Characterization of canopy openness before and after a spruce budworm outbreak in the southern boreal forest[1]

Vincent D'Aoust, Daniel Kneeshaw, and Yves Bergeron

Abstract: We propose a simple method that uses aerial photographs to characterize the impacts of a spruce budworm (*Choristoneura fumiferana* (Clem.)) outbreak on canopy structure. Using aerial photographs taken at the beginning (1972) and after (1994) a major spruce budworm outbreak (1970–1987), we evaluated the change in canopy openness that occurred during the period of the outbreak, in five compositionally different stands. We compared canopy openness evaluated by photointerpretation with two independent field techniques and found a high degree of similarity between methods. Interpretation of the 1972 photographs (prior to the outbreak) shows that regardless of composition, four of our five analysed stands had about the same degree of mean canopy openness (17%–20%). Following the outbreak, openness increased in all stands except for the hardwood-dominated stand. The highest increase in openness (from 18% to 45%) occurred in the stand with the highest conifer content. Thematic maps and spatial analysis techniques were used to describe canopy openness distribution. Openness was low and uniformly distributed before the outbreak, whereas after the outbreak, the various degrees of openness had a patchy distribution in most stands. Furthermore, patch size increased with conifer content. Using the amount of increase in canopy openness and its specific distribution within stands, we propose guidelines for the development of silvicultural practices that mimic spruce budworm disturbances in boreal mixedwoods.

Résumé : Cette étude propose une méthode simple qui utilise l'interprétation de photos aériennes pour caractériser les impacts d'une épidémie de la tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* (Clem.)) sur la structure du couvert forestier. En utilisant des photos prises au début (1972) et après (1994) l'épidémie majeure qui a frappé notre secteur de 1970 à 1987, nous avons évalué les changements dans le degré d'ouverture du couvert forestier qui se sont produits dans cinq peuplements de composition différente. La méthode d'évaluation du degré d'ouverture par photo-interprétation a été comparée à deux méthodes d'estimation utilisées sur le terrain. L'interprétation des photos prises au début de l'épidémie montre qu'indépendamment de la composition, quatre des cinq peuplements étudiés avaient approximativement le même pourcentage d'ouverture moyen (17–20 %). L'épidémie a entraîné une augmentation du degré d'ouverture dans tous les peuplements à l'exception du peuplement dominé par les feuillus. Sur les photos prises après l'épidémie, l'ouverture augmente en fonction de la proportion de conifères. Le peuplement le plus affecté a atteint un degré d'ouverture de 45 % en 1994. L'analyse spatiale de nos résultats révèle que les degrés d'ouverture variables trouvés après l'épidémie sont distribués en îlots alors qu'ils étaient faibles et distribués uniformément avant l'épidémie. La taille de ces îlots augmente avec l'âge des peuplements. Ces résultats nous permettent de proposer un scénario préliminaire de pratiques sylvicoles basées sur les impacts causés par une épidémie de la tordeuse des bourgeons de l'épinette en forêt boréale mixte.

Introduction

In the North American boreal forest, fire is recognized as the most important disturbance initiating and controlling stand and landscape dynamics (Heinselman 1981; Payette 1992; Johnson 1995; Bergeron 2000). However, nonfire or secondary disturbances have recently gained more interest from the research community (Kuuluvainen 1994; Kneeshaw and Bergeron 1998; Cumming et al. 2000; Kneeshaw 2001; McCarthy 2001). In Quebec's southern boreal forest, recent studies suggest that the fire interval is increasing (Bergeron and Archambault 1993). Larger proportions of stands are therefore attaining old-growth status (Kneeshaw and Gauthier 2003). At these older stages, recurring spruce budworm (*Choristoneura fumiferana* (Clem.)) (SBW) outbreaks and small-scale disturbances tend to control forest dynamics. It

Received 28 March 2003. Accepted 20 November 2003. Published on the NRC Research Press Web site at http://cjfr.nrc.ca on 17 February 2004.

V. D'Aoust,[2] D. Kneeshaw, and Y. Bergeron. Groupe de recherche en écologie forestière interuniversitaire, Université du Québec à Montréal, C.P. 8888, succursale Centre-Ville, Montréal, QC H3C 3P8, Canada.

[1]This paper was presented at the 4th International Workshop on Disturbance Dynamics in Boreal Forests: Disturbance Processes and their Ecological Effects, held 9–14 August 2002, Prince George, B.C., and has undergone the Journal's usual peer review process.

[2]Corresponding author (e-mail: vdaoust@yahoo.com).

 doi: 10.1139/X03-278

has been suggested that the impacts of SBW outbreaks on the forest will increase as fire-return intervals increase (Blais 1983; Anderson et al. 1987; Bergeron and Leduc 1998).

Spruce budworm outbreaks are the most important of the secondary disturbances in the eastern boreal forest. In some decades they have affected more land area than forest fires (Kneeshaw 2001). Most studies on SBW outbreaks have been conducted in forests where host species of the insect are dominant; in these landscapes, severe outbreaks kill most adult balsam fir (*Abies balsamea* (L.) Mill.) (Blais 1983; MacLean 1984). In the southern part of the boreal forest, where the forest mosaic is more heterogeneous and species diversity is greater, SBW outbreaks are as frequent as they are in pure fir forests (Morin and Laprise 1989; Morin et al. 1993), but mortality of host species tends to be lower (Batzer and Popp 1985; Frelich and Reich 1995; Kneeshaw and Bergeron 1998; Needham et al.1999). For this reason, SBW outbreaks have been less studied in the southern boreal forest than in pure fir forests, and their effects on the forest canopy are still not well understood.

Budworm-caused disturbances have been mostly characterized at the regional level or at the individual-tree level. For example, there have been a number of studies focused on large-scale defoliation patterns (Brown 1970; Blais 1983; Candau et al. 1998; Gray et al. 2000; Jardon 2001), on the frequency of SBW outbreaks (Blais 1983; Morin et al. 1993), and on tree mortality and timber loss (Batzer and Popp 1985; Ostaff and MacLean 1989; MacLean and Ostaff 1989). Impacts on stand structure and forest composition have been studied to a much lesser extent. In spruce–fir forests of eastern Canada, Baskerville (1975), MacLean (1984, 1988), and Morin (1994) have shown that in the long term, SBW outbreaks act as a cycling mechanism, killing overstory adult trees and allowing the recruitment of preestablished balsam fir into the canopy. In Minnesota, Batzer and Popp (1985) looked at the short-term compositional changes caused by a SBW outbreak in spruce–fir stands. They found that 22 years after the outbreak, the basal area of the host species decreased from 70% to 31% in the overstory. In a recent study in boreal mixedwoods, Kneeshaw and Bergeron (1998) described the impacts of canopy gaps caused by an outbreak on forest composition. Small gaps generally promoted a gradual transition towards a more fir-dominated forest, whereas hardwoods and nonhost late-successional species (i.e., cedar (*Thuya occidentalis* L.)) increased in abundance over fir in the large gaps.

Despite Baskerville's (1975) insistence and the findings of Kneeshaw and Bergeron (1998) that preoutbreak stand composition and how postoutbreak canopy structure is impacted (newly open areas) within these compositionally different stands are important factors governing how stands will respond to SBW, most papers do not describe the impacts of the outbreak on canopy structure. In boreal mixedwoods, we suspect that the variation in species composition will lead to impacts that vary substantially in extent and severity within each stand, which would in turn influence the vegetation response. It is therefore crucial to understand the effects of SBW outbreaks on the canopy structure in compositionally different stands.

