Gap dynamics and replacement patterns in gaps of the northeastern boreal forest of Quebec[1]

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Abstract: The northeastern boreal forest of Quebec is characterized by a humid climate. Consequently, fires are less frequent and small-scale disturbances play an important role in forest dynamics. Natural mortality and nonfire disturbances such as insect outbreaks and windthrow lead to gap-driven processes. Changes in structure and species composition can result from gap dynamics. The objectives of this study were to characterize gaps and examine patterns of species replacement in gaps in old conifer stands. Line intersect sampling was used to sample stands dominated by balsam fir (*Abies balsamea* (L.) Mill.) and (or) black spruce (*Picea mariana* (Mill.) BSP). Results show that 54% of the forest was in expanded gaps and that canopy gaps are relatively small, since 87% of them were smaller than 100 m^2. The majority (94%) of the openings were caused by the mortality of less than 10 gap makers. Replacement probabilities show self-replacement of *A. balsamea* in *Abies* stands and of *P. mariana* in *Picea* stands. However, in *Abies–Picea* stands, there seems to be a reciprocal replacement of the two species. These results provide knowledge of the disturbance dynamics of the region as a basis for development of silvicultural practices that preserve the structural components of older forest stands.

Résumé : La forêt boréale du Nord-Est du Québec est caractérisée par un climat humide, de sorte que les feux y sont moins fréquents. La dynamique forestière est alors contrôlée par des perturbations secondaires (vent et insectes) ainsi que par la mortalité naturelle des arbres engendrant ainsi une dynamique de trouées. Des changements dans la structure et la composition des peuplements peuvent alors survenir. Les objectifs de la présente étude sont d'examiner les caractéristiques des trouées ainsi que les patrons de remplacement des espèces à l'intérieur des trouées de vieux peuplements résineux. Des transects ont été établis dans des peuplements de sapin baumier (*Abies balsamea* (L.) Mill.) ou d'épinette noire (*Picea mariana* (Mill.) BSP). La proportion de peuplements qui se présentent sous forme de trouée étendue atteint 54 % et 87 % des trouées de canopée ont une taille inférieure à 100 m^2. La majorité (94 %) des ouvertures est créée par la mortalité de moins de 10 individus. Les probabilités de remplacement indiquent qu'*A. balsamea* et *P. mariana* se succèdent à eux-mêmes dans les peuplements d'*A. balsamea* et de *P. mariana* respectivement mais qu'il y a un remplacement réciproque de ces espèces dans les peuplements d'*Abies–Picea*. Une meilleure compréhension de la dynamique naturelle permettra de développer des pratiques sylvicoles qui préserveront la structure des vieux peuplements.

Introduction

The importance of small-scale gap dynamics has been recognized for certain types of ecosystems such as temperate (Runkle 1981, 1982; Runkle and Yetter 1987) and tropical forests (Brokaw and Scheiner 1989; Denslow 1987; Whitmore 1989) but has been overlooked until recently in the boreal forest, where fire has long been considered to be the main disturbance (Kneeshaw 2001; Kneeshaw and Bergeron 1998; Kuuluvainen 1994; McCarthy 2001). However, fire regimes across the boreal forest are quite variable, as they are largely affected by regional climate. In drier regions, the fire cycle varies from 50 to 100 years, while in maritime and humid climates, the cycle can exceed 200 years (Gauthier et al. 2001; Heinselman 1981; Johnson 1992).

Long periods of time without fire give increased importance to nonfire disturbances. Such disturbances include insect outbreaks and wind. This type of disturbance regime can generate large patches as well as smaller gaps. In cases where the fire interval exceeds the life span of the tree spe-

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cies, individuals approaching senescence die of natural mortality and the dynamics of these stands become driven by gap dynamics.

The North Shore region of Quebec, where the study was conducted, is characterized by a humid maritime climate. The fire regime has yet to be described, but a study by Foster (1983) in an adjacent region determined a fire cycle of 500 years. Consequently, nonfire disturbances are important in controlling forest dynamics. Insects such as spruce budworm (*Choristoneura fumiferana* (Clem.)) and hemlock looper (*Lambdina fiscellaria fiscellaria* (Guen.)) are known to be important causes of mortality in the region (Blais 1983*a*; MacLean 1980; Watson 1934), and a large proportion of the landscape is characterized by stands with an irregular size distribution (Boucher et al. 2003; De Grandpré et al. 2000).

In this study, we define a gap as an opening of the canopy caused by the mortality of single trees or small groups of trees. The release of advance regeneration or the establishment of new individuals can therefore occupy the available growing space (Oliver and Larson 1990). In gap-regenerating stands, individual or group replacement of trees leads to structural and compositional changes in the stands. Since tree species diversity is rather limited in the boreal forest, stand development occurs primarily through changes in structure (Harper et al. 2002). The formation of gaps often leads to multicohort stands with an uneven-aged structure.

The purpose of this study was to gain a better knowledge of the small-scale disturbance dynamics of old irregular conifer stands in the North Shore region. Specifically, our objectives were first to characterize different attributes of gaps such as gap fraction, gap size distribution, and number and mortality of gap makers by carrying out a gap inventory. Second, we wished to examine changes in composition associated with gap dynamics by computing transition probabilities from gap maker species to gap filler species. The effect of gap size on tree recruitment is also examined, since it is related to the availability of resources, particularly light (Brokaw and Scheiner 1989; Lieffers et al. 1999; Whitmore 1989).

A knowledge of the autoecology of dominant species allowed us to make some hypotheses about the variations in gap attributes and the success of replacing species. We hypothesized that gap characteristics should differ according to stand composition. In old stands on the North Shore, balsam fir (*Abies balsamea* (L.) Mill.) and black spruce (*Picea mariana* (Mill.) BSP) dominate (Rowe 1972). Since *A. balsamea* is a species with high vulnerability to causes of mortality such as defoliators and wind (Blais 1983*b*; Burns and Honkala 1990; MacLean 1980; Ruel 2000), we hypothesized that stands with high proportions of *A. balsamea* would have more gaps. Because *Abies* has a larger crown, we also expected to find larger gaps and therefore higher gap fractions in *Abies*-dominated stands. The number of dead trees should also be more important in these stands than in *P. mariana* dominated ones.

