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Mortality and stand renewal patterns following the last spruce budworm outbreak in mixed forests of western Quebec

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Abstract

We studied mortality caused by the last spruce budworm (*Choristoneura fumiferana* Clem.) outbreak (1972–1984) and the subsequent regeneration processes in the mixed conifer–hardwood forest zone of the Témiscamingue region, western Québec. Three kinds of late successional stands, undisturbed by human activities and representative of forest conditions on different sites, were studied using permanent plots, dendrochronology, and field data. The tree species affected directly by the spruce budworm, balsam fir (*Abies balsamea* L.), white spruce (*Picea glauca* Moench.), and black spruce (*Picea mariana* Mill.) suffered high overall mortality rates during the 1972–1996 period covered by the permanent plot measurements (97.6, 63.5, and 59.6%, respectively). The mortality of balsam fir and white spruce were positively correlated with pre-outbreak balsam fir basal area in the plots, as was the mortality of a non-host species, white birch (*Betula papyrifera* Marsh.). Mortality of host and non-host species following the outbreak might have been due in part to modified environmental conditions following canopy disruption, particularly on imperfectly drained sites that were dominated by balsam fir before the outbreak. This is also supported by the fact that radial increments of surviving white spruce trees remained significantly lower after the outbreak in balsam fir-dominated stands compared with other stand types. The outbreak has also favoured the emergence of an abundant sapling layer mostly dominated by balsam fir. Due to important fluctuations in the shape of canopy gaps over the years, the correlations between sapling abundance and actual canopy openings are low for all sapling species. In the present-day mixed species stands, density and species composition of the sapling layer seem to depend more on the presence of suitable micro-sites than canopy openings. These results suggest that the last outbreak gave rise to a gradient of stand regeneration patterns, depending on species composition before the outbreak and host and non-host mortality following it, ranging from overall stand mortality and replacement in balsam fir-dominated stands, dual-cohort structures in mixed boreal stands where mortality was partial, and quasi-gap dynamics in mixed hardwood stands dominated by yellow birch (*Betula alleghaniensis* Britton).

Keywords: Mixed forests; Spruce budworm; Mortality; Natural disturbances; Canopy gaps; Stand structure

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1. Introduction

Natural dynamics are not yet well understood in the sub-boreal mixed forest zone (Chen and Popadiouk, 2002). In the mixed woods of western Québec, repetitive spruce budworm outbreaks are known to have an important effect on the softwood component in late-successional forests (Bergeron and Leduc, 1998; Blais, 1981), while random gap-phase mortality is hypothesized as being a dominant form of mortality for non-host (mainly hardwood) tree species (Brown, 1981; Payette et al., 1990; Grondin et al., 1996). The relative importance of these two important disturbance types is however conjectural, especially in the case of mixed stands where host and non-host species are closely intermingled. The threshold at which spruce budworm outbreaks act as a stand replacing disturbance rather than a gap-level disturbance has been poorly studied.

Mortality following a spruce budworm outbreak can be almost total for balsam fir, but is usually inferior for white spruce and black spruce (Maclean, 1980). At the stand scale, a relationship has been established between mortality caused during an outbreak and factors including tree species composition, or soil characteristics such as drainage and/or productivity. Lower mortality in mixed stands has been observed when compared with pure balsam fir stands (Maclean, 1980; Bergeron et al., 1995; Su et al., 1996; Maclean and MacKinnon, 1997), but lower mortality is also observed on mesic compared to xeric or humid sites (Dupont et al., 1991; Archambault et al., 1990). In fact, the results obtained by these different studies are sometimes at odds and appear to vary on a regional basis (see Bergeron et al., 1995; Maclean and MacKinnon, 1997). These two predictor variables (composition and site) are also often correlated, and their respective effects cannot always be separated clearly (Osawa, 1994).

Other than mortality patterns, the distribution of regeneration within a stand will aid in determining whether the gap or the stand perspective is more appropriate for understanding forest dynamics after disturbance. When regeneration is restricted to, or more abundant in canopy openings created by disturbances, or when its composition is strongly influenced by parameters such as gap size (Kneeshaw and Bergeron, 1998, 1999), the gap perspective is more adequate. However, in boreal forests, light often penetrates into the understory elsewhere than under gaps created recently by the death of large trees (Ban et al., 1998). Numerous very small canopy openings can remain unfilled for long periods as a result of the low branch plasticity of most boreal tree species (Bartemucci, 2002) and the angle of solar radiation at higher latitudes (Canham et al., 1990; Ban et al., 1998). These characteristics allow for relatively high light levels throughout the stand (Bartemucci, 2002), and may thus facilitate the emergence or maintenance of a seedling or sapling cohort that is not restricted to canopy openings. Thus, mortality following a spruce budworm outbreak can result either in gap-centered regeneration (Kneeshaw and Bergeron, 1998), bimodal age structures at the stand scale (Pominville et al., 1999; Morin, 1994), or even-aged stands where mortality had been near total (Ghent et al., 1957; Baskerville, 1975; Morin, 1994).

In this paper, our goal is to evaluate the effect of a spruce budworm outbreak on stand dynamics along a gradient of biotic and abiotic conditions found in three stand types: balsam fir-dominated stands, mixed stands dominated by other boreal tree species, and mixed stands dominated by yellow birch. Tree mortality is examined in these stands, and residual forest structure and regeneration patterns are analyzed in the two mixed species stand types where mortality was partial. In particular, we evaluate whether the stand or gap perspective is more appropriate for predicting future stand development, and we use this information to draw implications for forest management in the context of spruce budworm outbreaks.

2. Methods

2.1. Study area

Our study area is located in the Témiscamingue region, in the western portion of the province of Québec (Canada). It is entirely within the balsam fir–yellow birch domain according to the current bioclimatic classification (Ministère des Ressources Naturelles du Québec, 2000). This is a transitional vegetation zone between the boreal forest to the north and the temperate northern hardwoods forest zone to the south, also corresponding to the

Missinaibi-Cabonga (B.7) forest zone of Rowe (1972). The study area spans over 3600 km^2 and comprises a landscape dominated by glacial deposits, essentially tills of various thicknesses but also a few outwash plains as well as glacio-lacustrine deposits. 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), the only one located within our study area.

