Forest dynamics following spruce budworm outbreaks in the northern and southern mixedwoods of central Quebec

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Abstract: The effects of 20th century spruce budworm (*Choristoneura fumiferana* (Clem.)) outbreaks on forest dynamics was examined in the southern and northern parts of the mixedwood forest zone in central Quebec, Canada. In each region, three study areas were placed in unmanaged stands that had not burned for more than 200 years. Disturbance impacts and forest succession were evaluated using aerial photographs and dendrochronology. Spruce budworm outbreaks occurred around 1910, 1950, and 1980 in both regions. The 1910 outbreak seemed to have limited impact in both regions, and the 1950 outbreak caused heavy mortality in conifer stands (mostly of balsam fir, *Abies balsamea* (L.) Mill.) in the southern region. The 1980 outbreak caused major mortality in the northern region, but had little impact in the southern region. Successive spruce budworm outbreaks led to a massive invasion by hardwood species in the last century in the southern region but not in the northern region. The reason for such contrasting dynamics between regions is unknown, but we hypothesize that differences in disturbance intensities, influenced by climate, played a major role. Results from this study emphasize that generalizations about the effect of spruce budworm outbreaks on forest dynamics cannot be derived from observations made during a single outbreak or at a single location.

Résumé : L'effet des épidémies de tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* (Clem.)) du 20e siècle sur la dynamique forestière a été examiné dans les parties sud et nord de la zone de forêt mixte du centre du Québec, au Canada. Dans chaque région, trois aires d'étude ont été placées dans des peuplements non-aménagées n'ayant pas brûlé depuis plus de 200 ans. L'impact des perturbations et la succession forestière ont été évalués à l'aide de photographies aériennes et de la dendrochronologie. Des épidémies de tordeuse des bourgeons de l'épinette sont survenues vers 1910, 1950 et 1980 dans les deux régions. L'épidémie des années 1910 parait avoir eu un impact limité dans les deux régions, et l'épidémie des années 1950 a causé une mortalité sévère dans les peuplements conifériens (principalement du sapin baumier, *Abies balsamea* (L.) Mill.) dans la région sud. L'épidémie des années 1980 a causé une mortalité sévère dans la région nord, mais a eu un faible impact dans la région sud. Les épidémies successives de tordeuse des bourgeons de l'épinette ont conduit à une invasion massive par les essences feuillues dans la région sud, mais pas dans la région nord. La raison expliquant un tel contraste entre les régions demeure inconnue, mais nous proposons l'hypothèse que des différences dans l'intensité des perturbations, influencées par le climat, ont joué un rôle important. Les résultats de cette étude suggèrent que des généralisations portant sur les effets d'épidémies de tordeuse des bourgeons de l'épinette sur la dynamique forestière ne peuvent être dérivées à partir d'observations effectuées dans une seule région ou après une seule épidémie.

Introduction

Boreal and subboreal forests of eastern Canada are characterized by recurrent spruce budworm outbreaks. This insect causes extensive mortality in areas where balsam fir (*Abies balsamea* (L.) Mill.) or spruces (*Picea* spp.) are abundant. Most recent studies suggest that spruce budworm populations reach outbreak levels more or less synchronously over very large areas at intervals of ca. 35 years (Royama 1984; Williams and Liebhold 2000; Jardon et al. 2003). However, within the distribution range of the spruce budworm, there are large variations in the amount of damage caused during individual outbreaks. At both the stand and landscape scales, outbreaks caused higher defoliation and mortality in older balsam fir stands (MacLean 1980; Erdle

and MacLean 1999). Mixed stands are also generally less vulnerable than pure coniferous stands, with mortality rates for host species being proportional to the conifer content in a stand (Bergeron et al. 1995; Erdle and MacLean 1999). At regional or subcontinental scales, climatic factors are also known to affect the length and intensity of defoliation episodes (Pilon and Blais 1961; Blais 1961, 1983; Gray et al. 2000; Volney and Fleming 2000; Candau and Fleming 2005). These spatial variations in the intensity of defoliation episodes are generally expected to cause corresponding variations in the amount of mortality for the host species (Jardon et al. 2003; Pothier and Mailly 2006).

In terms of forest dynamics, postoutbreak colonization patterns by different tree species are also expected to vary spatially. At the landscape scale for example, Bouchard et al.

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(2006b) found that sites on upper slope positions are more favorable for the invasion of birch species in mixed forests of western Quebec. Over regional or subcontinental spatial scales, conditions for the recruitment of balsam fir are generally adequate in boreal or maritime regions (MacLean and Ostaff 1989; Morin 1994; Leblanc and Bélanger 1998), whereas invasion by nonhost species following spruce budworm outbreaks is frequently mentioned in subboreal or continental climates (Batzer and Popp 1985; MacLean 1988; Osawa 1994; Kneeshaw and Bergeron 1998, 1999; Bouchard et al. 2005). However, postoutbreak stand dynamics have rarely been compared directly between regions with a homogenous methodology, with the exception of Ghent et al. (1957), who found that the short-term effect of the 1950 spruce budworm outbreak on forest regeneration varied at different locations along the Quebec–Ontario border. Comparing the effects of past outbreaks in regions with different climatic and compositional characteristics may permit a better understanding of the relationships between climate, preoutbreak forest composition, outbreak impacts, and stand dynamics. Such information could be useful to help forest managers design the most appropriate practices in the new context of nature-based forest management and climate change.

