

Relationships between change in fire frequency and mortality due to spruce budworm outbreak in the southeastern Canadian boreal forest

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Abstract. We present a simple empirical model that allows an estimation of mortality due to spruce budworm (*Choristoneura fumiferana*) outbreak in relation to fire frequency and site characteristics. The occurrence of a recent spruce budworm outbreak around Lake Duparquet (48° 30' N, 79° 20' W, ca. 300 m a.s.l.) in northwestern Québec permitted a reconstruction of the stand composition before the outbreak, and also of the mortality of *Abies balsamea* due to the outbreak. The basal area of *A. balsamea* increases with time since fire in all site types but with increasing values for (1) rock and shallow till, via (2) till and mesic clay up to (3) hydric clay. Mortality (measured as percentage loss of basal area due to the outbreak) increases with time since fire but did not vary with site type. The increasing abundance of *A. balsamea* with time since fire is mainly responsible for this increase in mortality. Mortality for a specific basal area is, however, lower for the more recently burned stands suggesting a significant residual effect of time since fire. A landscape model integrating mortality due to the outbreak for stands of different age is developed. Both absolute and relative losses of basal area increased with the length of the fire cycles. According to this model, changes in fire cycle could explain a large portion of the spatio-temporal variations observed in outbreak mortality in the southeastern boreal forest of Canada.

Keywords: *Abies balsamea*; Climate change; Disturbance; Landscape model; Vegetation model.

Nomenclature: Hosie (1972).

Introduction

Fires (Payette 1992; Johnson 1992) and outbreaks of spruce budworm (*Choristoneura fumiferana*) (MacLean 1984) are widespread disturbances in the eastern Canadian boreal forest. These disturbance regimes are not independent, and changes in one regime might affect the other. Frequent fires would limit the abundance of late successional species that host the insect, thus decreasing mortality due to the outbreak (Bergeron et al. 1995). On the other hand, susceptibility to fire may be enhanced by severe spruce

budworm outbreaks (Stocks 1987). The understanding and prediction of how change of one disturbance may affect the other, is important in the context of global change as the effects of climate change on disturbance dynamics might have a greater impact on forest composition than climate per se (Davis 1989; Overpeck et al. 1990). Several studies have shown the possible effects of warming on decreasing or increasing the fire activity (Flannigan et al. 1998). These temporal changes in fire frequency would in turn affect the forest composition that potentially would affect the mortality due to the outbreak.

We generally recognize that, in the North American boreal forest regions potentially dominated by *Abies balsamea*, fire is a more important disturbance in the mixed-wood stands in the West while spruce budworm outbreaks are the main disturbance in the East (Baskerville 1975; MacLean 1984; Morin et al. 1993). In most of the area, however, both disturbances interact producing a complex forest mosaic (Bergeron & Dansereau 1993). While defoliation may occur in the total range of *Abies balsamea* (Hardy et al. 1986), mortality due to outbreaks appears to be more important in regions where *Abies balsamea* is dominant (Blais 1983).

Studies on past outbreaks have reported a direct correlation between mortality and abundance of the host species (MacLean 1980; MacLean & Ostaff 1989; Bergeron et al. 1995). Recent studies (e.g. Bergeron et al. 1995; Cappucino et al. 1998) suggest that these relationships do not only hold at the stand level but also at the landscape level; stands of host trees are less severely affected if surrounded by post-fire deciduous stands. Proportion of host species basal area (*Abies balsamea*, *Picea glauca* and *P. mariana*) increases with time since fire (Bergeron & Dansereau 1993). Therefore, mortality due to the outbreak may be a direct function of fire frequency as host species become more abundant with longer fire intervals. Here, we present a simple empirical model that allows an estimation of spruce budworm mortality due to the outbreak in relation to fire frequency and site characteristics.

Study area

Empirical data were collected in *Abies balsamea* forest near Lake Duparquet (48° 30' N, 79° 20' W, elevation ca. 300 m a.s.l.) in northwestern Québec. Lake Duparquet is part of a vast watershed that drains northward through Lake Abitibi to James Bay. The surrounding region is part of the northern Clay Belt of Québec and Ontario, a large physiographic region created by lacustrine deposits left after the maximum post-Wisconsinian extension of the proglacial lakes Barlow and Ojibway (Veillette 1994). The meteorological station closest to our study area is at La Sarre, which is situated 42 km to the north of Lake Duparquet.