The repeated occurrence of past wildfires in this region has been studied, and the length of the natural fire cycle has been estimated at 200 years (Grenier, 2003). This mixed forest region is dominated by species such as balsam fir (BF), yellow birch (YB), white birch (WB), white cedar (WC, *Thuja occidentalis* L.), black spruce (BS), white spruce (WS), red maple (RM, *Acer rubrum* L.) and sugar maple (*A. saccharum* Marsh.). Trembling aspen (*Populus tremuloides* Michx.), jack pine (*Pinus banksiana* Lamb.), and red pine (*P. resinosa* Ait.) are also abundant but regenerate mostly after fire under natural conditions. Eastern white pine (*P. strobus* L.), an economically important species, regenerates abundantly after surface fires but also occurs in late-successional stands where sparse old individuals can reach considerable sizes. The tree height of the forest canopy generally varies between 15 and 25 m, with a few large trees such as white spruce or white pine occasionally reaching 30 m or more. Understory species such as mountain maple (MM, *A. spicatum* Lam.), hazelnut (HN, *Corylus cornuta* Marsh.) and speckled alder (*Alnus rugosa* (DuRoi) Spreng.) are widespread in many late-successional stands.

2.2. Stand types

For late-successional stands in this region, composition correlates relatively well with site factors (Gosselin et al., 1998). Three major late-successional stand types—mixed hardwoods, mixed boreal, and balsam fir-dominated stand types—were studied in detail. These stand types correspond to categories commonly used for forest mapping and forest management in Québec as well as elsewhere in northeastern North America. In our study region, mixed hardwood stands are characterized by the significant presence of yellow birch and are associated with mesic sites or well-drained sites on up-slopes. Mixed boreal stands, where coniferous species (white cedar, fir, spruces) dominate in association with white birch and red maple, tend to occur on mid-slopes, and stands dominated by balsam fir (before the outbreak) generally occur on imperfectly drained down-slope sites.

The recent dynamics of the three selected stand types were studied using dendroecology and data from permanent inventory plots. In addition, current canopy structure and regeneration were evaluated from field transects in the two mixed species stands. The sampled stands were not significantly affected by logging and had not burned for at least 150 years. Three major spruce budworm outbreaks occurred in our study area during the last century, the last one between 1972 and 1984.

2.3. Recent forest dynamics and mortality

To quantify the composition, structure and recent dynamics of the main late-successional stand types, we used permanent plots established and maintained by the provincial Ministry of Natural Resources that are located in the study area. These plots were established in 1972 and were remeasured in 1979 and 1996. In each plot, diameter at breast height (DBH) and species of every tree with a DBH of more than 9 cm were recorded individually during the periodic measurements. The methodology used for the establishment and subsequent remeasurement of these 400 m^2 circular plots are described in full elsewhere (Anonymous, 2000). Characteristics such as canopy composition, soils, potential vegetation, and disturbance history were used to select plots corresponding to mixed boreal, mixed hardwood, and balsam fir-dominated late-successional stand types. Plots that were subjected to heavy partial cuttings during the period, those that were located in areas that had burned within the last 150 years (as determined from fire maps, stand composition, and maximal tree age), and those located in other stand types were not considered. This yielded 22, 14, and 27 plots for mixed-boreal, mixed-hardwood, and balsam fir-dominated stand types, respectively. Some dendrometric and compositional characteristics of these stands are given in Table 1.

We used these records to quantify the mortality that occurred in the three stand types. The mortality rate

Table 1
Tree composition in mixed hardwood, mixed boreal, and balsam fir-dominated stand types, according to permanent plot measurements and variable radius plots located along the field transects

Species/stand type	Basal area (m^2/ha)				Stand density (no./ha)			
	Permanent plots			Transects	Permanent plots			Transects
	1972	1979	1996	2002	1972	1979	1996	2002
Black ash								
Mixed hardwood	0	0	0	0.6	0	0	0	21
Mixed boreal	0.1	0.1	0	0.1	5	3	0	7
Balsam fir-dominated	0	0	0	–	0	0	0	–
Trembling aspen								
Mixed hardwood	0	0	0	0	0	0	0	0
Mixed boreal	1.8	1.6	1.1	0	35	27	14	0
Balsam fir-dominated	0.4	0.5	0.1	–	12	11	4	–
White birch								
Mixed hardwood	2.6	2.1	2.4	2.7	96	84	71	59
Mixed boreal	7	7.3	7.6	4.3	207	213	208	156
Balsam fir-dominated	2.7	3	2.2	–	102	113	116	–
Yellow birch								
Mixed hardwood	9.1	8.6	7.3	8.2	152	145	114	121
Mixed boreal	0.6	0.6	0.7	1.5	10	11	17	31
Balsam fir-dominated	0.4	0.5	0.6	–	13	13	14	–
White cedar								
Mixed hardwood	6.3	6.1	6.7	5.4	136	134	150	140
Mixed boreal	2.8	3.2	4.7	9.3	84	138	126	258
Balsam fir-dominated	1.3	1.6	2.2	–	55	22	80	–
Balsam fir								
Mixed hardwood	6.7	4.5	1.1	1.5	341	250	96	107
Mixed boreal	7.5	4.8	0.8	2	481	295	103	172
Balsam fir-dominated	13.5	6.7	0.4	–	767	408	65	–
Red maple								
Mixed hardwood	1.6	2	2.2	0.8	45	48	43	30
Mixed boreal	0.8	1	1.2	0.8	48	52	53	26
Balsam fir-dominated	0.1	0.1	0.2	–	11	11	14	–
Sugar maple								
Mixed hardwood	0.3	0.3	0.2	0	4	4	9	1
Mixed boreal	0.1	0.1	0.3	0	3	3	6	3
Balsam fir-dominated	0	0	0	–	0	0	0	–
Eastern white pine								
Mixed hardwood	0	0	0	0.1	0	0	0	2
Mixed boreal	0.7	0.8	0.9	0.6	6	5	3	2
Balsam fir-dominated	0.1	0	0	–	3	1	0	–
Black spruce								
Mixed hardwood	0.2	0.1	0.1	0	4	2	5	0
Mixed boreal	0.9	0.7	0.4	0.9	35	28	20	46
Balsam fir-dominated	3.6	3.1	2.9	–	163	144	128	–
White spruce								
Mixed hardwood	1.6	1.6	1.1	1.4	46	41	32	38
Mixed boreal	4	3.9	2.1	1.3	108	101	59	30
Balsam fir-dominated	1	0.9	0.3	–	31	28	14	–