The general objective of this paper is to compare how successive outbreaks that occurred over the last century have affected forest structure and composition in two contrasting regions of central Quebec. One region is located in the northern mixedwoods, at the interface with the boreal forest zone, and the second in the southern mixedwoods, closer to the northern hardwoods forest zone. Specifically, our objective is to verify if spruce budworm effects on forest dynamics can be generalized based on patterns observed in one region.

Methods

Study areas

The two studied regions are located in the northern and southern parts of the subboreal or mixedwoods forest zone. In Quebec, this zone comprises the balsam fir / white birch and balsam fir / yellow birch bioclimatic domains as defined by Saucier et al. (1998). The sampled northern mixedwoods region is characterized by a mean fire return interval of ca. 127 years (Lesieur et al. 2002) and is dominated by tree species such as black spruce (*Picea mariana* (Mill.) BSP), jack pine (*Pinus banksiana* Lamb.), and trembling aspen (*Populus tremuloides* Michx.) in areas recently affected by fires. Balsam fir, white spruce (*Picea glauca* (Moench) Voss), and white birch (*Betula papyrifera* Marsh.) also occur and are mostly found on small hills that have not been affected by fire for long periods (i.e., >150 years). The fire regime has not been specifically studied in the southern mixedwoods region; however, because fire-dependant species (jack pine and aspen) are relatively rare on the eastern side of the Saint-Maurice River, we can reasonably assume that the fire return interval is longer than 200 years, which would correspond to what is observed in the lower Saint-Maurice Valley (Barrette 2004). In the southern mixedwoods region, stands that have not been logged heavily are generally dominated by tree species such as balsam fir, white birch, yellow birch (*Betula alleghaniensis* Britt.),

Fig. 1. Location of the six study areas (squares) and of the Réservoir Gouin, Rapide-Blanc (RB), and La Tuque meteorological stations (triangles). The shaded area indicates the provenance of the jack pines used to build the nonhost chronology (Lesieur et al. 2002).
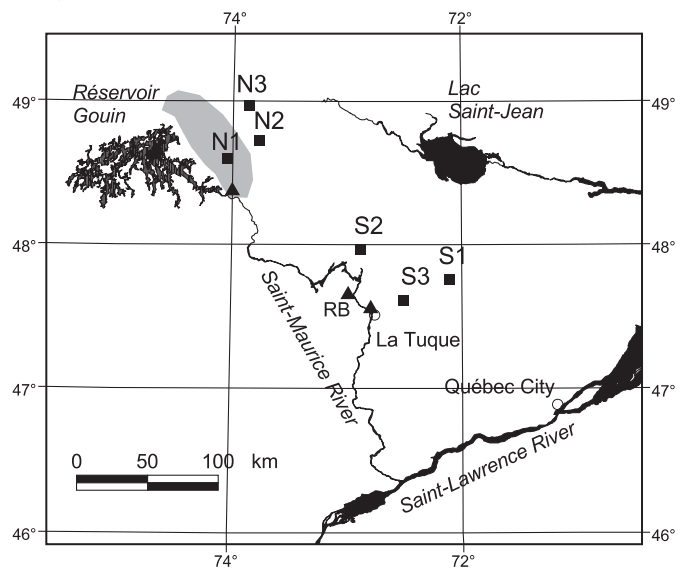
and white spruce. During the 1951–1980 period, a mean annual temperature of 0.8 °C and mean annual precipitation of 948.4 mm were recorded at the Barrage Gouin weather station (elevation 404 m a.s.l.), which is located in the northern mixedwoods region (Fig. 1). In the southern mixedwoods region, mean annual temperatures of 2.0 and 3.6 °C, and total annual precipitations of 1037.2 mm and 951.6 mm were recorded at the Rapide-Blanc (272 m a.s.l.) and La Tuque (125 m a.s.l.) stations, respectively (Environment Canada 1981) (Fig. 1).

We evaluated the effect of past spruce budworm outbreaks by making dendrochronological and photointerpretation surveys in six study areas, with three areas being placed in each region (Fig. 1). All study areas covered between 70 and 90 ha (Table 1). They were located on sites with mesic ecological characteristics: relatively thick surficial till deposits with loamy textures, on a gently undulating terrain. These areas were not affected by fires for periods of ≥200 years at the time of sampling, as evaluated from the age of the dominant trees. We selected unburned areas to make sure that temporal variations in forest structure and composition were not due to the legacies of past fires. Tree species assemblages were mostly dominated by balsam fir and white birch in both regions, with a component of yellow birch present only in the southern mixedwoods (Table 1). Jack pine and aspen were absent in the study areas, with the exception of very sparse trembling aspens that occurred in two study areas (N1 and N2), but these trees were relatively young when the sampling took place, suggesting that they did not recruit after fire. It is known that aspen propagules can germinate or sucker long after the demise of the initial postfire aspen cohort and up to 200 years after a stand initiating fire (Lavertu et al. 1994; Kneeshaw and Bergeron 1998, 1999). We also made sure that the study areas were not directly affected by past forest management activities. All study areas were located near the

Table 1. Description of the six study areas located in the northern and southern mixedwoods of central Quebec.