Abies balsamea is a late-successional species and several studies have suggested that it replaces *P. mariana* (Bergeron and Dubuc 1989; De Grandpré et al. 2000; Gauthier et al. 2000). Kneeshaw and Bergeron (1998) found that spruce budworm mediated gaps promoted the transition to *Abies*-dominated forests. *Abies balsamea* also has the ability to persist in a suppressed state for long periods and to grow rapidly with an increase in light levels (Messier et al. 1999; Morin and Laprise 1997). Consequently, we predicted that replacement processes in gaps should favour *A. balsamea* in *Abies* stands. However, because of its ability to regenerate by layering (Burns and Honkala 1990; Stanek 1961), *P. mariana* should be able to maintain itself in *Picea* stands with low productivity (Newton and Jolliffe 1998; Sirois 1997). For other species, partitioning by gap size might favour the establishment of shade-intolerant species such as birch in very large gaps (Kneeshaw and Bergeron 1998; Kuuluvainen and Juntunen 1998; Whitmore 1989).

Materials and methods

Study area

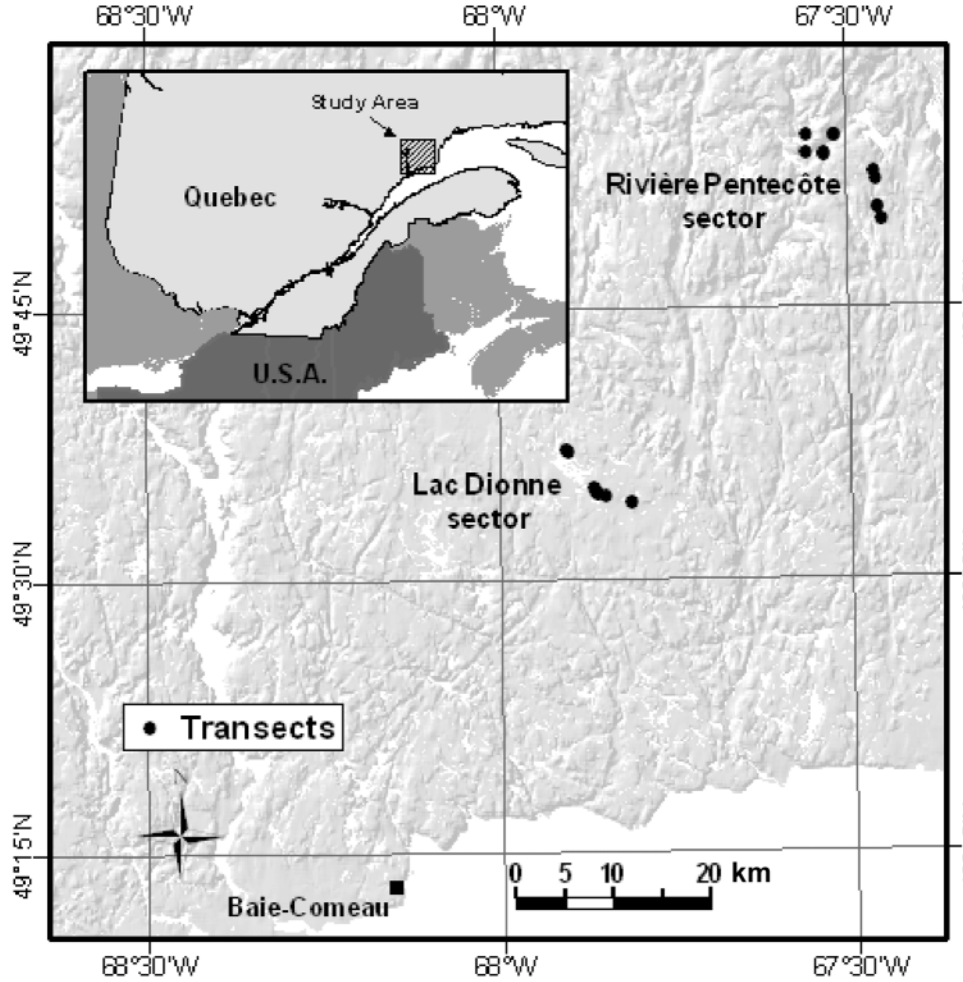
The study was conducted in Quebec's North Shore region, which is part of the humid boreal forest (49°30′–50°00′N, 67°30′–69°00′W), more specifically at Lac Dionne, 50 km north of Baie-Comeau, and at Rivère Pentecôte, 110 km east of Baie-Comeau (Fig. 1). The topography is characterized by moderate slopes and the maximum altitude is 500 m. The climate is cold and maritime and the average annual temperature fluctuates between –2.5 and 0.0 °C. Mean annual precipitation is between 1100 and 1300 mm, 35% of which is in the form of snow (Robitaille and Saucier 1998). Rocky outcrops represent close to 40% of the area and are present on summits, close to bodies of water, and on steep slopes. Undifferentiated glacial till deposits constitute most of the remaining surficial deposits and are found on gentle slopes and in depressions (Robitaille and Saucier 1998).

This area corresponds to Rowe's (1972) Chibougamau–Natashquan region and is part of the eastern boreal forest. The southern part of the study area is located in the bioclimatic domain of *A. balsamea* – paper birch (*Betula papyrifera* Marsh.), while the northern part is in the *P. mariana* – moss bioclimatic domain (Robitaille and Saucier 1998). The dominant species found in the region are *A. balsamea*, *P. mariana*, white spruce (*Picea glauca* (Moench) Voss), jack pine (*Pinus banksiana* Lamb.), *B. papyrifera*, and trembling aspen (*Populus tremuloides* Michx.) (Rowe 1972).

