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A comparison of gap characteristics in mixedwood old-growth forests in eastern and western Quebec

Julie Messier, Daniel Kneeshaw, Mathieu Bouchard, and André de Römer

Abstract: Canopy gaps play an important role in the dynamics of old-growth forests, although it is not well known how gap dynamics differ among regions. To further our understanding of natural gap dynamics in mixedwood forests, this study compares mixed stands located in eastern (Gaspésie region) and western (Témiscamingue region) Quebec. We tested whether the gap fraction in mixedwood stands was similar in these two regions. Data from field transects were used to characterize current canopy gaps, and aerial photos were used to contrast gap characteristics before and after the most recent spruce budworm (*Choristoneura fumiferana* Clem.) outbreak, which occurred from 1973 to 1991 in Gaspésie and from 1972 to 1984 in Témiscamingue. The current gap fraction was found to differ between the two regions: it varied from 2% to 48% with an average of 25.6% for the Gaspésie region and from 24% to 52% with an average of 36.6% for the Témiscamingue region. While the last spruce budworm outbreak coincided with a significant increase in canopy openings in the Témiscamingue region ($p = 0.047$), no such effect was observed in Gaspésie. These results suggest that the temporal pattern of small-scale disturbances can vary among regions, even when similar forest types are compared.

Résumé : On sait que les trouées de canopée sont importantes pour la dynamique des peuplements de fin de succession, mais nous disposons de peu d'informations sur la variabilité inter-régionale. Dans le but d'améliorer nos connaissances sur la création des trouées en forêt mixte, cette étude compare des peuplements mélangés de l'est (Gaspésie) et l'ouest (Témiscamingue) du Québec. Nous avons vérifié si le pourcentage d'ouverture de la forêt, pour un même type de forêt, est similaire dans ces deux régions. Des données provenant de transects établis sur le terrain on permis de caractériser les ouvertures actuelles, et des photographies aériennes ont été utilisées pour comparer la proportion de trouées avant et après la dernière épidémie de tordeuse des bourgeons de l'épinette *(Choristoneura fumiferana* Clem.), qui a eu lieu entre 1973 et 1991 en Gaspésie et de 1972 à 1984 au Témiscamingue. Les résultats obtenus indiquent que le degré d'ouverture de la canopée diffère entre les deux régions : en Gaspésie, le pourcentage d'ouverture de la forêt varie de 2 à 48 % avec une moyenne de 25,6 % alors qu'au Témiscamingue il varie de 24 à 52 % avec une moyenne de 36,6 %. Alors que la dernière épidémie de tordeuse des bourgeons de l'épinette a coïncidé avec une augmentation significative des ouvertures de canopée dans le Témiscamingue ($p = 0,047$), un tel effet n'a pas été observé en Gaspésie. Ces résultats suggèrent que le taux de création de petites ouvertures peut varier entre les régions, même lorsque des types forestiers similaires sont comparés.

Introduction

Recent research has shown that old-growth forests and small-gap dynamics are more common in the boreal zone than was previously assumed (McCarthy 2001; Kneeshaw and Gauthier 2003). This is also thought to be the case in the mixedwood forest zone further south, even if forests is this zone are often managed in an even-aged fashion using clear-cutting practices (MacDonald 1995; Bergeron et al. 1999). The ecosystem management approach suggests the use of interventions that mimic natural disturbances (Franklin 1993; Bergeron et al. 1999; Kneeshaw et al. 2000). It is therefore imperative to better understand the gap dynamics in these older forests while some still remain, both for ecological reasons and to design forest management practices that emulate late-successional dynamics.

Knowing the proportion of a forest in gap phase (i.e., gap fraction) and whether this proportion is variable among stands in the same forest type is critical for better understanding and emulating gap dynamics. Because most gap studies are conducted at limited spatial and temporal scales, it is not known how representative gap regimes are across larger spatial scales. However differences have been observed in large-scale disturbance regimes among regions, which suggests that gap dynamics may also differ. For example, there has

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J. Messier,[1] D. Kneeshaw, M. Bouchard, and A. de Römer. Groupe de recherche en écologie forestière interuniversitaire, C.P. 8888, succursale Centre-ville, Montréal, QC H3C 3P8, Canada.