Region	Study areas	Location	Photointerpreted area (ha)	Years of photographs			Forest composition (% stand types)[a]				
				1940s	1960s–1970s	1990s	wBbF	yBbF	bFbS	bSbF	SM
Northern mixedwoods	N1	Lac du Milieu	73.75	1945	1970	1990	36	0	22	13	30
	N2	Lac du Nippon	86.00	1947	1969	1997	5	0	12	19	63
	N3	Lac Lamandois	72.75	1945	1964	1997	0	0	4	54	42
Southern mixedwoods	S1	Lac Aberdeen	77.25	1947	1975	1997	74	21	0	5	0
	S2	Rivière Trenche	72.00	1946	1972	1997	68	28	0	3	0
	S3	Lac Croche	74.25	1945	1972	1996	47	43	9	0	0

[a]Species codes: wB, white birch; yB, yellow birch; bF, balsam fir; bS, black spruce. For the stand types, the first species is dominant, and the second species subdominant. SM, Severe mortality (>75%) due to the 1980 spruce budworm outbreak. This information comes from contemporary forest maps published by the ministère des Ressources naturelles du Québec.

Table 2. Information on field samplings and cored trees.

Study area	Transect length (km)	No. of plots	Total no. of trees per species[a,b]				
			yB	wB	wS	bS	bF
N1	1.9	9	—	20 (2)	16 (2)	4 (1)	48 (3)
N2	1.1	10	—	14 (0)	19 (4)	3 (1)	84 (5)
N3	1.5	12	—	5 (0)	18 (2)	14 (2)	68 (9)
S1	2.2	12	20 (3)	28 (1)	23 (4)	7 (4)	24 (1)
S2	1.6	11	1 (0)	37 (6)	26 (3)	—	51 (0)
S3	1.7	12	14 (2)	22 (1)	23 (0)	—	44 (1)

[a]Values in parenthesis are the numbers of trees that could not be aged accurately (because of rot or missed centers).

[b]Species codes: yB, yellow birch; wB, white birch; wS, white spruce; bS, black spruce; bF, balsam fir.

height of the land on the eastern side of the Saint-Maurice River watershed (Fig. 1).

Dendrochronology

The dendrochronological part of this study had two objectives. The first objective was to build a spruce budworm outbreak chronology for each area based on the growth patterns of white spruce, a host species that tends to survive through outbreaks and, hence, is more suitable for historical reconstructions (Blais 1961). Our second objective was to construct tree age structures in each area to confirm whether past outbreaks caused sufficient mortality to initiate a recruitment pulse in the studied stands.

To acquire representative data, three or four linear transects with random orientation were placed within each study area. When an area was recently logged (after 2000), the transects were established in remnant forest patches >10 ha, having characteristics representative of the larger photointerpreted patches: similar forest type, absence of anthropogenic disturbances, and located on mesic sites. For one area (F1), which was not accessible by road, the transects were established in representative forest patches located less than 2 km from the photointerpreted area. Along each transect, the sample plots were placed perpendicular to locations where large white spruce trees were found, such that we respected a minimal distance of 50 m between plots. Sample trees were selected with a prism (factor $k = 2$), which gave a greater weight to large trees compared with a tree-selection criteria based on abundance. Concentrating the sampling on larger trees permitted us to obtain more information on trees originating before the last outbreak (which is already well described on forest maps and defoliation surveys). Every second tree that was included in the prism plot was cored.

In addition to this, all white spruces larger than 20 cm DBH present within a radius of 20 m from the plot centre were cored. Nine to 12 plots were established for each study area (Table 2). For each white spruce tree, two cores were taken at 1 m in height with an angle, on a horizontal plane, of 90° to 180° between the two cores. For the other species, only one core was collected at 1 m height. Each core was glued to a wooden holder, dried, and sanded (400 or 600 grit). In each study area, we cored about 100 trees of different species in this manner (to satisfy our second objective), including a minimum of 10 large white spruce trees (to satisfy the first objective).

Precise ring-width measurements were done for each white spruce tree. The measurements (0.01 mm precision) were done with a tree-ring measuring table (Velmex Inc., Bloomfield, N.Y.) connected to a computer. Crossdating was done with the program COFECHA (Holmes 1997) to validate the accuracy of the ring count and locate missing rings. This measurement and crossdating procedure was repeated for all white birch cores, because this species is particularly susceptible to having missing rings. Other species (balsam fir, black spruce, and yellow birch) were not crossdated. For each tree, we also identified growth releases when a tree's growth increased by 100% over a given 10 year period compared with the preceding 20 year period. A relatively long 20 year period prior to release was used to insure that the releases were due to canopy openings and not simply an artefact of the cessation of insect defoliation. This criterion is relatively conservative compared with other studies using similar growth release criteria (Lorimer and Frelich 1989; Parish et al. 1999).

To detect past spruce budworm outbreaks, standard chronologies were built for each site with the program ARSTAN

Table 3. Information on host (white spruce) and nonhost (jack pine) residual chronologies.

| Study area | No. of trees | Ss > 0.80[a] | Time span | Mean ring width (mm) | Sensitivity | | Intertree correlation |
					Mean	SD	
N1	14	1893	1858–2004	1.49	0.240	0.714	0.563
N2	16	1877	1764–2004	1.23	0.237	0.649	0.594
N3	15	1845	1775–2004	1.19	0.230	0.656	0.540
S1	21	1873	1782–2004	1.55	0.305	0.986	0.580
S2	16	1899	1832–2004	1.65	0.266	0.963	0.550
S3	22	1857	1778–2004	1.34	0.278	0.763	0.593
Nonhost	34	1835	1767–1998	1.05	0.213	0.589	0.559

[a]Year in which signal strength (variance agreement between finite and theoretical infinite sample size; Holmes 1997) becomes greater than 0.80.