The climate is cold temperate with a mean 1961-1990 annual temperature of 0.8 °C and a mean total annual precipitation of 850 mm (Anon. 1993). Snow represents 25 % of the yearly precipitation. Most liquid precipitation falls during the growing season but evaporation can limit plant growth in both June and July. The mean frost free period is 64 days but freezing can occur at any time.

Lake Duparquet is located in the southeastern boreal forest which forms part of Rowe's (1972) Missinaibi-Cabonga forest section. *Abies balsamea* is the dominant late-successional species while *Picea mariana*, *Picea glauca*, and *Betula papyrifera* are important components of the forest as well. Stands of pioneer species, such as *Pinus banksiana*, *Populus tremuloides*, and *Betula papyrifera* occupy large areas following disturbance (Bergeron & Dubuc 1989).

The periodic occurrence of fires since the end of the last glaciation (about 8000 BP) has been documented from lake sediments (Liu 1990; Richard 1993). The fire regime during the last 300 years has been reconstructed by Bergeron (1991) and Dansereau & Bergeron (1993). The mainland fire regime is characterized by high intensity fires covering large areas, especially in flat topography. The fire cycle has been estimated at 63 yr for the period before 1870. Since 1870 the fire cycle has dramatically increased and the last major fire occurred in 1944. Three major spruce budworm outbreaks from 1919-1929, 1930-1950 and 1970-1987 have been reported for this century (Morin et al. 1993). Forest harvesting started in the region when the transcontinental railway was opened in 1910. However, it was not until 1978 that large-scale clearcuts disturbed the western part of the Lake Duparquet area (Harvey & Bergeron 1989).

Methods

Field sampling

Stands were selected in forest areas which originated after a major fire and varied in post-fire age. A stand initiation map, previously created using fire-scars and the systematic dating of post-fire tree cohorts by Bergeron (1991) and Dansereau & Bergeron (1993), was used to select nine burned areas, covering each at least 100 ha and representing a chronosequence of 230 yr. Two post-fire forests of about the same age, having burned in 1916 (35 ha) and 1919 (104 ha), were combined for the analysis because of their small extents. One should note that, while time since fire is equivalent to average stand age during the first 100 years of the chronosequence, average age of the stand is younger than time since fire in the older stands as a new cohort of trees has replaced the post-fire cohort.

Forest composition and *Abies balsamea* mortality were assessed in 16 m × 16 m quadrats which for logistic reasons were systematically located every 50 m along transects established across the different forest areas. Transects were located in such a way that they crossed most of the site conditions characteristic of the area. An ecological map (Béland et al. 1992), indicating surficial deposits and drainage was used for this purpose. Each fire year was represented by 72 to 87 quadrats for a total of 540 quadrats where *A. balsamea* occurred.

In each plot, all living and dead trees greater than 5 cm DBH were tallied in 5-cm diameter classes. Great care was taken to identify all dead stems. Sampling was done during the summers of 1991 and 1992, seven to eight years after a maximum mortality had taken place (Morin et al. 1993). *Abies balsamea* trees which were killed during the budworm outbreak were easily identified because most of them were still standing (75 % on average) or were present on the forest floor with bark and branches still intact. MacLean & Ostaff (1989) reported that the natural mortality not related to the budworm average 2 % of the basal area per year. Since it is known that wood of *A. balsamea* decomposes rapidly (Lambert et al. 1980), we believe that in using trees with bark and branches, we might have included only few years of natural mortality in our estimate of the total mortality. We expect that, by including natural mortality occurring prior to the outbreak, we might have overestimated the mortality (% of basal area) caused by the budworm outbreak by less than 10%.

Statistical analysis and modeling

To determine whether differences exist between site types in the temporal pattern of increase in *Abies balsamea* basal area, we used covariance analysis (ANCOVA) with site type as a main effect and time since fire as a covariate. ANCOVA was also used to compare relationships between mortality caused by the outbreak (included as a dependent variable) and the *A. balsamea* basal area before the outbreak (as a covariate), obtained at different site types (as a main effect) or in different fire years (as a main effect). To adjust the model for a certain departure from linearity of the relationship, we considered the square term of the covariate. *T*-tests performed on differences between parameters (testing for $H_0 = 0$) are used in order to identify which particular site types or fire years are responsible for the global differences detected by ANCOVA.