[1]Corresponding author (e-mail: messier_julie_@hotmail.com).

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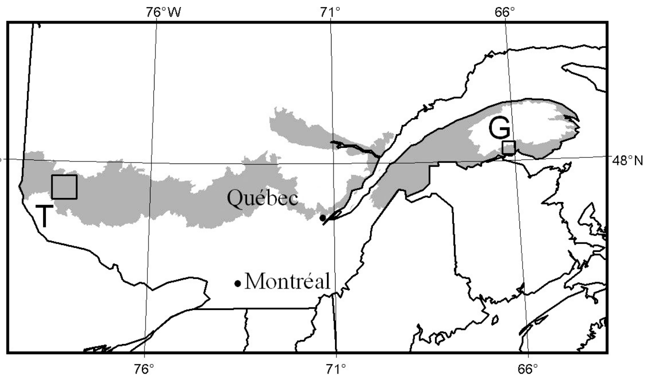
Fig. 1. Location of the two studied areas within the Témiscamingue (T) and Gaspésie (G) regions, Quebec, Canada. The shaded area represents the balsam fir – yellow birch bioclimatic domain.



been some suggestion that the fire cycle and old-growth abundance may vary among regions in the mixed forest zone in Quebec (Gauthier et al. 2001). In late-successional old-growth stands, the duration and severity of spruce budworm (*Choristoneura fumiferana* Clem.) outbreaks, a main cause of tree mortality, may also vary on a regional basis (Blais 1983; Gray et al. 2000).

The objective of this paper is to compare the current gap fraction in late-successional stand types present in mixed-wood forests in the same bioclimatic domain in eastern and western Quebec (respectively Gaspésie and Témiscamingue regions). We also look at temporal changes in the gap fraction before and after the latest spruce budworm outbreak. We hypothesize that the current gap fraction should be similar for both regions, and that the gap fraction should increase after a spruce budworm outbreak.

Study areas

The two study areas, located in northern Témiscamingue and southern Gaspésie, are, respectively, at the western and eastern ends of the balsam fir – yellow birch bioclimatic domain in Quebec (Fig. 1; Saucier et al. 1998). As the study areas are located in the northern part of the transitional zone between the boreal and temperate forest biomes, they can also be designated boreal mixedwoods or sub-boreal forests (Pastor and Mladenoff 1992).

The Gaspésie peninsula is the northeastern extremity of the weathered Appalachian mountain chain, which is of sedimentary origin. Deposits are composed of a mix of glacial tills and alteration rocks. In Témiscamingue the topography is generally flatter, with glacial deposits (boulders, gravel, and loams) of various thicknesses covering the Precambrian igneous rocks of the Canadian Shield (Robitaille and Saucier 1998). The climate is similar in both study areas, with a mean annual precipitation of 1220 mm and a mean annual temperature of 2.6 °C in the southern part of Gaspésie (Saint-Elzéar weather station, 48°10′N, 65°21′W), and a mean annual precipitation of 996 mm and a mean annual temperature of 1.9 °C in northern Témiscamingue (Belleterre weather station, 47°23′N, 78°42′W) (Environment Canada 2005).

In both regions natural succession is significantly influenced by disturbances such as fire and recurring spruce budworm epidemics. The natural fire cycle has been estimated to be approximately 190 years in northern Témiscamingue (Grenier et al. 2005) and between 200 and 250 years in southern Gaspésie (Lauzon 2004), although Wein and Moore (1977) suggest fire cycles up to 340 years for neighbouring New Brunswick. The last spruce budworm outbreak occurred between 1973 and 1991 in the Gaspésie region, and between 1972 and 1984 in the Témiscamingue region (Gray et al. 2000), causing extensive mortality in late-successional stands dominated or codominated by balsam fir (*Abies balsamea* (L.) Mill.).

Table 1. Species composition (mean basal area ± SD, m^2/ha) for the sampled stands in the Gaspésie and Témiscamingue regions.

