The two lidar datasets were co-registered in x, y and z for temporal comparisons using the methods presented in Vepakomma, St-Onge & Kneeshaw (2008). Various visualization strategies (e.g. hill shading, transparency and swiping) (i) between Digital Terrain Models (DTMs, created using classified ground returns, representing surfaces of the underlying terrain), (ii) between Digital Surface Models (DSMs, created using classified vegetation returns, representing canopy surfaces), (iii) trends in sloping terrain on the arithmetic difference of the DTMs, showed no apparent planimetric shift. Bias in z of 22 cm in the 1998 dataset was estimated as the average altimetric difference using (iv) all the corresponding ground returns for 2003 falling within a 10-cm radius of the 1998 hits (matched pairs), and (v) all ground returns within a few rare patches of bare ground. The bias in z of the 1998 lidar set (both ground and vegetation returns) was then corrected.

Table 1. Specifications of lidar data used

Data characteristics	1998	2003
Lidar acquisition system	ALTM1020	ALTM2050
Acquisition date	28 June	14–16 August
Power (μJ)	140	200
Flight altitude (m AGL)	700	1000
Flight speed (m s^{-1})	65	70
Divergence (mrad)	0.3	0.2
Footprint size at nadir (cm)	21	20
Pulse frequency (Hz)	4000	50 000
Scan repetition rate (Hz)	16	35
Maximum scan angle (degrees)	10	15
Mean density of first return (hits m^{-2})	0.3	3
Density range of first return (% of the study area with at least 1 hits m^{-2})	0–14 (60)	0–12 (90)
Mean density of ground returns combined from both surveys (hits m^{-2})	0.3	0.3
Density range of ground returns combined from both surveys (hits m^{-2})	0–6	0–6
Classification software	REALM	TERRASOLID

The CHM for the study area was generated for both years by calculating the difference between the elevations of the respective canopy surface (DSM) and the underlying terrain (DTM). Assuming that the terrain conditions did not change over the study period, we combined the ground returns from both surveys to improve the average point density from 0.03 to 0.3 hits m^{-2}. Rasterization of point data to generate surfaces was performed by choosing the highest laser return (and lowest for ground) within a grid cell of 0.25 m, and supplementing the missing values (40% for 1998 and 10% for 2003 canopy surfaces) with the Inverse Distance Weighting algorithm interpolated heights of the neighbouring cells.

DELINEATION OF CANOPY GAPS ON LIDAR SURFACE

In this study, we defined a gap as an opening in the canopy caused by the fall of a single canopy tree or a group of canopy trees such that the height of any remaining stem is $<$ 5 m in height (fixed based on field observations). The edge of a gap is defined as the vertical projection of the canopy crown of trees adjacent to the gap. Features like streams, rock outcrops or marsh lands were not considered to be a part of canopy gaps. On the basis of image classification of Quickbird imagery, these features were eliminated from the lidar CHMs. The resulting area for the study was thus slightly lower than 6 km^2. We then identified gaps on the lidar CHMs as individual objects of contiguous binary grid cells determined by a gap indicator function (eqn 1), that have a minimum size of 5 m^2 (to avoid interstitial spaces and because this was equivalent to the minimum tree size measured on the field) and which were represented by at least three lidar vegetation returns (Vepakomma, St-Onge & Kneeshaw 2008). A gap indicator function G was defined for a given grid cell at (x,y) on the CHM$_i$ as:

$$G_i(x,y) = \left\{ \begin{matrix} 1 & \text{if } \mathrm{CHM}_i(x,y) < a \\ 0 & \text{otherwise} \end{matrix} \right\}, \qquad \text{eqn 1}$$

where $a = 5$ m in this study, CHM$_i$(x,y) is the lidar height of the canopy surface in the ith year at location (x,y). A region-growing algorithm, which joins cells of similar characteristics, applied to this binary grid identified individual gap objects of non-null adjacent cells. An example of gap identification as determined by lidar and the corresponding high-resolution image is presented in Fig. 1. A comparison of 29 field-measured gaps along 980 m of transect with lidar-delineated gaps made in the earlier study showed a strong 96.5% match for the number of gaps identified and an overall 73.4% match for the total gap length measured along the transects (only one transect had less than a 92% match).

Combinatorics for the two lidar surfaces and gap objects were applied to identify the nature of each gap event: new gap area or closed gap area. New gap area was further subdivided into random new gaps or gap expansions, and closed gap area was further subdivided into laterally closed gaps or vertically closed gaps. New gap area was defined as a gap in the canopy that opened between 1998 and 2003. New gap area that shared the edge with a gap that existed in 1998 was classified as gap expansion, while the remaining new gap area was identified as 'random new gap' (see Vepakomma, St-Onge & Kneeshaw 2008). Areas with vegetation > 5 m in height were considered to be closed forest. Gap closure occurred when the average vegetation height increased from below 5 m in 1998 to over 5 m by 2003. A gap can be closed by crown displacement (or expansion through lateral growth), or by vertical growth of regeneration (see Vepakomma, St-Onge & Kneeshaw 2008). Coalescing gaps formed when gap expansions connected two existing gaps to form a single large gap (Fig. 2a,b). Shifting gaps were those existing gaps that experienced both expansion and also closure that split a gap over the evaluated time period (Fig. 2c,d). The criteria for minimum size of an object and number of vegetation returns on each of the lidar CHMs were extended to all gap events to increase reliability of their identification.

The estimated bias in using unequal point return density of vegetation was found to be reasonably low to efficiently capture gap dynamics in these boreal forests. More details and analyses are provided in Appendix S1 in Supporting Information.

GAP DISTURBANCE CHARACTERISTICS

Gap characteristics like percentage of land area in gaps (gap fraction), number of gaps per unit area (gap density per hectare), gap-size distribution based on the frequency of gaps per hectare, annual rates of opening and closure of gaps and turnover were calculated within the ArcGIS 9.2 environment based on the standard guidelines for evaluating forest gaps (Runkle 1992). Gap size and gap perimeter were determined as the gap object area and gap object perimeter. We note that although this method gives a near-complete survey of canopy