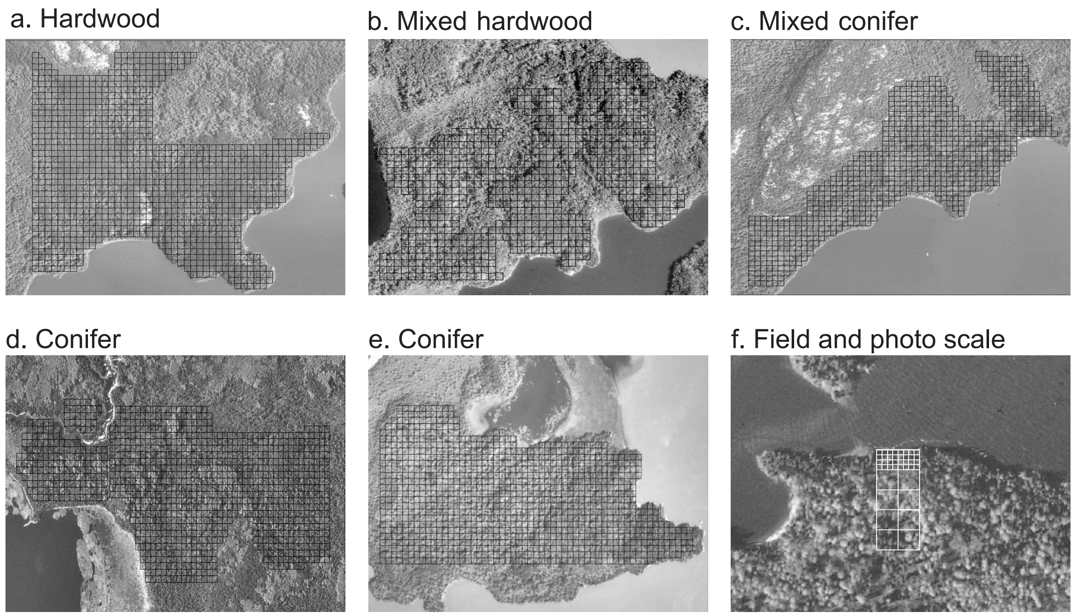
Canopy gap structure of forests has generally been characterized by conducting field surveys. However, there are important limitations to field sampling methods: they are restricted to evaluating current forest conditions, and they are time consuming to apply over large areas. The analysis of aerial photographs, especially across a time series, has the potential to solve these problems. Until now, however, they have only been used to describe stand composition and large-scale patterns in disturbances and have rarely been used to detect small stand-scale changes in canopy coverage. Nakashizuka et al. (1995) and Tanaka and Nakashizuka (1997) developed an excellent method to characterize the canopy structure of a temperate deciduous forest by making digital elevation models of the forest using aerial photographs (1:8000) taken in winter (without leaves) and in summer (with leaves). This method, however, cannot be used in coniferous (or mixed) forests, since the ground is not visible in winter. Similarly, high resolution aerial photographs are often not available for reconstructing historic conditions. Other methods have been proposed using digital image analysis techniques (Bucchheim et al. 1985; Laframboise and Beaubien 1985; Ahern et al. 1986; Blackburn and Milton 1997; St-Onge and Cavayas 1997; Sommerfeld et al. 2000), but most of these methods only detect defoliation patterns at a very large scale, while others are not easily accessible because of costs and technological requirements.

To acquire more detailed information on the impact of SBW outbreaks on canopy structure in boreal mixedwoods and to avoid labour-intensive ground surveys, we undertook to develop and validate a simple method using aerial photographs.

Study area

Our study sites are located in a 40-km^2 area of forest on the west shore of Lake Duparquet, south of Lake Abitibi in northwestern Quebec. The surrounding region is at the southern limit of a large physiographic region known as Quebec and Ontario's northern Clay Belt. It is characterized by clay deposits from the postglacial lakes Barlow and Ojibway (Vincent and Hardy 1977). The climate is cold temperate with an average annual temperature of 0.8 °C and average precipitation of 857mm/year (Environment Canada 1993). Lake Duparquet is in the southeastern boreal forest within Rowe's (1972) Missinaibi–Cabonga forest section. The dominant species is balsam fir, but black spruce (*Picea mariana* (Mill.) BSP), white spruce (*Picea glauca* (Moench) Voss), paper birch (*Betula papyrifera* Marsh.), and trembling aspen (*Populus tremuloides* Michx.) are also well represented. Species occurrence generally follows a succession pattern where pioneers such as jack pine (*Pinus banksiana* Lamb.), trembling aspen, and paper birch occupy recently disturbed sites. With time, shade-tolerant conifers replace the pioneer species and eventually dominate these sites (Bergeron 2000). Cedar generally occurs on sites where the forest has not burned for long periods. The fire cycle was estimated at 63 years for the period ranging from 1700 to 1870 and at more than 99 years from 1870 to 1990 (Bergeron 1991; Bergeron and Dansereau 1993). Three major SBW outbreaks have been reported in the last century: 1919–1929, 1930–1950, and 1970–1987 (Morin et al. 1993).

Fig. 1. Representation of the 500-m^2 cell grid overlaid on the five studied stands (*a–e*) and scale adjustments for field (small white cells = 25 m^2) and photograph (large white cells = 400 m^2) interpretations (*f*).



Materials and methods

To measure the changes in canopy coverage in compositionally different stands, five areas (approx. 40–50 ha) representing each of the major stand types were evaluated: (*i*) an intolerant hardwood dominated stand (greater than 65% hardwoods, primarily aspen with some paper birch) originating from a fire in 1870 (stand A) (see Kneeshaw and Bergeron (1998) for a more complete description), (*ii*) a mixed hardwood stand (50%–65% hardwood) originating from a fire in 1823 (stand B), (*iii*) a mixed conifer stand (50%–65% conifer, primarily fir with some white spruce and cedar) originating from a fire in 1797 (stand C), and (*iv*) two conifer-dominated stands (greater than 65% conifer) originating from a fire in 1760 (stands D and E). All stands were selected and characterized using the 1972 aerial photographs, 1975 forest inventory maps, and field data from the area (Bergeron and Dansereau 1993, Dansereau and Bergeron 1993, Kneeshaw and Bergeron 1998; Bergeron 2000). Nonsymmetric shapes were delineated to avoid nonforested areas or large changes in vegetation type.

The method consists of using a grid (made up of 500-m^2 square cells) overlaid onto 1 : 15 000 aerial photographs (Fig. 1) and visually estimating canopy openness (%) for every cell using a stereoscope and × 8 magnifying lens. The 500-m^2 cell size was chosen for its suitability in detecting within-stand spatial patterns in openness while being coarse enough for evaluations to be done over large continuous areas. The ability to evaluate openness precisely and continuously (difficult in smaller cells) and the total amount of work involved were also considered. Individual-tree deaths or small gaps (which would be 4 to 30 m^2 in size) are very difficult to observe and even harder to delineate on 1 : 15 000 aerial photographs. Additionally, these have been covered elsewhere in the literature (Baskerville and MacLean 1979; MacLean and Piene 1995; Kneeshaw and Bergeron 1998). Because this was not our goal and because we wanted to describe the patchiness of the various degrees of openness over larger areas, we opted for the 500-m^2 cell size. This scale will also be more useful in forestry planning for boreal mixedwoods than the individual-tree scale. Canopy openness, which normally refers to the relative amount of sky that is visible from a point beneath the forest canopy (Fraser 2000), was inversed to refer to the relative amount of ground or understory visible from a point above the forest canopy. Canopy openness was evaluated in the same manner as cover estimations of herbaceous vegetation in the field. Openness percentage was estimated to the nearest 5%. Percent openness for each cell was then entered into a geographic information system where a properly scaled digitized version of the grid was created as a "layer", accepting data for each of the cells. All stands were evaluated in this manner with aerial photographs (1 : 15 000) taken at the beginning (June 1972) and after (July 1994) the outbreak, which occurred from 1970 to 1987 (Morin et al. 1993). Because tree death only begins to occur after several years (>5) of severe defoliation (Blais 1981; Baskerville and MacLean 1979; MacLean 1984, 1988), we did not expect to miss any outbreak-induced openness because of the 2-year lag between the beginning of the outbreak and the time the aerial photographs were taken.

Thematic maps were produced allowing for visual representation of the spatial distribution of the various degrees of canopy openness. Openness percentages were divided in three classes (5%–34%, 35%–64%, and 65%–99%) to improve and simplify visual detection of patterns. A series of spatial statistics were conducted using these classes. Horizontally or vertically connecting cells that had a percent openness in the same class were aggregated to form patches. These patches could then be analyzed using "patch analyst", an ArcView extension, to obtain information on class type distribution and patch characteristics.

A spatial autocorrelation analysis was also performed to detect and characterize spatial patterns in canopy openness distribution. We tested for positive autocorrelation (values of openness tend to be similar at a given distance) and negative autocorrelation (values of openness tend to be different at a given distance). When both positive and negative autocorrelations are detected, this confirms the presence of patches of different openness values. Because an autocorrelation value is obtained for each chosen distance class, the scale at which a spatial pattern occurs can also be determined. Spatial autocorrelation is usually measured using Moran's I and (or) Geary's C (Legendre and Fortin 1989; Duncan and Stewart 1991). Formulas and specifics are detailed in Legendre and Legendre (1998). To tests the significance of the I values (Moran's I), we used the standard normal deviates, $z(d)$ (where d is distance class), calculated using the normal variance of I. Since sample size was so high (>800), we did not need to use the variance under the null hypothesis of randomization; in fact both values (normal and random) were almost exactly the same (Legendre and Legendre 1998). We relied on the Bonferroni correction for the significance level of the correlogram as a whole (Legendre and Fortin 1989). This correction states that because several tests are performed at the same time (for each distance class) and that these tests are not independent, at least one value should be significant at $\alpha = \alpha/k$, for the correlogram to be significant (where k is the number of distance classes). To air on the conservative side, we used the same correction method to test the significance of Moran's I for each individual distance class. To examine spatial autocorrelation results, correlograms for each stand were drawn with $z(d)$ values plotted for each distance class. At the 0.05 significance level ($\alpha = 0.05/k$; $k = 40$), the corresponding z is 3.23.