Table 1 (*Continued*)

Species/stand type	Basal area (m^2/ha)				Stand density (no./ha)			
	Permanent plots			Transects	Permanent plots			Transects
	1972	1979	1996	2002	1972	1979	1996	2002
Other species[a]								
Mixed hardwood	0.6	0.1	0.2	0	18	5	21	0
Mixed boreal	0	0.2	0.1	0	2	5	1	0
Balsam fir-dominated	0.1	0.1	0.1	–	5	6	5	–
Total								
Mixed hardwood	29	25.4	21.4	20.8	841	713	543	520
Mixed boreal	26.5	24.3	19.7	20.9	1024	882	611	747
Balsam fir-dominated	23.2	16.7	9.1	–	1161	756	438	–

[a] The “other species” are pin cherry, mountain ash (*Sorbus* spp.), largetooth aspen (*Populus gradidentata*) and willows (*Salix* spp.).

for the main tree species was calculated by observing the proportion of mature trees present at the beginning of the period which had died due to natural causes by the end of the period. The three periods considered were 1972–1978 (7 years), 1979–1996 (17 years), and 1972–1996 (24 years). Periodic mortality rates correspond to the proportion of the trees that died during the period, and annual mortality rate to that number divided by the number of years covered by the period. We used the chi-square goodness of fit test to evaluate the significance of the differences between expected and observed annual mortality rates for the 1972–1978 and the 1979–1996 periods. The expected mortality is based on the annual mortality rate for the whole 1972–1996 period.

Mortality for some dominant host and non-host species in each plot was also correlated (Spearman rank correlations) with pre-outbreak balsam fir basal area (BA), a commonly used variable to explain defoliation or mortality caused by this insect (Bergeron et al., 1995; Su et al., 1996). The use of other predictors was also explored (proportion of hardwood BA, proportion of non-host species BA) but they did not add additional information and were therefore ignored. This was tested only for the 1972–1996 period, because mortality caused by the outbreak overlapped both measurement periods, and probably continued for some years following the end of defoliation in 1984 (Blais, 1981).

2.4. Radial growth of surviving white spruce

In order to examine host species recovery following the outbreak as a function of stand type, we compared radial growth of surviving white spruce trees in the three different stand types by coring 62 living white spruce in a ca. 5 km^2 area (47°12′N, 78°16′W) where all late-successional stand types were present and untouched by past logging. The sampling included the coring of 16 white spruce trees located in mixed boreal stands, 21 in mixed hardwood stands, and 25 in stands formerly dominated by fir. The cored trees were selected randomly among the dominant canopy trees and were located at least 30 m apart. Field observations within a 25-m radius of each cored trees (coarse woody debris, tree species composition) and aerial photos taken in 1965 were used to determine the stand type. Two cores per tree were taken at height of 1 m, they were stored in straws and later mounted on wooden holders. The cores were sanded and measured to an accuracy of 0.01 mm using a Velmex Uni Slide measuring table connected to a computer. The COFECHA computer program (Holmes, 1997) was used to test for possible dating or measurement errors.

The radial growth of cored white spruces was divided into three periods: pre-outbreak (1965–1973), outbreak (1974–1984), and post-outbreak (1985–2001). The “outbreak” period considered here begins later than the actual outbreak because growth reductions only begin a few years after the first years of defoliation (Blais, 1958). For each of these periods, we compared average tree basal area increment between stand types with the Wilcoxon rank test. The use of basal area increments, rather than linear radial increments, and the fact that average tree diameter before the outbreak is the same for all stand types (Table 4) allow us to make direct comparisons between stand types while minimizing the effect due to tree age or size. The DBH of the sampled trees before outbreak (1971) was estimated by subtracting cumulative growth from the 2002 DBH (with bark).

2.5. Canopy structure and regeneration in mixed hardwood and mixed boreal stands

The mixed hardwood and mixed boreal stand types were sampled by field transects during the summer of 2002. Stands formerly dominated by balsam fir had less than 75% in residual tree cover following the last spruce budworm outbreak according to forest cover maps. These stands had a discontinuous canopy of residual live trees, and consequently no gap studies were undertaken there.

The transects were positioned with the use of provincial forest cover maps and aerial photographs. The criteria used to select stands for transect measurements were mostly the same as those used for the categorization of permanent plots in the different stand types. The transects were located between 0.5 and 75 km from each other, in areas where there were no burns for at least 150 years (as deduced from the age of the dominant trees), where early successional species such as aspen or pines were absent, and where traces of past loggings were either sparse or absent. The transects were 400 m in length unless we encountered stand types other than those targeted or signs of significant logging, in which case the transects were stopped at a minimal distance of 10 m from the boundary. In all we measured 17 transects, for a total of 2000 m in mixed boreal stands and 3500 m in mixed hardwood stands.

For each 0.5 m of transect we noted all canopy trees, defined as trees of DBH > 7.1 cm, whose crown was present immediately above the transect (vertical projection). The species and DBH for every tree was recorded. The data were collected to characterize the canopy, including canopy openings where no foliage occurred. Saplings (diameter between 1.1 and 7.0 cm at 1.3 m height) were counted by species in plots measuring 5 m long × 4 m wide, placed in a continuous manner all along the transects, for a total of 700 micro-plots in mixed hardwood stands and 400 in mixed boreal stands. To directly associate canopy structure of the stands and their dendrometric characteristics, variable radius plots (metric prism, basal area factor of 2) were established every 40 m along each transect. Tree species and DBH were noted as well for every canopy tree in these plots.

The Mann–Whitney rank test was used to compare sapling abundance among transects in both stand types. For each stand type, we verified if sapling abundance in individual micro-plots was influenced by the percent of canopy opening directly overhead, and if the different species reached maximal abundance in the same plots. The effect of canopy opening on sapling abundance for the different species was verified with linear regressions for the two stand types separately, a log transformation being used when necessary. Inter-species correlations were calculated with Spearman rank correlations based on sapling abundances for each stand type, and based on these correlations the species were clustered for each stand type using Ward's method (Legendre and Legendre, 1998).