Our empirical model is based on three components. First, the pre-outbreak *Abies balsamea* basal areas for the four site types – 1: rock outcrop/shallow till; 2: till; 3: clay with moderate drainage and 4: moist clay – were related to time since fire.

Second, absolute mortality (m²/ha) and relative mortality (percentage of basal area) were computed for all stands. These values were related to time since fire and *A. balsamea* basal area. As previously outlined, covariance analyses were used to test if the relationships between mortality and abundance of balsam fir (m²/ha) varied among: (1) site type and (2) time since fire. Simple relationships between mortality (absolute and percentage) and time since fire were developed.

Third, in order to assess the variation of mortality in relation to different fire cycles a model describing the distribution of stand age (time since fire) for fire cycles ranging from 50 to 300 yr (using an increment of 50 yr) was developed. Given a constant fire frequency and an equal probability of burning for any stand age, the expected forest age-class distribution in a specific equilibrium landscape should follow a negative exponential distribution (Johnson

Table 1. Regressions of *Abies balsamea* basal area (m²/ha) against time since fire for the different site types. Mean values (\pm S.E.) are given for each site type. *R*² and *P*-values refer to regression analyses.

Site type	<i>N</i>	<i>Abies balsamea</i> basal area (m ² / ha)	<i>R</i> ²	<i>P</i> -value
Hydric clay	72	14.58 \pm 1.00	0.33	< 0.0001
Mesic clay	298	11.43 \pm 0.41	0.25	< 0.0001
Till	115	8.91 \pm 0.67	0.45	< 0.0001
Rock and shallow till	55	4.96 \pm 0.76	0.22	0.0013

& Van Wagner 1985; Bergeron & Dansereau 1993). Equal probability of burning for any stand age is generally assumed for the boreal forest (Johnson 1992) and the negative exponential distribution has been successfully used to describe forest age-class distribution (Johnson & Van Wagner 1985; Bergeron 1991). We thus computed the expected forest age-class distribution associated to fire cycles of 50 to 300 yr using a 50-yr increment. We then assigned specific outbreak mortality to each forest age class (time since fire) and integrated it over all classes. The same process was repeated for all fire cycles.

Results

Abies balsamea basal area increased with time since fire in all cases but with increasing values as follows: rock/shallow till < till = mesic clay < hydric clay (Table 1). Basal area declined slightly after 150 yr on both rock outcrops/shallow till and till deposits. The ANCOVA full model showed that regression equations obtained for each site type differ in slope (as tested by the interaction term) but not in origin (as tested by the main effect of site type; Table 2). Model testing for slope homogeneity confirmed this result and showed that the ranking from rock/shallow till < till = mesic clay < hydric clay is statistically significant (Table 2).

Mortality (as % basal area) increased with the increase in *A. balsamea* basal area, due to the outbreak (Table 3). This relationship, however did not vary with site type (neither in slope nor in origin, Table 4).

Table 2. Covariance analysis comparing the relative importance of site conditions and time since fire on the variation of *Abies balsamea* basal area (m²/ha).

Source of variation	df	SS	<i>F</i> -ratio
Full model			
<i>R</i> ² : 0.38			
Model	11	11951	30.04***
Error	528	19097	
Site type	3	171	1.57
Time since fire (TSF)	1	1248	34.51***
Square of TSF	1	395	10.91**
Site type \times TSF	3	188	1.73
Site type \times square of TSF	3	139	1.28
Model testing for slope homogeneity			
<i>R</i> ² : 0.36			
Model	5	11738	64.92***
Error	534	19310	
Time since fire	1	1898	52.49***
Square of time since fire	1	638	17.65***
Site type \times TSF	3	2858	26.34***

* = 0.01 < *P* < 0.05; ** = 0.001 < *P* < 0.01; *** = *P* < 0.001.

Table 3. Regressions of mortality of *Abies balsamea* (measured as % basal area) against basal area of *A. balsamea* (m²/ha) for the different site types. Mean values (± S.E.) are given for each site type. R² and P-values refer to the regression analyses.