The correlograms presented in this paper are all directional. A condition to produce all-directional correlograms is to find isotropy in the analysed variables. This basically means that spatial autocorrelation should be constant in all directions, or in our case, that the similarity or dissimilarity of canopy openness at a chosen distance remains constant in all directions. Because we suspected anisotropy in our data, which is often the case in ecology, we produced directional correlograms to verify if the spatial distribution of our variable showed isotropy. We found some differences for large distance classes depending on the direction chosen. However, all directions showed very similar autocorrelation values for approximately the first 10–15 distance classes. Isotropy was also found for larger distance classes in the conifer-dominated stands. We therefore present all-directional correlograms for classes 0–25, where distance class 1 includes data points within 0–25 m, distance class 2 includes data points located within 25–50 m, and so on.

Testing photointerpretations

To gage the value of our photointerpretation, we compared the evaluation of canopy openness on the 1994 photographs with openness evaluated in the field by this study (2001) and a 1993–1994 study (Kneeshaw and Bergeron 1998). Although a series of factors contribute to complicate such a comparison (positioning in the field and on the photographs, scale adjustments, year differences, and the use of different methods), the results from two independent studies should, nonetheless, show whether photointerpretation allows us to accurately estimate canopy openness.

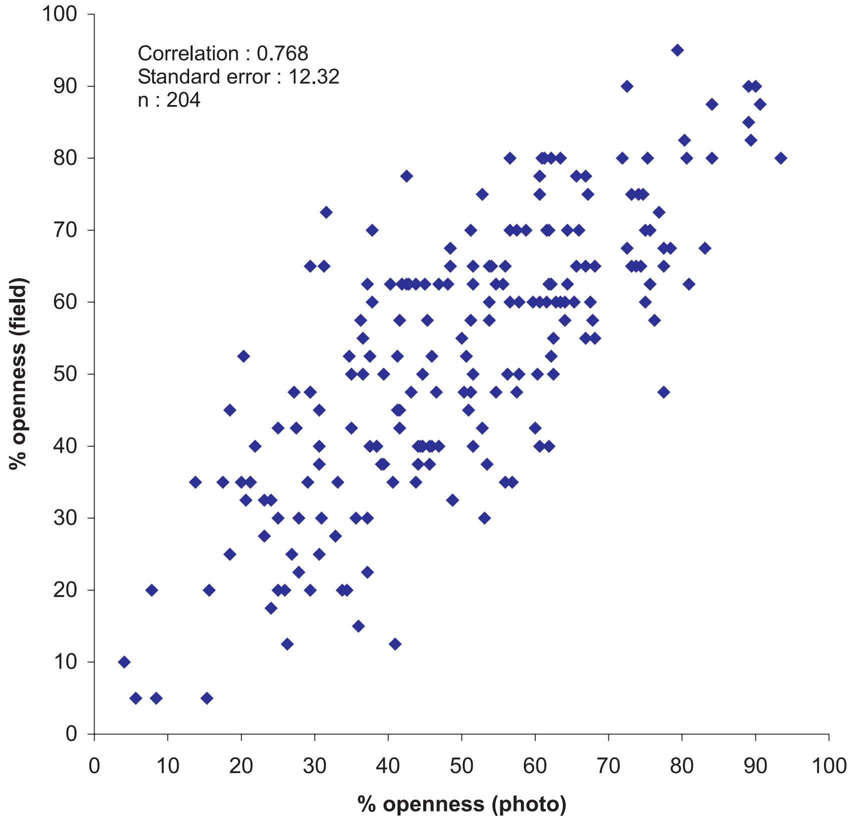
We designed two comparisons between field and photograph evaluations: one at the cell scale and one at the stand scale (mean openness). At the cell scale, we evaluated 204 (400 m^2) cells for openness in the field and on the photographs. The 400-m^2 cell size was chosen to facilitate comparisons between field measurements and aerial photographs; however, the complete photointerpretation work was done at the 500-m^2 cell size to improve interpretation speed and facility and to use a cell size that could more easily be scaled up (e.g., 500, 1000, 1500 m^2, etc). Twenty field transects, each composed of 8–12 cells, were distributed randomly in all stand types within the study area. For field evaluations, each 400-m^2 cell was divided into smaller, more easily interpretable 25-m^2 cells (Fig. 1*f*). We evaluated percent openness (to the nearest 5%) in the 25-m^2 cells by standing in the centre of the cell and looking straight up at the canopy, delimitating the canopy 2.5 m to the east, west, south, and north. Openness for all 25-m^2 cells contained in the larger 400-m^2 cell was then averaged and compared with openness obtained from photointerpretation of the actual 400-m^2 cell. To be as close as possible to evaluating precisely the same area in the field as on the photographs, all transects were established near the lakeshore, where field marks (trees, rocks, bays, or points) were used to locate starting points. We used a global positioning system unit to confirm position, and if required, the position on the photograph was corrected upon return from the field before photointerpretation. Field interpretations were done in 2001, and the photographs are from 1994. No important disturbances occurred in the area during this time interval.

Our second evaluation was done at the stand scale by using field results from Kneeshaw and Bergeron (1998). They used three to eight linear transects per stand totalling between 2.5 and 8.5 km of transects to establish the mean percent openness for each stand. We compared these results with our evaluations from aerial photographs obtained by averaging percent openness of all cells within the same stands.

Pre- and post-outbreak evaluations

In addition to evaluating canopy openness before (1972) and after (1994) the outbreak, we specifically quantified the change in canopy openness that occurred during the outbreak period by subtracting percent openness obtained in 1972 from percent openness obtained in 1994. This gave us the net change in canopy openness occurring during the 22-year period for every cell and thus allowed us to detect the process of the canopy opening or closing. Since no other significant disturbances occurred in the area during this period (Bergeron 2000) and since new openings due to small gaps were more or less balanced by canopy closure, we assume that important increases in canopy openness can primarily be attributed to the outbreak. To visually represent the spatial distribution of these results we divided the degree to which cell openness changed between 1972 and 1994 into four classes: (1) decrease in canopy openness (11%–95% decrease), (2) no important change in coverage (0%–10% increase or decrease), (3) moderate increase in canopy openness (11%–39% increase), and (4) important increase in canopy openness (40%–99% increase). Relative frequencies

Fig. 2. Comparison between field and aerial photograph estimations of canopy openness in 204 (400 m^2) cells distributed in 20 transects throughout all stand types. Field estimations for each 400 m^2 cell were obtained by averaging openness values from the 16 smaller 25 m^2 cells contained in the 400 m^2 cells. Aerial photograph estimations were obtained at once for each 400-m^2 cell.



of the degree of change in canopy openness for each stand were also calculated.

Results

Field and photograph openness evaluations

At the individual-cell scale, field and photograph estimations of canopy openness were well correlated (0.77, $p < 0.01$) (Fig. 2). Photointerpretations provided a slightly higher estimate (2%) of openness compared with field interpretations in more open areas and a slightly lower estimate (2%) of openness in closed canopies. At the stand scale, mean openness evaluated in the field with the line transect method (Kneeshaw and Bergeron 1998) was also well correlated (0.96, $p < 0.05$) with openness measured on the aerial photographs (Fig. 3). Despite the excellent correlation, the same slight tendency (less than 3%) of estimating greater openness by photointerpretation was present. Overestimation was most important in the mixed conifer stand (8%).

Preoutbreak condition

Conditions of canopy openness before the outbreak were consistent and low in all stand types. In fact, despite age and compositional differences, all stands, with the exception of the mixed conifer stand (which showed a mean openness of 30%), had a mean openness between 18% and 20% in 1972 (Table 1). In these preoutbreak stands, canopy openness (Fig. 4) was low and uniformly distributed. With the exception of the mixed conifer stand, the 18% mean openness found in the remaining stands reflects high canopy coverage with a small gap distribution. Since 18% of 500 m^2 equals 90 m^2, we can say that most gaps were equal or smaller than this, with few exceptions due to larger gaps found in two or more connecting cells. This openness reflects the canopy openness caused by small-scale regular disturbance events in a nonoutbreak period.