Fig. 2. Chronologies for spruce budworm host and nonhost species for the six study areas. Dotted lines are the reference jack pine chronology (nonhost; Lesieur et al. 2002), and the continuous lines are the white spruce chronologies (host species). Each host chronology is based on more than 10 white spruce trees.
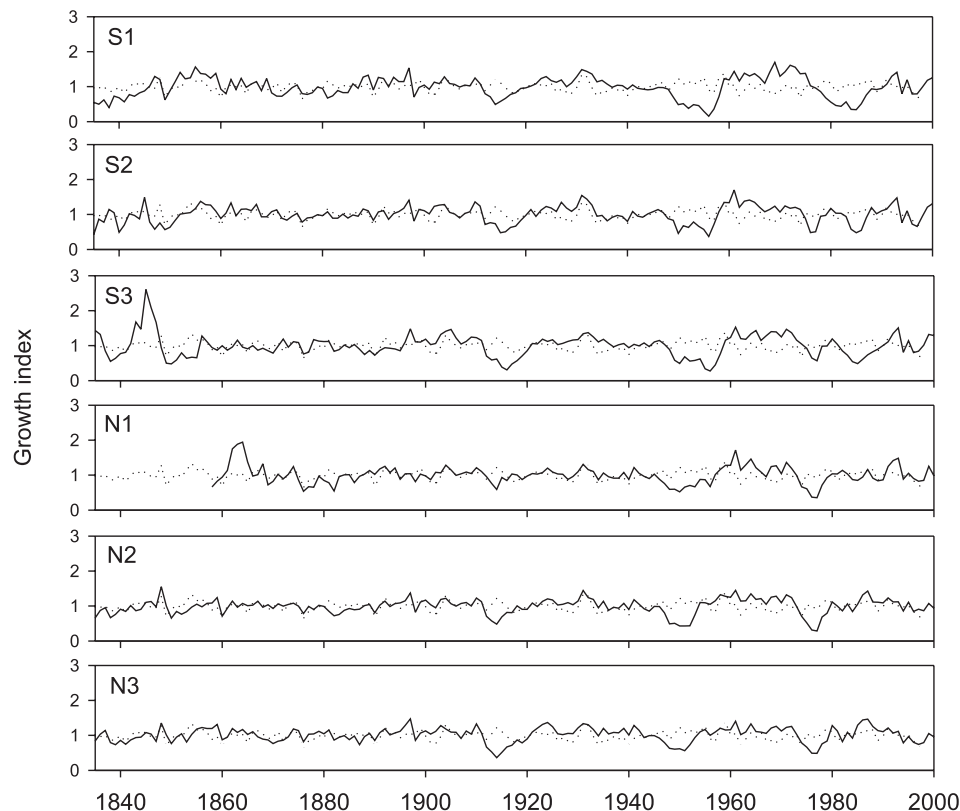
(Holmes 1997), using a cubic smoothing spline to detrend the series (with a 50% frequency response cutoff of 60 years). A jack pine chronology was used as a reference non-host chronology. Jack pine trees were sampled in the eastern Réservoir Gouin sector, ≤50 km from the study areas in the northern mixedwoods region and about 100 to 150 km from the sampling areas in the southern mixedwoods (Fig. 1; refer to Lesieur et al. (2002) for a description of the sampling procedure for jack pine). A standard chronology was obtained for jack pine tree-ring measurements by using the same statistical procedure as for white spruce. Each individual white spruce chronology was then compared visually with this reference jack pine chronology (Blais 1965). Growth reductions specific to white spruce indicated potential spruce budworm outbreaks.

Photointerpretation

A procedure similar to the one used by Bouchard et al. (2006b) was used to obtain information from aerial photographs. The goal was to quantify the impact of successive outbreaks in term of area affected and examine successional pathways following severe budworm impact.

The three areas were subdivided using a grid with a 50 m × 50 m cell size. The width of a cell represents about two or three times the average mature tree length in these forests and enables us to focus on patch- or stand-scale disturbance and regeneration patterns rather than gap-scale processes. The changes in vegetation composition and structure through the years were measured from aerial photographs available from federal or provincial government records.

Photographs taken in the 1940s, 1960s–1970s, and 1990s were available for all three areas (cartographic scales between 1 : 13 000 and 1 : 16 000). Photographs taken in 1930 were available for three study areas (N1, S1, and S3; scales between 1 : 10 000 and 1 : 15 000). We printed the 50 m × 50 m grid on an acetate paper at a scale corresponding to the photographs from each area and each period and conducted the photointerpretation with this grid overlaid on the photographs.

We considered that a tree was part of the overstory when its crown was high and large enough to be distinguished from adjacent trees, which according to field evaluations corresponds to a vegetation height of 8–10 m or more. The proportion of the cell covered by conifer and hardwood species was evaluated on aerial photographs for each period and for each cell by using the following classification: ≤5%, 6%–15%, and by every 10% up to the 86%–95% category. The remaining area within each cell was considered to be open. The midpoint value of each of these categories was subsequently used for analysis. The photographs taken in 1930 were not used to evaluate canopy composition, because they were not of sufficient quality to quantify species composition. They were only used to assess canopy openness.