Changes in species composition following fire were described by De Grandpré et al. (2000) for the region. Two major postfire successional trends were revealed by that study. Young postfire stands were generally dominated by *P. mariana*, by intolerant boreal species such as paper birch and trembling aspen, or by mixed cover. With time elapsed since fire, stands dominated by *P. mariana* evolved towards dominance by either *P. mariana* or *A. balsamea* or a mixture of both (De Grandpré et al. 2000). *Abies balsamea* seemed to be the replacing species in shade-intolerant deciduous or mixed stands. In both cases, the size structure of stands became more irregular with time elapsed since fire, which resulted in a multilayered forest (De Grandpré et al. 2000).

Fire history has not been precisely reconstructed over the area, except for some recent major fires. However, according to De Grandpré et al. (2000), our study area had not burned for at least 225 years. Moreover, a very long fire cycle has

Fig. 1. Location of the study area in the North Shore region of Quebec, Canada.



been estimated for this region by Gauthier et al. (2001). A study in a neighbouring region of southeastern Labrador revealed a fire rotation of approximately 500 years (Foster 1983).

A severe spruce budworm outbreak began in the 1970s and affected an area of more than 9 × 10^6 ha (Blais 1983*a*, 1983*b*) in the North Shore region. A lighter and restricted outbreak occurred during the 1940s, but for the past 130 years, no other spruce budworm attacks have been recorded (Blais 1983*a*, 1983*b*). Another defoliator known to be affecting stands is the eastern hemlock looper, which caused severe damage to *A. balsamea* at the end of the 1920s and during the 1970s (Benoît and Desaulniers 1972; Watson 1934). Another outbreak of hemlock looper took place during 1999 and 2000. A very large windthrow affecting an area of 65 km by 3–4 km was recorded for 1964 (Anonymous 1964) just west of our study area.

Sampling

Three stand types were investigated: (*i*) *A. balsamea* dominated stands, (*ii*) *A. balsamea* – *P. mariana* dominated stands, and (*iii*) *P. mariana* dominated stands. These stand types were classified based on the percentage of the basal area occupied by living stems of each tree species. This classification is based on the percentage of basal area occupied by each living tree species (ministère des Ressources naturelles 1995). *Abies balsamea* and *P. mariana* stands had 75% or more of the total basal area occupied by *Abies* and *Picea*, respectively (Appendix). An *A. balsamea* – *P. mariana* dominated stand is a stand in which *Abies* occupies 50%–74% of the basal area and where *Picea* is the second most important species.

A total of 18 sites were sampled and the number of sampled sites per stand is not equal (Appendix). These sites were located in stands presenting an irregular size structure and were chosen with the use of maps and aerial photographs. Since this study aimed to focus on small-scale gaps, very large gaps caused by windthrow or insect defoliation were avoided.

In each site a 200-m-long transect was established. Line intersect sampling, which is commonly used to measure gap fraction and gap size (Battles et al. 1996; Runkle 1982), was applied to these transects. In our study, two types of gaps are considered: canopy gaps and expanded gaps. A canopy gap is defined as the land surface directly under the canopy opening and the expanded gap consists of the area of the canopy gap plus the area that extends to the trunks of the trees surrounding the gap (Runkle 1982). Two criteria were used to define a gap. In old conifer stands, interstitial space between crowns can be important, and therefore, the opening

Table 1. Decay classes for gap makers.

Decay class	Large branches	Fine branches	Foliage	Bark	Wood decomposition
Very young	Present	Present	Present, green	Intact	None
Young	Present	Present	Present, red or brown	Intact	None
Medium	Present	Occasional	Absent	Sloughing	Little
Medium–old	Present	Absent	Absent	Mostly sloughed off	Moderate
Old	Occasional to absent	Absent	Absent	Mostly absent	Advanced

had to result from the mortality of at least one tree. The regeneration that was released or that established after gap formation had to be lower than two thirds of the height of the surrounding dominant trees.

To obtain the proportion of stands under expanded gaps, we divided the total distance of the transect in expanded gaps by the length of the whole transect. All gaps encountered along the transect were recorded. Then, five gaps from each transect (total of 90 gaps) were randomly chosen to evaluate gap area. To determine the size of the gap, the length of the longest axis passing through the opening was measured for the canopy gap and expanded gap separately. The lengths of secondary axes (three to six depending on the size of the gap) at a 90° angle from the main axis and at 2- or 3-m intervals along it were also measured. The surface of the resulting polygons was calculated to obtain gap area for both canopy and expanded gaps.

In each of the 90 gaps, mortality and recruitment were evaluated. We noted the species, diameter at breast height (DBH), and mode of mortality (uprooted, snapped, or standing dead) of gap makers and attributed a decay class to each of them (Table 1; modified from Liu and Hytteborn 1991). A gap maker is defined as a tree with DBH >9 cm whose mortality contributed to the opening of the canopy. The orientation of fallen trees was also measured in cases where gap makers were logs. To establish the patterns of replacement of gap makers by gap fillers (individuals growing in a gap), we collected data on the regeneration in each of the 90 gaps. Species and height (classes: (1) 1.3–2 m, (2) 2–3 m, (3) 3–4 m, (4) 4–5 m, (5) 5–10 m, and (6) 10–15 m) were recorded for all saplings growing within the expanded gap with DBH >1 cm. In some gaps, no saplings over 1 cm DBH were encountered. The presence of various tree species was then noted.

Data analysis

To compare the characteristics of gaps between the three stand types, analysis of variance using PROC GLM (SAS Institute Inc. 1990) was performed on the proportional area of stands in expanded gap and the number of gaps intercepted per 200-m-long transects. A mixed linear model (PROC MIXED) was used to compare the ratio of expanded gap to canopy gap between stand types (fixed effect) and a nested random effect of transect within stand type.

We used the nonparametric Kolmogorov–Smirnov two-sample test (Sokal and Rohlf 1995) to compare the distribution of (*i*) canopy gap size, (*ii*) expanded gap size, (*iii*) the number of gap makers per gap, and (*iv*) the number of gap makers in the different decay classes among the three stand types. This test detects differences in dispersion and skewness of the distributions.