3. Results

3.1. Stand attributes

The mean post-outbreak basal area of mixed boreal and mixed hardwood stands are similar, respectively 19.7 and 21.4 m^2/ha for permanent plot measurements, and 20.9 and 20.8 m^2/ha for prism plots (Table 1). For balsam fir-dominated stands, the post-outbreak mean basal area of 9.1 m^2/ha in permanent plots is much lower. In spite of a similar basal area, the two mixed species stands differ in some respects. As measured using variable radius plots and transects, stems of smaller sizes (i.e. less than 30 cm) generally represent a larger portion of total basal area (Fig. 1A), and a higher proportion of total stem count (Fig. 1B) in mixed boreal stands compared with mixed hardwood stands. The frequency distributions of prism plots according to their BA values show that both stand types are very heterogeneous. Only 39 and 51% of the prism plots have BA values between 15 and 25 m^2/ha in mixed boreal and mixed hardwood stands, respectively (Fig. 1D).

There are also fewer canopy openings in the mixed hardwood stand type than in the mixed boreal stand type (Table 2). We observed 42 and 27% of the forest in canopy openings for mixed boreal and mixed hardwood stands, respectively. Small canopy openings

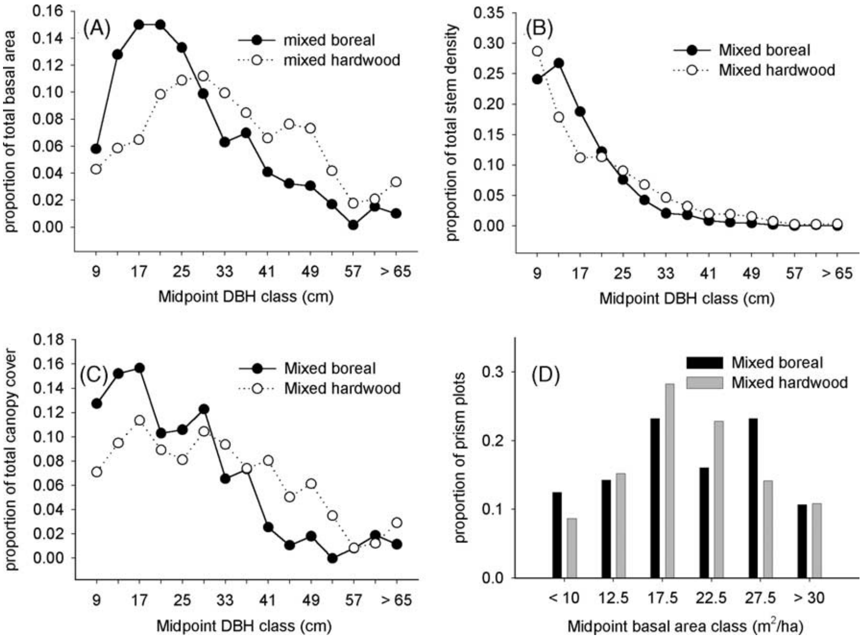

Fig. 1. Structure of mixed boreal and mixed hardwood stand types. Relative frequency distribution of basal area (A), canopy cover (B), and stem density (C) in relation to DBH classes, and relative frequency of prism plots by category of basal area (D).

represent an important fraction of the total: canopy openings of 6 m or less in length account for 14.3% of the total transect length in mixed hardwoods, and 18.8% in mixed boreal stands (Table 2). Large openings, more than 20 m, account for 1.3% of the total transect length in mixed hardwood stands, and 2.4% in mixed boreal stands (Table 2). The most important species in the dominant canopy in mixed hardwood stands are, in decreasing order of importance, yellow birch, white cedar, white birch, and balsam fir (Table 2). In mixed boreal stands the canopy is dominated by white cedar, white birch, balsam fir,

Table 2
Description of horizontal canopy structure and composition by tree species for the two mixed stand types

Canopy variable (% of total transect length)	Mixed hardwood (%)	Mixed boreal (%)
Horizontal structure		
Canopy openings	26.9	42.0
Canopy openings <6 m	14.3	18.8
Canopy openings >20 m	1.3	2.4
Crown overlap	24.5	14.2
Canopy composition		
Black ash	2.4	0.1
White birch	9.6	18.8
Yellow birch	48.4	7.0
White cedar	12.2	19.8
Balsam fir	6.9	7.2
Red maple	4.5	4.2
Eastern white pine	0.3	2.4
Black spruce	0.0	1.4
White spruce	5.5	2.6

and yellow birch (Table 2). In mixed boreal stands, trees of smaller diameter also generally represent a larger part of the total canopy cover (Fig. 1C).

3.2. Recent mortality

Analysis of the permanent plot data reveals that both in the case of balsam fir and white spruce, maximal mortality for the 1972–1996 period occurred in the balsam fir-dominated stands (98.8 and 73.0% respectively, for the two species), and the least amount of mortality occurred in mixed hardwood stands (93.7 and 40.7%) (Table 3). As for black spruce, most of the mortality took place in mixed boreal stands (78.6%), the least in fir stands (56.6%), and this species was absent in mixed hardwood stands (Table 3).

Species which are host or non-host to the spruce budworm show mortality rates which vary by species

Table 3
Mortality rates for the main tree species by period and stand type

Species/stand type	No. of living trees in 1972	Mortality rate by period (number of years)		
		1972–1978 (7 years)	1979–1996 (17 years)	1972–1996 (24 years)
Trembling aspen				
Mixed hardwood	0	–	–	–
Mixed boreal	29	0.24	0.59	0.69
Balsam fir-dominated	12	0.08	0.64	0.67
White birch				
Mixed hardwood	49	0.06	0.23	0.27
Mixed boreal	180	0.06	0.20	0.24
Balsam fir-dominated	109	0.07	0.46	0.52
Yellow birch				
Mixed hardwood	88	0.10	0.18	0.27
Mixed boreal	10	0.20	0.20	0.40
Balsam fir-dominated	14	0.07	0.14	0.21
White cedar				
Mixed hardwood	76	0.09	0.15	0.23
Mixed boreal	73	0.01	0.05	0.06
Balsam fir-dominated	58	0.03	0.17	0.19
Balsam fir				
Mixed hardwood	190	0.33	0.89	0.94
Mixed boreal	416	0.41	0.94	0.97
Balsam fir-dominated	824	0.47	0.97	0.99
Red maple				
Mixed hardwood	25	0.00	0.39	0.38
Mixed boreal	42	0.07	0.35	0.43
Balsam fir-dominated	11	0.09	0.33	0.36
Black spruce				
Mixed hardwood	1	0.00	0.00	0.00
Mixed boreal	30	0.23	0.68	0.79
Balsam fir-dominated	159	0.16	0.49	0.57
White spruce				
Mixed hardwood	27	0.15	0.30	0.41
Mixed boreal	95	0.08	0.64	0.66
Balsam fir-dominated	37	0.14	0.69	0.73
All species				
Mixed hardwood	462	0.19	0.46	0.56
Mixed boreal	890	0.24	0.55	0.66
Balsam fir-dominated	1232	0.36	0.72	0.83

