

FOREST DYNAMICS AFTER SUCCESSIVE SPRUCE BUDWORM OUTBREAKS IN MIXEDWOOD FORESTS

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Abstract. In order to assess the long-term spatiotemporal influence of the spruce budworm in sub-boreal mixedwood forests, we studied the effect of three successive outbreaks in a region of western Quebec, Canada. We used dendrochronology to detect past outbreaks in three areas (111–185 ha), based on the recruitment age of balsam fir (*Abies balsamea*) and on growth patterns of white spruce (*Picea glauca*), the two main host species of this defoliating insect. We also used a series of aerial photographs taken between 1935 and 2003 to evaluate overstory mortality and post-outbreak succession patterns in these same areas. Individual outbreaks had a spatially homogenous impact on host species throughout the region, but successive outbreaks differed in intensity: the two outbreaks around 1910 and 1980 caused widespread mortality in the overstory, but an outbreak around 1945 had little impact, probably because the forest mosaic had not yet recuperated from the 1910 outbreak. No clear outbreak was detected in the later part of the 19th century. In portions of the study areas where the 1910 outbreak had a major impact, between 36% and 50% of the stands were reoccupied by balsam fir stands in the period up to the 1980 outbreak (cyclic succession), the rest being at least partly replaced by nonhost species such as *Betula* spp. Changes in forest composition after the 1910 outbreak were mostly associated with upper-slope positions in all study areas. The 1980 outbreak also had a higher impact than earlier outbreaks in lower-slope positions dominated by black spruce (*Picea mariana*)–balsam fir mixtures. These results suggest that, at the regional scale, the abundance of mature or over-mature balsam fir stands does not determine the outbreak cycle. When an outbreak occurs, however, its impact will be strongly constrained by forest characteristics such as stand composition and structure, which are themselves influenced by previous disturbances and slope position.

Key words: *Abies balsamea*; *Betula*; birch dieback; Choristoneura fumiferana; forest dynamics and succession; mixedwoods; natural disturbances; outbreaks; *Picea*; spruce budworm.

INTRODUCTION

Spruce budworm outbreaks are a major large-scale natural disturbance throughout most of the range of balsam fir in eastern North America. Outbreaks occur synchronously over subcontinental spatial scales (Williams and Liebhold 2000), but the intensity and duration of the defoliation episodes vary on a regional or subregional basis (Blais 1983, Williams and Liebhold 2000). As a result of this variability in outbreak severity, the impact of an outbreak can range from temporary growth reductions in individual trees, to extensive tree mortality affecting entire stands. Based on dendroecological reconstructions and archival records, we also know that spruce budworm populations generally reach outbreak levels with a frequency varying between 30 and 40 years (Royama 1984, Jardon et al. 2003, Boulanger and Arseneault 2004). Significantly longer intervals, up

to 100 years, could occur in some regions (Blais 1983), perhaps because some intermediate outbreaks remain undetected (Royama 1984, Royama et al. 2005).

For a given level of defoliation, an outbreak tends to cause more mortality in older stands compared with younger ones, and in balsam fir-dominated stands compared to stands dominated by spruce species (MacLean 1980, Blais 1985, Bergeron et al. 1995). Outbreak impact is thus usually constrained by the abundance of mature balsam firs within the forest mosaic, which itself depends on the legacies of previous disturbances. For instance, after stand-replacing fires, balsam fir will increase in importance progressively over a period of 150–200 years, causing a corresponding increase in the impact of spruce budworm outbreaks (Frelich and Reich 1995, Bergeron and Leduc 1998). Forest characteristics can also be modified directly by the spruce budworm itself: when it causes extensive mortality, a severe outbreak can reduce the vulnerability of stands and forests to future budworm attack for intervals of 50 years or more (Blais 1981a, Erdle and MacLean 1999).

Manuscript received 27 July 2005; revised 17 January 2006; accepted 7 February 2006. Corresponding Editor: J. A. Jones.

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Several studies indicate that most balsam fir stands killed during an outbreak will be replaced by stands of similar composition, because balsam fir stands often contain an abundant seedling bank (Ghent et al. 1957, MacLean 1980, 1984, Blais 1983, 1985, MacLean and Ostaff 1989, Morin 1990, 1994). Other studies, essentially conducted in warmer or dryer climates where fir is less ubiquitous, indicate that nonhost species may invade in larger canopy openings (Baskerville 1975, Batzer and Popp 1985, Osawa 1994, Kneeshaw and Bergeron 1998, 1999) or when the balsam fir seedling bank is less dense (Déry et al. 2000). The fate of these nonhosts is uncertain, and some or all of them may disappear in the years following the disturbance (MacLean 1984, Osawa 1994). An increased abundance of nonhost species after a spruce budworm outbreak has also been observed in studies carried out over large spatial scales (Frelich and Reich 1995, D'Aoust et al. 2004), but it is not clear whether these outbreaks accelerated postfire succession or triggered successional processes of their own.

Forest management activities such as logging and fire suppression could also be responsible for an increase in balsam fir content in some regions (Blais 1983), a factor that may be responsible for an increase in outbreak severity during the 20th century in eastern Canada (Blais 1983, Jardon et al. 2003). However, this temporal change in outbreak patterns may also be due to factors unrelated directly to forest characteristics, such as the impact of climate and stochastic factors on population dynamics of the insect and its natural enemy complex (Royama 1984, Royama et al. 2005).

Our objectives in this study were to measure spruce budworm outbreak impacts in terms of overstorey mortality and succession at various spatial scales, and evaluate the possible influence of previous disturbances on these patterns. We used a combination of dendrochronological reconstructions and the interpretation of old aerial photographs to study the effect of successive outbreaks in three mixed-species unlogged areas (113–183 ha) that have not been affected by major fires for at least 200 years.