Table 2. Expanded gap fraction and mean number of gaps intercepted by 200-m-long transect for different stand types in the northeastern boreal forest of Quebec (n = 18 transects).

	Gap fraction (%)			
Stand type	Min.	Max.	Mean	No. of gaps per transect
Abies balsamea	30	74	47	10
Abies balsamea – Picea mariana	40	82	53	10
Picea mariana	54	74	60	13
Mean			54	11

Using a one-way contingency table, we tested the hypothesis of a homogeneous distribution of the frequency of dead standing, snapped, and uprooted trees using a χ^2 test. Two-way contingency tables were built to test if the gap makers' mode of mortality differed among stand types or among tree species, also using a χ^2 test.

Uprooted logs were divided into two groups according to the direction in which they fell on the ground. One group consisted of trees that had fallen in the direction of the prevailing winds (towards the southeast) and the other group contained all of the remaining trees, which fell towards either the northeast, the northwest, or the southwest. Again, a χ^2 test was used to assess whether the orientation of the fallen logs was related to the prevailing wind direction. The expected frequencies for the χ^2 were unequal (null hypothesis: 25% for trees falling in the southeast direction and 75% for trees falling in the remaining directions). Snapped trees were not considered in this analysis, since it was impossible to determine whether the tree was alive when snapped.

To determine if there was a change in species composition within gaps, we constructed Markovian transition matrices to obtain replacement probabilities for each of the tree species. These probabilities were based solely on the current composition and did not take into account differential mortality or subsequent tree replacement. To calculate the transition probabilities, we compared the proportion of gap fillers by species with the proportion of gap makers by species using each of the 90 gaps as entities. To take into consideration that the tallest individuals in a gap are more likely to fill the gap than smaller ones, each gap filler was weighted according to its height class (0.2 for 1.3–2 m, 0.4 for 2–3 m, 0.6 for 3–4 m, 0.8 4–5 m, and 1.0 for >5 m). In gaps where no saplings over 1 cm DBH were encountered, tree seedlings were used as the gap filler species. The replacement probabilities were calculated for each of the three stand types and for different size classes of expanded gaps. For each gap of a particular stand type or size class, all possible combinations of gap filler to gap maker ratio were first calculated. For ex-

Table 3. Canopy gap and expanded gap size characteristics for different stand types in the northeastern boreal forest of Quebec (n = 90 gaps).

	Canopy gap (CG) area (m^2)				Expanded gap (EG) area (m^2)				
Stand type	Min.	Max.	Mean	Median	Min.	Max.	Mean	Median	Ratio of EG to CG by stand type
Abies balsamea	0.5	230.3	39.5	19.6	12.3	294.8	75.2	58.2	5.6c
Abies balsamea – Picea mariana	2.3	435.2	54.0	40.9	20.1	521.8	89.5	76.8	2.4b
Picea mariana	3.6	222.6	71.0	47.2	12.4	278.0	105.7	79.6	1.7a

Note: Values with different letters are significantly different at the $\alpha = 0.05$ level.

ample, if four species of gap makers and two species of gap fillers were present in a gap, eight different ratios would be computed. The mean of these ratios was then calculated for each stand type and gap size class. The means were summed by gap makers species and the replacement probabilities (R) were obtained by dividing each mean gap filler (Gf) to gap maker (Gm) ratio by this sum:

$$R(i) = \frac{\mathrm{Gf}(i)/\mathrm{Gm}}{\sum \mathrm{Gf}(i)/\mathrm{Gm}} \qquad \text{for } i = 1,\ldots,n \text{ species}$$

Results

Gap characteristics

Expanded gaps occupied from 39% to 82% of stand area with an average of 54% and an average of 11 gaps per 200-m-long transect (Table 2). The analysis of variance showed no significant difference in these two parameters among stand types (F = 1.00, df = 2, p = 0.3895 and F = 3.34, df = 2, p = 0.0633, respectively). However, the two stand types including *Abies* had a greater difference between the minimum and maximum gap fraction than *Picea*-dominated stands (Table 2).

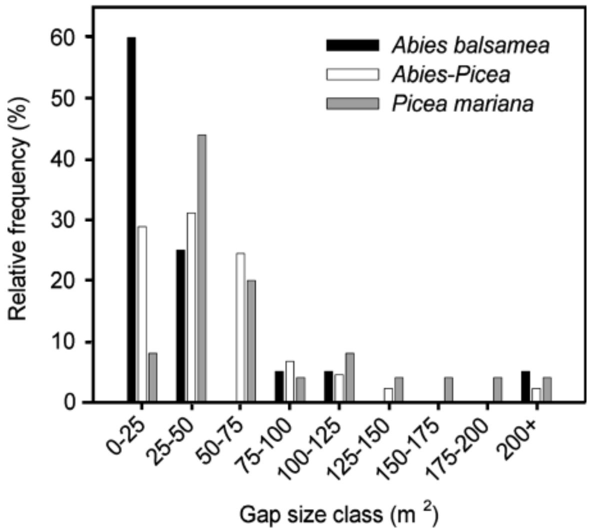
The size of canopy gaps was highly variable (see Appendix for details). The smallest canopy gap was 0.5 m^2, while the largest was 435.2 m^2 (Table 3). The comparison of the size distribution of canopy gap size among stand types shows that *A. balsamea* dominated stands were significantly different from both *Abies–Picea* stands and *P. mariana* stands (Kolmogorov–Smirnov tests, p = 0.005 and p = 0.001, respectively). Figure 2 shows the size distribution of canopy gap and we can see that a much higher proportion (60%) of gaps in *A. balsamea* stands were in the smallest size class (0–25 m^2). Overall, 87% of all canopy gaps covered less than 100 m^2 (Fig. 2).

The minimum size for an expanded gap was 12.3 m^2 and the maximum size was 521.8 m^2 (Table 3). Expanded gap size distribution did not differ among stand types (Kolmogorov–Smirnov tests, p > 0.05). The size distribution of all expanded gaps resembles a normal distribution, with a high proportion of expanded gaps larger than 200 m^2 in *P. mariana* stands but with 71% of all expanded gaps less than 100 m^2 (Fig. 2).