	Gaspésie		Témiscamingue	
Species	Mean	SD	Mean	SD
Abies balsamea	5.0	4.7	1.7	2.8
Picea mariana	0.0	0.0	0.3	1.7
Picea glauca	1.0	1.4	1.4	2.1
Acer saccharum	4.6	6.0	0.0	0.2
Acer rubrum	1.4	2.9	0.9	1.9
Betula alleghaniensis	3.6	3.0	5.7	5.7
Betula papyrifera	2.9	3.6	3.3	4.1
Prunus pensylvanica	0.1	0.5	0.0	0.0
Thuja occidentalis	0.0	0.0	6.7	7.4
Pinus strobus	0.0	0.0	0.3	1.1
Fraxinus nigra	0.0	0.0	0.5	2.6

Note: Composition is based on 64 prism plots (factor k = 2) taken at regular intervals along the transects in the Gaspésie region, and on 142 plots in the Témiscamingue region.

Materials and methods

Two methods were used to characterize canopy gap regimes: line intersect sampling of gaps in the field, and the study of line transects using aerial photographs. The surveyed stands are of mixed composition, are located on mesic sites, and have not burned since at least 150 years, as determined by fire studies conducted in these areas (Lauzon 2004; Grenier et al. 2005) and the maximum tree age in each stand.

In the field, 13 transects ranging from 100 to 460 m in length were measured in the Gaspésie area for a total of 3.66 km, and 12 transects ranging from 150 to 420 m were measured in the Témiscamingue area for a total of 3.96 km. These transects were dispersed across an area of approximately 500 km^2 in the Gaspésie region and of approximately 800 km^2 in the Témiscamingue region. The chosen sites presented old-growth attributes such as the presence of old trees and fallen trees at different stages of decomposition, an irregular stand structure, no evidence of tree cutting, and a mixed composition (Table 1). Transects started and ended at a minimal distance of 50 m from stand edges. Following Runkle (1992), a gap was defined as the vertical projection onto the ground of the opening in the forest canopy resulting from the death of one or more canopy trees. The presence of a snag or a dead log was used to confirm that the opening was due to tree mortality rather than to an edaphic feature or to the lack of tree recruitment at that location. A gap was considered closed when the height of gap fillers reached two-thirds of the height of the tree canopy (Battles and Fahey

Table 2. Mean, 25th and 75th quartiles, and minimum and maximum values of gap fraction (%) for the sampled transects from field data and aerial photographs before and after the spruce budworm outbreak.

	Field data (2000s)		Pre-budworm aerial photograph data (1970s)		Post-budworm aerial photograph data (1990s)	
	Gaspésie	Témiscamingue	Gaspésie	Témiscamingue	Gaspésie	Témiscamingue
Mean	25.6	36.6	44.0	33.2	37.0	44.4
25th–75th quartile	13.3–38.7	28.6–46.9	39.0–48.8	29.0–39.0	31.2–43.5	38.0–48.9
Min.–Max.	2.4–48.4	24.0–51.7	32.0–52.6	20.0–42.0	25.0–45.0	30.0–64.0

2000). The gap fraction for each transect was calculated as the proportion of transect occupied by open forest, and results were averaged per region.

We measured the proportion of open forest before and after the last spruce budworm outbreak. For this we used aerial photographs (scale 1 : 15 000) taken in 1965 and 1991 for the Témiscamingue region, and photographs taken in 1972 and 1992 for the Gaspésie region. Nine 300-m transects were dispersed across mixedwood stands on six aerial photographs per region for a total of 2.7 km in each region. The transects were interrupted 75 m on each side of any road, river, or steep slope so that measurements were made on flat or gently undulating terrain. This precaution was deemed necessary because gap fraction and gap density may vary with topographic position, elevation, and slope inclination (Battles et al. 1995). The gap fraction was calculated in the same way as when using field data.

Only gaps with an intercept length shorter than 25 m were considered, which represent gap sizes smaller than 500 m^2 if it is assumed that gaps have a circular shape and that the intercept represents the gap diameter. This was done so that we did not measure patches (i.e., large disturbed areas), since we consider that they have their own dynamic (sensu McCarthy 2001). This 25-m cutoff length was based on our own field observations and on literature on gaps in coniferous or mixed boreal forests (Kneeshaw and Bergeron 1998; Bartemucci et al. 2002). The gap size varied from 1 to 25 m in intercept length for field data and from 1.5 to 25 m for preoutbreak and postoutbreak aerial photograph data.