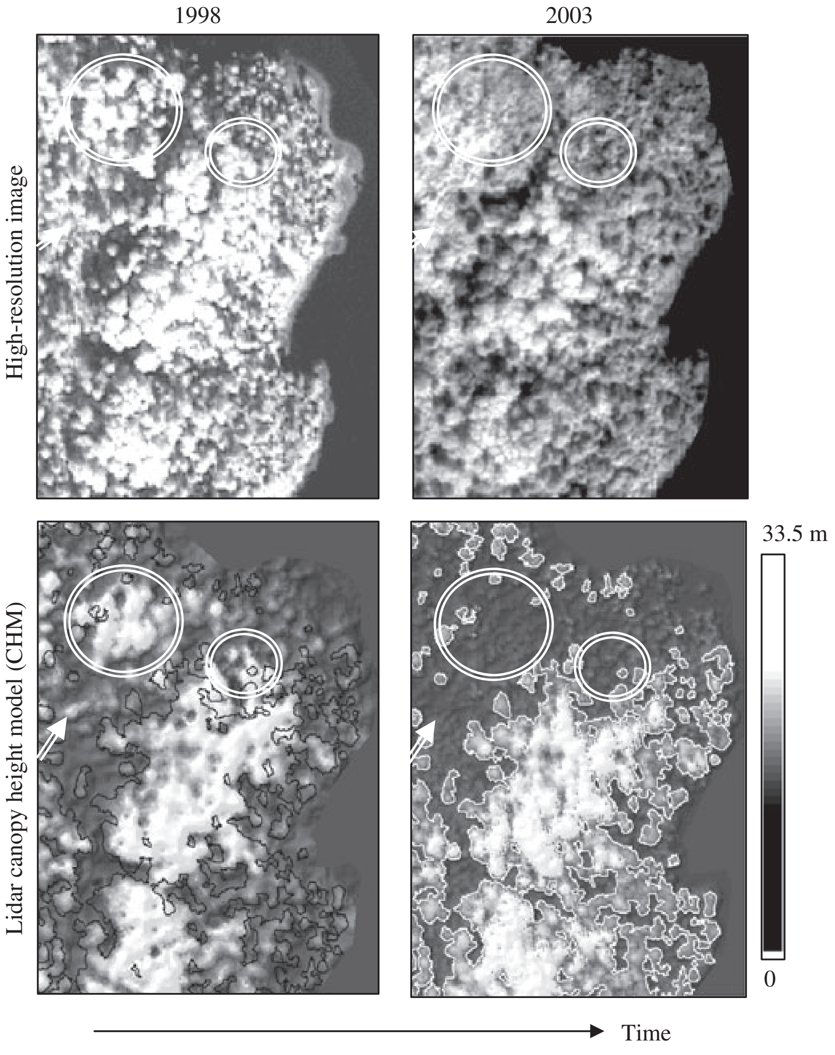

Fig. 1. Example showing delineation of gap opening in 2003 on the lidar CHM (black lines on CHM 1998, white lines on CHM 2003) and high-resolution images in a 120 × 180 m window. New gaps formed by single tree (arrow) and group of trees (double line circle) falls, during 1998–2003 are automatically identified on both high-resolution images (above) and lidar surfaces (below).

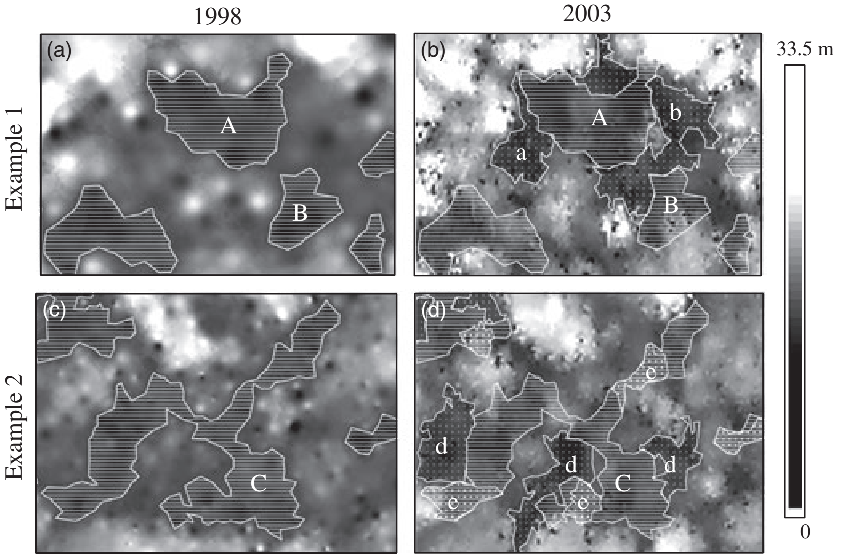

Fig. 2. Coalescing (top set) and shifting (bottom set) gaps during the period 1998–2003 delineated on lidar surfaces seen in a 50 × 40 m window. (a) Gaps in 1998 (e.g. objects A and B) overlaid on CHM 1998. (b) Gap expansion and coalition of objects A and B (by objects a and b to a single large gap object) during the period 1998–2003, overlaid on CHM 2003. (c) Gaps in 1998 (e.g. object C) overlaid on CHM 1998. (d) Gap expansion (object d) and gap closure (object e that splits the object C) during 1998–2003, overlaid on CHM 2003. Polygons filled with horizontal lines show gaps in 1998; polygons with crosses are new gap expansions; dotted line indicates gap closure from 1998 to 2003.

gaps on the lidar surface, due to the constraints set on minimum object size and vegetation returns, many small objects were eliminated. As a result, the sum area (and hence their proportions) of all the gap events and non-gap objects for a given year do not completely add up to the total area under study.

Gap fraction for the assessment year *i*, GF_i, is a proportion of forest area under gaps in year *i*, and was estimated using:

$$\mathrm{GF}_i = \sum_{k=1}^{T} \mathrm{AG}_k^i \Big/ A, \qquad \text{eqn 2}$$

where AG_k^i is the area (in m^2) of the *k*th gap object in the *i*th year and *A* is the total study area.

The annual rate of gap opening

$$\begin{aligned}\mathrm{GO} &= (\text{proportion of land area in new gaps of age} \le n \text{ years old})/\\ &\quad n \text{ years} \times 100\\ &= \left[\sum_{l=1}^{p} \mathrm{AN}_l^{ij} \Big/ An\right] \times 100, \ n = 5 \qquad \text{eqn 3}\end{aligned}$$

where AN_l^{ij} is the area (in m^2) of the *l*th new gap object during the period (i,j), $i < j$, *p* is the total number of new gap objects in the study area.

The annual rate of gap closure is

$$\begin{aligned}\mathrm{GC} &= (\text{proportion of land area where the canopy closed}\\ &\quad \text{in the gaps})/n \text{ years} \times 100\\ &= \left[\sum_{f=1}^{q} \mathrm{AC}_f^{ij} \Big/ An\right] \times 100, \ n = 5, \qquad \text{eqn 4}\end{aligned}$$

where AC_f^{ij} is the area (in m^2) of the *f*th gap closure object during the period (i,j), $i < j$ and *q* is the total number of gap closure objects in the study area.