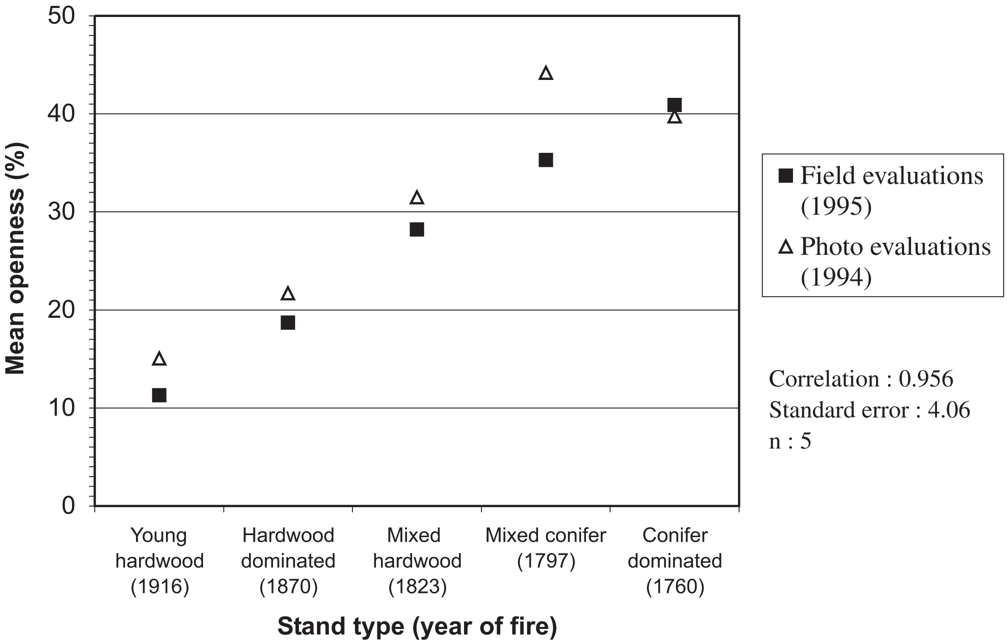
The greatest canopy structural heterogeneity occurred in the mixed conifer stand (Fig. 4). This stand had many sections of more open forest (35%–64% openness class), which was found to be due to the presence of more rocky outcrops (field observations).

Our patch analysis (Table 2) reflects the same patterns of preoutbreak canopy openness. In most stands, statistics show the presence of one or a few large patches of forest with 5%–34% openness. The correlograms (Fig. 5) also show similar patterns in all stand types before the outbreak, but these patterns are not the same as those seen on the maps and depict a finer-scale patchiness that cannot be seen with a coarse classification such as the 5%–34% openness class. Positive autocorrelation is present and significant at small scales (distance classes 3–4 = approx. 75–100 m), after which significance drops, and practically no negative autocorrelation is found.

Postoutbreak conditions

Important changes in canopy coverage occurred during the outbreak. Aside from the hardwood-dominated stand, mean percent openness increased by 14% to 27% (Table 1).

Fig. 3. Comparison between field and aerial photograph estimations of mean canopy openness at the stand scale. Mean openness in the field was obtained in 1995 by calculating the proportion of open versus closed canopy in three to eight (1 km) linear transects for each stand type. Aerial photograph estimations were obtained on the 1994 photographs by averaging openness values of all cells contained in our stands.



Increases were larger in the older conifer-dominated stands, such that postoutbreak canopy openness increased with stand age.

The hardwood-dominated stand is the only stand where little change in canopy openness was observed. The percentage of cells in which canopy openness increased moderately (17%) was balanced by cells in which the canopy closed (16%) (Table 1). Cells that experienced no change in canopy openness represent 65% of the stand and were uniformly distributed throughout the stand (Fig. 4). One patch of forest (1000 m^2) was severely impacted in the lower centre of the stand, but field observations confirmed that this was due to beaver activity.

In the mixed hardwood stand, 49% of cells experienced no changes in openness, and 41% experienced moderate increases. The spatial distribution analysis showed that cells of both these categories were mostly aggregated into specific sections. Cells showing a 40%–95% increase in openness were rare and occurred in small patches of one to four cells (1000 m^2). They represented 8% of all cells.

Impacts to the mixed conifer stand were not lessened by the prior conditions of canopy openness. Openness increased by 14% (Table 1). Spatial distribution of the impacted areas, however, was more randomlike, making spatial patterns harder to observe (Fig. 4). The most obvious and observable pattern in this stand concerns cells that showed important increases in openness. These cells were clumped into groups of eight or more, forming a few patches of open forest each approximately 5000 m^2 in size.

Openness in conifer stand D increased by 16%. Most of the cells showing an increase were located in the western section of the stand, while cells that showed little change in openness were clumped together in a large area in the south-central – southeastern portion of the stand (Fig. 4*d*). Cells showing an important increase in canopy openness were once again aggregated into medium to large patches (approx. 5000 – 10 000 m^2) in the centre of the stand. In the second conifer-dominated stand (stand E), close to 80% of its area showed either moderate (48%) or important (30%) increases in openness following the outbreak (Table 1). This stand opened up 27% from the preoutbreak condition. Cells where openness increased importantly were mostly found in a single large patch (6.4 ha) of open forest at the west end of the stand (Fig. 4*e*). Most of the remaining cells were moderately impacted and are now in the 35%–64% openness class.

From 1972 to 1994 the number of patches (all openness classes) tripled in three of the four mixed and conifer stands (Table 2). Mean patch size was reduced by more than half. The amount of edge also increased dramatically, and patch types were more evenly distributed (Shannon's evenness index). The result of these observations is that we are now (after the outbreak) in the presence of a much more complex and diversified forest environment in terms of canopy openness. In the two conifer-dominated stands, the number of patches of highly open forest (65%–99% openness) increased dramatically after the outbreak. Although most of these patches (64%) are smaller than 0.1 ha, in terms of area, these small patches represent only 21% of the highly open areas, while the few large patches of open forest (>1 ha) represent 47% of the new highly open areas (65%–99% openness) (Fig. 6).

Spatial autocorrelation

After the outbreak, differences among stand types could also be observed on the correlograms (Fig. 5). Although preoutbreak and postoutbreak plots were similar in the hardwood and mixed hardwood stands, important differences began to appear in the mixed conifer and conifer stands:

Table 1. Stand size, mean canopy openness in 1972 and in 1994, and net change in canopy openness as divided in four classes for the five stands studied in the boreal forest of Quebec.

Stand type (year of fire)	Stand size (ha)	Mean openness (%) 1972	Mean openness (%) 1994	% of cells showing an increase or decrease in openness: Decrease (>10%)	No change (≤10%)	Moderate increase (11%–39%)	Important increase (≥40%)	Total change (% increase)
A. Hardwood (1870)	58	20	22	16	65	17	2	2
B. Mixed hardwood (1823)	37	18	32	2	49	41	8	14
C. Mixed conifer (1797)	45	30	44	6	49	32	13	14
D. Conifer (1760)	47	18	34	3	44	38	15	16
E. Conifer (1760)	49	18	45	3	19	48	30	27

positive autocorrelation was greater at small distance classes and lasted into larger distance classes. The highest distance class for which autocorrelation remained significant (4, 9, and 15 for stands C, D, and E, respectively) can be interpreted as the approximate patch size or the scale length over which the openness values are similar. At distance classes 17–25, most stands showed significant negative autocorrelation after the outbreak, which confirms the presence of distinct patches of both open and closed forest.

Discussion

Field and photograph openness evaluations

Comparisons between field and aerial photograph canopy openness estimations showed a good correlation between the two methods at both the cell and stand scale (Figs. 2–3). Estimations at the cell scale were affected by the difficulty in ensuring that the exact same area (cell) was evaluated in the field as on the photograph. Field marks and global positioning system coordinates did not always coincide perfectly on the aerial photographs, leaving room for small positioning errors. A deviation of even 1 or 2 m between the field location and the aerial photograph may explain some of the variation observed at the scale of the individual cell. The very slight (2%) overestimation of openness evaluated on the aerial photographs may be due, in part, to the lag time (and thus some vegetation recovery) between field measurements and the time at which the photographs were taken.

The use of aerial photographs permits both the estimation of canopy openness over larger areas than field studies and the estimation of canopy openness at different moments in time. At a local scale, however, delineating individual gaps on (1 : 15 000) aerial photographs would be an enormous and tedious task. It should, however, be considered with finer-scale photographs. Nonetheless, the precision obtained by our method allowed us to adequately characterize the general spatial distribution and degree of canopy openness.

Preoutbreak conditions

Aside from one stand (the mixed conifer stand), where openness was higher because of more rocky outcrops, the percentage of the forest in canopy gap in 1972 (i.e., prior to the effects of the outbreak) did not vary much among stand types. This canopy openness reflects the natural small-scale disturbance or mortality occurring in stands during non-outbreak periods. The fact that openness was similar among stands is in contrast with what has been reported in studies of different forest types, that is, the tendency for coniferous stands to generally show more openness than hardwood stands (McCarthy 2001; Kneeshaw 2001). Openness in the hardwood stand (20%) was at the high end of what is reported for temperate hardwood forests (2%–20%, median: 10%; McCarthy 2001) and was also slightly greater than the values reported for our conifer stands in the preoutbreak period (18%). These high openness values may reflect the beginning of the breakup of the intolerant-hardwood stand (Bergeron 2000; Cumming et al. 2000). This is further supported by the fact that our hardwood stand is quite old, as it originated from a fire in 1870. It has been reported that a peak in aspen mortality for stands in this area can be observed for individuals between 110 and 150 years (Senecal et al. 2004). In the mixed and conifer-dominated stands, the openness percentages showed that prior to SBW disturbance, openness fell within the range reported in McCarthy's (2001) review of other studies of boreal and subalpine forests (6%–36%).