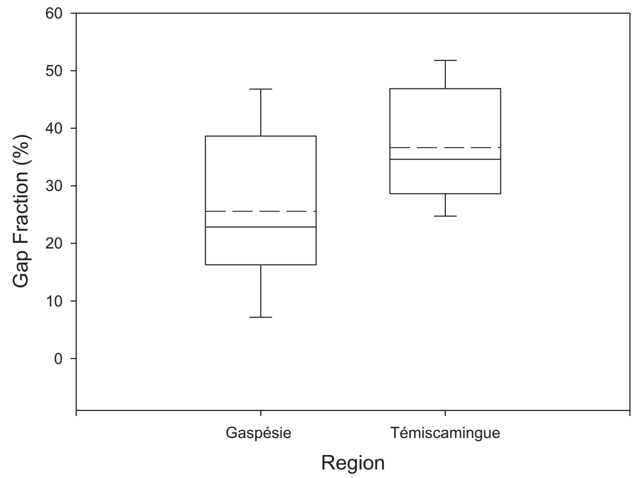
Independent *t* tests were used to compare current gap fractions from field transects for the two regions. For aerial photograph data, paired *t* tests were used to compare the gap fraction of each region before and after the last spruce budworm outbreak. All data distributions were tested for normality and homoscedasticity. Differences were considered significant at $\alpha = 0.05$.

Results and discussion

Field data

The average gap fraction measured in field transects was 25.6% in the Gaspésie region and 36.6% in the Témiscamingue region (Table 2 and Fig. 2). These results are within the range of gap fractions (from 6% to 36%) obtained in studies of boreal small-gap regimes (McCarthy 2001). Kneeshaw and Bergeron (1998) found the gap fraction to be 40.4% in 234-year-old coniferous stands but only 7% in a 50-year-old deciduous stand in northwestern Quebec, at the southern limit of the boreal forest. Brunet (2002) measured a 38% gap fraction in balsam fir dominated stands of the northern part of the Gaspésie region. Perkins et al. (1992) found the gap fraction to be 40% in subalpine forests affected by red spruce (*Picea rubens* Sarg.) decline in the Appalachian Mountains of Vermont. The gap fractions in our study are thus slightly lower than those in other mixed conifer–hardwood forests. A reason for this may be that our stands have, on average, a higher proportion of hardwoods, which can result in more lateral filling of gaps and less susceptibility to spruce budworm infestation.

Fig. 2. Stand gap fractions in Gaspésie and Témiscamingue as measured in the field. The extremities of the boxes are the 75th and 25th percentile values. The solid middle line is the mean, and the broken line is the median. The top and bottom bars are the 5th and 95th percentiles.