Canopy turnover time was estimated based on total new gap formation and new gap closure independently using:

$$(\mathrm{GO})^{-1}, \qquad \text{eqn 5}$$

and

$$(\mathrm{GC})^{-1}. \qquad \text{eqn 6}$$

To determine the extent to which random new gaps are indeed occurring randomly in relation to distance from a given existing gap, we compared the relative frequency distributions of the occurrence (geographic location) of a random new gap area with respect to its distance from the nearest existing gap edge. We conjectured that the occurrence of random new gaps in this study area is influenced by the presence of an existing gap. Here, we assume that such a distribution should be uniform if the occurrence of new gaps is random (validation is presented in Appendix S2). Distance was calculated as the Euclidean distance from the centroid of a random new gap opening to the nearest edge of a gap existing in 1998.

DATA ON STAND INITIATON

We used the stand initiation maps created by Danserau & Bergeron (1993) for this area to identify the different times of origin since fire (TSF) for each stand. The stand chronosequence was 248, 206, 133, 123, 96 and 84 years TSF. In other terms, the stands originated in 1760, 1797, 1870, 1880, 1907 and 1919. The stands covered 38%, 30%, 27.5%, 1.4%, 1.69% and 1.85% of the study area, respectively. In this study, these stands represent stand developmental stages and throughout the text stand 'age' is used when referring to TSF.

CLASSIFICATION OF SPECIES COMPOSITION

High-resolution multi-spectral images acquired on 27 September 1997 and 13 June 2004 in leaf-on condition were used to classify vegetation in the study area into conifer- or hardwood-dominated forests. The 1997 dataset consisted of 150 photo captures of near-nadir aerial videography data (0.50-m resolution) in green (520–600 nm), red (630–690 nm) and near infrared (760–900 nm) bands. The 2004 data were an 'ortho-ready' (standard image with minimal adjustments) Quickbird satellite image acquired in panchromatic (0.61-m resolution, 450–900 nm) and multispectral modes (2.44-m resolution, spectral windows similar to videography). Theoretically, minimal changes occurred between the acquisition of videography (end of growing season in September 1997) and the first lidar dataset (beginning of the growing season in June 1998). Similarly, few changes are expected between the collection of the second lidar dataset (near the end of the growing season in August 2003) and the capture of Quickbird images (beginning of the growing season in June 2004). Generally leaf-fall begins mid-October in this region (B. Harvey, LDTRF, personal observations). Change in foliage colour had no impact on the accuracy of classification of hardwood species.

The Quickbird images were ortho-rectified with reference to the lidar DSM of 2003 based on modified rational polynomials (for more details refer to St-Onge *et al.* 2005). A simple first-order polynomial rectification was then performed for each of the individual photo captures using the ortho-rectified Quickbird data as the horizontal geometric reference and then mosaicked in PCI GEOMATICA v9.01. Canopy height derived from the lidar data was integrated with the spectral signatures of the image data (both years independently) to extract automatically individual image objects using a standard nearest-neighbourhood classification procedure in ECOGNITION v. 3.0 (Definiens GmbH, Munich, Germany). This method helped us to separate successfully shadows from vegetation, a problem otherwise inherent in high-resolution imagery. Open areas and delineated shadows were merged into a miscellaneous class. Features like streams, rock outcrop, roads and marsh lands were eliminated from the study. We validated the image classification using 40 (for 1998) and 30 (for 2003) hardwood and softwood field-identified trees, and 24 non-forest locations. A confusion matrix – a plot used to evaluate actual and predicted classifications – yielded an overall accuracy of 84% and 87.5%, respectively. The errors found were largely due to softwoods mixing with the shadow class.

Results

CHARACTERIZATION OF GAP DYNAMICS

Extent of canopy opening

In general, the percentage area under gaps decreased from 38 to 32, with 23.45% of the gap area continuing to remain open over the 5-year study period (Table 2 and Fig. 3a). The total number of gaps per hectare decreased from 17.1 to 13.6. However, the number of gaps > 1 ha in size increased from 23 to 30 during the study period. This may be due to partial closure

Table 2. Gap dynamic characteristics in a 6-km^2 area of the south-eastern boreal forest during 1998 and 2003 as derived from lidar data

				New gap area			Closed gap area		
Statistic	Gaps in 1998	Gaps in 2003	Common open areas	Expansion	Random	Total new gap area	Lateral growth	Regeneration height growth	Total gap closure
Gap frequency per hectare	17.09	13.55	15.83	11.16	0.79	11.95	19.00	60.25	33.85
Minimum gap size (m^2)	5.0	5.0	5.0	5.0	5.0	5.0	3.0	5.0	5.0
Maximum gap size (m^2)	9.8 ha	9.2 ha	5.9 ha	2182.5	223.1	2182.5	63.5	402.5	451.4
Mean gap size (m^2)	156.4	202.3	149.2	24.6	14.6	23.9	7.1	9.3	17.7
Median gap size (m^2)	19.6	24.5	23.6	13.7	11.1	13.4	5.7	6.6	12.1
Standard deviation gap size (m^2)	1708.6	2075.7	1308.8	60.4	14.5	58.5	4.4	12.5	20.3
95% confidence limit of mean gap size (m^2)	121.9–190.9	156.4–248.2	122.2–176.1	23.1–26.1	13.0–15.9	22.6–25.4	7.1–5.7	9.1–9.4	17.4–17.9
Percentage of area under gap	38.0	32.0	23.45	2.75	0.11	2.87	1.34	4.64	5.98
Percentage frequency of gaps < 100 m^2	86.7	85.08	85.04	100	97.58	97.71	99.99	99.7	99.04
Number of gap of size > 1 ha.	23	30	17	0	0	0	0	0	0
Gap fraction (in %)	35.03	31.54	27	2.75	0.12	2.87	1.34	4.64	5.98
Annual rate of gap formation (opening and closure) in %	–	–	–	0.55	0.024	0.57	0.27	0.93	1.2
Turn over time (in years)	–	–	–	–	–	175	–	–	83.6
% Hardwood in gap areas that have opened or closed	–	–	–	36	31	35	54	50	50
% Softwood in gap areas that have opened or closed	–	–	–	64	69	65	46	50	50