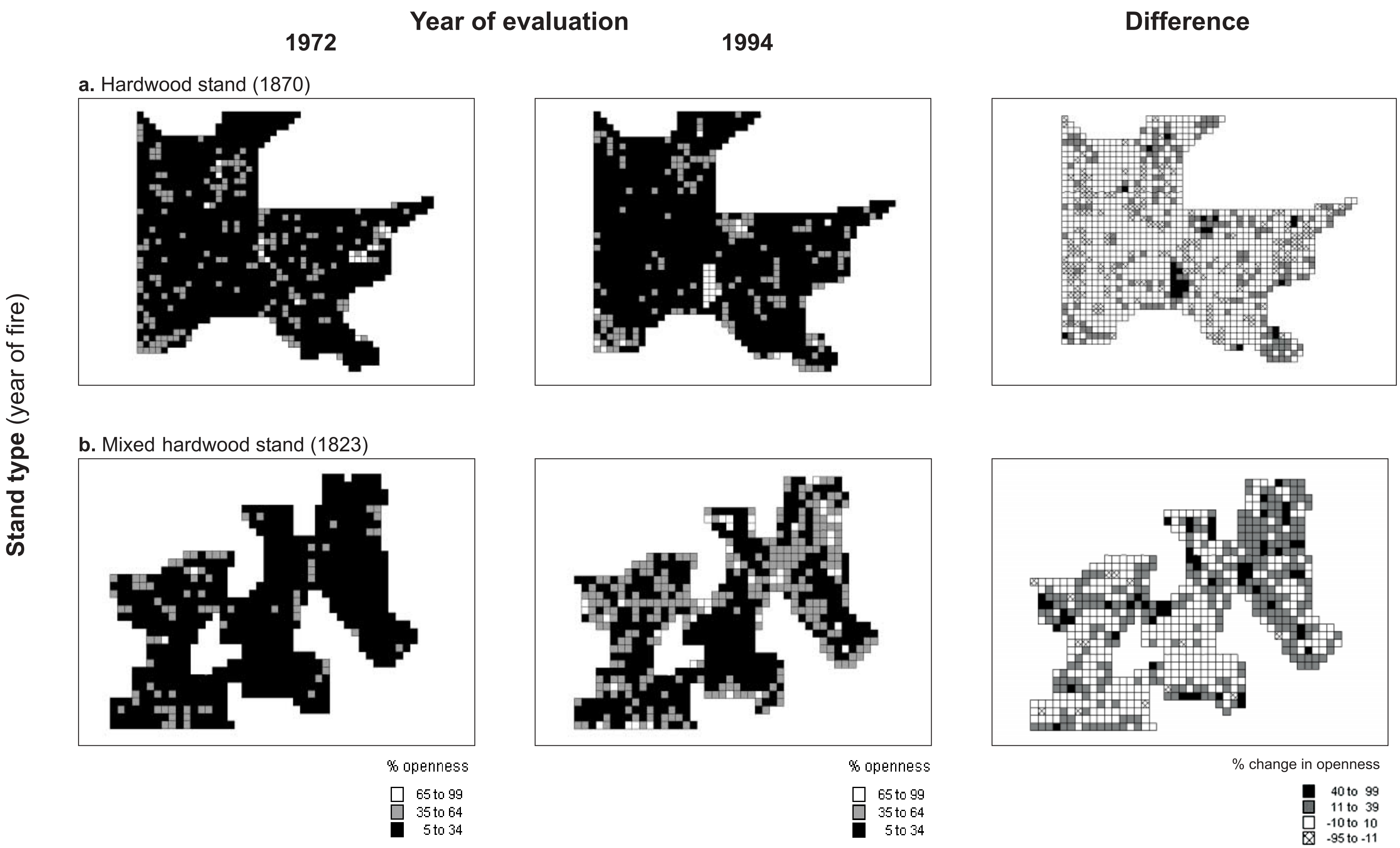
The fact that all stands had similar and low canopy openness in 1972 suggests that pre-SBW disturbances were limited to small-scale natural group and single-tree mortality. The fact that preoutbreak openness did not increase with conifer content suggests that the SBW outbreak that occurred before this period (1930–1950; Morin et al. 1993) may have been less severe and (or) that regeneration filled in most of the open areas during the 20-year period between the last two outbreaks.

Postoutbreak conditions

After the budworm outbreak, canopy openness increased substantially in all but the hardwood-dominated stand. The young hardwood-dominated stand did not experience important changes in canopy openness, presumably because of its species composition (predominance of species that are not SBW hosts). That is not to say that no changes occurred, but rather that the small percentage of the canopy that opened because of mortality was mostly balanced by areas in which the canopy closed because of new growth. This stand is thus in a dynamic balance (Frelich 2002).

In the mixed and conifer-dominated stands, postoutbreak mean openness increased substantially to between 32% and 45%. These figures fall at the high end of the reported range (McCarthy 2001). Postoutbreak, canopy openness generally increased with time since fire (as stands become increasingly

Fig. 4. Canopy openness before (1972) and after the outbreak (1994) as divided in three openness classes. The "difference" column represents the net change (openness in 1994 minus openness in 1972) in canopy openness.



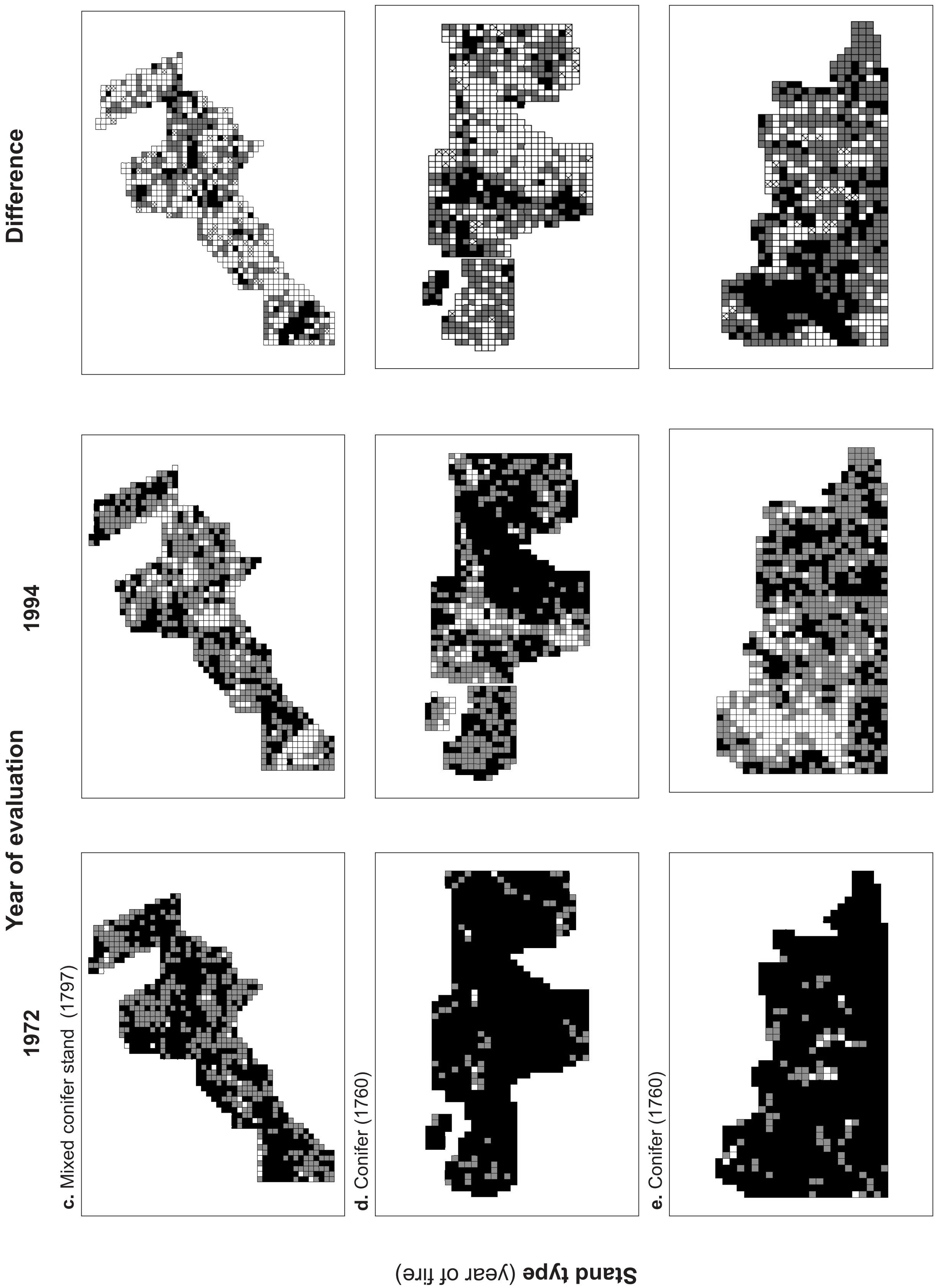


Fig. 4 (*concluded*).

