

Temporal, spatial, and structural patterns of adult trembling aspen and white spruce mortality in Quebec's boreal forest¹

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Abstract: Temporal, spatial, and structural patterns of adult trembling aspen (*Populus tremuloides* Michx.) and white spruce (*Picea glauca* (Moench) Voss) mortality were studied in intact 150-year-old stands in the southwestern boreal forest of Quebec. For both species, mortality decreases (number of dead trees/total number of trees) with distance from the lake edge until 100–150 m, from which point it slightly increases. Strong peaks in mortality were found for 40- to 60-year-old aspen mainly between 1974 and 1992. Such mortality in relatively young aspen is likely related to competition for light from the dominant canopy trees. Also, the recruitment of this young aspen cohort is presumably the result of a stand breakup that occurred when the initial aspen-dominated stand was between 90 and 110 years old. For spruce, strong peaks in mortality were found in 110- to 150-year-old trees and they occurred mainly after 1980. No clear explanation could be found for these peaks, but we suggest that they may be related to senescence or weakening of the trees following the last spruce budworm outbreak. Suppressed and codominant aspen had a much higher mortality ratio than spruce in the same height class, while more surprisingly, no difference in mortality rate was found between dominant trees of the two species. Most spruce trees were found as standing dead, which leads us to reject the hypothesis that windthrow is an important cause of mortality for spruce in our forests.

Résumé : Les patrons de mortalité temporel, spatial et structurel ont été établis pour le peuplier faux-tremble (*Populus tremuloides* Michx.) et l'épinette blanche (*Picea glauca* (Moench) Voss) adultes dans des forêts de 150 ans situées dans le sud-ouest de la forêt boréale du Québec. Chez les deux espèces, on observe une diminution de la mortalité (nombre d'arbres morts / nombre d'arbres total) du bord du lac jusqu'à 100–150 m et une faible augmentation par la suite. La mortalité était importante chez les peupliers de 40 à 60 ans et s'était produite entre les années 1974 et 1992. Cette mortalité chez les jeunes peupliers est probablement reliée à la compétition pour la lumière venant des arbres dominants. Le recrutement de cette jeune cohorte de peuplier est présumé être le résultat d'une ouverture assez soudaine du peuplement mature de peuplier entre les années 90 et 110 ans. Chez l'épinette blanche, une mortalité importante fut observée pour les arbres âgés entre 110 et 150 ans et s'est produite surtout après 1980. Nous croyons que cette mortalité est induite par la sénescence des arbres, ou en raison de leur affaiblissement suite à l'épidémie de la tordeuse des bourgeons de l'épinette. Les peupliers supprimés et codominants avaient un taux de mortalité beaucoup plus élevé que les épinettes, mais il n'y avait pas de différence entre les arbres dominants des deux espèces. La plupart des épinettes étaient morts debout, ce qui rejette l'hypothèse voulant que le vent soit une cause importante de mortalité chez l'épinette.

Introduction

The composition, structure, and dynamics of forests can be attributed, in part, to processes that kill trees and create conditions for different successional pathways (Lugo and

Scatena 1996). The pattern of mortality of adult trees is, however, still poorly understood, and literature on adult mortality in intact boreal forests of North America is extremely rare (Yao et al. 2001). In the boreal forest of North America, large-scale disturbance is largely due to fire and insect outbreaks (Baskerville 1986; Bergeron et al. 2001). However, in eastern Canada over the last century, intervals between fires have increased and the effects of fire have been reduced (Archambault and Bergeron 1992; Bergeron et al. 2001) so that secondary disturbances have become much more important. Until quite recently, there has been little interest in studying natural mortality in forests whose age (or time since burning) exceeded the average life span of the tree (Kneeshaw and Gauthier 2003). In these successional stands, individual tree mortality is related to both exogenous and endogenous factors (Pedersen 1998).

One of the more important exogenous factors contributing to mortality, wind, has been evaluated in many regions of the globe (Skatter and Kucera 2000; Dunham and Cameron 2000; Canham et al. 2001). Windthrow hazard depends on

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the interaction of numerous biological factors such as tree size, species, and morphology (Dyer and Baird 1997; Webb 1988; Peterson and Pickett 1991; Cameron and Dunham 1999) and disease (Lewis and Lindgren 2002). Another important secondary exogenous factor is the important increase in tree mortality following severe insect outbreaks (Bergeron et al. 1995).