STUDY REGION

Vegetation and disturbances

Our study took place in the Témiscamingue region, in the western portion of the Province of Quebec (Canada), within the transitional vegetation zone between the boreal forest and the temperate northern hardwood forest zone, corresponding to the balsam fir/yellow birch bioclimatic domain according to the latest provincial classification (Saucier et al. 1998). Soils in the study region are dominated by glacial deposits, and the sampled areas were mostly located on tills at least 1 m thick. A mean annual temperature of 1.9°C and a mean annual precipitation of 995.9 mm (including 290.8 cm as snow) were recorded during the 1971–2001 period at Belleterre's meteorological station (47°23' N, 78°42' W).

In this region, the topographic gradient is linked to variations in factors known to be important for the establishment and growth of the different tree species, such as drainage, nutrient availability, soil depth, and microclimate (Fraser 1954, MacHattie and McCormack 1961, Geiger 1965, Brown 1981). In forests that have not been affected by fire for a long period, mesic-xeric hilltops are often dominated by sugar maple (*Acer saccharum*), upper-slope mesic sites have mixed stands dominated by yellow birch (*Betula alleghaniensis*), middle-slope or lower-slope mesic sites have mixed stands dominated by boreal species (balsam fir, white birch [*Betula papyrifera*] or white cedar [*Thuja occidentalis*]), and imperfectly drained lower slopes or lowlands are dominated by black spruce together with some balsam fir and white cedar. The length of the natural fire cycle has been estimated to be 200 years (Grenier et al. 2005), and fire-adapted species such as aspen (*Populus tremuloides*) and jack pine (*Pinus banksiana*) are also present in the region.

Aerial surveys conducted during the last century confirm that major defoliation episodes by the spruce budworm occurred in the area between 1909 and 1918 (Swaine and Craighead 1924, Brown 1970), between 1938 and 1948 (Brown 1970), and between 1972 and 1984 (Hardy et al. 1986). For the rest of this paper, these three outbreaks will be referred to as the 1910, 1945, and 1980 outbreaks, respectively. The history of spruce budworm outbreaks during the 19th century has also been studied in surrounding regions through dendrochronology, but some uncertainties remain. For the region to the southeast of Témiscamingue, Blais (1981b) found that no outbreaks occurred during the 19th century. For the Lake Duparquet area, ~150 km to the northwest of our study sites, Morin et al. (1993) found evidence of an outbreak occurring ca. 1830. In another study covering a large sector of western Québec, Jardon et al. (2003) found minor outbreaks occurring close to our study sites around 1860 and 1890.

Study areas

Three areas were selected for detailed photointerpretation and dendroecological analysis. All sites had a minimum area of 100 ha, contained all the main late-successional mixed-stand types present along the toposequence, had no evidence of harvesting, and had not burned for at least 200 years based on the age of dominant trees. The extensive tree harvesting in the region in recent decades made the location of sites difficult, and the three chosen areas, which are separated by at least 25 km, are probably the last remaining virgin late-successional stands in the region. For each of these areas, we excluded from the analysis the portions of the stands where spruce budworm host species have been very rare throughout the 20th century (sugar maple stands on hilltops, swamps, or inundated areas), and a few stands affected by disturbances other than by spruce budworm outbreaks during the 1935–2003 period.