Table 2. Spatial statistics of patches of three different classes of canopy openness in the five studied stands in Quebec at the time period before (1972) and after (1994) a spruce budworm outbreak (patches were formed by merging horizontally or vertically contiguous cells (Fig. 5) of the same openness percentage class).

	Percent openness class							
	5%–34%		35%–64%		65%–99%		Landscape (all classes)	
Spatial statistics	1972	1994	1972	1994	1972	1994	1972	1994
Hardwood stand (1870 fire)								
No. of patches	6	9	89	68	11	10	106	87
Mean patch size (ha)	8.39	5.37	0.10	0.12	0.08	0.14	0.57	0.67
Largest patch (ha)	49.89	47.39	0.69	0.59	0.25	0.79	49.89	47.39
Edge density (m/ha)	256.84	224.98	195.73	173.94	21.42	24.30	473.99	423.22
% of land	0.84	0.83	0.15	0.14	0.02	0.02	na	na
Shannon's evenness index	na	na	na	na	na	na	0.76	0.79
Mixed hardwood stand (1823 fire)								
No. of patches	1	31	43	67	2	29	46	127
Mean patch size (ha)	33.62	0.67	0.09	0.21	0.06	0.08	0.82	0.29
Largest patch (ha)	33.62	10.15	0.32	3.56	0.07	0.16	33.62	10.15
Edge density (m/ha)	256.10	354.31	140.76	383.52	5.42	87.93	402.29	825.75
% of land	0.90	0.56	0.10	0.38	0.00	0.06	na	na
Shannon's evenness index	na	na	na	na	na	na	0.65	0.87
Mixed conifer stand (1797 fire)								
No. of patches	34	70	59	42	18	40	111	152
Mean patch size (ha)	0.74	0.18	0.31	0.57	0.06	0.21	0.40	0.30
Largest patch (ha)	9.56	1.64	4.15	8.72	0.11	1.90	9.56	8.72
Edge density (m/ha)	361.58	295.29	349.68	415.87	38.22	171.37	749.49	882.53
% of land	0.57	0.28	0.41	0.53	0.02	0.19	na	na
Shannon's evenness index	na	na	na	na	na	na	0.78	0.95
Conifer stand 1 (1760 fire)								
No. of patches	5	44	41	78	6	29	52	151
Mean patch size (ha)	9.28	0.59	0.10	0.24	0.07	0.18	0.98	0.33
Largest patch (ha)	44.81	16.45	0.24	2.18	0.10	1.49	44.81	16.45
Edge density (m/ha)	191.85	301.04	104.69	345.10	12.48	110.26	309.02	756.40
% of land	0.91	0.52	0.08	0.37	0.01	0.11	na	na
Shannon's evenness index	na	na	na	na	na	na	0.72	0.92
Conifer stand 2 (1760 fire)								
No. of patches	2	66	41	56	11	41	54	163
Mean patch size (ha)	22.85	0.24	0.11	0.47	0.08	0.26	0.94	0.32
Largest patch (ha)	45.64	1.71	0.40	10.88	0.20	6.41	45.64	10.88
Edge density (m/ha)	175.61	281.06	105.48	408.20	24.71	162.66	305.80	851.92
% of land	0.90	0.30	0.09	0.50	0.02	0.20	na	na
Shannon's evenness index	na	na	na	na	na	na	0.81	0.94

dominated by conifers) (Table 1). Since canopy openness before the outbreak (1972 photographs) was similar among stands, this suggests that the increase in canopy openness observed in the 1994 photographs was probably caused by the budworm outbreak. In conifer-dominated stands, the complex interactions between budworm and nonbudworm disturbances may not be completely accounted for by the evaluation of preoutbreak and postoutbreak photographs in this study. However, patches of windthrow (i.e., patches of blowndown trees) were not observed in this area in the field (Kneeshaw and Bergeron 1998) or in the analysis of the photographs. Other smaller-scale disturbances such as natural tree mortality were accounted for as part of the initial background rate of openness observed in the first set of photographs.

The large increases in openness from the preoutbreak to the postoutbreak period in the mixed and coniferous stands (from 18% to almost 45%) cover much of the wide range in values of gap fraction (because of endogenous and natural exogenous events (except fire)) reported for coniferous forests (Worral and Harrington 1988; Spies et al. 1990; Lertzman and Krebs 1991; Qinghong and Hytteborn 1991; Battles and Fahey 1996). The fact that this variation was found at different times within the same stands suggests that the "time of evaluation" is critical in assessing canopy openness. Therefore, although the evaluation of openness at one point

Fig. 5. Spatial correlograms of canopy openness before (1972) and after (1994) the outbreak for all stands. The statistic $z(d)$ is the standard normal deviate of Moran's I for each distance class (d), the 0.05 significance level of deviations ($z(d)$) from expected values of Moran's I is 3.23 (dotted lines). The size of our distance classes is 25 m. Distance class 1 is 0–25 m, distance class 2 is 25–50 m, and so on. Therefore the $z(d)$ represents the similarity (positive z) or dissimilarity (negative z) of values of canopy openness for neighbors located within the distance range of distance class (d).

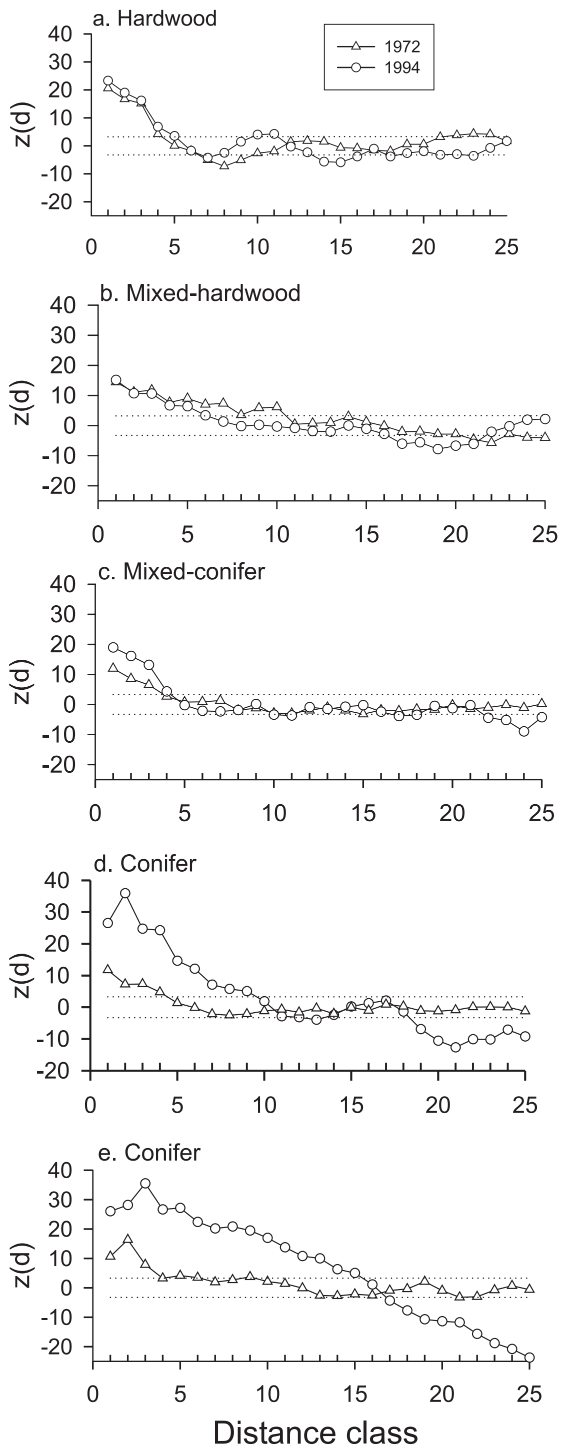
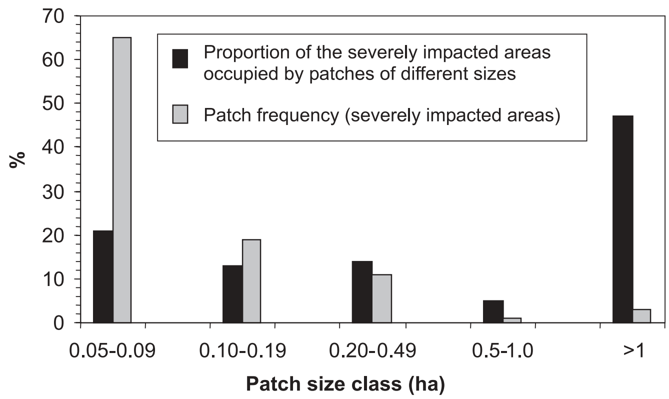


Fig. 6. Postoutbreak patch size distribution for patches of severely impacted areas in the two conifer-dominated stands and the proportion of the severely impacted areas that they occupy within these two stands.



in time may reflect the current state of the forest (Runkle 1982, 1985; Krasny and Whitmore 1992; Yamamoto 1992, 1993), only evaluations compiled over the course of time can truly reflect the dynamic aspect of a forest's disturbance regime (Tanaka and Nakashizuka 1997).