Site type	N	Mortality (% basal area)	R ²	P-value
Hydric clay	72	59 ± 4	0.47	< 0.0001
Mesic clay	298	52 ± 2	0.26	< 0.0001
Till	115	46 ± 3	0.37	< 0.0001
Rock and shallow till	55	39 ± 5	0.23	0.0011

Table 4. Covariance analysis comparing the relative importance of site conditions and basal area (m²/ha) of *Abies balsamea* on the variation of mortality (% basal area) due to the outbreak of the spruce budworm.

Sources of variation	df	SS	F-ratio
Full model			
R ² : 0.33			
Model	11	22.94	23.57***
Error	528	46.72	
Site type	3	0.30	1.14
<i>Abies balsamea</i> basal area	1	5.41	61.09***
Square of <i>Abies balsamea</i> basal area	1	0.99	11.25***
Site type × basal area	3	0.31	1.17
Site type × square of basal area	3	0.50	1.88
Model without interaction terms			
R ² : 0.32			
Model	5	22.08	49.56***
Error	534	47.58	
Site type	3	0.26	0.99
<i>Abies balsamea</i> basal area	1	9.26	103.93***
Square of basal area	1	2.99	33.61***

*** = P < 0.001.

Table 5. Regressions of mortality of *Abies balsamea* (measured as % basal area) against basal area (m²/ha) of *A. balsamea* for the different times since fire. Mean values (± S.E.) are given for each time since fire. R² and P-values refer to regression analyses.

Time since fire (yr)	N	Mortality (% basal area)	R ²	P-value
230	79	76 ± 3	0.06	> 0.05
193	66	75 ± 3	0.23	0.0003
167	74	68 ± 3	0.08	0.0470
143	78	56 ± 3	0.13	0.0068
120	73	51 ± 3	0.16	0.0025
74	60	36 ± 4	0.12	0.0250
46	64	11 ± 2	0.33	< 0.0001
26	46	8 ± 4	0.01	> 0.05

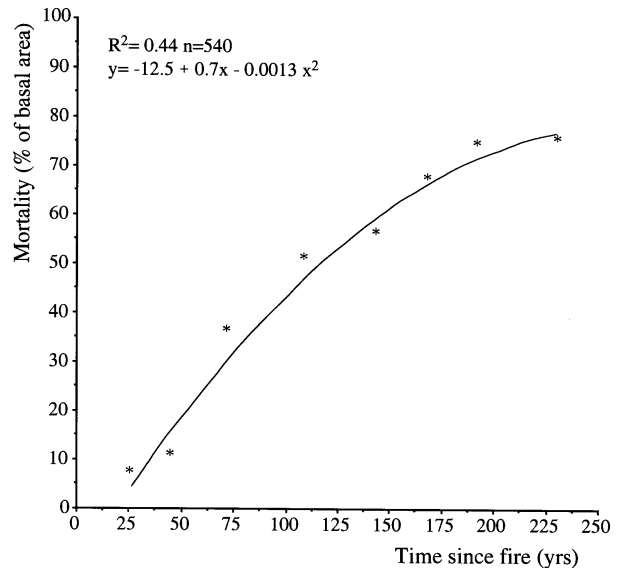


Fig. 1. Regression of mortality in *Abies balsamea* (measured as % basal area) against time since fire for all surficial deposits. Asterisks indicate mean values of mortality for each time since fire.

Table 6. Covariance analysis comparing the relative importance of time since fire and *Abies balsamea* basal area (m²/ha) on the variation of mortality (% basal area) due to the outbreak of spruce budworm.

Sources of variation	df	SS	F-ratio
Full model			
R ² : 0.52			
Model	23	36.04	24.04***
Error	516	33.63	
Time since fire (TSF)	7	2.54	5.58***
<i>Abies balsamea</i> basal area	1	0.57	8.71**
Square of <i>Abies balsamea</i> basal area	1	0.01	0.24
TSF × basal area	7	0.30	0.67
TSF × square of b.a.	7	0.2	0.46
Model without interaction terms			
R ² : 0.51			
Model	9	35.42	60.92***
Error	530	34.25	
Time since fire (TSF)	7	13.61	30.09***
<i>Abies balsamea</i> basal area	1	2.04	31.64***
Square of basal area	1	0.66	10.25**

** = P < 0.001; *** P < 0.001.

This suggests that the different basal area losses observed for different site types are explained solely by differences in the abundance of *A. balsamea* (Tables 2 and 3) and not by different mortality rates according to site type characteristics.