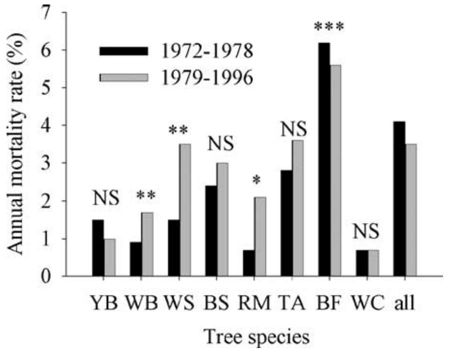

Fig. 2. Mortality rates for the main tree species by period (1972–1978, 1979–1996). *, ** and *** represent significant differences according to the chi-square test ($P < 0.05$, 0.01 and 0.001, respectively). See Section 2.1 for the species names abbreviations.

and between periods (Fig. 2). Balsam fir had a higher annual mortality rate during the first period (6.2% versus 5.6%; $P < 0.001$), while white birch (0.9% versus 1.75%; $P < 0.01$), red maple (0.7% versus 2.1%; $P < 0.05$), and white spruce (1.5% versus 3.5%; $P < 0.01$) died more often than expected during the second period (Fig. 2). For yellow birch, black spruce, white cedar, and trembling aspen no differences were found in mortality rates between the two periods.

Pre-outbreak stand composition had an influence on the mortality rate of some species, as observed during the 24-year period covered by the permanent plot measurements. Significant positive Spearman correlations exist between initial balsam fir basal area and mortality for balsam fir and white spruce, but not for black spruce even though a similar trend is apparent ($P = 0.053$; Fig. 3). Among the two non-host species sufficiently abundant to be tested, white birch mortality is positively related with initial balsam fir basal area, but no significant relation exists for white cedar (Fig. 3). Whereas the relationship appears roughly linear for white spruce and white birch mortality, balsam fir mortality was almost total in stands that had an initial balsam fir BA of more than 5 m^2/ha (Fig. 3).

3.3. *Effect of stand type on white spruce post-outbreak recovery*

All the cored white spruce trees measured more than 15 cm DBH, and before the outbreak the DBH of trees in the different stand types did not differ significantly (Wilcoxon rank test, $P = 0.98$; Table 4). Increments were low for all stand types during the outbreak period (Fig. 4), but without significant differences between stand types (Table 4). After the outbreak, the white spruce trees located in mixed hardwood stands and mixed boreal stands recovered radial increments near to their pre-outbreak values. In comparison, radial increments remained at levels

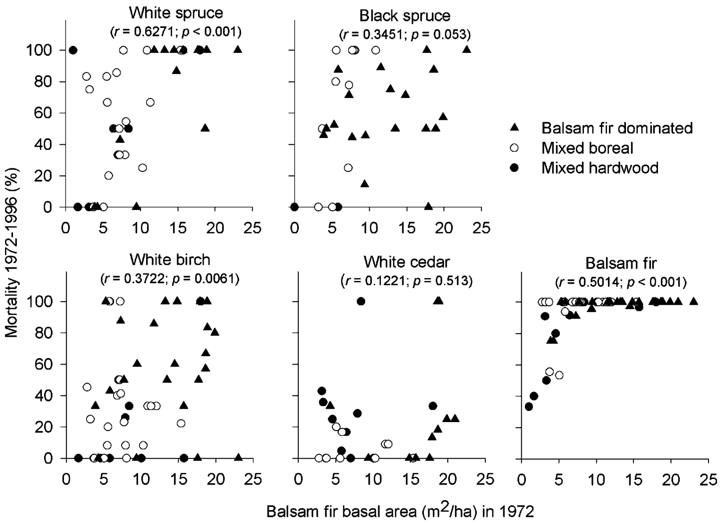

Fig. 3. Mortality for three hosts and two non-host species as a function of initial (1972) balsam fir basal area in permanent plots. Spearman rank correlations coefficients (r) and corresponding P-values are indicated for each species.

Table 4
Pre-outbreak DBH and mean annual increments of surviving white spruce trees before, during, and after the spruce budworm outbreak for three stand types

Outbreak status/years	Variable	Stand type			P^*
		Mixed hardwood	Mixed boreal	Balsam fir-dominated	
DBH (cm)					
Pre-outbreak	Mean	29.9	29.5	29.6	NS
1974	S.D.	10.1	10.5	7	–
Annual increment (cm^2/year)					
Pre-outbreak	Mean	16.3	13.7	13.4	NS
1965–1973	S.D.	1.6	1.9	1.5	–
During outbreak	Mean	7.1	5.4	5.6	NS
1974–1984	S.D.	0.8	0.9	0.7	–
Post outbreak	Mean	14.9	12.7	8.3	<0.001
1985–2001	S.D.	1.3	1.5	1.2	–

[*] From Wilcoxon rank test comparing mean values among the three stand types; NS, not significant ($P > 0.05$).

close to the outbreak period for trees located in balsam fir-dominated stands (Fig. 4). The increments were significantly lower in balsam fir-dominated stands compared with mixed boreal and mixed hardwood stand types only for this last period (Wilcoxon rank test, $P < 0.01$; Table 4).