Mortality of balsam fir caused by the last outbreak in our area was evaluated in the same stand types by Bergeron et al. (1995). Mortality rates varied from 22% in deciduous stands to 51%–57% in mixed stands and 71% in conifer stands. The increase in mortality rates with conifer content compares well with the greater increase in openness in stands dominated by conifers.

The spatial distribution of our data is reported by three means: thematic maps (Fig. 4), descriptive spatial statistics (Table 2), and spatial autocorrelation analysis (Fig. 5). All three methods show how openness became more heterogeneously distributed after the outbreak because of the presence of patches with different openness percentages. In the mixed hardwood and mixed conifer stands, impacts to the overstory canopy reflect the balance between the host and nonhost species content of these stands — important increases in openness were rare and came in small patches (Fig. 4) because of the lower abundance of fir (Bergeron 2000) and also presumably because fir mortality does not always increase canopy openness where hardwood coverage is important. Nonimpacted and moderately impacted areas formed larger distinct patches either because few fir were present (nonimpacted sections) or because where fir was present, it was usually found interspersed with nonhost species (moderately impacted sections). Furthermore, Su et al. (1996), Cappucino et al. (1998), and Bergeron et al. (1995) also suggest that fir mortality is reduced in mixed stands. This observation of nonimpacted and moderately impacted areas in mixedwood forests also agrees well with the finding that these forests are dominated by small- and medium-size gaps (Kneeshaw and Bergeron 1998).

The same pattern of spatial aggregation of different impacts was even more obvious in the conifer-dominated stands. Nonimpacted and moderately and severely impacted cells were aggregated into large patches in these stands (Figs. 4 and 5). Spatial patterning was also reported at smaller scales (approx. 50 m or less) in mortality studies (Baskerville and MacLean 1979; MacLean and Piene 1995). In our study, the aggregation of cells showing no increase, moderate increases, or important increases in openness into large patches is presumed to be caused by variable pre-outbreak concentrations of mature balsam fir (MacLean 1980), which were identified on the 1974 forest inventory maps and from photointerpretation of canopy composition in 1972. Frelich and Reich (1995) also demonstrated that stands that have not burned for long periods acquire a patchy character in which small groups of trees of the same species are interspersed at different spatial scales. Our results tend to support this and further suggest that the patchy distribution of canopy openness following a SBW outbreak may accentuate this phenomenon. Over the short term important changes in composition may occur in variable ways (within a stand). A study of the (postoutbreak) within-stand vegetation responses based on these findings should be considered.

Management implications

The results of this study have direct implications for forest managers who seek silvicultural and management strategies with a natural disturbance based underpinning. First, it should be stated that SBW outbreaks are not the only factor leading to canopy openness. Before an outbreak all stands generally experience some openness (approximately 15%–20%), as they may have been in a dynamic stable state (i.e., with openness and closure balancing each other through time). Periodic outbreaks may remove another 20%–25% of conifers in conifer-dominated stands. It is our preliminary recommendation that managing boreal mixedwoods could involve removal of a similar proportion of conifers in partial harvesting operations that mimic budworm-caused mortality while ensuring that not more than 45% of the canopy is opened to remain within natural limits. In conifer-dominated stands, openings could be distributed into patches of different sizes to generate highly impacted areas similar to budworm-origin patches. As our results show, patches of highly open areas (65% and more openness) represent between 11% and 20% of these stands (Table 2). Our results, although from a limited sample size, suggest that a small number of these patches can attain areas of 1 to 6 ha. The large patches that we observe represent only 3% of the total number of patches of highly open areas, but in terms of area they represent 47% of the highly open areas (Fig. 6). To maintain the gradient of openness classes, the remainder of the harvested areas should, however, be in the smaller patch size classes.

References

Ahern, F.J., Bennett, W.J., and Kettela, E.G. 1986. An initial evaluation of two digital airborne imagers for surveying spruce budworm defoliation. Photogramm. Eng. Remote Sens. **52**: 1647–1654.

Anderson, L., Carlson, C.E., and Wakimoto, R.H. 1987. Forest fire frequency and western spruce budworm outbreaks in Western Montana. For. Ecol. Manage. **22**: 251–260.

Baskerville, G.L. 1975. Spruce budworm: super silviculturist. For. Chron. **51**: 138–140.

Baskerville, G.L., and MacLean, D.A. 1979. Budworm-caused mortality and 20-year recovery in immature balsam fir stands. Can. For. Ser. Marit. For. Res. Cent. Inf. Rep. M-X-1025.

Battles, J.J., and Fahey, T.J. 1996. Spruce decline as a disturbance event in the subalpine forests of the northeastern United States. Can. J. For. Res. **26**: 408–421.

Batzer, H.O., and Popp, M.P. 1985. Forest succession following a spruce budworm outbreak in Minnesota. For. Chron. **61**: 75–81.

Bergeron, Y. 1991. The influence of island and mainland lakeshore landscapes on boreal forest fire regimes. Ecology, **72**: 1980–1992.

Bergeron, Y. 2000. Species and stand dynamics in the mixed woods of Quebec's southern boreal forest. Ecology, **81**: 1500–1516.

Bergeron, Y., and 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. Holocene, **3**: 255–259.

Bergeron, Y., and Dansereau, P.R. 1993. Predicting forest composition under different fire cycles in the southeastern boreal forest of Canada. J. Veg. Sci. **4**: 827–832.

Bergeron, Y., and Leduc, A. 1998. Relationships between change in fire frequency and mortality due to spruce budworm outbreak in the southeastern Canadian boreal forest. J. Veg. Sci. **9**: 492–500.

Bergeron, Y., Leduc, A., Morin, H., and Joyal, C. 1995. Balsam fir mortality following the last spruce budworm outbreak in northwestern Quebec. Can. J. For. Res. **25**: 1375–1384.

Bescond, H. 2002. Reconstitution de l'historique de l'exploitation forestière sur le territoire de la forêt d'enseignement et de recherche du lac Duparquet au cours du 20ème siècle et influence sur l'évolution des peuplements forestiers. M.Sc. thesis. Université du Québec à Montréal, Montréal, Que.

Blais, J.R. 1981. Mortality of balsam fir and white spruce following a spruce budworm outbreak in the Ottawa River watershed in Quebec. Can. J. For. Res. **11**: 620–629.

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.

Blackburn, G.A., and Milton, E.J. 1997. An ecological survey of deciduous woodlands using airborne remote sensing and geographical information systems (GIS). Int. J. Remote Sens. **18**: 1919–1935.

Brown, C.E. 1970. A cartographic representation of spruce budworm, *Choristoneura fumiferana* (Clem.), infestation in eastern Canada, 1906–1966. Can. Dep. Fish. For. Can. For. Serv. Publ. 1263.

Bucchheim, M.P., Maclean, A.P., and Lillesand, T.M. 1985. Forest cover type mapping and spruce budworm defoliation detection using simulated SPOT imagery. Photogramm. Eng. Remote Sens. **51**: 1115–1122.

Candau, J.N., Fleming, R.A., and Hopkin, A. 1998. Spatiotemporal patterns of large-scale defoliation caused by the spruce budworm in Ontario since 1941. Can. J. For. Res. **28**: 1733–1741.

Cappucino, N., Lavertu, D., Bergeron, Y., and Regnière, J. 1998. Spruce budworm impact, abundance and parasitism rate in a patchy landscape. Oecologia, **114**: 236–242.

Cumming, S.G., Schmiegelow, F.K.A., and Burton, P.J. 2000. Gap dynamics in boreal aspen stands: Is the forest older than we think? Ecol. Appl. **10**: 744–759.