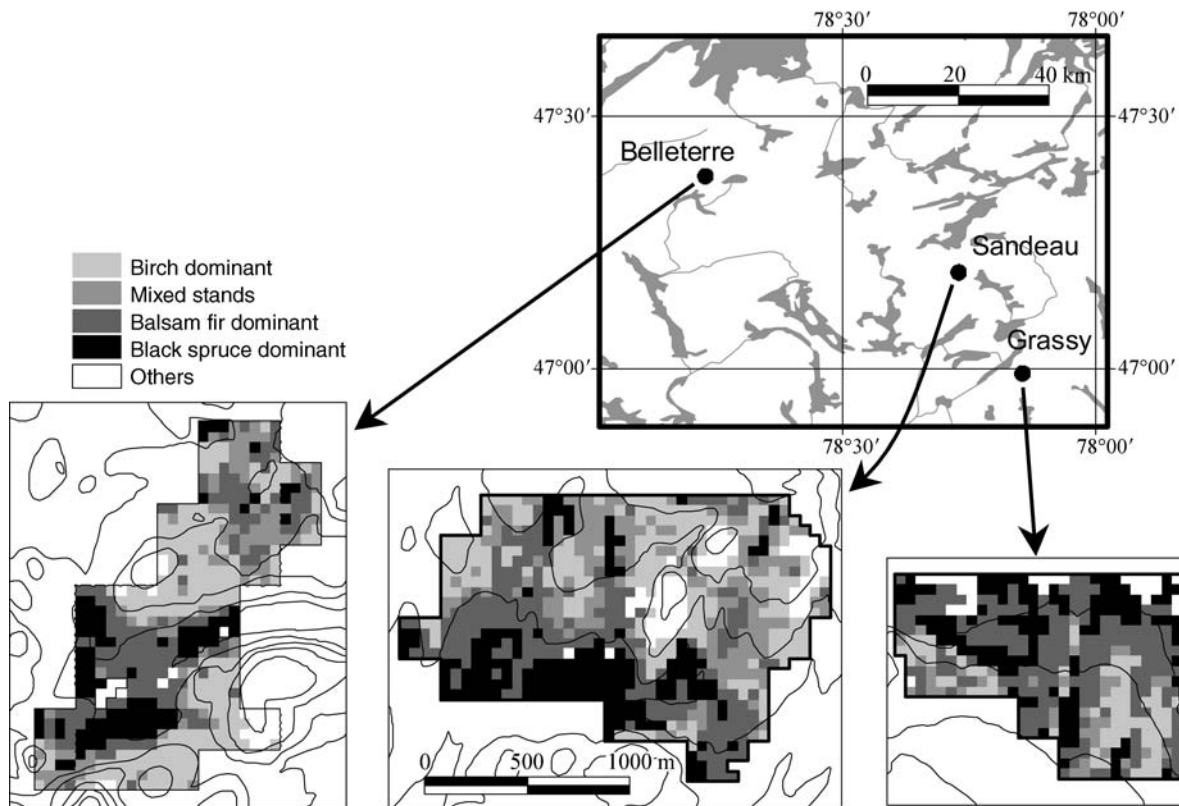


FIG. 1. Location of the areas studied (outline map) and canopy composition (shaded maps) in 1965 (Belleterre and Sandeau) and 1971 (Grassy). Open cells within the three photo-interpreted landscapes were not considered in the analyses because host tree species were absent or because they were affected by disturbances other than spruce budworm outbreaks (see *Study regions: Study areas* for details).

(partial cuttings in the Belleterre area and local windthrows in the Grassy area) (see open cells in Fig. 1).

The westernmost area (124.0 ha) is located near the town of Belleterre, and is characterized by a hilly topography and relatively few flat surfaces. The largest area (185.5 ha), located near Lake Sandeau, features a few small hills, and a large, relatively flat surface in the southwest portion. The easternmost area (111.0 ha), located near Lake Grassy, features an extensive flat surface throughout the northern part. The range of elevations is less in the Grassy area (30 m), compared with 40 and 50 m in the Sandeau and Belleterre areas, respectively (Fig. 1).

METHODS

Dendrochronology

Spruce budworm outbreak chronologies were developed for each of the three studied areas based on white spruce growth patterns. White spruce was selected for the analysis rather than balsam fir because it often survives attacks, which allows for longer time series compared with balsam fir. Twenty-three trees were sampled in the Belleterre area, 34 in the Sandeau area, and 35 in the Grassy area. Large trees dispersed on

mesic sites throughout the study areas were used. Two cores per tree were taken at a height of 1 m, stored in elongated containers, and later mounted on wooden holders and sanded. The width of growth rings was measured to an accuracy of 0.001 mm using a Velmex Uni Slide measuring table (Velmex Incorporated, Bloomfield, New York, USA) connected to a computer. The COFECHA computer program (Holmes 1997) was used to test for possible dating or measurement errors.

The detection of past spruce budworm outbreaks from tree ring measurements was done following standard dendrochronological techniques (Jardon et al. 2003, Boulanger and Arseneault 2004). Standard chronologies were built for each tree with the program ARSTAN (Holmes 1997), using a cubic smoothing spline to detrend the series (with a 50% frequency response cutoff of 60 years). For each tree chronology we considered that a growth reduction was significant when it lasted >5 years and included at least one year when growth was reduced below the mean by 1.28 standard deviations or more (Speer et al. 2001). All calculations for the detection of possible outbreak periods were done using the OUTBREAK program (Holmes and Swetnam 1996). Since outbreak detection was more efficient when based solely on host species growth responses for known

20th-century outbreaks, no correction was applied by standardizing with a nonhost control species. In each study area, we inferred outbreak occurrence from the proportion of the trees alive during a given decade that showed significant growth reductions.

To assess the age distribution of the balsam fir cohort that died during the last outbreak, 100 dead balsam firs were sampled in each of the three areas. The logs and snags were selected systematically along randomly disposed transects on mesic sites across the areas. As most of these trees were very rotten at the base, disks were cut at 1 m height. Age was not corrected for the time to reach 1 m in height because we consider that tree age at 1 m is a valid indicator of the stand replacement process. Most trees could be cross-dated visually through the presence of marker years, such as a pale ring (1956), narrow rings caused by spruce budworm defoliation (1946–1947), and narrow rings unrelated to spruce budworm defoliation (1960, 1967). When any doubt arose during visual cross-dating, dates were validated with the COFECHA program by comparing ring-width series with a reference chronology built from a subsample of living balsam fir trees from each area.

Photo-interpretation

The three areas were subdivided using a grid with 50 × 50 m cell size. The width of a cell represents ~2–3 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 1945, 1981, 1991, and 2003 were available for all three areas. Photographs taken in 1965 were used for the Belleterre and Sandeau areas, 1971 photographs for the Grassy area only, and 1935 photographs for the Belleterre area only. Photographs taken in 1965 and 1971, at a time when a mature canopy covered most of the study areas, were used to classify the cells into four broad stand types (Fig. 1). An elevation class was derived from topographic maps (10-m contours), and values were attributed to each cell.

Because very few permanent and stable open areas such as roads or rock outcrops could be identified, no formal spatial corrections were made when superimposing the grid to the photos from different periods. To maximize the accuracy and precision of grid overlay we used transient control points such as very large pine trees, stand boundaries, breaks in land relief, and small ponds or swamps. Errors due to distortion are considered to be minor because the relief is not strongly accentuated.

The impact of spruce budworm outbreaks was determined on aerial photos 0–30 years after their occurrence. We described the impact as “major” when no overstory was present in 65% or more of the area

within a given cell; based on field observations and previous research conducted in these forests (Bouchard et al. 2005), we consider that >65% consisting of canopy openings is sufficient to initiate recruitment of an even-aged sapling layer. 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. In the case of the oldest photographs available (1935 or 1945), we considered that outbreak impact was major when 65% or more of the area within a cell was occupied by young even-aged thickets; corings and field checks performed in several stands in each area corroborated that these former thickets were even aged, and that they originated from a past outbreak. 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%, 5%–15%, and every 10% thereafter up to 85–95%. The midpoint value of each of these categories was subsequently used for analysis.