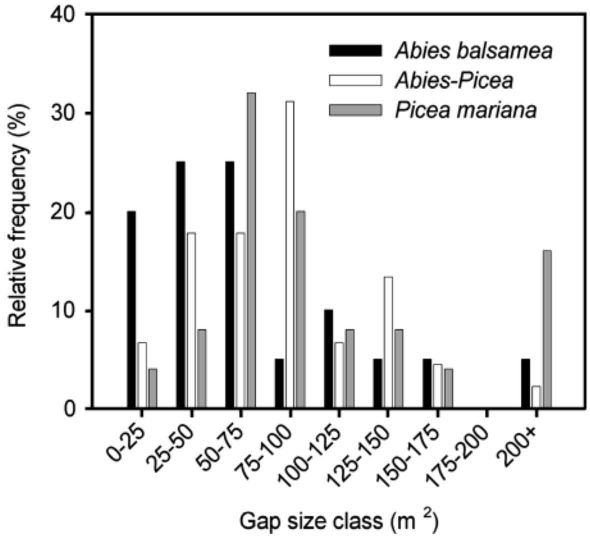
When we examined the relationship between the size of canopy gaps and expanded gaps, we found that the ratio of expanded gap size to canopy gap size was significantly different among stand types (F = 6.21, df = 2 for stand types and df = 15 for random effect of transect within stand type, p = 0.01). Indeed, in *A. balsamea* stands, expanded gap size was 5.6 times larger than canopy gap size (Table 3). In *Abies–Picea* stands, it was 2.4 times larger, while in *P. mariana* stands, expanded gaps were 1.7 times larger than canopy gaps (Table 3).

Fig. 2. Relative frequency of gap size distribution for (*a*) canopy gaps and (*b*) expanded gaps for different stand types in the northeastern boreal forest of Quebec.

(a) Canopy gaps



(b) Expanded gaps



Mortality

There were no significant differences in the distribution of the number of gap makers per gap among the three stand types (Kolmogorov–Smirnov tests, $p > 0.05$). The majority of gaps (94%) resulted from the mortality of less than 10 gap makers. Only 13% of gaps were the result of single-tree mortality, 74% had four gap makers or less, and a maximum of 23 gap makers was recorded for one gap (Fig. 3).

The distribution of gap makers over the decay class differed significantly among stand types (Kolmogorov–Smirnov tests, $p < 0.01$). More than 60% of gap makers in *Abies–Picea*-dominated stands were in medium–old to old decay classes, while in *P. mariana* stands, over 40% of gap makers were in young decay classes (Fig. 4).

We found a significant difference in the frequency of occurrence among the different modes of mortality of gap makers ($\chi^2 = 17.5966$, df = 2, $p = 0.0002$). Indeed, of the 352 gap makers, 37% were snapped trees, 40% died standing, and 23% were uprooted (Table 4). This pattern is similar in each of the stand types even though there seems to be a high proportion (52%) of trees that died standing in *P. mariana* stands (Table 4). In one specific site, almost all gap makers were found standing dead. An unidentified pathogen is most likely the cause of this.

The orientation of fallen logs, which consisted of 80 uprooted trees, appeared to be related to the direction of prevailing winds ($\chi^2 = 28.9$, df = 1, $p = 0.0001$), since 46% of trees fell in that direction.

Gap maker – gap filler comparisons

Transition probabilities calculated for stand types showed that in *A. balsamea* dominated stands, gap makers of *A. balsamea*, *B. papyrifera*, *P. glauca*, and *P. mariana* were replaced by *Abies* with probabilities varying from 0.71 to 0.79 (Table 5). The same self-replacement pattern is observed in *P. mariana* dominated stands where all species were replaced primarily by *P. mariana* with replacement probabilities of 0.74, 0.71, and 0.79, respectively, for *A. balsamea*, *B. papyrifera*, and *P. mariana* gap makers (Table 5). However, in mixed stands, *A. balsamea* tended to be replaced by *P. mariana* with a probability of 0.72, while *B. papyrifera* and *P. mariana* were replaced by *A. balsamea* with probabilities of 0.51 and 0.63, respectively. It thus appears that reciprocal replacement may occur in these stands (Table 5).

Patterns of reciprocal replacement of the two most frequent species, *A. balsamea* and *P. mariana*, are noticeable again when we examine the transition probabilities calculated for different size classes of expanded gaps for all stand types combined (Table 6). With the exception of *P. mariana* in very large gaps, which shows an equal probability of being replaced by *Abies* or *Picea*, reciprocal replacement is observed in all other situations (Table 6). In small gaps, gap makers of *B. papyrifera* are more likely to be replaced by *Abies* (Table 6). The same goes for *B. papyrifera* in large gaps (Table 6). However, in medium-sized gaps, *B. papyrifera* has a higher probability of replacement by *P. mariana* (Table 6). In very large gaps, *B. papyrifera* and *P. glauca* have a slightly higher probability of being succeeded by *P. mariana* than by *Abies* (Table 6).

Discussion

Gap characteristics

In the old conifer forests that we studied on the North Shore, the high percentage of stand area in expanded gaps (54% for all three types of stands; Table 1) is comparable with the percentages found in some studies in coniferous forests (Bartemucci et al. 2002; Kneeshaw and Bergeron 1998; Lertzman and Krebs 1991) but is greater than what is found for temperate forests (Runkle 1982). Gap-forming processes seem important in our stands and the high gap fraction is attributable to numerous factors. First, at high latitudes, the shorter growing season means that filling of the gaps by regeneration takes longer (Bartemucci et al. 2002). Second, there is little filling of the edges of gaps by surrounding canopy because of the restricted ability of conifers to grow branches into openings, as compared with deciduous species (Kuuluvainen 1994). Moreover, conifer stands show very open canopies owing to interstitial space between trees caused by the narrow conical crowns. The greater variability in gap fraction observed between stands where *A. balsamea* is present may be explained by the higher susceptibility of that species to disturbance agents when compared with *P. mariana*. The timing of disturbances between stands will

Fig. 3. Relative frequency of gap makers per gap for all forest types combined in the northeastern boreal forest of Quebec.