3.4. Sapling abundance and distribution

The variability in sapling abundance among the transects for the different stand types indicates an important overall heterogeneity (Table 5). Some species are very well distributed in the stands, especially balsam fir, which is present in 91% of the micro-plots in mixed boreal stands and 66% of the micro-plots in mixed hardwood stands. Shrub species are present in 35 and 79% of the micro-plots in these stands, respectively (Table 5). White birch and balsam fir are significantly more abundant in mixed boreal stands, whereas red maple and hazelnut are more abundant in mixed hardwood stands (Table 5). The abundance of balsam fir ($r^2 = 0.031$, $P = 0.002$) and white birch ($r^2 = 0.016$, $P = 0.029$) saplings is also significantly, but weakly correlated with percent canopy openings in mixed boreal stands, whereas the abundance of hazelnut ($r^2 = 0.012$, $P = 0.004$) saplings is positively related to canopy openings in mixed hardwood stands. However, these relationships explain a very small portion of the variance (Table 6), and saplings of most species are distributed in the stands without being closely associated with the canopy openings overhead.

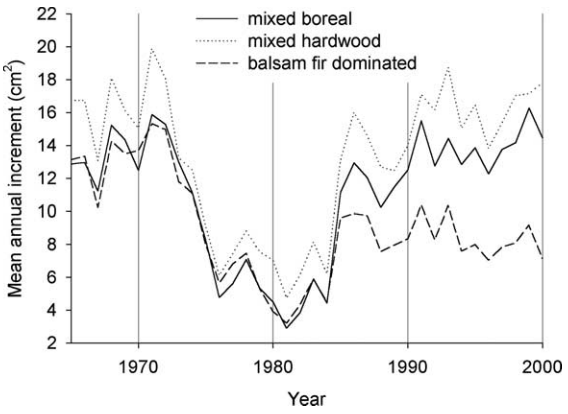

Fig. 4. Mean annual basal area increments (cm^2/year) of dominant white spruce trees sampled in mixed boreal, mixed hardwood, and balsam fir-dominated stand types.

The cluster analysis resulted in the same three main clusters of species for the two stand types (Fig. 5). One cluster is composed of black spruce and white cedar, and the two other clusters are dominated, respectively, by balsam fir (comprising also red maple, white birch, and white spruce) on the one hand, and mountain maple (comprising also hazelnut) on the other. The negative correlations between species belonging to these two groups are often significant (Table 7), even when species pairs are both positively associated with canopy openings, e.g. balsam fir and hazelnut

Table 5
Comparison of sapling density and stocking in transects located in the mixed boreal and mixed hardwood stand types

Species	Sapling stocking (% plots with presence)			Sapling density (stems/ha)		
	Mixed boreal	Mixed hardwood	P[a]	Mixed boreal	Mixed hardwood	P[a]
Shrubs						
Speckled alder						
Mean	8	3	NS	211	35	NS
Range[b]	0–15	0–19	–	0–656	0–271	–
Hazelnut						
Mean	4	18	NS	59	333	0.04
Range	0–23	2.44	–	0–353	24–1013	–
Mountain maple						
Mean	19	56	NS	396	1287	NS
Range	0–80	1–100	–	0–2125	6–3192	–
Red maple						
Mean	10	29	NS	268	465	0.04
Range	2–20	0–73	–	10–156	0–1263	–
Shrubs combined						
Mean	35	79	–	723	2085	–
Range	8–85	59–100	–	20–2450	593–3944	–
Trees						
White birch						
Mean	19	3	0.03	233	22	0.03
Range	0–34	0–6	–	0–488	0–50	–
Yellow birch						
Mean	5	8	NS	27	59	NS
Range	0–13	0–18	–	0–63	0–138	–
White cedar						
Mean	33	28	NS	532	415	NS
Range	8–66	0–62	–	50–1010	0–829	–
Balsam fir						
Mean	91	66	0.02	6176	2036	0.02
Range	41–99	31–81	–	559–8619	462–2881	–
Black spruce						
Mean	13	2	NS	143	14	NS
Range	0–44	0–13	–	0–500	0–100	–
White spruce						
Mean	10	13	NS	75	97	NS
Range	0–18	0–38	–	0–150	0–375	–
Trees combined						
Mean	96	82	–	7185	2643	–
Range	47–100	55–96	–	676–9644	1038–3556	–

[a] The P-value represents the probability of significant differences between the two stand types according to the Wilcoxon rank test on mean transect values. NS stands for a non-significant difference ($P > 0.05$).

[b] Range values represent the minimal and maximal values recorded for each variable and each species.

Table 6
Linear regression coefficients of sapling abundance on percent canopy opening

Species	Mixed boreal		Mixed hardwood	
	r^2	P	r^2	P
Speckled alder	0.000	NS	0.000	NS
Yellow birch	0.000	NS	0.000	NS
White birch	0.016	0.029	0.000	NS
Hazelnut	0.000	NS	0.012	0.004
White spruce	0.000	NS	0.000	NS
Black spruce	0.000	NS	0.000	NS
Mountain maple	0.000	NS	0.001	NS
Red maple	0.000	NS	0.000	NS
Balsam fir	0.031	0.002	0.004	NS
White cedar	0.000	NS	0.002	NS

Most sapling abundances were log-transformed. NS means a non-significant regression.

($P = 0.004$ in mixed boreal and $P < 0.001$ in mixed hardwood stands; Table 7). Yellow birch is not very abundant in either stand type, and is not negatively correlated with any other species. This species is associated with the mountain maple cluster in mixed boreal stands, and the balsam fir cluster in mixed hardwood stands.

4. Discussion

4.1. Mortality and its effect on canopy gaps

Lower levels of mortality caused by the spruce budworm in mixed species stands compared with balsam fir stands have also been observed in other regions, and have been explained by composition variables which are hypothesized to enhance the natural enemies complex (Kemp and Simmons, 1979; Capuccino et al., 1998; Bergeron et al., 1995), or else lower the dispersal potential of reproducing moths in mixed species stands (Maclean and MacKinnon, 1997). In our region, the balsam fir stands that sustained the heaviest mortality are also usually found on imperfectly drained sites (Brown, 1981; Gosselin et al., 1998), which is another factor that has been found to influence spruce budworm-induced mortality in some regions (Dupont et al., 1991; Archambault et al., 1990). Considering the covariation between stand composition and site, it is impossible at present to clearly separate the effect of these factors on defoliation and mortality rates, especially in the case of balsam fir since mortality was so overwhelming for that species in every stand type.