Generally, we interpreted a decrease in canopy cover as evidence of overstory tree mortality. Following a major spruce budworm impact, an increase in the percentage of canopy cover was interpreted as resulting from new trees recruited to the canopy level.

Data analysis

We examined mortality and successional patterns following spruce budworm outbreaks at three spatial scales: the cell (0.25 ha), the slope position (or hillslope scale, 1–180 ha), and the region (~2000 km²). Within each study area, cells were grouped according to their position along the slope, which is strongly correlated with species composition. Depending on their elevation the cells were associated with upper-slope, middle-slope, or lower-slope positions, with the exception of the Grassy area where upper-slope positions were not present within the photo-interpreted area (Table 1). A second categorization was made by grouping the cells that experienced similar impact during the same outbreaks, for instance major impact following only the 1910 outbreak, only the 1980 outbreak, or both 1910 and 1980 outbreaks. A chi-square test for goodness of fit (two-way contingency table [Legendre and Legendre 1998:356]) was used to compare the actual vs. expected frequencies of these different “outbreak sequences” as a function of slope position. We also looked at changes in canopy composition for each outbreak sequence to gain some understanding of the underlying ecological mechanisms. Patterns at the regional scale were evaluated by contrasting tree mortality and succession between the three areas.

RESULTS

Spruce budworm outbreaks chronology

The occurrence of growth reductions in the white spruce trees sampled in this study coincide well with the

TABLE 1. Percentage of cells with major outbreak impact for each study area.

Study area and slope position	Elevation (m above sea level)	No. cells	Percentage of cells with major outbreak impact†			
			1910 only	1980 only	1910 and 1980	None
Grassy‡						
lower	310–329	280	7	31	41	20
middle	330–339	164	20	16	30	35
all			12	25	37	26
Sandeau						
lower	380–389	200	7	25	32	37
middle	390–399	301	26	7	20	47
upper	400–419	241	22	1	2	75
all			19	10	18	53
Belleterre						
lower	310–329	115	13	17	43	28
middle	330–339	238	32	5	16	48
upper	340–359	143	28	0	1	71
all			26	6	18	50

† The criterion for a major impact is a canopy cover of <35% on aerial photos taken 0–30 years following known spruce budworm outbreaks.

‡ No upper-slope positions occurred in the Grassy area.

timing of spruce budworm outbreaks previously reported on large-scale defoliation maps for the 1910, 1945 (Brown 1970), and the 1980 (Hardy et al. 1986) outbreaks (Fig. 2). Growth reductions were relatively synchronous for the Grassy and Sandeau areas, but were delayed by a few years in the Belleterre area for the 1910 and 1980 outbreaks. In terms of the proportion of trees affected by significant growth reductions at the peak of the outbreaks, the most intense was the 1910 outbreak, followed by the 1980 and 1945 outbreaks; this was true for all three areas (Fig. 2).

Synchronous growth reductions were less obvious during the 19th century. An outbreak may have occurred around 1825 in the Belleterre area (Fig. 2), and although this interpretation is based on only a few trees, it coincides with an outbreak detected ~150 km to the northwest by Morin et al. (1993). Defoliation caused by the budworm might also have occurred in 1840 or earlier (Sandeau), 1860 (Belleterre and Grassy), and 1890 (Belleterre), but only 30–40% of trees had significant growth reductions during those events (Fig. 2). Thus even if some outbreaks may have occurred during the 19th century, they were probably not very severe compared with those observed during the 20th century.

Mortality and composition fluctuations at the regional scale

Two important mortality episodes caused by the spruce budworm were detected on aerial photographs. We attributed the high number of cells showing major disturbance impacts on the 1935 and 1945 photographs to the 1910 outbreak (Table 1). The recruitment age of dead balsam firs sampled in all three areas points to the importance of this outbreak: tree recruitment to 1 m in height reached a peak in the 1920s decade in all three areas, a few years after the cessation of the 1910

outbreak (Fig. 2). Very few of these trees reached a height of 1 m later than 1930 or before 1910. The effect of the 1945 outbreak is not visible on the 1945, 1965, or 1971 photographs, and surveys in the studied areas revealed no stand that could have originated from this event. The second major conifer mortality episode was a consequence of the 1980 outbreak. We infer from the presence of extensive mature conifer stands in 1965–1971, and from the age distribution of dead balsam firs, that virtually all balsam firs were 50 years old or more (at 1-m height) when the 1980 outbreak began. Canopy breakup during this event began earlier and was more important in the Grassy area (Fig. 3A), where the proportion of conifer stands was particularly high before the outbreak. The 1980 outbreak also had a major impact in some cells that had not suffered a major impact in 1910, including a high proportion of cells where black spruce had been dominant (Table 2).

The abundance of hardwood species fluctuated as well during the 1935–2003 period (Fig. 3A). A slight decrease in hardwood canopy cover was observed during the 1945–1965 (Sandeau) and 1945–1971 (Grassy) periods, but this cannot be considered as a major impact disturbance at the cell scale since far less than 65% of the canopy was opened up. This minor decrease coincides with the birch dieback that has been reported in southeastern Canada following severe spring thaw–frost events, especially in the years 1944 and 1945 in western Québec (Braathe 1995). A second, more pronounced hardwood decline occurred after 1980 in all three areas, following a sharp increase in hardwood canopy cover (Fig. 3A). This second decline was a relatively gradual process, taking place between 1980 and 2003, and mostly occurred as an indirect consequence of spruce budworm outbreaks (see *Discussion* for further details).