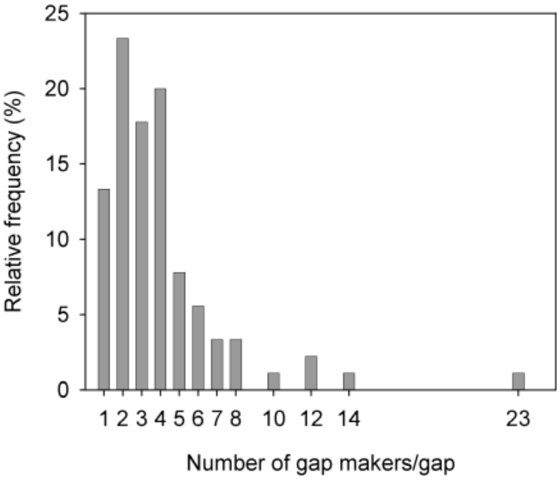


Fig. 4. Relative frequency of decay class distribution of gap makers for different stand types in the northeastern boreal forest of Quebec.

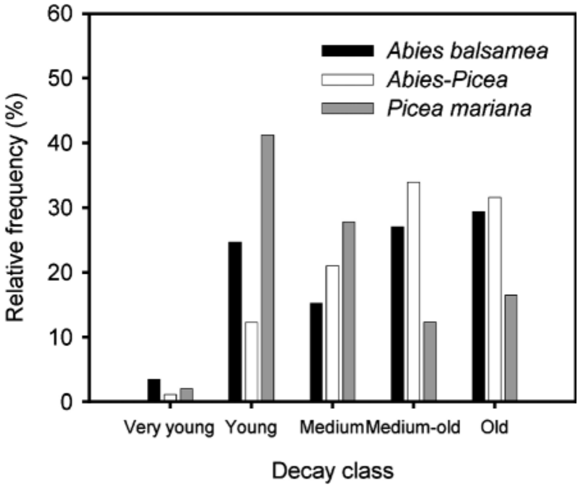


Table 4. Mode of mortality of gap maker by species and stand type in the northeastern boreal forest of Quebec (n = 352 gap makers).

	Snapped	Standing dead	Uprooted	Total
Species				
Abies balsamea	57 (36%)	66 (42%)	34 (22%)	157
Betula papyrifera	3 (19%)	7 (44%)	6 (38%)	16
Picea glauca	2 (100%)	0	0	2
Picea mariana	65 (37%)	69 (40%)	40 (23%)	174
Undetermined	2 (67%)	0	1 (33%)	3
Total	129 (37%)	142 (40%)	81 (23%)	352
Stand type				
Abies balsamea	30 (35%)	32 (37%)	24 (28%)	86
Abies balsamea – Picea mariana	66 (39%)	60 (36%)	43 (25%)	169
Picea mariana	33 (34%)	50 (52%)	14 (14%)	97
Total	129 (37%)	142 (40%)	81 (23%)	352

Note: Percentage in parentheses is the proportion of trees of a given mode of mortality for one species.

Table 5. Transition probabilities from gap maker species to gap filler species by stand type in the northeastern boreal forest of Quebec.

(A) *Abies balsamea* dominated stands (n = 20 gaps).

	Gap maker				
Gap filler	*Abies balsamea* (74%)	*Betula papyrifera* (5%)	*Picea glauca* (2%)	*Picea mariana* (17%)	Unknown (1%)*
Abies balsamea	0.79	0.73	0.73	0.71	0.73
Betula papyrifera	0.09	0.16	0.18	0.09	0.18
Picea glauca	0.03	0.02	0.01	0.07	0.01
Picea mariana	0.09	0.09	0.08	0.13	0.08

(B) *Abies balsamea – Picea mariana* dominated stands (n = 45).

	Gap maker			
Gap filler	*Abies balsamea* (53%)	*Betula papyrifera* (6%)	*Picea mariana* (40%)	Unknown (1%)*
Abies balsamea	0.28	0.51	0.63	0.53
Betula papyrifera	<0.01	0.05	0.08	0.05
Picea glauca	<0.01	<0.01	0.01	0.01
Picea mariana	0.72	0.43	0.28	0.41

(C) *Picea mariana* dominated stands (n = 25).

	Gap maker		
Gap filler	*Abies balsamea* (3%)	*Betula papyrifera* (2%)	*Picea mariana* (95%)
Abies balsamea	0.25	0.28	0.20
Betula papyrifera	<0.01	0.02	0.01
Picea mariana	0.74	0.71	0.79

Note: Percentage in parentheses is the proportion of the gap maker species by stand type.
*Gap makers whose species could not be determined because of advanced decay.

also affect the variability in gap fraction. In the North Shore, there were two spruce budworm outbreaks officially reported in the last century (Blais 1983*a*, 1983*b*) and two eastern hemlock looper outbreaks (Benoît and Desaulniers 1972; Watson 1934). It is obvious that the sampled stands were not affected by all these disturbances or did not experience the same mortality; thus, at the moment of sampling, they were at a different period of recovery following disturbance, explaining the higher variability in gap fraction in stands with *A. balsamea*.

Gap size was highly variable among transects, but we did observe a higher proportion of small canopy gaps in *A. balsamea* stands. The ratio of expanded gap area to canopy gap area reflects the difference in crown dimension of tree spe-

Table 6. Transition probabilities from gap maker species to gap filler species by expanded gap size for all forest types combined in the northeastern boreal forest of Quebec.

(A) Small gaps: 0–50 m^2 (n = 23 gaps).

Gap filler	Gap maker *Abies balsamea* (60%)	*Betula papyrifera* (2%)	*Picea mariana* (37%)	Unknown* (2%)
Abies balsamea	0.27	0.64	0.66	0.61
Betula papyrifera	0.03	0.04	0.11	0.08
Picea glauca	<0.01	<0.01	0.01	<0.01
Picea mariana	0.71	0.32	0.22	0.30

(B) Medium gaps: 50–75 m^2 (n = 21 gaps).