White spruce can sustain longer periods of defoliation before dying (Blais, 1981), and this probably explains the higher annual mortality rate for that species in permanent plots during the 1979–1996 period, compared with balsam fir which had higher mortality rates during the 1972–1978 period. For dominant white spruce trees, the radial increments are statistically similar among the different stand types during the outbreak, suggesting that differences in defoliation pressure among stand types were not major during that period. The persistence of weak growth rates for the trees located in balsam fir-dominated stands after the end of defoliation in 1984 points toward a site-related effect, perhaps because of a lower capacity for recovery

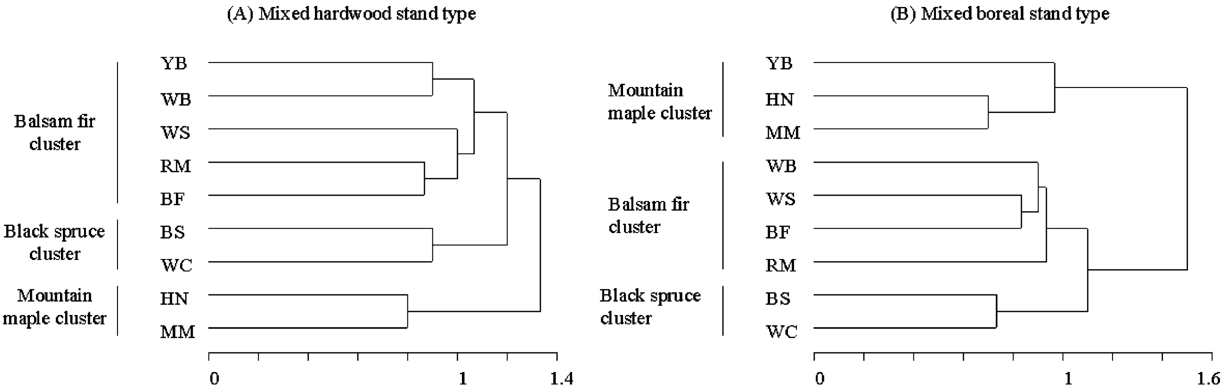

Fig. 5. Sapling species clusters for the mixed boreal and mixed hardwood stand types. Clustering was done with the Ward method, based on Spearman rank correlations of species abundances. Between-species similarity is inversely correlated with distance values indicated beneath the dendrograms. See Section 2.1 for species names abbreviations.

Table 7
Significant ($P < 0.05$) Spearman rank correlations (r) between sapling abundances for two stand types

Species pair		Mixed boreal		Mixed hardwood	
Species 1	Species 2	r	P	r	P
White birch	Yellow birch	0.099	0.011	–	–
White cedar	Hazelnut	−0.153	0.000	−0.127	0.027
White cedar	Mountain maple	−0.122	0.002	−0.259	0.000
White cedar	Black spruce	–	–	0.284	0.000
Balsam fir	Hazelnut	−0.140	0.000	−0.165	0.004
Balsam fir	Mountain maple	−0.259	0.000	−0.278	0.000
Balsam fir	Red maple	0.126	0.001	–	–
Balsam fir	Black spruce	–	–	0.122	0.034
Balsam fir	White spruce	–	–	0.120	0.037
Mountain maple	White birch	−0.083	0.033	–	–
Mountain maple	Yellow birch	0.099	0.011	0.183	0.001
Mountain maple	Hazelnut	0.180	0.000	0.329	0.000
Mountain maple	Black spruce	–	–	−0.164	0.004
Red maple	Hazelnut	−0.106	0.007	–	–
Red maple	Mountain maple	−0.300	0.000	−0.118	0.040
Black spruce	White spruce	–	–	0.134	0.020

on more humid sites where tree vigor is inferior (Blais, 1958) or because of environmental modifications following canopy disruption and surrounding mortality, for instance, a rise in the water table following reduced evapotranspiration at the stand scale (Dubé et al., 1995). Blais (1981) has previously observed that significant mortality occurs in the years immediately following an outbreak, but our results also indicate that in balsam fir-dominated stands the trees can remain weakened for long periods.

Initial gap creation resulting from host species mortality is not random in our area, but corresponds to the disposition of pre-disturbance balsam fir trees. Significant mortality also occurred during the post-outbreak period for some host (white spruce) and non-host (white birch, red maple) species. The higher mortality during the 1979–1996 period for some non-hosts and the positive correlation between white birch mortality and initial balsam fir basal area (Fig. 2) strongly suggest that the outbreak can accelerate or synchronize non-host mortality. Most of these trees are not part of a fire origin cohort, and therefore synchronized mortality during the 1979–1996 period is not a consequence of post-fire succession. However, a certain number of non-host trees originate from recruitment pulses following previous outbreaks, and at the regional scale it is possible that many of these trees were close to attaining maturity or senescence during the years 1979–1996 and therefore were more prone to environmental stresses. This would especially be the case for relatively short-lived species like red maple and white birch. Although white birch decline after canopy disruption has already been studied (Burns and Honkala, 1990; Roy et al., 2001), such effects have so far rarely been linked with natural disturbances such as spruce budworm outbreaks.

The delayed mortality in hosts and non-hosts probably increased the size and modified the shape of canopy gaps in mixed boreal stands. In mixed hardwood stands, however, there are fewer canopy openings in spite of a similar pre-outbreak abundance of balsam fir. This probably reflects at the same time a lower abundance of the decline-susceptible white birch in these stands, and a higher presence of yellow birch which more easily expands its branches into canopy openings (Battles et al., 1995; Payette et al., 1990).

4.2. Sapling distribution in mixed stands

In our study, the relationship between actual sapling abundance and canopy openings is generally weak. Significant positive relationships between hazelnut, balsam fir, mountain maple, and white birch saplings with more open conditions have been reported elsewhere, especially following spruce budworm outbreaks (Batzer and Popp, 1985; Osawa, 1994; Kneeshaw and Bergeron, 1999). At the stand scale, the light levels appear to have been maintained above the threshold needed to allow for numerous seedlings to reach the sapling layer, particularly in the mixed boreal stands where balsam fir is found in 91% of the micro-plots. Subsequent changes in the configuration of canopy openings following mortality and crown expansion events are also a likely explanation for the discordance between sapling abundance and actual canopy openings. The relationship with canopy gaps might also have been improved for some species if we had used methods other than stem counts to assess sapling abundance, in particular for competitive shrub species that may react to increased light levels by creating more foliage (Jobidon, 1995; Lei and Lechowicz, 1998).