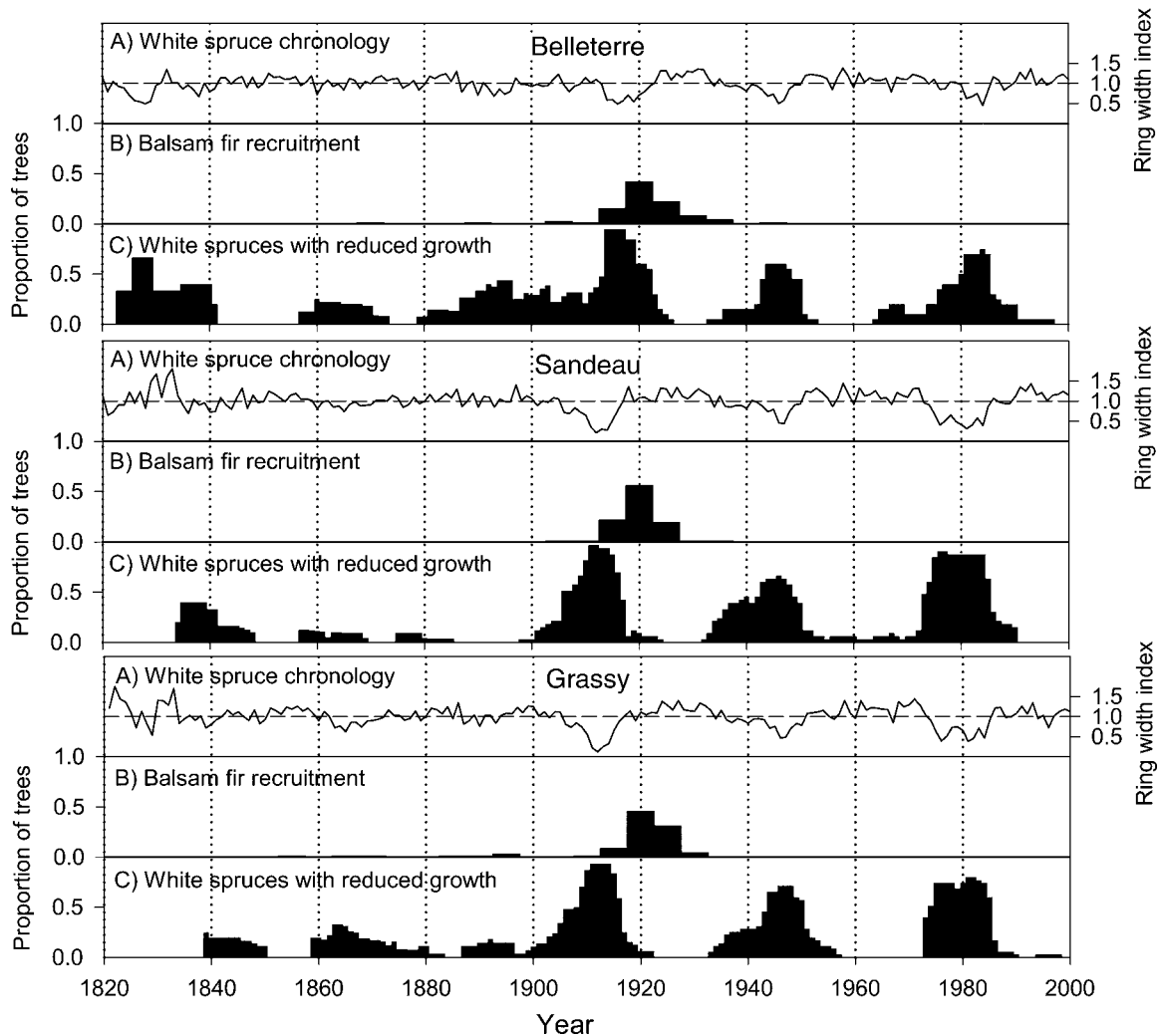


FIG. 2. For each study area, (A) white spruce standardized ring width indices, (B) proportion of balsam fir trees that recruited (first tree ring at 1-m height) during a given five-year period, and (C) proportion of white spruce trees showing significant growth reductions (i.e., five consecutive years with growth inferior to mean standardized ring width, including at least one year with growth below the mean standardized ring width by ≥ 1.28 sd).

Outbreak impact and post-outbreak succession at the hillslope scale

Each photointerpreted cell was categorized into three possible outbreak sequences for the 20th century: major impact only in 1910, only in 1980, or in both 1910 and 1980 (Table 1). The 1945 outbreak was not considered because it did not produce any detectable impact. Of the total number of photo-interpreted cells in the Belleterre, Sandeau, and Grassy areas, 50%, 47%, and 74%, respectively, experienced a major budworm impact during the 1910 and/or the 1980 outbreak (Table 1). The three outbreak sequences are also significantly associated with slope position in the three areas according to the goodness-of-fit test ($P < 0.001$; Fig. 4). The differences between expected and observed frequencies are consistently positive on middle- and

upper-slope positions for the cells with major impact only in 1910, but this difference is negative on lower positions (Fig. 4). The trend is opposite for cells with major impact in 1980 only and those affected both in 1910 and 1980, which are positively associated with the lower part of the topographic gradient (Fig. 4).