Gap filler	Gap maker *Abies balsamea* (44%)	*Betula papyrifera* (2%)	*Picea mariana* (52%)	Unknown* (2%)
Abies balsamea	0.15	0.43	0.59	0.41
Betula papyrifera	<0.01	0.04	0.07	0.04
Picea glauca	<0.01	0.01	0.01	0.01
Picea mariana	0.85	0.52	0.33	0.55

(C) Large gaps: 75–100 m^2 (n = 20 gaps).

Gap filler	Gap maker *Abies balsamea* (54%)	*Betula papyrifera* (4%)	*Picea mariana* (42%)
Abies balsamea	0.41	0.63	0.76
Betula papyrifera	<0.01	0.09	0.14
Picea glauca	<0.01	0.01	0.02
Picea mariana	0.59	0.27	0.07

(D) Very large gaps: 100 m^2 and over (n = 26 gaps).

Gap filler	Gap maker *Abies balsamea* (36%)	*Betula papyrifera* (5%)	*Picea glauca* (1%)	*Picea mariana* (57%)	Unknown * (1%)
Abies balsamea	0.26	0.45	0.46	0.50	0.46
Betula papyrifera	<0.01	0.06	0.05	0.00	0.05
Picea glauca	<0.01	<0.01	<0.01	<0.01	<0.01
Picea mariana	0.74	0.49	0.48	0.50	0.48

Note: Percentage in parentheses is the proportion of the gap maker species by gap size.
*Gap makers whose species could not be determined because of advanced decay.

cies. *Picea mariana* has a fairly narrow, conical crown compared with *A. balsamea*, *P. glauca*, or *B. papyrifera*. This explains why we obtained a smaller ratio for *Picea* stands. In *Abies* stands, most gap makers were *Abies*, and thus the difference between expanded gap area and canopy gap area is accentuated, since the latter is delimited by the projection of the tree crown to the ground and the former by the distance to the trunk. The same interpretation applies to *Abies–Picea* stands where more than half of the gap makers are large-crowned *Abies* and *Betula* (see Table 5).

Overall, in old conifer stands, the majority of gaps were smaller than 100 m^2 for both canopy (87%) and expanded gaps (71%), which is consistent with the findings in other studies (Bartemucci et al. 2002; Liu and Hytteborn 1991; Lertzman and Krebs 1991). Gaps are therefore small but frequent.

Mortality

Gap size is dependent on the number of trees whose mortality generated the gap (Kuuluvainen 1994). Since gaps were small, it was logical to find that a small number (1–4; Fig. 3) of gap makers created the majority of gaps. The maximum number of gap makers found by Lertzman and Krebs (1991) was 16, and Liu and Hytteborn (1991) established that the number of gap makers rarely exceeded 10 individuals per gap. As in Lertzman and Krebs' study (1991), gaps seemed to result from successive events of tree mortality separated in time so that increases in light are gradual. Very few gaps resulted from the simultaneous death of all gap makers, as most gaps had gap makers of many different decay classes.

The most common mode of mortality of gap makers in all stand types was standing dead, followed by snapped stems. The small gap areas that we obtained are consistent with a mortality of standing trees, which creates smaller openings in the canopy than fallen trees. A portion of the snapped trees were probably standing dead at some time owing to insect attack and subsequently snapped. A small proportion of trees was uprooted, therefore creating some disturbance of the forest floor (Schaetzl et al. 1989). A large proportion of these uprooted trees had been blown down by wind, as many of them fell in the same direction as the prevailing winds of the region. The release of resources differs according to the cause of tree mortality (Krasny and Whitmore 1992), and gaps with remaining standing dead trees probably transmit less sunlight than ones with uprooted or snapped stems.

Gap maker – gap filler comparisons

Transition probabilities calculated by stand type suggest self-replacement trends for the two dominant species of the region at the stand scale. This means that *A. balsamea* is the most frequent successor in *Abies* stands and *P. mariana* is the most likely replacement species in *Picea* stands regardless of the species of gap maker. Gap fillers of both species were probably present before gap formation. It is common to observe saplings of *Abies* trees that are suppressed for many years before a growth release can be observed as a result of an opening in the canopy. For *Picea*, most of the regeneration comes from layering, which is independent of gap creation. Therefore, we would expect that the species composition of stands would be maintained in time in both *Abies* and *Picea* stands. However, when we examine replacement probabilities in the mixed *A. balsamea – P. mariana* stands, there seems to be a reciprocal replacement of *Abies* gap makers by *P. mariana* gap fillers and vice versa. *Abies*, however, does show slightly higher replacement probability when the mortality is due to other species.

Many studies on species coexistence mention species partitioning by gap size such that large gaps would favour shade-intolerant tree species (Brokaw and Scheiner 1989; Denslow 1987; Runkle 1982; Whitmore 1989). This did not seem to be the case in our study; *B. papyrife*ra was not a gap filler more frequently found in larger gaps. Because of the low angle of the sun at our latitude and the narrow conifer crowns, light is probably not a main limiting factor for tree recruitment into the forest understory. Bartemucci et al. (2002) found similar light levels for gap and nongap areas in boreal forests. Hubbell et al. (1999) also found that species richness in tropical forests did not differ in gap and nongap areas. Thus, other factors might be limiting, such as proper germination beds. The main mode of mortality (standing dead) does not provide adequate regeneration microsites such as would be created by uprooted trees or snapped trees after they decayed. This could be unfavourable to *Betula* as well as to *P. glauca* (Galipeau et al. 1997).

Irrespective of stand type, reciprocal replacement is again noticeable for all gap sizes, which is inconsistent with other studies on replacement trends in gaps (Busing 1996; Lertzman 1992). This could be explained by the fact that half of the gaps were in mixed coniferous stands, where reciprocal replacement probabilities were highest. Kneeshaw and Bergeron (1998) showed that *A. balsamea* was the most frequent successor, but its potential to succeed diminished with gap size; thus, shade-intolerant species were maintained in patches affected by spruce budworm.