As for endogenous factors, competition for space (self-thinning) and resources (e.g., light) is probably the single most important factor affecting the mortality of young trees (Lee 1998). Research has generally shown that shade-tolerant tree species are less sensitive, in term of mortality, to reductions in growth caused by resource depletion than shade-intolerant ones (Kobe et al. 1995). Several studies have demonstrated that mortality of seedlings and saplings increases with a reduction in radial growth (Glitzenstein et al. 1986; Kobe et al. 1995; Lin et al. 2001), but this phenomenon is poorly documented for adult trees (but see Manokaran and Kochummen 1987). In old trees, senescence is the cause of much of the mortality attributable to endogenous factors. Large reductions can be observed in the number of individuals as trees age beyond their normal life spans (Noo-dén 1988; Peet and Christensen 1988). Such old-age mortality is known to vary greatly among tree species.

This study examines differences in the pattern of mortality at the adult stage for two contrasting species in the boreal forest. The first species, trembling aspen (*Populus tremuloides* Michx.), is the most important deciduous tree species in the North American boreal forest, both ecologically and commercially. This clonally reproducing species is considered shade intolerant, with adult trees having a wide crown found at the top of a long bole and a root system deeper than that of many competing species (Burns and Honkala 1990). The second species, also an important commercial tree for both pulpwood and lumber, is the shade-tolerant, sexually reproduced white spruce (*Picea glauca* (Moench) Voss). It is coniferous with a shallow root system and a long narrow tree crown.

The spatial, temporal, and structural patterns of mortality of these two species were investigated. We hypothesized that adult aspen mortality, because of its shade intolerance, its relative wind firmness (compared with white spruce), and its short life span, is largely driven by endogenous factors (e.g., senescence and shade intolerance). This would suggest a peak in mortality (as a clonal species, we anticipated that such peaks would be concentrated in time) as trees approach their reported longevity and that understory trees would have a greater probability of dying than overstory trees. In contrast, it was hypothesized that the mortality of adult white spruce is mainly driven by exogenous factors (e.g., wind), since spruce is recognized to live longer, to be more shade tolerant, and to be more susceptible to wind than aspen (Nienstaedt and Zasada 1990). Therefore, we expect to observe most dead trees as having uprooted or snapped.

Materials and methods

The study sites are in the forests surrounding Lake Duparquet, located south of Lake Abitibi in northwestern Quebec (79°1'W, 48°30'N). The geomorphology of this region is characterized by a postglacial lacustrine phase that formed

the Northern Clay belt, covering a vast area in east-central Canada (Vincent and Hardy 1977). To standardize for the effects of soil, all study sites were located on clay deposits with a moderate moisture regime (Brais and Camiré 1992). The closest meteorological station to the study area is at Roquemaure, approximately 8 km to the north. The climate is cold and temperate with a mean (1961–1990) annual temperature of 0.8 °C and a mean annual precipitation of 856.8 mm (Environment Canada 1993). Most liquid precipitation falls during the growing season, but evaporation can limit plant growth in both June and July. Prevailing winds come from the southwest, but high-speed winds can originate from all directions, although they tend to come from the southwest. The average wind speed is 21 km/h and the highest events can reach 77 km/h (Environment Canada 2002).

Balsam fir (*Abies balsamea* L.) and trembling aspen are the dominant species; black spruce (*Picea mariana* (Mill.) BSP), white spruce, and paper birch (*Betula papyrifera* Marsh.) are codominant species. Stands of pioneer species, such as jack pine (*Pinus banksiana* Lamb.), aspen, and paper birch, occupy large areas following a disturbance (Bergeron and Bouchard 1984).

Aspen and white spruce adult tree mortality was evaluated in three different mixedwood stands. The age of these stands was approximately 150 years, and they are dominated by aspen, balsam fir, and white spruce. We were able to find relatively abundant white spruce and aspen growing together in only a few stands that were located at the eastern, southeastern, and southwestern parts of the lake.

Three to five transects were established in each of the three stands. The starting point of each transect was randomly located at the first tree (≥ 7 cm diameter at breast height (DBH)) nearest to the lake and the orientation was perpendicular to the lake. The transect was discontinued when a minimum of 40 dead trees were sampled for each species or when the composition of the forest changed suddenly. If the transect was stopped because of a change in composition, a second was started 50–100 m away and parallel to the first one. At each site, transects were parallel to each other. Each transect was 10 m wide and the length varied from 100 to 480 m. All trembling aspen and white spruce greater than 7 cm DBH were measured. For both dead and live trees, the following data were collected: DBH; distance of each tree to the lakeshore; distance of each tree to the center of the transect line; tree canopy position as either dominant (in the canopy), codominant (located in the canopy but clearly under dominant trees), or suppressed (very clearly well under the canopy); and a notation of wounds or distinctive signs (insects, disease, presence of fungus, cracks, etc.).