Observed differences between stands are not apparent at the micro-plot scale since sapling species associations are similar in the mixed boreal and mixed hardwood stand types. The presence of species positively correlated with canopy openings in both the mountain maple and the balsam fir-dominated clusters and our knowledge of the autecology of these species suggest that segregation at the micro-plot scale may instead be linked with soil conditions. A range of factors such as drainage, nutrient richness, slope, exposition, soil depth, and others are known to play an important role in the establishment and growth of these species (Brown, 1981; Burns and Honkala, 1990; Jobidon, 1995). For example, the mountain maple cluster might be linked with globally richer micro-sites, the balsam fir cluster with poorer ones, and the black spruce cluster would be present in the moister part of the environmental gradient where *Sphagnum* species are often abundant on the ground.

The increased distribution of shrub species in mixed hardwood stands (79% of plots) compared with mixed boreal stands (35% of plots) was also observed by Levesque (1997) in a similar bioclimatic context. In our study, the competition created by these species apparently did not structure the post-outbreak species composition as much as observed in other studies. For instance, mountain maple apparently did not exclude balsam fir in larger openings as observed by Kneeshaw and Bergeron (1998). If competitive exclusion occurs in the stands we studied, it may be restricted to richer micro-sites where mountain maple and hazelnut perform well (Jobidon, 1995). Also, the within-stand heterogeneity observed in sapling densities might be due to the gently rolling topography generally characteristic of till deposits, which may contrast with the more uniform topography and more fertile soils usually associated with the glacio-lacustrine deposits more typical of the claybelt (Kneeshaw and Bergeron, 1998). Other shade-intolerant species (aspen, raspberry (*Rubus* spp.), pin cherry (*Prunus pensilvanica* L.)), often reported to take advantage of larger post-outbreak canopy gaps to get established (Osawa, 1994; Kneeshaw and Bergeron, 1998, 1999; Marchand, 1990), are totally absent from our transects. This may be due to the absence of seed sources or root suckers in close proximity, since most of the stands studied here have not been disturbed by humans or fire for a long time.

4.3. Natural stand dynamics

The patterns of stand mortality (Table 3) and regeneration (Table 6) may be summarized as follows for the three stand types used in this study. In balsam fir-dominated stands, more than 80% of the trees were killed during or shortly after the last spruce budworm outbreak. In these stands, the outbreak had a stand replacing effect similar to what is often mentioned in the literature for uncontrolled severe outbreaks in pure stands in eastern Canada (Baskerville, 1975; Morin, 1994). Balsam fir regeneration was also extremely abundant in these stands at the time this study took place (M. Bouchard, pers. obs.).

In mixed boreal stand types, the last spruce budworm outbreak was almost stand replacing in effect, or at least initiated a dual-cohort structure. Two elements suggest this, namely the high overall mortality rate for host and non-host species, and the good spatial distribution of saplings within these stands. Furthermore, competitive shrub species are not very abundant, and balsam fir is ubiquitous in the understory and will likely constitute a large part of future stands. White cedar, which sustained low mortality rates and is well represented in the sapling layer, might increase in proportion in the long term, as suggested by Kneeshaw and Bergeron (1998) for boreal stands that have been spared by fires for long periods of time. White spruce, which formed an important proportion of the pre-outbreak stands, may have suffered unusually high mortality rates during the last outbreak compared to the preceding ones (see Blais, 1981). White spruce regeneration appears scarce in the sapling layer (75 saplings/ha, 80 times less than balsam fir), and therefore the pre-outbreak proportion of mature white spruce (108 stems/ha, of which 36 survived) may not be reconstituted from the present generation alone, even if this species generally has a higher survival rate than fir during the stem exclusion phase (Fye and Thomas, 1963).

A form of gap dynamics may be driving forest succession in the mixed hardwood stands, given the significant presence of a long-lived species (yellow birch) able to close canopy openings laterally (Payette et al., 1990). However, there are important differences from typical hardwood forests further south, such as the absence of northern hardwood species which intercept light efficiently (e.g. sugar maple and beech), the relatively open canopies and the ubiquitous sapling community. Thus the traditional gap/non-gap contrast is probably less stark in our mixed hardwood stands as it is in deciduous forests. The outbreak also has had a long-term effect on species composition, and as in mixed boreal stands, white cedar's abundant regeneration and low mortality indicate that this species is likely to take advantage of the recent openings to increase its presence in future stands. The case of yellow birch is more complex: even if saplings are relatively scarce (59 stems/ha), mature individuals can persist for 200 years or more in the dominant canopy, and the occasional accession of isolated saplings might be sufficient to sustain this species in unmanaged conditions.

5. Conclusions

The last spruce budworm outbreak had different consequences for the different stand types, ranging from a stand replacing effect in balsam fir-dominated stands, to the emergence of multi-level canopy structures in mixed boreal stands and quasi-gap dynamics in mixed hardwood stands. All these regeneration patterns seem to be part of a spatial continuum linked with site factors. Our results also indicate that these mortality and regeneration events occurred in a synchronized manner at the regional scale following massive host species mortality caused by the last spruce budworm outbreak.

From a silvicultural perspective, researchers have suggested for a long time that by promoting mixed species stands, the softwood component could be protected against future infestations by the budworm (Miller and Rusnock, 1993). Our permanent plot and radial growth data indicate that at the local scale, and notwithstanding the technical feasibility of such a measure, this might be of limited applicability because site characteristics also appear to be an important factor in the region. In northern Témiscamingue, late-successional coniferous stands are mostly restricted to humid, relatively nutrient poor locations where boreal hardwoods (aspen, white birch) usually perform poorly. Our study concentrated on the stand scale and we did not specifically examine the effect of tree species composition on mortality at the landscape scale (e.g. Bergeron et al., 1995; Su et al., 1996), however the overall observed mortality rates for host species were so high in all stand types that any such landscape-scale effect must have been limited. In our region, investing in particular management strategies to diminish mortality rates through the promotion of specific mixtures would probably be largely ineffective in the face of a spruce budworm outbreaks of a magnitude similar to the last outbreak of the 20th century.

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