To measure the spatial extent of mortality caused by 20th century disturbances, we considered that the impact of a disturbance was major when ≥65% of a cell was open. This was determined on aerial photographs taken 0–30 years after the occurrence of a given outbreak. Based on earlier studies, we estimate that, from this threshold, mortality due to the spruce budworm should initiate stand replacement processes rather than gap-phase dynamics. To confirm that canopy openings were due to spruce budworm outbreaks, we verified prior dominance by host species, which was possible for outbreaks occurring after the earlier photographs were taken. For older photographs, we validated outbreak occurrence by cross referencing the photointerpretation results with the dendrochronology results.

Results

Dendrochronology

A total of 633 trees were cored (Table 2). In each of the six study areas, we found several trees 150 years or older, which confirms that these areas were not affected by stand-replacing fires for long periods. From the comparison of Tables 1 and 2, we conclude that some species were oversampled (balsam fir and white spruce) and others undersampled (birches and black spruce) relative to their abundance in the overstory as indicated by contemporary forest maps. This bias may have been caused by the plot-location procedure, which required the presence of white spruce for dendroecological dating of the spruce budworm outbreaks. However, we believe that the overrepresentation of balsam fir should not cause bias in the detection of recruitment or growth release pulses. It is also worth mentioning that balsam fir was more abundant before the 1980 outbreak.
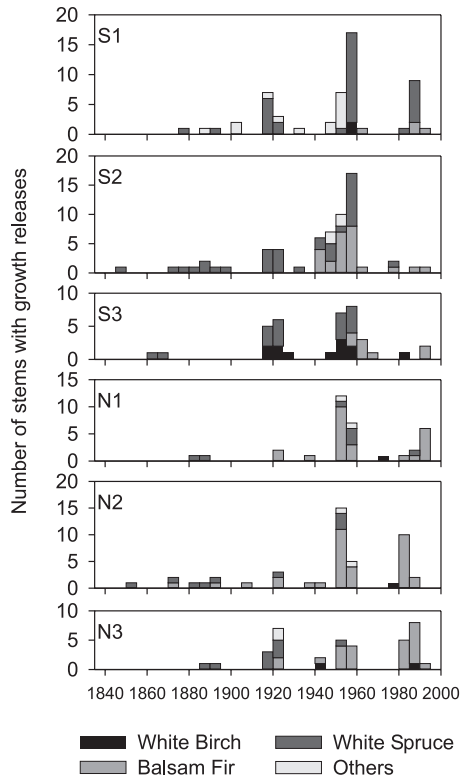
The nonhost (jack pine) residual chronology exhibits lower mean sensitivity and standard deviation compared with the host (white spruce) chronologies (Table 3). This suggests that jack pine is less influenced by interannual var-

Fig. 3. Year of recruitment at 1 m height for all trees cored in the six study areas between 1840 and 2000.
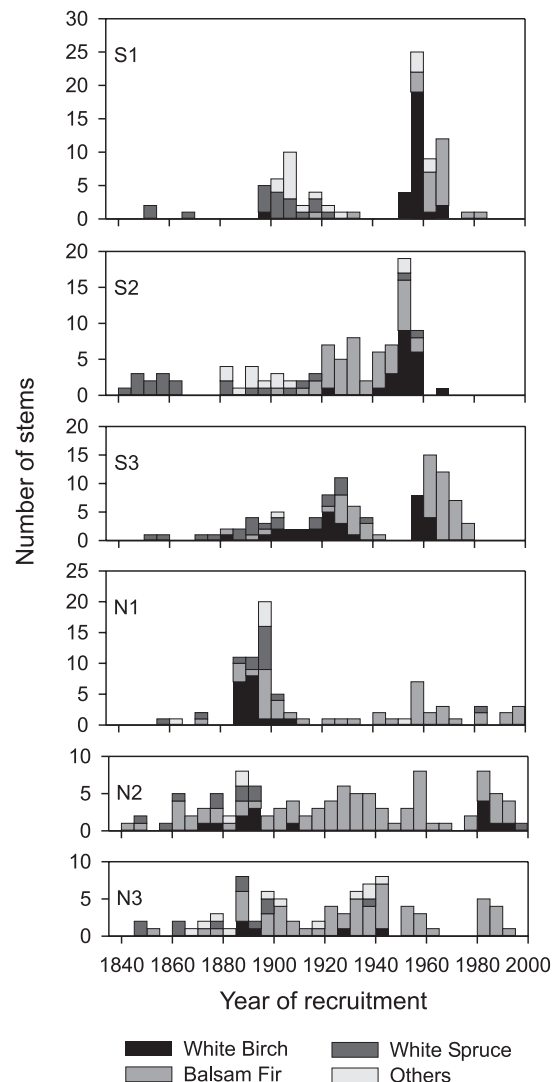
iations in environmental conditions such as climate or insect defoliation. Based on the comparison between the growth patterns of white spruce and jack pine, three growth depressions corresponding to potential outbreaks were identified in the 20th century in all areas: around 1910, 1950, and 1980, with beginning and ending dates varying from one site to the other (Fig. 2). These outbreaks have been directly or indirectly observed by several researchers in neighbouring regions (Swaine and Craighead 1924; Blais 1965; Brown 1970; Morin 1994; Leblanc and Bélanger 1998; Jardon et al. 2003). Growth reductions specific to host species were also detected around 1840 and 1880 in some areas (Fig. 2). However these growth depressions were less pronounced than those found during the 20th century, and they were not synchronous among the six study areas.