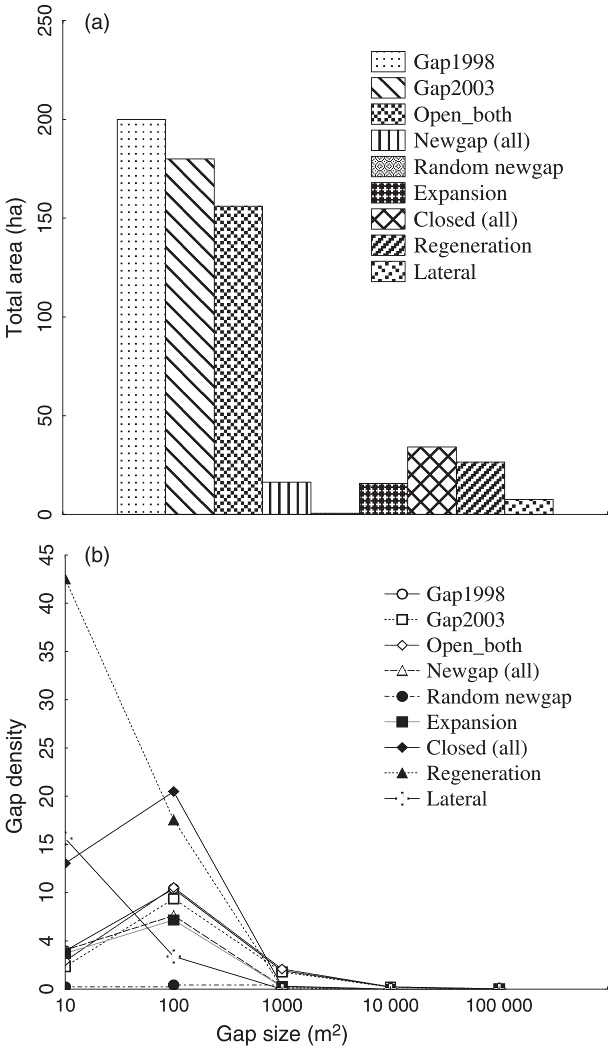

Fig. 3. Gap processes that occurred from 1998 to 2003. (a) The area under different gap events. (b) The gap-size distribution of different gap events. *X*-axis shows the upper limit of the gap-size class. Gap1998, gaps in 1998; gap2003, gaps in 2003; open_both, areas open in both 1998 and 2003; newgap(all), new openings (random gaps and gap expansions combined) that occurred from 1998 to 2003; random new gap, random gap opening during the period 1998–2003; expansion, gap expansion from 1998 to 2003; closed (all), gap closure (height growth of regeneration and lateral closure combined) during the period 1998–2003; regeneration, gap closure due to height growth of regeneration during the period 1998–2003; lateral, gap closure due to lateral expansion during the period 1998–2003.

of very large gaps (> 5 ha) in 1998. The mean and median gap sizes were 156.4 and 19.6 m^2, respectively, in 1998 but they increased to 202.3 and 24.5 m^2, respectively, in 2003. The gap-size frequency distribution based on frequency per unit area for both years is approximately lognormal, with the modes occurring in the 10- to 100-m^2 size class for all gap characteristics. Exceptions are seen in the case of closure due to vertical growth of regeneration and lateral extension, for which the distributions decrease monotonically (Fig. 3b). The distribution pattern of gap size did not change over time, especially for existing and new gaps, but the magnitude of frequency was found to vary. Hence, the distributions of gap sizes are significantly different (Kolomogorov–Smirnov test, $P < 0.01$) between all types of gap events.

New gap area

A total area of about 16.37 ha in 6826 gaps opened within the canopy during the evaluated 5-year period. The size of the new gaps ranged from 5 to 2182 m^2, with an average size of 25 m^2 (Table 2). On the basis of their size, 97% of the gaps were formed due to a single or a few trees disappearing from the canopy (Fig. 3b). Although the average gap size increased over time due to gap expansions and gap coalescing (Fig. 2), the size of new gaps was significantly smaller than that of older ones (Mann–Whitney *U*-test, $P < 0.01$). Based on these recent gap openings, gap density is *c.* 12 ha^{-1}, which is slightly lower than the gap density based on all the gaps in 2003. The estimated annual rate of new gap area is 0.57% with an estimated turnover of 175 years.

Gap expansions versus random new gaps

Out of the 6826 new gaps that opened between 1998 and 2003, 94% are gap expansions from gaps existing in 1998 (Table 2). There is more area in gap expansions (15.70 ha) than that formed by random new gaps (0.66 ha). The mean area that was added to an existing gap, i.e. gap expansion is 25 m^2 while that of the random new gaps is 15 m^2. Maximum size of gap expansion is 2182 m^2, while the maximum size of random new gaps is 223 m^2. With the exception of two large gap expansions and one large random new opening (both > 1 ha) that opened near streams, nearly 87% of the gap expansions and 90% of the random new openings are smaller than 55 m^2. This suggests that canopy opening is caused by the death of one or very few trees. However, the size distribution of gaps that expanded is significantly greater than that of random new gaps that formed during the study period (Kolmogorov–Smirnov test, $P < 0.001$). Gap density over the 5 years and annual rates of opening of gap expansions are 11.2 gaps ha^{-1} and 0.55% vs. 0.8 gaps ha^{-1} and 0.02%, respectively, for random new gap openings.

New gap expansions coalesced about 409 existing gaps at an annual average rate of 286 m^2 during the study period. We also note that about 989 existing gaps with a mean gap size of 1173 m^2 in 1998 both expanded and closed. Gap-size distribution indicates that such coalesced gaps were larger than 100 m^2. Although the overall rate of closure is higher than that of new gap opening in these boreal forests (Table 2), the opposite was noted for gaps that were both expanding and closing during 1998–2003. Of the new gaps that coalesced, over 2.6% of the existing area in canopy opening was closed but another 13% opened as gap expansions.

Gap closures

Overall, in these forests the annual rate of canopy closure was 1.2%, which is twice as fast as the creation of new canopy openings (0.6% annually). Between the two time periods, a total of 34.15 ha of canopy closed and maximum size of the closure was 451 m^2. However, of the 19 329 objects that underwent closure, 99% were smaller than 100 m^2.

Lateral versus vertical growth

The majority of gaps that closed in these forests did so due to vertical growth of the regenerating vegetation (56.5% of the total number of gaps that closed during the 5 years). The total area that closed laterally was 7.7 ha whereas the total area that closed through height growth of the regenerating vegetation was 26.5 ha (Table 2). Gaps that closed due to lateral extension ranged from 5.0 to 10.9 m^2 in size while gaps that closed due to height growth of regenerating vegetation ranged from 5.0 to 403.0 m^2.