Dansereau, P.R., and Bergeron, Y. 1993. Fire history in the southern boreal forests of northwestern Quebec. Can. J. For. Res. **23**: 25–32.

Duncan, R.P., and Stewart, G.H. 1991. The temporal and spatial analysis of tree age distributions. Can. J. For. Res. **21**: 1703–1710.

Environment Canada. 1993. Canadian climate normals 1961–1990. Canadian climate program. Atmospheric Environment Service, Downsview, Ont.

Fraser, G.W., Trofymow, J.A., and Lertzman, K.P. 2000. Canopy openness and leaf area in chronosequences of coastal temperate rainforests. Can. J. For. Res. **30**: 239–256.

Frelich, L.E. 2002. Forest dynamics and disturbance regimes: studies from temperate evergreen-deciduous forests. Cambridge University Press, Cambridge, U.K.

Frelich, L.E., and Reich, P.B. 1995. Spatial patterns and succession in a Minnesota southern-boreal forest. Ecol. Monogr. **65**: 325–346.

Gray, D., Regnière, J., and Boulet, B. 2000. Analysis and use of historical patterns of spruce budworm defoliation to forecast outbreak patterns in Quebec. For. Ecol. Manage. **127**: 217–231.

Heinselman, M.L. 1981. Fire and succession in the conifer forests of North America. *In* Forest succession: concepts and application. *Edited by* D.C. West, H.H. Shugart, and D.B. Botkin. Springer-Verlag, New York. pp. 374–405.

Jardon, Y. 2001. Analyses spatiales et temporelles des épidémies de la tordeuse de bourgeons de l'épinette. Ph.D. thesis, Université du Québec à Montréal, Montréal, Que.

Johnson, E.A. 1995. Fire and vegetation dynamics: studies from the North American boreal forest. Cambridge Studies in Ecology. Reprint edition. Cambridge University Press, Cambridge, U.K.

Kneeshaw, D.D. 2001. Are non-fire gap disturbances important to boreal forest dynamics? *In* Recent research developments in ecology. *Edited by* S.G. Pandalarai. Transworld Research Press, Kerala, India. pp. 43–58.

Kneeshaw, D.D., and Bergeron, Y. 1998. Canopy gap characteristics and tree replacement in the southeastern boreal forest. Ecology, **79**: 783–794.

Kneeshaw, D.D., and Gauthier, S. 2003. Defining old-growth boreal forests at stand and landscape levels: a dynamic perspective. Environ. Rev. **11**: 99–114.

Krasny, M.E., and Whitmore, M.C. 1992. Gradual and sudden forest canopy gaps in Alleghany northern hardwood forests. Can J. For. Res. **22**: 139–143.

Kuuluvainen, T. 1994. Gap disturbance, ground microtopography, and the regeneration dynamics of boreal coniferous forests in Finland: a review. Ann. Zool. Fenn. **31**: 35–51.

Laframboise, P., and Beaubien, J. 1985. Digital airborne imagery for spruce budworm damage assessment. *In* Pecora 10; Remote Sensing in Forest and Range Resource Management: Proceedings, 20–22 August 1985, Fort Collins, Colo.

Legendre, P., and Fortin, M.J. 1989. Spatial pattern and ecological analysis. Vegetatio, **80**: 107–138.

Legendre, P., and Legendre, L. 1998. Numerical ecology. Dev. Environ. Model. 20. 2nd ed. Elsevier, Amsterdam.

Lertzman, K.P., and Krebs, C.J. 1991. Gap-phase structure of a sub-alpine old-growth forest. Can. J. For. Res. **22**: 1730–1741.

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. 1988. Effects of spruce budworm outbreaks on vegetation, structure and succession of balsam fir forests on Cape Breton Island, Canada. *In* Plant form and vegetation structure. *Edited by* M.J.A. Werger, P.J.M. van der Aart, H.J. During, and J.T.A. Verhoeven. Academic Publishing, The Hague, Netherlands. pp. 253–261.

MacLean, D.A., and Ostaff, D.P. 1989. Patterns of balsam fir mortality caused by an uncontrolled spruce budworm outbreak. Can. J. For. Res. **19**: 1087–1095.

MacLean, D.A., and Piene, H. 1995. Spatial and temporal patterns of balsam fir mortality in spaced and unspaced stands caused by spruce budworm defoliation. Can. J. For. Res. **25**: 902–911.

McCarthy, J. 2001. Gap dynamics of forest trees: a review with particular attention to boreal forests. Environ. Rev. **9**: 1–59.

Morin, H. 1994. Dynamics of balsam fir forests in relation to spruce budworm outbreaks in the Boreal Zone of Quebec. Can. J. For. Res. **24**: 730–741.

Morin, H., and Laprise, D. 1989. Analyse dendroécologique d'une sapinière issue d'un chablis dans la zone boréale, Québec. Can. J. For. Res. **20**: 1753–1758.

Morin, H., Laprise, D., and Bergeron, Y. 1993. Chronology of spruce budworm outbreaks near Lake Duparquet, Abitibi region, Quebec. Can. J. For. Res. **23**: 1497–1506.

Nakashizuka, T., Katsuki, T., and Tanaka, H. 1995. Forest canopy structure analyzed by using aerial photographs. Ecol. Res. **10**: 13–18.

Needham, T., Kershaw, J., MacLean, D.A., and Su, Q. 1999. Effects of mixed stand management to reduce impacts of spruce budworm defoliation on balsam fir stand level growth and yield. North. J. Appl. For. **16**: 19–24.

Ostaff, D.P., and Maclean, D.A. 1989. Spruce budworm populations, defoliation and changes in stand condition during an uncontrolled spruce budworm outbreak on Cape Breton Island, Nova Scotia. Can. J. For. Res. **19**: 1077–1086.

Payette, S. 1992. Fire as a controlling process in the North American boreal forest. *In* A systems analysis of the global boreal forest. *Edited by* H.H. Shugart, R. Leemans, and G.B. Bonan. Cambridge University Press, Cambridge, U.K. pp. 144–169.

Qinghong, L., and Hytteborn, H. 1991. Gap structure, disturbance and regeneration in a primeval *Picea abies* forest. J. Veg. Sci. **2**: 391–402.

Rowe, J.S. 1972. Forest regions of Canada. Environment Canada, Ottawa, Ont.

Runkle, J.R. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. Ecology, **63**: 1533–1546.

Runkle, J.R. 1985. Disturbance regimes in temperate forests. *In* The ecology of natural disturbance and patch dynamics. *Edited by* S.T.A. Pickett and P.S. White. Academic Press, New York. pp. 17–33.

Senecal, D., Kneeshaw, D., and Messier, C. 2004. Temporal, spatial, and structural patterns of adult trembling aspen and white spruce mortality in Quebec's boreal forest. Can. J. For. Res. **34**: 308–316.

Sommerfeld, R.A., Lundquist, J.E., and Smith, J. 2000. Characterizing the canopy structure of a disturbed forest using the Fourier transform. For. Ecol. Manage. **128**: 101–108.

Spies, T., Franklin, J.F., and Klopsch, M. 1990. Canopy gaps in Douglas-fir forests of the Cascade mountains. Can. J. For. Res. **20**: 534–544.

St-Onge, B.A., and Cavayas, R. 1997. Automated forest structure mapping from high resolution imagery based on directional semivariogram estimates. Remote Sens. Environ. **61**: 82–95.

Su, Q., MacLean, D.A., and Needham, T.D. 1996. The influence of hardwood content on balsam fir defoliation by spruce budworm. Can. J. For. Res. **26**: 1620–1628.

Tanaka, H., and Nakashizuka, T. 1997. Fifteen years of canopy dynamics analyzed by aerial photographs in a temperate deciduous forest, Japan. Ecology, **78**: 612–620.

Turner, K.B. 1952. The relation of mortality of balsam fir, *Abies balsamea* (L.) Mill., caused by the spruce budworm, *Choris-*

toneura fumiferana (Clem.), to forest composition in the Algoma forest of Ontario. Can. Dep. Agric. Publ. 875.

Vincent, J.S., and Hardy, L. 1977. L'évolution et l'extinction des grands lacs glaciaires Barlow et Ojibway en territoire Québécois. Géogr. Phys. Quat. **31**: 357–372.

Worral, J.J., and Harrington, T.C. 1988. Etiology of canopy gaps in spruce–fir forests at Crawford Notch, New Hampshire. Can. J. For. Res. **18**: 1463–1469.

Yamamoto, S.-I. 1992. Gap characteristics and gap regeneration in primary evergreen broad-leaved forests of western Japan. Bot. Mag. Tokyo, **105**: 29–45.

Yamamoto, S.-I. 1993. Gap characteristics and gap regeneration in a subalpine forest on Mt. Ontake, central Honshu, Japan. Ecol. Res. **8**: 277–285.