Cells showing a major outbreak impact in both 1910 and 1980 were considered as cases of cyclic succession, where dominance by conifers (essentially balsam fir) existed both before and after the 1910 outbreak (Fig. 3C). For cells experiencing major impact in 1910 but not in 1980, we assume that invasion by nonhost species (or species change) took place after 1910. This is based on the logical inference that overstory balsam firs showed a $>95\%$ mortality rate during the last outbreak (Bouchard et al. 2005), and hence all cells without major impact

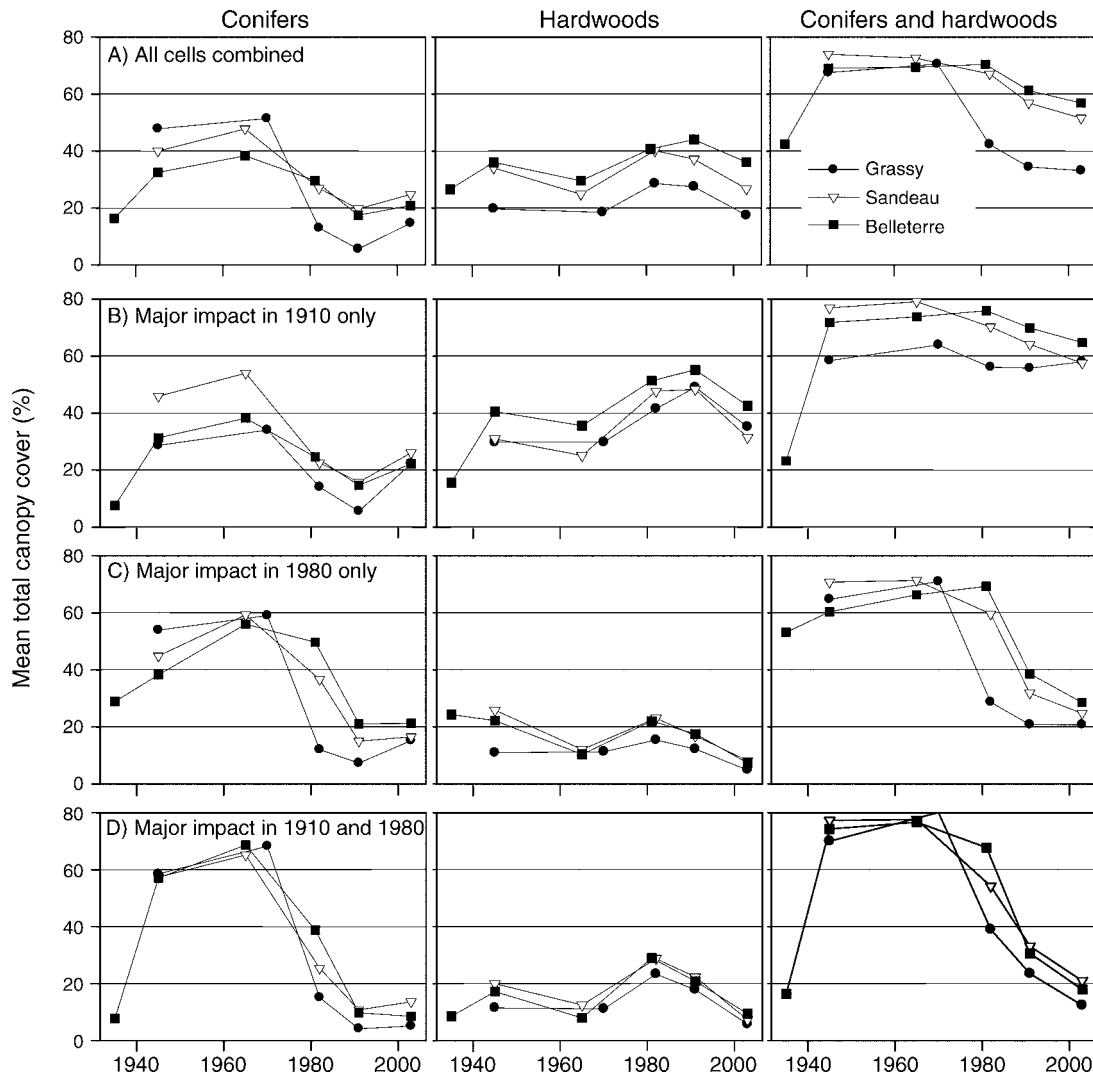


FIG. 3. Changes in conifer, hardwood, and total canopy cover in the three study areas, based on aerial photos taken during the period 1945–2003 (Grassy and Sandeau areas) or 1935–2003 (Belleterre area): (A) All cells combined, major and nonmajor impact; (B) cells with major impact following the 1910 outbreak only; (C) cells with major impact following the 1980 outbreak only; and (D) cells with major impact following both outbreaks. Labels in left-hand panels pertain to the entire row.

during the 1980 outbreak were dominated by other species. The evolution of canopy composition in these cells (Fig. 3B) confirms that hardwood content was much higher than for the other outbreak sequences. Species change in the overstory occurred in 60%, 51%, and 24% of the cells with major impact in 1910 in the Belleterre, Sandeau, and Grassy areas, respectively (Table 1).

DISCUSSION

Each of the three successive spruce budworm outbreaks that occurred during the 20th century had consistent impacts in terms of mortality and succession at the regional scale. Within each study area, however, the type of post-outbreak succession varied depending on slope position. Our results indicate that two spatial

scales, region (~200 000 ha in the present study) and hillslope (~50–500 ha), are important to consider in order to understand the effects of past spruce budworm outbreaks on forest dynamics.

TABLE 2. Predisturbance composition in cells with major impact only after the 1980 outbreak.

Study areas	No. cells	Pre-outbreak dominant composition (%)			
		Hardwoods	Black spruce	Mixed	Balsam fir
Grassy	113	0.9	94.7	1.8	2.7
Sandeau	73	8.2	60.3	15.1	16.4
Belleterre	30	6.7	60.0	6.7	26.7

Note: Composition was obtained by interpretation of aerial photographs from 1965 (Belleterre and Sandeau) and 1971 (Grassy).