GAP DYNAMICS IN STANDS IN DIFFERENT DEVELOPMENTAL STAGES

Gap fraction was reduced in all stands from 1998 to 2003, with the exception of the youngest stand, while the greatest decrease occurred in the oldest conifer-dominated stand (Table 3). New gaps opened more frequently in the oldest stands (burned in 1760 and 1797) than in the remaining younger stands with rates of gap opening of 0.88% and 0.6%, respectively. Over 60% of the new gaps were formed due to gap expansions. Although the maximum gap sizes varied significantly, the variation in mean gap sizes was not significant across the stands. The rates of gap closure were consistently higher than the rates of opening in all stands, but gap closures were highly fragmented with a mean size lower than the mean size of new gaps. Gap turnover was shortest in the oldest stands (114 years) and longest in the youngest stand (643 years). The percentage of area in gap closures increased with stand age, largely due to regenerating vegetation closing gaps from beneath. Closure from the side, i.e. lateral expansion, was noted in all stands with the most occurring in the oldest stands.

The gap density distribution for all gap dynamic characteristics is approximately lognormal in all stands with the peak in frequency occurring mostly in the 10–100 m^2 size class. Interestingly, the pattern did not differ from the gap density distribution observed at the forest level (Figs 3 and 4). In all but the youngest stand, gap expansions occur more frequently than random new gaps. Gap closures in the oldest stand are the most fragmented compared to the other stands. However, differences in the gap density distributions of all gap dynamics events between the differently aged stands are highly significant (Kruskal–Wallis ANOVA by ranks and Median tests, $P \approx 0$).

Random new gaps appeared at a distance of 0.5–38 m from the edge of an existing gap in 1998. The range of gap density increased from 2.2 to 7.4 ha^{-1} with stand age (Table 3). The number of random new gap occurrences varied with distance from the existing gaps and increased with stand age (Fig. 5). Nonetheless, the majority of the random new gaps (75% of random new gaps in older stands and 60–75% of random new gaps in younger stands) appeared within 2.5 m of the existing gap edge irrespective of the openness of the stand (Fig. 5a–d).

Table 3. Gap characteristics for different aged stands in the south-eastern boreal forest (1998–2003)

Statistic/time since fire (years)	84	96	123	133	206	248
Gap fraction in 1998 (in %)	16.20	42.52	11.59	16.26	45.90	36.10
Gap fraction in 2003 (in %)	20.19	34.48	8.59	13.89	40.18	33.90
New gap area						
New gap density ha^{-1}	5.0	15.5	9.9	10.9	18.1	21.5
Maximum gap size (m^2)	289.4	57.4	48.5	2107.6	867.9	2182.5
Mean gap size (m^2)	17.8	13.2	11.9	22.9	16.9	20.8
Median gap size (m^2)	7.7	9.4	9.9	12.5	10.6	11.7
% Area under new gaps	0.78	1.89	1.10	2.47	3.01	4.4
% New gap area that was hardwood	30.00	27.00	24.71	46.96	33.13	30.06
% New gap area that was softwood	70.00	73.00	75.29	53.04	66.87	69.94
Annual rate of gap opening (%)	0.16	0.38	0.22	0.5	0.6	0.88
Gap turnover (years)	643	265	455	202	166	114
Gap expansion – gap fraction (gap density)	0.61 (2.84)	1.31 (9.18)	0.67 (4.89)	1.92 (6.47)	2.31 (11.85)	3.57 (14.05)
Random new gap opening – gap fraction (gap density)	0.17 (2.2)	0.57 (6.29)	0.43 (4.89)	0.55 (4.4)	0.67 (6.23)	0.83 (7.4)
Gap closure						
% Area closed to the total area	2.19	10.27	3.68	4.93	7.59	6.15
Annual rate of gap closure (%)	0.44	2.05	0.74	0.98	1.52	1.23
Closure turnover (years)	228	49	136	101	66	81
Area closing from side – gap fraction (gap density)	0.22 (3.76)	1.28 (20.16)	1.45 (20.89)	1.06 (14.44)	1.49 (21.92)	1.48 (18.3)
Area closing from below – gap fraction (gap density)	1.97 (2.75)	8.99 (19.16)	2.24 (8.0)	3.86 (5.08)	6.10 (21.88)	4.67 (17.18)
% Closure that is hardwood	57.50	48.43	54.04	41.63	47.08	48.82
% Closure that is softwood	42.50	51.57	45.96	58.37	52.92	51.18

Underlined figures are the highest values for a given statistic.

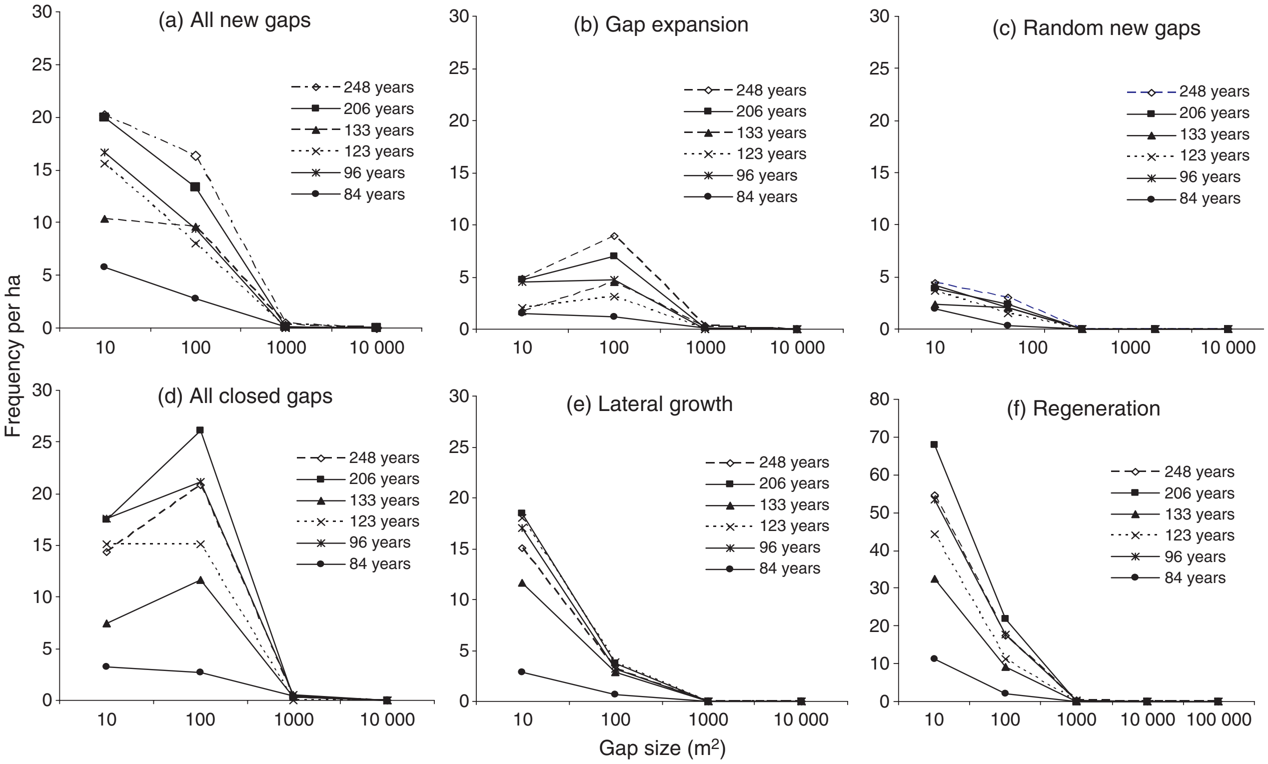

Fig. 4. Gap density distributions of various gap dynamical characteristics in stands originated from different origin (times since fire). Gap-size class upper limits are shown on *x*-axis. Note the differences in scale on the *y*-axes.