Fox (1977) justified the alternation of species in gaps by a reciprocal replacement of American beech (*Fagus grandifolia* Ehrh.) and eastern hemlock (*Tsuga canadensis* (L.) Carrière). However, Runkle's (1981) study of the same region did not reveal the same patterns of reciprocal replacement. There was rather a self-replacement of species where the gap maker species influenced the species composition of its successors. According to Runkle (1981), reciprocal replacement would be more likely to occur in species-poor stands, which is the case with northern coniferous forests. A disturbance-mediated process could, however, explain the reciprocal replacement observed in our mixed coniferous stands. *Abies balsamea* is more shade tolerant than *P. mariana* but is highly vulnerable to defoliators such as the spruce budworm and the hemlock looper (Martineau 1984). Both defoliators can cause severe mortality in all sizes of trees, but the hemlock looper causes higher mortality in stems of less than 11 cm DBH (MacLean and Ebert 1999), while larger trees are more susceptible to spruce budworm (Bergeron et al. 1995). The action of both disturbances may explain the high probability of *P. mariana* gap fillers replacing *A. balsamea* gap makers. On the other hand, when canopy mortality does not result from species-specific disturbances, *A. balsamea* should be a more successful gap filler than *P. mariana*, as it is more shade tolerant than *P. mariana* and can regenerate under a closed canopy.

Our case study indicates that although minor fluctuations in species might occur at a fine scale, the overall species composition of stands should be maintained over time within gap phase processes, whether it is by self-replacement or reciprocal replacement. However, we did not take into account stand age when computing replacement probabilities. Frelich and Reich (1995) mentioned that transition probabilities vary with stand age; therefore, different stand ages might produce different results as to the potential successor species.

Openings in the canopy exist in a continuum of sizes. However, McCarthy's (2001) review on gap dynamics in boreal forests stressed the difference between two types of processes. Large-scale disturbances generally affect an entire stand or a large portion of it, creating canopy openings over 200 m^2. Therefore, mortality occurs for a large number of trees in a catastrophic way such as found after very large windthrows or severe insect outbreaks. Such a process, operating at a coarse scale, undoubtedly exists in the region, since a history of spruce budworm (Blais 1983*a*, 1983*b*) and hemlock looper (Benoît and Desaulniers 1972; Watson 1934) outbreaks in addition to very large windthrow events (Anonymous 1964) has been recorded for the area. It is finer scale disturbances that break up the more uniform patches into a mosaic of openings (Spies and Franklin 1989) and we concentrated on these finer scale dynamics.

Frelich (2002) emphasized the importance of understanding the scale-dependent nature of succession. He also pointed out that the best possible way to assess succession is probably by multiscale and multitemporal analysis. The processes inherent to large-scale gap dynamics might result in different patterns of recruitment and succession than what were reported here.

Gap formation is probably the source of the structural heterogeneity found in old stands, and the structural components (snags, coarse woody debris, etc.) have been shown to provide wildlife habitat (Kuuluvainen 2002). Perhaps traditional even-aged management practices (such as clear-cutting) should be reexamined and diversified if our goal is to emulate gap dynamics to maintain old-growth attributes of the stands.

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Appendix A

Appendix appears on the following page.

Table A1. Characteristics of sampled stands in the northeastern boreal forest of Quebec.

	Basal area (%)				Stem density								Canopy gap area (m^2)		Expanded gap area (m^2)	
Stand type	*Abies balsamea*	*Betula papyrifera*	*Picea glauca*	*Picea mariana*	No./ha	m^2/ha	Snag density (no./ha)	Snag volume (m^3/ha)	Volume of logs (m^3/ha)	Minimum stand age (years)	Expanded gap fraction (%)	No. of gaps intercepted	Min.	Max.	Min.	Max.
Picea mariana	1	0	0	99	3300	0.76	200	30.87	42.90	143	54	10	3.63	162.10	12.42	227.00
	22	1	0	76	4875	1.67	75	19.28	61.50	212	62	14	39.36	111.28	71.80	153.57
	8	0	0	92	3225	1.11	125	18.18	34.34	171	74	16	31.31	140.09	48.27	209.84
	10	0	0	90	3175	1.31	175	24.35	24.30	171	56	13	44.12	222.58	68.81	277.98
	12	0	0	88	2675	1.37	200	35.26	69.64	160	56	11	37.39	89.85	60.15	135.08
Abies balsamea – Picea mariana	54	0	0	46	3725	1.26	125	56.04	64.96	242	44	9	2.27	139.00	21.90	174.92
	52	5	6	37	4500	1.31	100	18.40	41.66	219	40	7	9.92	70.50	30.33	125.40
	60	0	0	40	3750	1.22	275	35.25	29.16	219	45	11	8.32	61.35	20.13	90.85
	63	0	0	37	4300	1.46	75	13.37	40.95	221	41	9	5.88	83.22	22.49	136.30
	66	4	0	29	3375	1.40	125	24.79	42.31	221	46	12	13.11	40.17	57.03	85.40
	49	1	18	33	4850	1.26	125	36.95	178.78	226	82	13	4.73	38.67	32.88	62.82
	50	4	0	47	4775	0.79	25	2.66	56.94	156	50	9	15.94	123.40	38.53	158.25
	69	0	0	31	5275	0.71	300	48.64	62.90	171	67	11	48.45	435.19	77.23	521.79
	73	3	0	24	6950	0.81	200	23.62	22.60	180	60	10	29.05	94.20	54.71	133.40
Abies balsamea	77	0	14	9	2975	1.27	150	15.86	28.59	193	46	11	12.44	28.11	29.12	65.61
	76	1	12	12	6050	0.92	100	20.72	57.38	198	30	9	0.50	17.63	12.25	47.46
	88	6	5	1	4500	0.89	175	48.36	117.38	221	74	12	11.25	99.30	46.16	149.70
	79	1	0	20	5225	1.39	125	10.50	72.20	203	39	7	11.78	230.30	48.51	294.84