Pulses of recruitment by shade-intolerant tree species suggest significant mortality episodes in the dominant canopy. Recruitment of white birches was concentrated in the period following the 1950 outbreak in the southern mixedwoods (the S1, S2, and S3 areas) and around 1890 in the northern mixedwoods (the N1, N2, and N3 areas) (Fig. 3). An iso-

Fig. 4. Growth releases present in cores sampled at 1 m height.

White Birch   White Spruce
Balsam Fir   Others

Fig. 5. Variations in dominant canopy composition in each study area, based on the aerial photographs taken between 1945 and 1997. Percent canopy cover represents the mean canopy cover for all cells in a given study area (i.e., comprising cells with or without heavy impact).

lated pulse of recruitment by white birch also occurred around 1920–1925 in the S3 area. Recruitment pulses by shade-tolerant species (essentially balsam fir; Fig. 3) coinciding with growth releases (Fig. 4) occurred in the northern mixedwoods around 1950–1960, but no shade-intolerant tree species recruited during those events. Growth releases also occurred in the southern mixedwoods around 1915–1925 (Fig. 4), but they did not coincide with clear recruitment pulses (Fig. 3), suggesting that canopy openings were caused by a relatively diffuse mortality event.

Photointerpretation and composition changes

In terms of species composition, the study areas in the northern and southern mixedwoods had similar proportions of hardwood and softwood canopy cover in the 1940s photographs (Fig. 5). Following the 1950 outbreak, conifer cover decreased and stayed unchanged thereafter in the southern mixedwoods, whereas it initially increased or stayed unchanged in the northern mixedwoods and then decreased following the 1980 outbreak (Fig. 5). Conversely, hardwood content initially decreased and then stayed unchanged in the northern mixedwoods, whereas it stayed relatively constant and then increased strongly in the southern mixedwoods (Fig. 5). Generally, the photointerpreted cells were distributed much more evenly across canopy cover classes immediately after the severe disturbance episodes (Fig. 6).

Host-species mortality due to the 1950 and 1980 outbreaks could be assessed directly by comparing pre- and post-outbreak forest structure and composition, whereas the effects of the 1910 outbreak were estimated based on the abundance of young thickets and areas in regeneration in
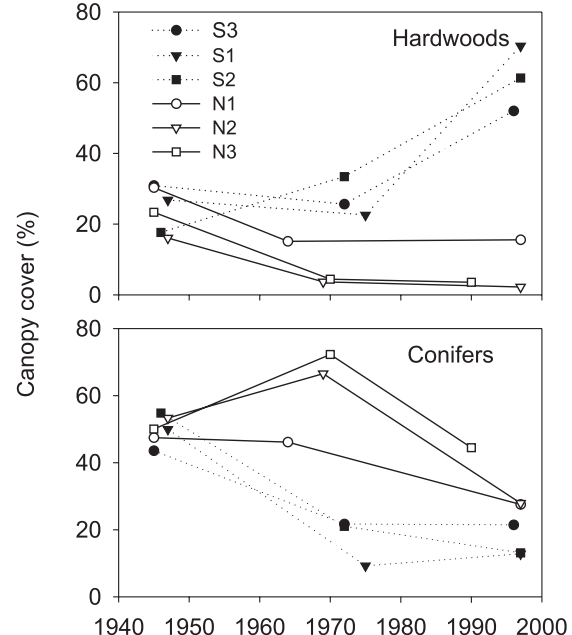
the study areas. In the southern mixedwoods, the proportion of photointerpreted cells affected by severe mortality was highest after the 1950 outbreak, whereas it was highest after the 1980 outbreak in the northern mixedwoods (Table 4). Most cells affected by heavy mortality during the 1980 outbreak were dominated by conifers in the 1960s–1970s (Table 5), which supports that this mortality was caused by the spruce budworm outbreak. However a certain proportion of the cells affected by tree mortality in the 1950s were dominated by hardwoods before the outbreak, especially in the N1 area (Table 6). This suggests that mortality in these areas, and perhaps also in the S1 area (Table 6), was due to a combination of both birch dieback and spruce budworm mortality. The occurrence of a large-scale birch dieback in 1956–1957 was observed by Lortie (1962). Although we did not have preoutbreak photographs for the 1910 outbreak, the fact that postoutbreak photographs (1930 and 1945) contained few cells at the regeneration stage, except for the S1 area (Table 4; Fig. 6), suggests that this outbreak killed individual trees instead of large groups of trees.

Long-term successional trends were assessed in both regions for the cells heavily affected by the 1950s outbreak (Table 6). The recruitment of conifers after this outbreak was more pronounced in the N1 area compared with study areas located in the southern mixedwoods (S1, S2, and S3) (Table 6). Successional trends were not examined in the N2 and N3 areas, because <20 cells were affected by severe mortality after the 1950 outbreak. Long-term trends following the 1910 outbreak were not examined, because this outbreak had little impact in the southern mixedwoods and no impact in the northern mixedwoods, which restricted comparisons between both regions.