To evaluate the effect of lake proximity on mortality, the mortality ratio (number of dead stems/total number of trees by species) was used. As the number of stems increases with proximity to the lake, this ratio was used to eliminate any possible effects of tree density on the results.

To estimate canopy position, visual estimates were made for snags. For downed logs, their horizontal length was compared with the height of the dominant surrounding canopy trees. For trees that had been dead for many years, a correction factor was applied to determine the correct class at the time of death for those that were in codominant and sup-

pressed tree classes at the time of sampling. Of course, for dead trees that were classified as dominant at the time of sampling, they would also have been classified as dominant at the time of death, since they could not gain in height over the surrounding live canopy. For live trees, the actual class was presumed to have been the same during their entire life. The correction factor for dead codominant and suppressed trees involves reassigning the current canopy position based on their diameter and the diameter of the surrounding trees at the time of death. The year of death was verified using dendroecological analyses (see below).

Each dead tree was categorized into one of five classes: 1, broken when dead; 2, snags (dead trees that were still standing); 3, bent or snapped (trees that were broken when alive); 4, uprooted (trees that blew over, exposing their root systems); 5, crushed (trees that were bent or knocked over when a larger tree fell on them). Trees in classes 1 and 3 were categorized by identifying wood structural differences at the point of breakage. Trees that were snapped while alive presented some of the following conditions: presence of fine branches and leaves, splintering at the point of breakage, jagged break-points that were unequal in height around the trunk of the tree, points of attachment, no discolored wood, etc. Dead trees were also classified by decay conditions (0 = dead leaves still present to 5 = dead tree incorporated into the soil) according to McCune et al. (1988). Finally, orientation for fallen trees and visual signs (e.g., woodpecker activity denoting the presence of wood-boring insects) indicating the possible cause of death were also noted.

Dendrological analysis

For live trees, each third specimen was systematically selected and two cores were taken at the base. Since the base of trunks may be oval, the first core was taken on the longest axis and a second one was taken at 90° to the first core (usually a short radius). Each dead tree was cut at the base and a disk was collected. If trunks were rotten, the disk was collected higher along the stem to a maximum of 2 m. If trunks were still rotten at 2 m, the sample was not retained.

The techniques used for measuring tree rings in cores and disks were the same as that used in previous dendroecological research in the same area (Archambault and Bergeron 1992; Dansereau and Bergeron 1993; Bergeron 2000). Tree-ring widths were measured using a Henson incremental measuring stage to a precision of 0.01 mm. Two radii were measured per sampled disk. The first radius was measured on the longest axis of the disk and the second was measured at 90° to the first one. If a measured radius reached a rotten part of the disk (this often occurred at the periphery), the radius was displaced until it occurred on solid, nonrotten wood (if possible). For the more decayed trees, many stem disks were collected on the same tree. These disks were gathered from different parts of the trunk, although we attempted to take at least one disk close to the base. As the reconstruction of mortality moves back in time, the probability of finding dead specimens decreases (Storaunet and Rolstad 2002) because of decomposition. Small trees usually disappear quickly. Analyses are thus more accurate for recent years from which a greater number of small logs could be obtained. However, since standing trees decompose slowly (Newbury et al. 2004) and since most sampled trees were found stand-

ing, we are confident that we have obtained good results, especially in recent decades.

Each chronology was cross-dated with a master chronology from living trees to identify the year of mortality and the age of the dead tree. Cross-dating accuracy was verified using the COFECHA program (Holmes 1983).

Data analysis

The effect of distance to an opening (the lake) as a function of the ratio of dead trees to all trees for white spruce and aspen was examined using a polynomial quadratic regression. To test the effect of canopy position on mortality, an ANOVA was used. Mortality was compared, with an ANOVA, between the three different canopy classes by species in the mixed stand. The independent variable included is position in the canopy and the dependent variable is the mortality ratio (number of dead trees/total number of trees).

Logistic regression models were developed to evaluate predictors of mortality in mixed stands. The response variable was the probability of a tree being dead. Explanatory or independent variables included in the model were position in the canopy, DBH (at 1.3 m height), and annual diameter increment during each of the last 5 years (complete years of growth) preceding death. The response variable γ (dependent variable) is a binary variable indicating whether a tree is dead ($\gamma = 1$) or alive ($\gamma = 0$). The logistic model was formulated as follows:

$$P = \frac{1}{1 + e^{-(\beta_0 + \beta_1 x_1 + \dots + \beta_k x_k)}}$$

where $\beta = (\beta_0, \beta_1, \dots, \beta_k)$ are unknown parameters. The stepwise procedure was used in selecting independent variables at a significance level of $P < 0.05$.