Mortality for a specific basal area was, however, lower for stands from the more recent fires. This would suggest a significant effect of time since fire (Tables 5 and 6). Moreover, the effect of time since fire appeared only as a difference regarding the origin of regression equations whereas the slopes of various regressions showed non-significant differences (Table 6). The actual mortality (m^2/ha) in a specific stand can thus be estimated using both abundance of *A. balsamea* and time since fire. Since this abundance is also a function of time since fire, a simple relationship between time since fire and mortality (% basal area) can be described (Fig. 1).

Fig. 2 presents a generalization of the relationships between mortality and length of the fire cycle for different site types and for specific fire cycles. Both absolute and relative mortality in the basal area increased with the length of the fire cycle. Change in relative mortality is independent of site types and can be directly predicted (Fig. 2a). However, as the proportion of site types may vary from one landscape to the other, estimated gross mortality has to be weighted in relation to area covered by each site type.

Discussion

Outbreaks of spruce budworm form a major and widespread disturbance in the eastern Canadian boreal forest, even if other insect outbreaks occur as well (Bergeron et al. 1998). Results from our modeling exercise can explain the west-east gradient in mortality due to the outbreak of spruce budworm observed for eastern Canada (Blais 1983; Morin et al. 1993). Although *Abies balsamea* is present in all of the southern boreal forest, it is the dominant species of most of the stands only in the east where the climate is more humid. As *A. balsamea* can form vigorous pure stands in most of its distribution range (cf. Simard et al. 1998), direct effects of climate on growth and reproduction do not appear a valid explanation for this variation in abundance.

While pre-settlement fire cycles of less than 100 yr are reported for the western part of the *A. balsamea* distribution (Heinselman 1983), fire cycles increase eastward and it is over 500 yr in the maritime region (Furyaev et al. 1983). Such an increase in the fire cycles may lead to a landscape dominated by old growth forests with an abundance of shade-tolerant *A. balsamea*

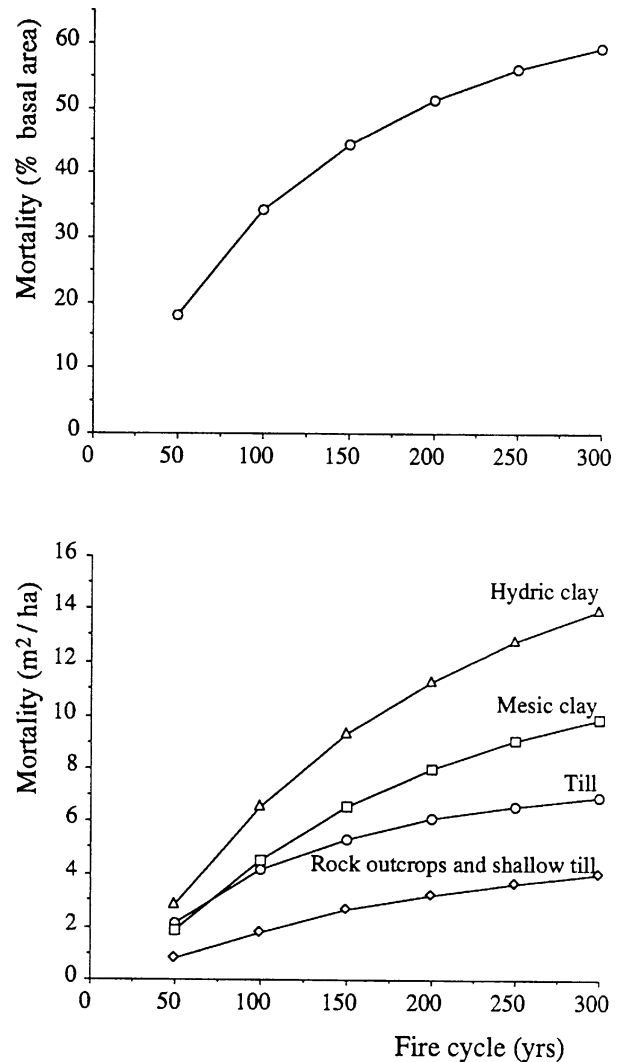


Fig. 2. a. Mortality of *Abies balsamea* (% basal area) for hypothetical fire cycles of 50 to 300 yr using 50 yr increment. **b.** The same but for net mortality (m^2/ha) and for the different site types.