GAPS VERSUS CHANGES IN SPECIES COMPOSITION

A comparison of the percentage distribution of class of species composition over the 5-year period shows that the proportional area covered by hardwoods increased over the study period not only across the entire study forest (Table 4) but also in all individual stands (Fig. 6). Softwoods, on the other hand, showed a considerable increase in the younger stands with marginal changes in the older ones. Nearly 70% of the newly opened area (mostly composed of gaps smaller than 500 m^2) in all stand types was due to the loss of softwood trees (Tables 3 and 4, Fig. 6), with a large proportion (50% at the level of the entire forest) being in gap expansions (Table 2). Gaps created only by hardwood trees were usually found to be large (three

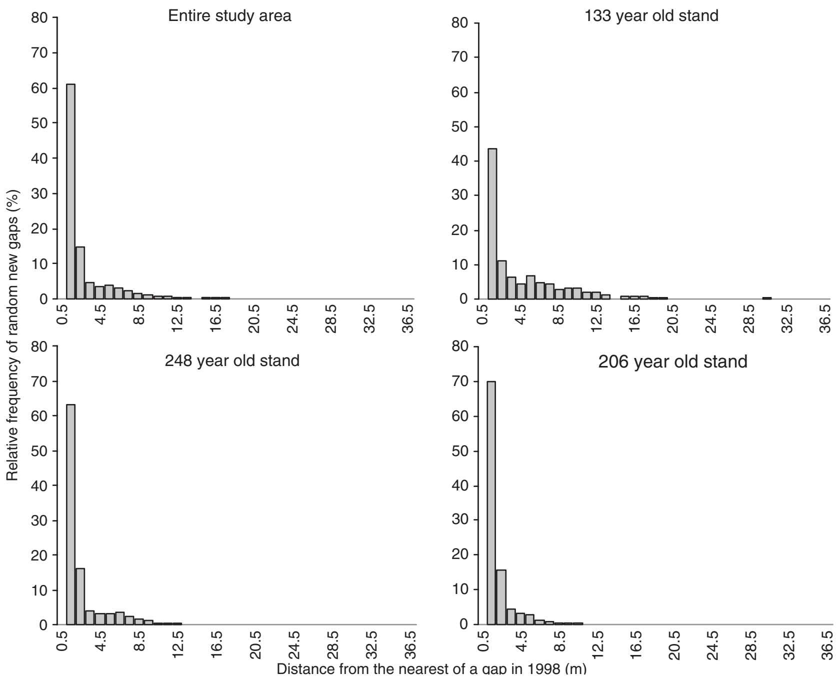

Fig. 5. Gap density distributions of random new gaps as a function of distance from the nearest existing gap for stands having originated from different times since fire stands of the boreal forests. Gap-size class upper limits are shown on *x*-axis.z

Table 4. Broad species compositional changes (given in area ha) from 1998 to 2003 in the mixed-wood boreal forest around Lake Duparquet, Quebec, Canada

	2003				
1998	Hardwood	Softwood	Miscellaneous*	Total	Percentage of the total area
Hardwood	62.76	25.44	21.86	110.06	19.13
Softwood	48.17	50.86	45.45	144.48	25.11
Miscellaneous	44.17	45.5	231.19	273.88	55.75
Total	155.12	121.82	298.5	575.46	
Percentage of the total area	26.96	21.17	51.87		

*Miscellaneous class includes shadows and open areas; Features likes streams, rock outcrops, marsh lands are eliminated from the study.

gaps were over 1 ha, seven were over 500 m^2) and all were close to lakes or streams, suggesting that they may have been created by beaver damage (field observations, Senecal, Kneeshaw & Messier 2004). In general, the number of gaps closed by the growth of hardwoods or softwood species is the same, with hardwood lateral growth being marginally greater than that of the softwoods (Table 2). Although a slightly higher proportion of softwoods in the closed gaps was noted in most of the stands, gaps closed by height growth of hardwood regeneration in the older stands were observed to be large (exceeding 100 m^2).

By examining the changes that occurred in the two broad species groups with respect to their status in 1998, we noted that the gain in the proportion of intolerant hardwoods is much higher than the loss, and that these gains steadily increased with stand age (Table 4 and Fig. 6). Although shade-intolerant hardwoods and shade-tolerant softwoods had similar rates of closing, softwoods gained less area than they lost, and the area gained decreased with the age of stands. Hardwoods topped softwoods at a greater rate in the older stands while softwoods tended to outgrow hardwoods in the younger stands. A higher proportion of the increase in area