Fig. 6. Frequency distributions of the photo-interpreted cells as a function of canopy cover classes. The frequency distributions are shown separately for the six study areas and three periods. The thick black vertical line indicates the threshold value below which a cell is considered heavily disturbed (i.e., < 35% canopy cover).
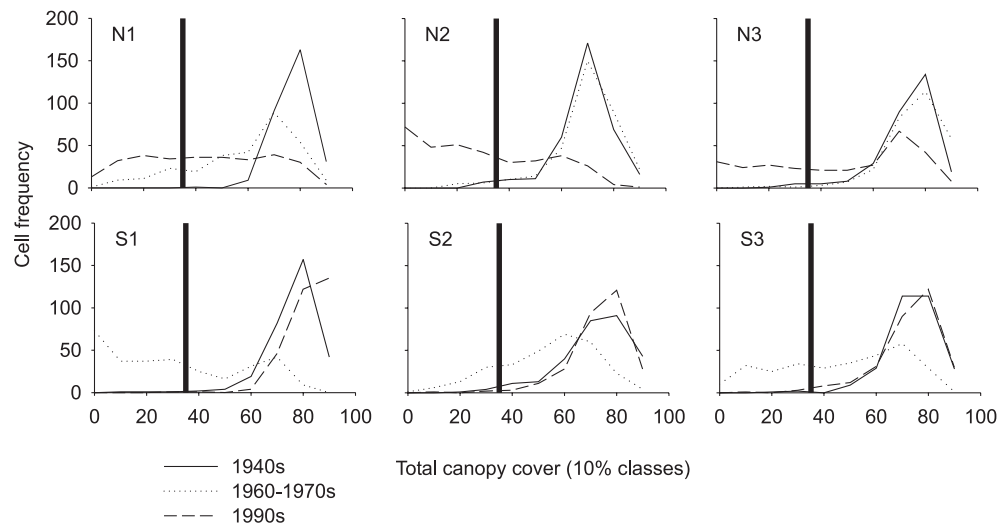

Table 4. Proportion of cells (0.25 ha) in each study area that were affected by severe mortality based on aerial photographs from the 1940s, 1960s–1970s, and 1990s.

| Year of photographs | Percentage of cells affected | | | | | |
| | Southern mixedwoods | | | Northern mixedwoods | | |
	S1	S2	S3	N1	N2	N3
1940s	18.8	5.9	2.0	0.0	2.0	2.7
1960s–1970s	49.8	17.0	33.3	14.9	3.2	1.4
1990s	0.3	0.3	1.3	38.3	61.3	35.7

Note: Most of the mortality observed on these photographs is due to outbreaks that occurred around 1910, 1950, and 1980, respectively. Heavy impact within a given cell was recorded when the canopy cover of mature trees was less than 35%.

Table 5. Preoutbreak canopy composition in cells with heavy disturbance impact during the 1980 outbreak (i.e., ≤35% of remaining canopy in a given cell) based on the 1960s–1970s aerial photographs.

| Composition before the 1980 outbreak | Percentage of cells affected | | |
	N1	N2	N3
Hardwood	0	0	0
Mixed[a]	38	3	2
Conifer	62	97	98

Note: Only study areas with more than 20 cells with heavy impact are shown (S1, S2, and S3 areas had only one, one, and four cells with heavy impact, respectively).

[a]A cell was categorized as mixed when the difference between conifer and hardwood canopy cover is less than 20%. Otherwise, the cells are categorized as either hardwood or conifer.

Discussion

Spruce budworm-caused mortality

The impacts of successive spruce budworm outbreaks on forest dynamics were assessed using several indicators. We have shown that such impacts varied in space (i.e., among regions and study areas) and in time (among successive outbreaks). During the 20th century, the 1910 outbreak had a relatively minor impact in terms of stand mortality, essentially concentrated in one study area of the southern mixedwoods. This concurs with the observations made by Blais (1965) in Laurentide Park and suggests that this outbreak probably caused little mortality in central Quebec, contrasting with the large-scale devastations reported in western Quebec (Swaine and Craighead 1924; Bouchard et al. 2006b) or the Maritime Provinces (MacLean and Ostaff 1989) during the same period. The 1950 outbreak caused heavy mortality in the southern mixedwoods, which was easily detectable on aerial photographs. In contrast, only one area experienced some heavy mortality in the northern mixedwoods during this outbreak (N1 area). The 1980 outbreak also caused heavy mortality but only in the northern mixedwoods. The duration and intensity of the defoliation episode in the southern mixedwoods during the 1980 out-

break, as determined from growth reductions in white spruce (Fig. 2), suggests that this outbreak was severe in this region as well but had little impact in terms of stand mortality, because mature balsam fir stands had already been mostly eliminated following the 1950 outbreak.

During the 19th century, growth reductions in white spruce were observed around 1880–1885 in both regions. A potential outbreak around these years was also detected by Jardon et al. (2003) for their sampling points located in the Saint-Maurice Valley and by Morin (1994) in the neighbouring Lac Saint-Jean region. Some recruitment, including shade-intolerant birches, occurred in the 10–20 years following this possible outbreak, particularly in the study areas located in the northern mixedwoods.

Birch dieback

A hardwood decline was observed on photographs from the 1960s–1970s, probably corresponding to the white birch dieback mentioned by Lortie (1962), which started in 1956–1957. This dieback could be due either to climatic irregularities such as thaw–frost events, to the synchronous mortality of a senescent cohort, or to both reasons (Lortie 1979; Au-

Table 6. Successional pathways for the photointerpreted cells exhibiting severe disturbance impact on the 1960s–1970s aerial photographs.