All of the above statistical analyses were conducted using SAS ver. 8 (SAS Institute Inc. 2000).

Mortality rate

For both species, mortality rate was calculated for the three canopy classes, dominant, codominant, and suppressed, and for the three classes combined. Thus, four mortality rates were calculated for each species. Mortality rate m was calculated as

$$m = \left[\left(\frac{N_t}{N_0} \right) / t \right] \times 100$$

where N_t is the number of dead trees in the interval t , N_0 is the number of total stems, and t represents the interval of time. Since small (suppressed) trees possess high decay rates, analyses of mortality rates for all classes are restricted to data from the most recent 5 years ($t = 5$ years) to avoid biases resulting from not including already decayed smaller individuals. Thus, m is a good approximation of the instantaneous mortality rate.

The probability of tree mortality based on radial growth was tested with the model developed by Kobe and Coates (1997). This model, a maximum likelihood test, also provides a quantitative estimation of shade tolerance. The model uses the annual diameter increment of live and dead trees for a specific species and calculates the probability of mor-

tality as the product of the density function of prior growth rates for dead individuals and the density function of prior growth rates for live individuals (see Kobe and Coates (1997) for a more detailed explanation). The model used had the form $m(g) = p(\text{death} | \text{growth}) = e^{-Cg}$, where $m(g)$ is the probability of mortality as a function of growth and C is a parameter to be calculated and has the biological interpretation of species shade tolerance. Lower C values indicate less tolerant species.

Results

Pattern of mortality as a function of distance to lake

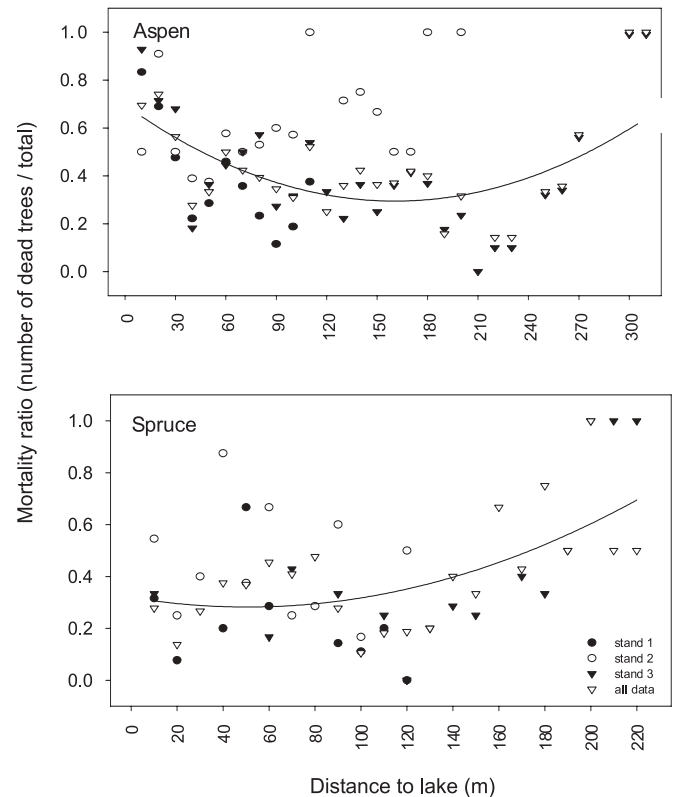
Both trembling aspen and white spruce were found to be more abundant (both living and dead stems) close to the lake, with the overall density of these trees decreasing with distance from the lake. The mortality ratio illustrates a pattern that we do not observe using only relative frequencies of dead trees along the transects (Fig. 1). For aspen, mortality was the highest near the lake (0.69), decreasing rapidly in the first 40 m (0.5) and then increasing with distance after 180 m. Higher mortality close to the lake was due to beaver activity. Our study suggests that beavers are responsible for cutting down 31.5% of all aspen in the first 30 m, with beaver-caused mortality increasing to close to 45% in the first 10 m. Up to 50 m, some live trees showed scars caused by beavers, but no beaver-killed trees are observed beyond 30 m.