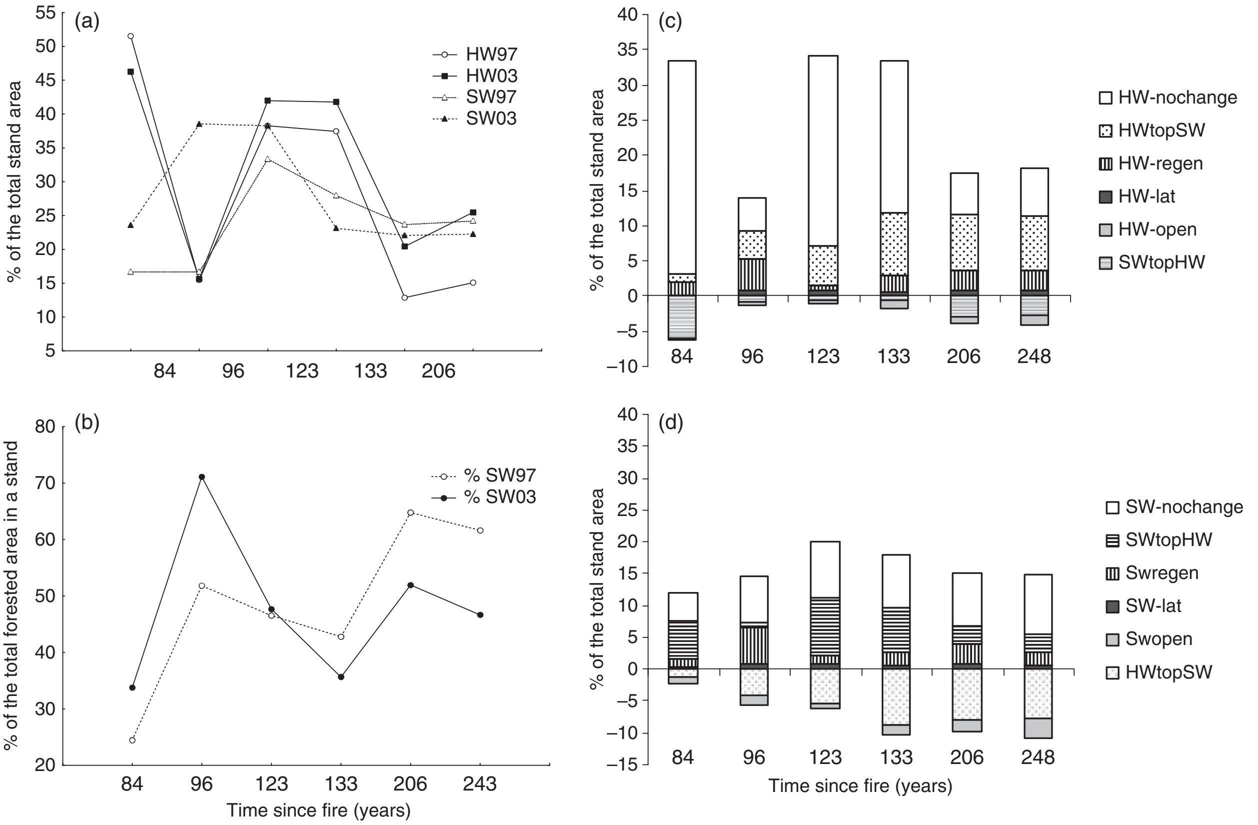

Fig. 6. Changes in the distribution of hardwood and softwood species during 1998–2003 for stands originating at different times since fire stands. (a) Overall changes in species composition in the stands. (b) Percentage distribution of softwood to the total forested area per stand. (c) Stacked graph of the percentage change in the total area of the hardwood of 1997 to various classes in the stands. (d) Stacked graph of the percentage change in the total area of the softwood of 1997 to various classes in the stands. HW, hardwood; SW, softwood; HW-close, hardwood closure; SW-close, softwood closure; HW-nochange, unchanged hardwood; SW-nochange, unchanged softwood; SWtopHW, softwood topping hardwood; HWtopSW, hardwood topping hardwood.

dominated by hardwoods occurred through lateral gap closures. The gain in softwood-dominated areas was mostly due to height growth in the younger stands and, where it occurred, primarily due to lateral growth in the older stands.

Discussion

GAP OPENING AND FILLING IN BOREAL FORESTS

This study reveals that boreal forests of all developmental stages (i.e. recruited after different stand replacing disturbances and then affected by one or multiple SBW outbreaks (Morin, Laprise & Bergeron 1993; Campbell, MacLean & Bergeron 2008) are changing quickly, even within a short time period. The opening of the studied boreal forest canopy over 5 years occurred both via new canopy gaps as well as gap expansions from openings created earlier. Although gap expansion is also a prominent feature in tropical and temperate forests (Foster & Reiners 1986; Lertzman & Krebs 1991; Runkle 1998; Worrall, Lee & Harrington 2005), gap expansions have not been described in other parts of the boreal forest. Previous single-time studies assumed that younger, vigorous boreal stands did not undergo gap expansion and thus they attributed abundant small gaps to random senescence and death of early successional species (Kneeshaw & Bergeron 1998; Bartemucci *et al.* 2002; Hill, Mallik & Chen 2005). Based on our multi-temporal lidar data analyses, we found that trees bordering canopy gaps were more vulnerable to mortality compared to interior canopy trees, and this occurred in all stands regardless of gap fraction. Gap expansions reported in other forests (Foster & Reiners 1986; Rebertus & Veblen 1993; Worrall, Lee & Harrington 2005; Quine & Malcom 2007) were mostly due to wind-throw of edge trees. Although very large expansions were observed, the majority of gap expansions and formation of random new gaps in our study area resulted in gaps smaller than 55 m^2 unlike in wind-driven *Picea–Abies* forests of New Hampshire (Worrall, Lee & Harrington 2005) and *Picea sitchensis* plantations in Britain (Quine & Malcom 2007) where gap expansions were also as frequent but larger in size compared to random new gaps.

The majority of the openings in our study were filled from below (i.e. due to height growth), with a smaller but significant proportion of the closures due to lateral growth of the gap edge trees. It has generally been acknowledged that in hardwood forests small gaps close from the sides while large ones fill from below (Runkle 1981; van der Meer & Bongers 1996; Tanaka & Nakashizuka 1997; Fujita *et al.* 2003). In boreal forests, gap closure from lateral in-filling has not been thought to be important due to the determinate growth and crown form of conifer trees (Nagel & Svoboda 2008). However, both types of canopy closure were observed in our study across a gradient of gap size, although gaps closing due to regeneration lead to larger closure sizes (403 vs. 11 m^2 maximum closed gap size). Furthermore, both hardwoods and softwoods close gaps laterally, which supports the conclusion made by Umeki (1995) that the lateral expansion of gap edge canopy trees towards the gap centre did not differ between conifers and hardwoods.

DYNAMIC STRUCTURAL CHANGES OF STANDS IN DIFFERENT DEVELOPMENTAL STAGES

Canopy gaps in these forests are dynamically expanding, coalescing old gaps to form large openings and closing rapidly during the study period. Openness in all stands generally decreased over time, however, older stands (i.e. those that have had a longer period of development since the last fire) had higher rates of new gap formation. Increased openings with stand development were also noted in 60- to 120-year-old stands in *Populus tremuloides* dominated boreal forests (Hill, Mallik & Chen 2005). This is probably due to the fact that these stands went through a period where canopy opening exceeded closure during the last SBW outbreak (D'Aoust, Kneeshaw & Bergeron 2004). Thus, gaps created during this period of high mortality, in the 1970s and 1980s, are now being filled in with lateral growth and regeneration height growth. Our results over the observed period indicate that the gap clo-