(Bergeron & Dansereau 1993). Therefore, according to our model (Fig. 2) this change in fire cycle could be responsible for at least doubling the mortality resulting from budworm outbreak.

A change in fire cycle may also explain the increasing mortality of the spruce budworm outbreaks during the 20th century (Blais 1983). This increasing mortality has been attributed to an increase in dominance of *A. balsamea* due to many factors, including selective cutting of *Picea*, clear-cutting, fire suppression and use of insecticides. Our results show that a change in the abundance of host species due to an increasing fire cycle can explain the observed increased mortality.

Doubling the fire cycle from 50 to 100 yr, as is observed for the 20th century in the Lake Duparquet area (Bergeron 1991), would more than double the mortality due to the outbreak from 15 % to 40 % in the mortality of *A. balsamea* – as reduction of basal area. Although fire suppression and selective cutting may have contributed to the increase in *A. balsamea*, in the southeastern boreal forest the phenomenon is synchronous with a decrease in fire frequency attributed to climate change (Bergeron & Archambault 1993). In this context, the possible increase in mortality due to the outbreaks can be seen as a natural response to a general change in fire frequency. As a continuous decrease in fire frequency is predicted with global warming in eastern Canada (Bergeron & Flannigan 1995; Flannigan et al. 1998), the mortality due to the outbreak could potentially increase. This change controlled by fire frequency may be more important than the possible direct effect of climate on the insect population dynamics (Holling 1992).

At the local scale, the model can predict different mortality levels in relation to the distribution of site types. However, at this scale the model is limited by the lack of inclusion of a spatial context. Our results clearly show that mortality is not a unique function of the amount of basal area of *A. balsamea* in a specific stand but also includes a significant effect of time since fire. We interpret this residual effect as being controlled by the forest composition at the landscape level.

We have observed that pure stands of host species are less severely damaged when surrounded by broad-leaved stands (Bergeron et al. 1995; Su et al. 1996). It appears that this situation could favor a better control of the budworm population by its natural enemies (Cappucino et al. 1998). The probability of having broad-leaved stands in the vicinity of susceptible *A. balsamea* stands decreases from short to long fire cycles but it is also affected by the size of the fire patches and distribution of site types that are also responsible for the forest composition. For a specific fire cycle, a regime of large fires would produce larger patches of mature forest in contrast to a regime of small fires. Similarly, a landscape dominated by large patches of very wet or very dry site types may have few broad-leaved stands. Both these factors would lead to a locally higher mortality due to the outbreak than is predicted by the model.

The fact that this model is based on data collected following a single outbreak and in only one region, is also limiting. Mortality may vary from one outbreak to another. It has been suggested that, because outbreaks occur roughly every 30 yr and *A. balsamea* stands take 60 yr to mature, severe outbreaks can occur regionally

only once for every two occurrences (Blais 1958, 1983). During the last outbreak in lake Duparquet area (1970–1986) most *A. balsamea* stands were mature (*Abies balsamea* average age of 57 ± 17 yr, Bergeron et al. 1995) and another outbreak in 30 yr may have a lower mortality. Moreover, the present age-class structure of the forest is not only a function of fire cycle but it is also influenced by harvesting and protection against the budworm. In this context, the inclusion of stand age in addition to stand composition could be an improvement to our model.

The model described here, is similar to the model previously developed for predicting forest composition and structure in relation to the occurrence of different fire cycles (Bergeron & Dansereau 1993; Gauthier et al. 1996; see also Angelstam 1998 for an approach in the European boreal forest) and it thus suffers from the same limitations. First, since we do not have stands that originate from fire older than 230 yr, the accuracy of the model decreases with long fire cycles. However, since *Abies balsamea* is very shade-tolerant and successfully replaces itself after budworm outbreaks, we supposed that forest composition would remain relatively constant after 230 yr.