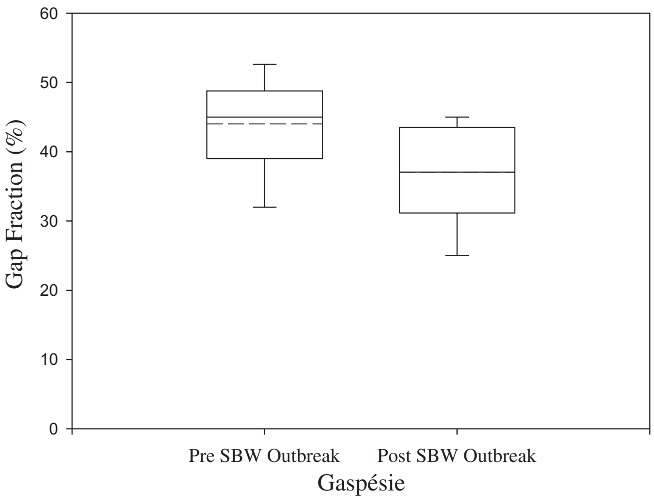


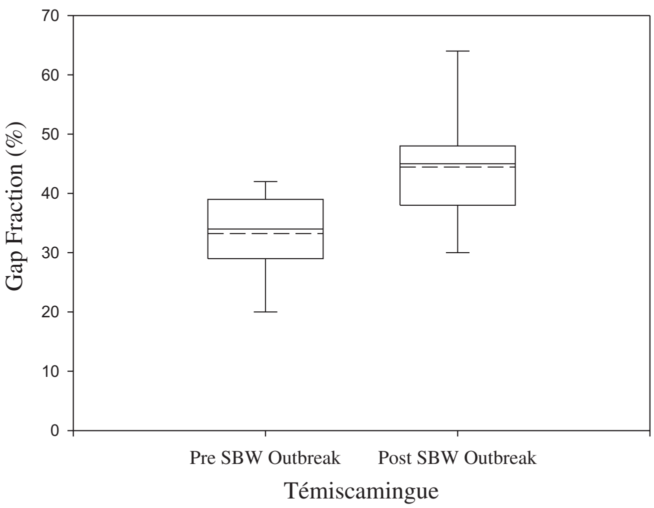
The significantly greater gap fraction in Témiscamingue ($p = 0.028$) did not correspond to our initial hypothesis that gap fraction should be the same in mixed stands irrespective of the region. This higher gap fraction in Témiscamingue may be due to a hardwood decline over the past few decades (Bouchard et al. 2005). Slight differences in species composition and disturbance regimes appear to lead to different gap dynamics in stands that are otherwise classified similarly in either region.

Temporal changes

In stands of the Gaspésie region the percentage of open forest tended to decrease during the period under study, although not significantly ($p = 0.091$), from 44.0% in 1972 to 37.0% in 1993. In contrast, the average gap fraction was found to increase ($p = 0.047$) for the Témiscamingue region from 33.2% in the 1960s to 44.4% in the 1990s (Table 2, Fig. 3). The 11.2 percentage points increase in canopy open-

Fig. 3. Stand gap fractions for each region, before and after the most recent spruce budworm outbreak as measured from aerial photographs (1965 and 1991 in Témiscamingue and 1972 and 1992 in Gaspésie). The extremities of the boxes are the 75th and 25th percentile values. The solid middle line is the mean, and the broken line is the median. The top and bottom bars are the 5th and 95th percentiles.





ness for the Témiscamingue region is very similar to the 14.3 percentage points increase in gap fraction (from 29.9% to 44.2%) estimated for the mixed-conifer forests of Abitibi (northwestern Quebec) following the last spruce budworm outbreak (D'Aoust et al. 2004). The differences between gap fraction values measured in the field and those obtained by photointerpretation for the Témiscamingue region may be due to the fact that the photographs used date from 1991 (11 years prior to our field measurements).

A number of reasons may explain why the gap fraction in the Gaspésie region did not increase. Possible explanations include differential gap-filling processes as well as the spatial distribution in the stand of deciduous tree species able to close gaps laterally (Park et al. 2005). The rate of gap closure can be significantly altered by the presence of hardwoods (Runkle 1990; Payette et al. 1990), especially since they are not directly affected by the spruce budworm

A more likely explanation for the relatively weak fluctuation of the gap fraction in the Gaspésie region would be that the last outbreak caused lower tree mortality for host species. The higher residual balsam fir basal area observed in the mixedwood forests of this region supports this conclusion (Table 1). Many studies have suggested that despite strong signals of spruce budworm outbreaks every 30 to 40 years, different regions are not necessarily equally affected (Blais 1983; Gray et al. 2000; Jardon et al. 2003). Indeed stands in the Gaspésie region were more open prior to the latest spruce budworm outbreak (Table 2), perhaps because the previous outbreak in the 1950s was longer and more severe in the Gaspésie région than in Témiscamingue region (Brown 1970; Gray et al. 2000).

These results suggest that while Kneeshaw (2001) considered that there is a predictable increase of gap fraction during the first hundred years after a fire, insect outbreaks such as those caused by the spruce budworm may alter this pattern. Furthermore, these variations are not synchronous among regions. Even though the Témiscamingue and Gaspésie mixedwood forests are both part of the balsam fir – yellow birch bioclimatic domain, they have different gap fractions and respond differently to spruce budworm outbreaks. Regional differences in the spatial and temporal pattern of disturbances suggest that the evaluation of gap dynamics should be conducted at relatively small spatial scales and, if possible, over relatively long temporal scales. Extrapolation of results to very large areas based on forest or stand types should therefore be done with caution. This is especially true if the specifics of the disturbance regime are used to justify management practices.

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