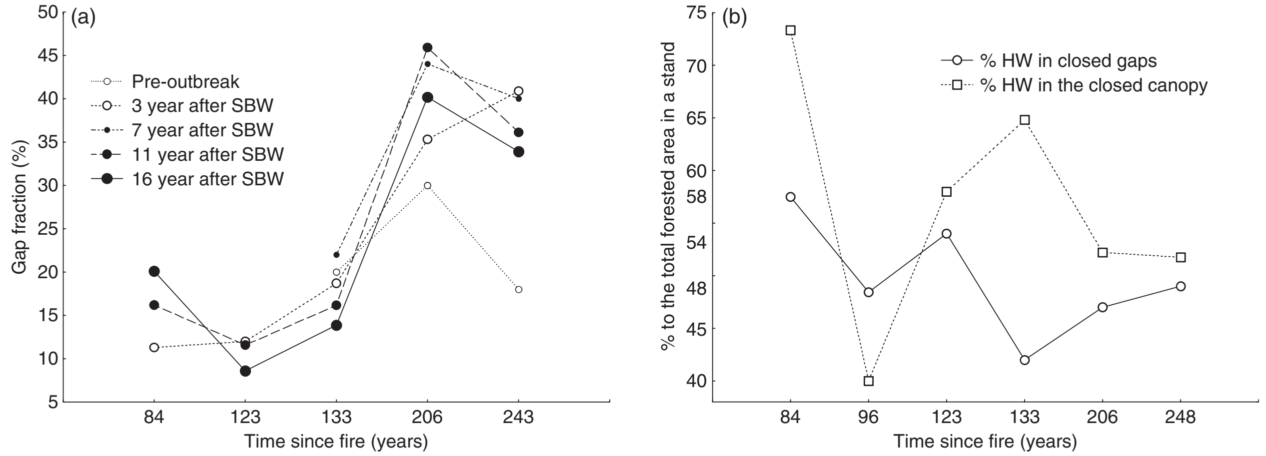

Fig. 7. (a) Comparison of gap fraction over time in different time since fire stands of the boreal forests. SBW, spruce budworm outbreak. Results of pre-outbreak conditions and 7 years after SBW adopted from D'Aoust, Kneeshaw & Bergeron (2004), while 3 years after SBW from Kneeshaw & Bergeron (1998). (b) Comparison of species composition between gaps closing due to height growth of regeneration and closed canopy.

sure rate is higher than the rate of canopy opening, which is in agreement with Brokaw (1985) and Valverde & Silvertown (1997). It should, however, be noted that despite higher rates of closure and the fact that older forests in this study area have been regenerating for 10–20 years following the last SBW outbreak (Morin, Laprise & Bergeron 1993), the forests still appear patchy and open as 78% of the old gaps did not fill and thus continued to remain open over the 5 years of our study (Fig. 7a). It has been suggested that short growing seasons and persistent snow accumulation may delay the filling of gaps in northern latitudes (Lertzman *et al.* 1996; Bartemucci *et al.* 2002; Parish & Antos 2004).

COMPOSITIONAL SHIFTS OF STANDS IN DIFFERENT DEVELOPMENTAL STAGES

In contrast to expectations, responses to the moderate- to small-scale disturbances in these mixed-wood boreal stands did not follow previously conceived successional patterns (Bergeron 2000). Previous research suggested that large gaps favour intolerant hardwoods while shade-tolerant softwoods successfully regenerate in small gaps (Kneeshaw & Bergeron 1998); however, this relationship was not observed here. An evaluation of gaps that totally closed from regeneration between lidar measurements in1998 and 2003 did not show a correlation between species groups and gap opening size. Overall, the proportion of softwood and hardwood regeneration within gaps was almost balanced with only a slight variation between the stands (Fig. 7b). The exception was in the oldest stand where, in contrast to our expectations, a considerable number of the large closures (over 100 m^2) were closed by hardwood regeneration.

In general, there was an increase in the presence of hardwoods in this forest over the study period. As seen in earlier studies in boreal forests (Kneeshaw & Bergeron 1998; Bouchard, Kneeshaw & Bergeron 2006) gaps created by SBW outbreaks seem to be the mechanism for hardwood maintenance in older conifer forests.

As we noted in this study, shifts in species composition in all stands are not just a result of gap dynamics but are also due to tree recruitment to the canopy without gap formation (Fig. 6). As the canopy dies, understorey softwoods assume dominance in younger stands without the formation of a gap although a decrease in canopy height is observed. This mechanism of species replacement may be important in mixed-wood stands in many forest types but is not quantified by standard gap studies. Although less frequent, such a transition without recording of a gap can also occur from conifers to hardwoods in the older stands. As the hardwoods are shade-intolerant and do not occur in the understorey, this suggests a rapid growth response from root suckers following canopy opening. These transitions both support and oppose earlier studies from chronosequences in this region that have shown a slow progression from hardwood-dominated, younger stands to mixed coniferous–deciduous stands due to small-scale disturbances and a continued increase in conifer dominance in mid-to-old aged stands (Bergeron 2000). However, most studies employing the chronosequence approach are carried out using single-time measurements based on a few representative sites from each stand to infer general patterns. Our results thus suggest that there is a large variation in forest response to openings within the generally observed trends in succession. An obvious advantage of using lidar and high-resolution image analysis of canopy gaps is the ability to repeat this near-complete census of canopy openings through time and over an extensive spatial area and hence to capture variations at local scales and across stands.

Conclusions

This spatially explicit fine-scale and short-term study of old-growth boreal forest dynamics counters the earlier assumption that the transition from one forest state to the next in boreal forests is slow, directional and influenced by the period of development since the last fire. Instead we show that that compositional changes within gaps both accelerate and reverse succession. Gaps are important for hardwood maintenance while non-gap replacement is the main mechanism for softwood recruitment in these mixed-wood boreal forests. These results stress the need for temporally analysing large contiguous spatial areas to reduce uncertainty in interpreting and extrapolating dynamics from a few representative sites. The study also provides a promising illustration of the strengths of combining lidar and high-resolution imagery in rapidly evaluating detailed and spatially extensive (a near-complete census of gaps in a large area) short-term dynamics of boreal forests. However, further analysis over a long time period is necessary to verify whether these observed dynamics are a temporary phenomenon or a characteristic that fluctuates with exogenous disturbances such as SBW outbreaks.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Bias in using lower and unequal vegetation return point density of lidar in delineating gap characteristics during the period 1998–2003.

Appendix S2. Occurrence of random new gap area.

Table S1. Gap opening and closure using different point return densities to estimate the bias using unequal as opposed to equal point return densities.

Figure S1. Summary of gap events delineated on surfaces of various lidar point return densities.

Figure S2. Relative frequency distribution of the distance of centroid of random new gaps (simulated and observed on the lidar CHM) to the nearest existing gap edge.