Mortality following 20th-century outbreaks

Two important spruce budworm outbreaks strongly affecting forest dynamics occurred over the last 100 years, one ca. 1910 and the other ca. 1980. The 1980 outbreak was apparently more severe, because it resulted in heavy mortality in stands dominated by black spruce that had been spared by the 1910 and 1945 outbreaks. Compared with balsam fir, black spruce is generally better able to survive a given level of defoliation (Blais 1957, Erdle and MacLean 1999, Nealis and Régnière 2004), but black spruce stands are more likely to die when trees are senescent (Erdle and MacLean 1999), or during flowering years (Blais 1957). With the information presently available, it is not possible to evaluate whether the higher impact in 1980 in these stands was due to a higher outbreak severity (i.e., intensity and duration of defoliation) or the presence of a weakened tree cohort. In forests of the Ottawa Valley to the south, Blais (1981a) came to the conclusion that both factors probably contributed to the unusually high mortality of white spruce during the same outbreak.

Our results suggest that all stands dominated by mature balsam fir could be killed during one outbreak, a phenomenon already observed in other regions (Blais 1954, 1981a, MacLean and Ostaff 1989, Bergeron et al. 1995). This circumstance was particularly pronounced in our study because apparently no immature stands (e.g., 15–50 years old) survived after the 1910 and 1980 outbreaks, and all stands dominated by balsam fir formed a roughly even-aged cohort at the regional scale (i.e., northern Témiscamingue). No major mortality resulted from the 1945 outbreak, even though aerial surveys confirm that defoliation occurred for a period of ~10 years (Brown 1970). In surrounding regions, extensive mortality was reported during this outbreak (Turner 1952, Ghent et al. 1957, Blais 1981a, Morin 1994). The minor impact observed in this region can be partly explained by the fact that most balsam firs had recruited after the 1910 outbreak and were still relatively young in 1945. It is well known that the survival of balsam fir trees and stands tends to decline gradually with age (MacLean 1980, Erdle and MacLean 1999). In agreement with previous research, we can conclude from the low impact of the 1945 outbreak that (1) outbreak indicators such as defoliation records or host tree ring widths may be misleading when evaluating the impact of an outbreak in terms of tree or stand mortality (Royama 1984, Jardon et al. 2003), and (2) at the regional scale the presence of aging stands of host species is not a prerequisite for an outbreak to occur (Royama 1984).

Forest succession after the 1910 outbreak

Based on variations in canopy composition in cells that experienced major impact as a result of the 1910 outbreak, it can be seen that the consecutive replacement by nonhosts can persist for long periods, and that different successional pathways occur according to slope position. To simplify the analysis, we regrouped these

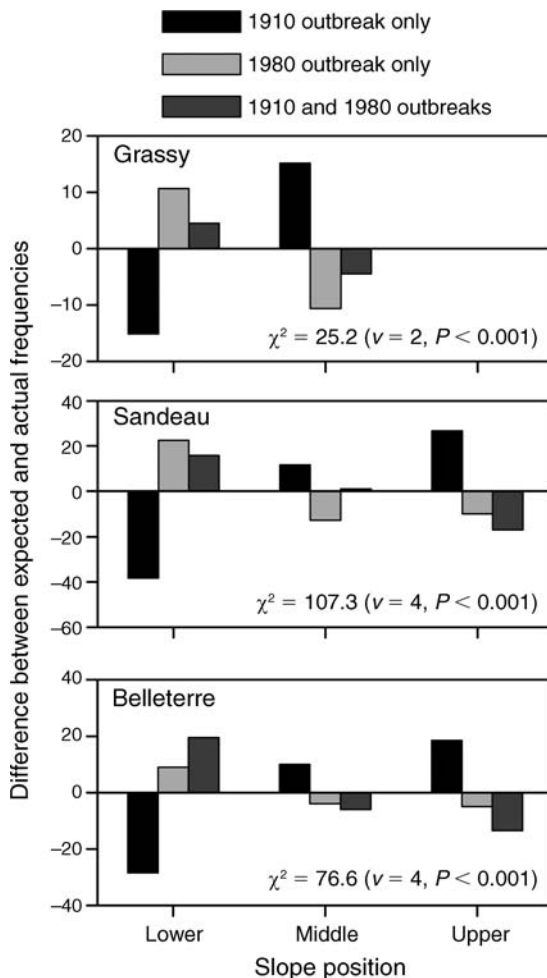


FIG. 4. Residual values from a two-way goodness-of-fit (chi-square) test of cells of the three study areas according to their topographic position and outbreak sequences. A high positive residual value, or difference between expected and actual frequencies, indicates a positive association between topographic position and outbreak sequence. No upper-slope positions occurred in the Grassy area.

pathways into two kinds: cyclic succession, where stand replacement does not bring about an important change in canopy composition, and compositional changes where nonhost species replace, at least partly, host species in overstory dominance.

Stand mortality caused by the spruce budworm is often expected to result in cyclic succession by balsam fir. This assumption has its roots in the well-known ability of balsam fir to form an extensive seedling bank under its own canopy (Baskerville 1975, MacLean 1984, Morin 1990, 1994). We observed cyclic replacement mostly in lower-slope positions, where patches of host species killed by the 1910 outbreak were colonized by dense conifer thickets, with a minor hardwood component (Fig. 3C). However between 24% and 59% of the cells with major budworm impact in 1910, mainly on upper-slope positions, were replaced by species mixtures

dominated by hardwoods (Table 1). The influence of slope position on post-outbreak succession is not surprising: lower slopes are cooler and more poorly drained than upper-slope positions, and such conditions are generally less favorable for the establishment and growth of birch species relative to balsam fir in this region (Fraser 1954, Brown 1981). Drier conditions on upper-slope positions could also be responsible for regeneration failures of balsam fir (Sims et al. 1990). We speculate that such failures might have been exacerbated during or before the 1910 outbreak, as this coincides with an exceptionally dry period in the greater region (Lefort et al. 2003). The post-1910 hardwood cohort began to break up after 1980, a decline probably associated with senescence, but also perhaps hastened and/or synchronized throughout the region by environmental modifications consecutive to conifer mortality in these stands (Bouchard et al. 2005). Causes of hardwood mortality can include cavitation and embolism following excessive evapotranspiration (Sperry et al. 1994), post-outbreak windthrows (Morin 1990), or the influence of secondary pathogens (Braathe 1995).