More important limitations extensively discussed in previous papers, are the use of empirical data rather than more mechanistic approaches (Shugart 1984; Prentice & Leemans 1990) and the fact that the model is not spatially explicit. Such improvements, which are currently under development, will provide a better predictive ability for this type of modeling. However, we believe that the model as it is presented here, gives a general framework that enables a new interpretation of spatio-temporal patterns of mortality due to the outbreak of spruce budworm in the forests of eastern Canada.

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References

- Anon. 1993. *Canadian climate normals 1961-90. Canadian climate program*. Environment Canada. Atmospheric Environment Service, Downsview, Ontario.
- Angelstam, P.K. 1998. Maintaining and restoring biodiversity by developing natural disturbance regimes in European boreal forests. *J. Veg. Sci.* 9: 593-602. (This issue.)
- Baskerville, G.L. 1975. Spruce budworm: super silviculturalist. *For. Chron.* 51: 138-140.
- Béland, M., Bergeron, Y., Harvey, B. & Robert, D. 1992. Quebec's ecological framework for forest management: a case study in Abitibi Forest. *For. Ecol. Manage.* 49: 247-266.
- Bergeron, Y. 1991. The influence of island and mainland lakeshore landscapes on the boreal forest fire regimes. *Ecology* 72: 1980-1992.
- Bergeron, Y. & Archambault, S. 1993. Decrease of forest fires in Quebec's southern boreal zone and its relation to global warming since the end of the Little Ice Age. *The Holocene* 3: 255-259.
- Bergeron, Y. & Dansereau, P. 1993. Predicting the composition of Canadian southern boreal forest in different fire cycles. *J. Veg. Sci.* 3: 827-832.
- Bergeron, Y. & Dubuc, M. 1989. Succession in the southern part of the Canadian boreal forest. *Vegetatio* 79: 51-63.
- Bergeron, Y. & Flannigan, M. 1995. Predicting the effects of climate change on fire frequency in the southeastern Canadian boreal forest. *Water Soil and Air Pollution* 82: 437-444.
- Bergeron, Y., Morin, H., Leduc, A. & Joyal, C. 1995. Balsam fir mortality following the last spruce budworm outbreak in northwestern Quebec. *Can. J. For. Res.* 25: 1375-1384.
- Bergeron, Y., Engelmark, O., Harvey, B., Morin, H. & Sirois, L. 1998. Key issues in disturbance dynamics in boreal forests: Introduction. *J. Veg. Sci.* 9: 461-466 (this issue).
- Blais, J.R. 1958. The vulnerability of balsam fir to spruce budworm attack in northwestern Ontario, with special reference to the physiological age of the tree. *For. Chron.* 34: 405-422.
- Blais, J.R. 1983. Trends in the frequency, extent and severity of spruce budworm outbreaks in eastern Canada. *Can. J. For. Res.* 13: 539-547.
- Cappucino, N., Lavertu, D., Bergeron, Y. & Regnière, J. 1998. Spruce budworm impact, abundance and parasitism rate in a patchy landscape. *Oecologia (Berl.)*. 114: 236-242.
- Dansereau, P. & Bergeron, Y. 1993. Fire history in the southern boreal forest of Quebec. *Can. J. For. Res.* 23: 25-32.
- Davis, M.B. 1989. Lags in vegetation response to greenhouse warming. *Clim. Change* 15: 75-82.
- Flannigan, M.D., Bergeron, Y., Engelmark, O. & Wotton, B.M. 1998. Future wildfire in circumboreal forests in relation to global warming. *J. Veg. Sci.* 9: 469-476.
- Furyaev, V.V., Wein, R.W. & MacLean, D.A. 1983. Fire influences in *Abies*-dominated forests. In: Wein, R.W. & MacLean, D.A. (eds.) *The role of fire in northern circumpolar ecosystems*, pp. 221-234. Scope 18. John Wiley and Sons, New York, NY.
- Gauthier, S., Leduc, A., & Bergeron, Y. 1996. Forest dynamics modelling under a natural fire cycle: a tool to define natural mosaic diversity in forest management. *Environ. Monitor. Assess.* 39: 417-434.