Successional pathways		Percentage of photointerpreted cells			
		Southern mixedwoods			Northern mixedwoods
Composition on 1940s photographs[a]	Composition on 1990s photographs[a]	S3	S2	S1	N1
Hardwood	Hardwood	0	0	9	2
Hardwood	Mixed	0	0	1	9
Hardwood	Conifer	6	0	0	**30**
Mixed	Hardwood	**11**	**10**	**34**	0
Mixed	Mixed	5	2	5	**20**
Mixed	Conifer	2	0	0	**25**
Conifer	Hardwood	**30**	**63**	**40**	5
Conifer	Mixed	**39**	**24**	**10**	7
Conifer	Conifer	6	0	1	2
Total		100	100	100	100

Note: Only cells with a heavy disturbance impact on the 1960–1970s photographs (i.e., ≤35% of remaining canopy in a given cell) and with more than 50% tree cover in the 1940s and the 1970s, are shown. Even though the 1950 spruce budworm outbreak was the main disturbance, some effect of birch dieback is perceptible in the N1 area. The N2 and N3 study areas are not shown, because they had less than 20 cells with heavy impact. Successional pathways representing >10% of the total number of cells for a given study area are given in boldface.

[a]A cell was categorized as mixed when the difference between conifer and hardwood canopy cover is less than 20%. Otherwise the cells are categorized as either hardwood or conifer.

clair et al. 1996). The possible presence of this senescent white birch cohort after 1956–1957 coincides well with the hypothesis of a hardwood recruitment pulse around 1880–1885. Even if individual white birch trees can live for periods much longer than 100 years, the breakup of an even-aged white birch stand can occur between 70 and 90 years after stand initiation, depending on soils and environmental conditions (Lortie 1979; Auclair et al. 1996; Pothier and Savard 1998; Bouchard et al. 2006b). A hardwood decline may also have occurred in the southern mixedwoods in the late 1930s (see Hatcher 1964; Braathe 1995), but we did not have predecline photographs to verify this.

Tree species composition and stand dynamics

Our results indicate that the hardwood–conifer balance was similar in the northern and southern regions of the mixedwood zone in the 1940s. This compositional similarity before the 1950 outbreak should be evaluated with caution, because there was probably a higher representation of black spruce in the conifer group in the northern region and a higher representation of yellow birch in the hardwood group in the southern region (Table 1). Composition subsequently diverged because of hardwood dieback in the northern mixedwoods and because of conifer mortality and postoutbreak hardwood invasion in the southern mixedwoods. This demonstrates that generalizations about forest dynamics from one region to another should be made with caution.

Postoutbreak invasion by hardwoods was a significant process in the southern mixedwoods. Such a large-scale compositional conversion from conifers to hardwoods has seldom been reported in the budworm literature. Balsam fir is usually reported to recruit abundantly after an outbreak because of the extensive seedling bank that this species is able to establish before the outbreak (MacLean 1984; Morin 1994). Two reasons could explain the lack of fir recruitment in the southern mixedwoods: the absence of a seedling bank prior to the outbreak or the killing of this seedling bank during an epidemic. The absence of a balsam fir seedling bank could be due to unfavorable litter or soil conditions (Greene et al. 1999), higher competition by shrubs prior to the outbreak (Kneeshaw and Bergeron 1999), or the absence of seed trees. As for the possibility that an outbreak completely eliminates the seedling bank, it is generally considered to be quite low (Morin and Laprise 1997; Ruel and Huot 1993). However, over longer time frames, intense and repetitive balsam fir mortality following successive outbreaks could reduce this species' ability to compete. Intense and repetitive fir mortality could provide the necessary growing conditions for nonhost tree species such as white birch. An increased severity of spruce budworm outbreaks has already been suggested as a mechanism explaining a greater abundance of birch in Quebec's mixed forest zone compared with the boreal zone (Richard 1993; Bouchard et al. 2006a).

Hardwood invasion was less important in the northern mixedwoods than in the southern mixedwoods. This was probably due partly to a lack of establishment opportunities for shade-intolerant species (i.e., outbreaks of lesser magnitude). It has been suggested that tree mortality following an outbreak is generally less important in northern regions (Blais 1983), perhaps because colder or more humid climates are less favorable to the proliferation of spruce budworm populations (Blais 1961, 1983; Volney and Fleming 2000; Candau and Fleming 2005). Even though our study does not provide direct evidence for such a latitudinal effect on outbreak intensity, it concurs well with this hypothesis. This is true especially in view of the important mortality during the 1950 outbreak in the southern mixedwoods, which had little effect in the northern mixedwoods.

Conclusion

It has been suggested that global warming will cause an increased virulence of spruce budworm outbreaks (Logan et al. 2003). If such a change occurs, we suggest that it may be accompanied by an increase in the abundance of nonhost tree species because of the opportunities created by disturbances for their recruitment. Replacement of fir by hardwoods would constitute a negative feedback loop between successive outbreaks, forbidding any linear increase in outbreak impact (Volney and Fleming 2000; Bouchard et al. 2006b). This is well illustrated by the case of the southern mixedwoods region described in this paper, where the stand-scale impact of the severe 1980 outbreak was low because few mature conifer stands were left after the 1950 outbreak. Sudden compositional or structural changes following insect outbreaks or other disturbance types should be integrated in forecasting models trying to predict the dynamics of these forests in response to climate change and forest management.

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