At the regional scale, the fluctuations in canopy cover for the broad categories “conifers” and “hardwoods” (Fig. 3A) are also likely to mask more subtle changes in overstory or understory composition. Observations of the current understory in these stands indicate that in the future, an important part of the stands invaded by hardwoods after the 1910 outbreak are likely to remain mixed with significant proportions of white birch, cedar, and yellow birch, in addition to balsam fir (Bouchard et al. 2005). An important part of the stands dominated by black spruce and affected only in 1980 may also be shifting in composition toward balsam fir (M. Bouchard, *personal observation*). Hence, even if constancy in species composition seems to occur at the cell scale in some topographic positions (lower slopes dominated by balsam fir), at the hillslope or regional scales the disturbance regime instigated by the budworm causes fluctuations in species composition, at least when considering a century-long time frame, such as the 20th century.

Long-term trends in outbreak impact

Some authors have speculated on an increase in outbreak severity, frequency, and extent during the 20th century. Whereas Blais (1983, 1985) attributed this mostly to an increase in balsam fir content in north-eastern America, Royama et al. (2005) proposed that changes in spruce budworm population cycles, and in their degree of synchrony over large areas, are more related to climate or stochasticity than to forest conditions. Without entering into the debate about which factors best explain outbreak occurrence over very large, subcontinental spatial scales, our data can improve the comprehension of insect/forest relations at the regional scale.

Although spruce budworm population or defoliation levels were not evaluated directly in this study, we have been able to show that the impact of successive outbreaks did not increase linearly during the 20th century. The most important outbreaks were the 1910 and 1980 outbreaks, separated by the less severe 1945 outbreak. Two mechanisms seem to impede any linear increase in the impact of successive outbreaks. The first is that over the long term, colonization of a substantial proportion of the stands by nonhost species diminishes the impact of future outbreaks by limiting the area occupied by host species, an effect that persisted for 70 years or more in Témiscamingue (Fig. 3B). This augmentation of nonhost species abundance may also diminish the mortality caused by future outbreaks, because the mortality of host species during an outbreak is usually negatively related to the abundance of nonhost species within a stand, which may be caused by a higher effectiveness of the budworm's natural enemy complex (Bergeron et al. 1995, Su et al. 1996, Capuccino et al. 1998). The second mechanism is that even if nonhosts do not invade, an outbreak causing high mortality levels at the regional scale will cause a shift in dominance toward very young balsam fir stands. As mentioned above, these younger forests will be more resistant for a period of 50 years or more, and any outbreak occurring within this interval is likely to have a relatively low impact.

We did not note the expected clear increase in frequency and extent of the outbreaks during the 20th century, but looking at longer temporal scales a different pattern is observable, with a change occurring between the 19th and 20th centuries. This has been noted by others, and may be due to the impact of climate change on the insect and its natural enemy complex (Fleming and Candau 1998), stochastic variations in the insect population cycles (Royama et al. 2005), or even to methodological difficulties in detecting past outbreaks (Boulanger and Arseneault 2004). A major pulse of large fires may also have triggered a synchronous postfire successional process throughout the region, resulting in balsam fir stands reaching maturity in time for the 1910 outbreak (Bergeron and Leduc 1998). Based on the age of the oldest trees cored in the studied areas, which were mostly yellow birches, we can estimate that if such a fire pulse occurred it was before the year 1800.

An increased abundance of balsam fir due to forest management activities has also been proposed as a factor explaining changes in outbreak patterns (Blais 1983). This is not likely in our region because the selective removal of some large white pines, which was the principal forestry practice carried out in southwestern Quebec during the second half of the 19th century (Brown 1981), is unlikely to have transformed the forest sufficiently to generate massive amounts of mature or overmature balsam fir stands in time for the 1910 outbreak. Some fires might also have been set off by early settlers before 1920 (Vincent 1995, Grenier et al. 2005), but the consequence of this would have

been a reduction of balsam fir content at the regional scale. On the whole, there is no indication that balsam fir content was highest toward the later part of the 20th century. Indeed, the very important impact of the 1910 outbreak suggests that the balsam fir component was highest at that time, at least in areas that had not burned recently.

Conclusion

A given outbreak can considerably modify the structure and composition of the forest, to the point of influencing the impact of outbreaks occurring 30 or 60 years later. Even if a link between the impact of successive outbreaks through forest characteristics was already reported at the stand scale (Morin 1994), this has rarely been measured directly at the regional scale. The only other well-documented occurrence of a single-age class of balsam fir occurring over a large area due to spruce budworm outbreaks is the Cape Breton area in Nova Scotia (MacLean and Ostaff 1989), but a long-term invasion by hardwoods was not reported in this region. The effect of successive outbreaks in northern Témiscamingue also appears to be different from the situation observed in some regions of eastern Canada, where successive outbreaks can lead to forest mosaics with stands in various stages of development (MacLean 1984, Morin 1994, Leblanc and Bélanger 1998). Our results confirm that even if spruce budworm populations reach outbreak levels synchronously over most of the range of the insect (Williams and Liebhold 2000, Jardon et al. 2003), the effect of successive outbreaks in terms of forest dynamics needs to be assessed on a regional basis.

ACKNOWLEDGMENTS

We thank H. Larose and S. Bujold for assisting with fieldwork, and D. MacLean, A. de Römer, and an anonymous reviewer for their comments on the manuscript. Funding for this study came from Tembec Inc., the CFS-NSERC Forest Research Partnership Program, and the Ministère de l'Éducation du Québec (FQRNT program).

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