- Hardy, Y., Mainville, M. & Schmitt, D.M. 1986. *An atlas of spruce budworm defoliation in eastern North America, 1938-1980*. U.S. Department of Agriculture Misc. Publ. 1449.
- Harvey, B. & Bergeron, Y. 1989. Site patterns of natural regeneration following clear-cutting in northwestern Quebec. *Can. J. For. Res.* 19: 1458-1469.
- Heinselman, M.L. 1981. Fire and succession in the conifer forests of northern north America. In: West, D.C., Shugart, H.H. & Botkin, D.B. (eds.) *Forest succession: Concepts and application*, pp. 374-406. Springer, New York, NY.
- Holling, C.S. 1992. The role of forest insects in structuring the boreal landscape In: Shugart, H.H., Leemans, R. & Bonan, G.B. (eds.) *A systems analysis of the boreal forest*, pp. 170-191. Cambridge University Press, Cambridge.
- Hosie, R.C. 1972. *Native trees of Canada*. Environment Canada, Forestry Service, Ottawa.
- Johnson, E.A. 1992. *Fire and vegetation dynamics - studies from the North American boreal forest*. Cambridge Studies in Ecology, Cambridge University Press, Cambridge.
- Johnson, E.A. & Van Wagner, C.E. 1985. The theory and use of two fire history models. *Can. J. For. Res.* 15: 214-220.
- Kneeshaw, D., Bergeron, Y. & de Grandpré, L. 1998. Early response of *Abies balsamea* seedlings to artificially created openings. *J. Veg. Sci.* 9: 543-550. (This issue.)
- Lambert, R.L., Lang, G.E. & Reiners, W.A. 1980. Loss of mass and chemical change in decaying boles of a subalpine balsam fir forest. *Ecology* 61: 1460-1473.
- Liu, K.-B. 1990. Holocene paleoecology of the boreal forest and Great Lake - St. Lawrence forests in northern Ontario. *Ecol. Monogr.* 60: 179-212.
- MacLean, D.A. 1980. Vulnerability of fir-spruce stands during uncontrolled spruce budworm outbreaks: a review and discussion. *For. Chron.* 56: 213-221.
- MacLean, D.A. 1984. Effects of spruce budworm outbreaks on the productivity and stability of balsam fir forests. *For. Chron.* 60: 273-279.
- MacLean, D.A. & Ostaff, D.P. 1989. Patterns of balsam fir mortality caused by an uncontrolled spruce budworm outbreak. *Can. J. For. Res.* 19: 1087-1095.
- Morin, H., Laprise, D. & Bergeron, Y. 1993. Chronology of spruce budworm outbreaks in the Lake Duparquet region, Abitibi, Québec. *Can. J. For. Res.* 23: 1497-1506.
- Overpeck, J.T., Rind, D. & Goldberg, R. 1990. Climate-induced changes in forest disturbances and vegetation. *Nature* 343: 51-53.
- Payette, S. 1992. Fire as a controlling process in the North American boreal forest. In: Shugart, H.H., Leemans, R. & Bonan, G.B. (eds.) *A systems analysis of the boreal forest*, pp. 144-169. Cambridge University Press, Cambridge.
- Prentice, I.C. & Leemans, R. 1990. Pattern and process and

- the dynamics of forest structure: a simulation approach. *J. Ecol.* 78: 340-355.
- Richard, P.J.H. 1993. Origine et dynamique postglaciaire de la forêt mixte au Québec. *Rev. Paleobot. Palynol.* 79: 31-68.
- Rowe, J.S. 1972. *Forest regions of Canada*. Environment Canada, Ottawa.
- Shugart, H.H. 1984. *A theory of forest dynamics*. Springer-Verlag, New York, NY.
- Simard, M.-J., Bergeron, Y. & Sirois, L. 1998. Conifer seedling recruitment in a southeastern Canadian boreal forest: the importance of substrate. *J. Veg. Sci.* 9: 575-582. (This issue.)
- Su, Q., MacLean, D.A. & Needham, T.D. 1996. The influence of hardwood content on balsam fir defoliation by spruce budworm. *Can. J. For. Res.* 26: 1620-1628.
- Stocks, B.J. 1987. Fire potential in the spruce budworm-damaged forests of Ontario. *For. Chron.* 63: 8-14.
- Veillette, J.J. 1994. Evolution and paleohydrology of glacial lakes Barlow and Ojibway. *Quat. Sci. Rev.* 13: 945-971.

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