Spruce displays an overall pattern similar to that of aspen, as the relative frequency of spruce (frequency of dead trees found on transects are reported as a percentage) was highest near the lake and decreased with distance away from the lake. The mortality ratio was, however, lower near the lake (0.30) and increased with distance away from the lake (to 0.65 at 220 m) (Fig. 1).

Mortality related to structural characteristics

The position of the tree in the canopy is an important factor that contributes to mortality (Table 1). Suppressed individuals were more susceptible to die, particularly for aspen. The mortality ratio (dead/total frequency by species) reveals that aspen located beneath the main canopy had more than twice the chance of dying (ratio of 0.83) than individuals

Fig. 1. Trembling aspen and white spruce mortality as a function of distance to lake. The line represents the tendency of all data.



considered in the dominant class (ratio of 0.30). Codominant aspen also had a mortality ratio much higher (ratio of 0.73) than individuals in the dominant class. Canopy position had much less of an effect on spruce mortality. Suppressed trees did have a higher mortality ratio than the other classes (a ratio of 0.49 compared with dominants with a ratio of 0.25 and codominants with a ratio of 0.37), but in contrast with aspen, mortality ratio did not differ among classes.

Size was found, in the logistic regressions, to be a predictor of mortality. For aspen, the canopy position of the tree as well as the last complete year of radial growth before death were found to be very highly significant ($P < 0.0001$, $R^2 = 0.21$) predictors of the probability of mortality.

$$P(\text{dead}) = 1/[1 + e^{-(0.2052 + 0.7566 \times \text{canopy position} - 1.5603 \times \text{growth}_1)}]$$

where canopy position corresponds to dominant (1), codominant (2), or suppressed (3) tree and growth_1 corresponds to the last year of radial growth (millimetres). Results for white spruce were similar, although DBH replaced canopy position in the equation as a more continuous measure of size. Recent radial growth was also found to be an important predicting factor.

$$P(\text{dead}) = 1/[1 + e^{-(1.6459 - 0.1095 \times \text{DBH (cm)} - 0.7663 \times \text{growth}_1 + 0.9145 \times \text{growth}_3)}]$$

where growth_3 corresponds to growth 3 years before death. The model for white spruce was also highly significant ($P < 0.0001$) but with a low coefficient of determination ($R^2 = 0.06$).

Characterization of the observed type of mortality revealed a similar overall pattern between spruce and aspen with the number of dead trees being observed in decreasing order as (i) standing, followed by (ii) those that died stand-

ing and were subsequently snapped, (iii) those that were snapped while alive, (iv) uprooted, and (v) crushed. There was minor variation between species: former snags now found on the ground as a result of windfall were higher for aspen (27%) than for spruce (21%). The proportion of dead individuals observed to be snags was quite similar for both species. Standing dead trees (67% for aspen and 65% for spruce) occurred more often than any other type of mortality

Table 1. Summary of trembling aspen and white spruce mortality ratios and mortality rates as a function of canopy class.

Canopy class	Mortality ratio (dead/total)	SD	Annual mortality rate (%)	Likelihood analysis
Aspen				
Suppressed	0.82	0.13a	15.5	
Codominant	0.67	0.14a	11.5	
Dominant	0.27	0.07b	3.2	
Overall	0.43		5.9	3.4*
Spruce				
Suppressed	0.44	0.20a	6.6	
Codominant	0.35	0.17a	5.5	
Dominant	0.24	0.08a	3.4	
Overall	0.40		4.0	4.2*

Note: Likelihood analysis provides an estimation of shade tolerance. A lower value indicates higher mortality under shade. Different letters identify statistically different groups.

*Significant differences between canopy classes ($P < 0.05$).

(<0.001). There was more uprooted spruce (3.1%) than aspen (0.7%), while the proportion of crushed trees was similar for both species (0.26% for spruce and 0.61% for aspen). The biggest difference was in snapped trees (those trees that were alive when snapped). Spruce deaths from this type of windfall (9.9%) occurred approximately four times more often than aspen deaths (2.3%).

Temporal patterns of mortality

Past mortality of aspen and white spruce is different. Aspen has a mortality pattern that follows a wave form (Fig. 2). The upper part of the wave corresponds to a major increase in mortality in 1974. Mortality decreased gradually afterwards until 1983 and then returned to a constant level that could be associated with background mortality. Unfortunately, we were not able to reconstruct mortality patterns into the past far enough to be able to observe other waves. Although mortality of trembling aspen was dated back until 1957, such individuals (that were dead for so long) were rare because of decomposition. There is, however, a relatively high frequency of individuals dated as having died since the late 1960s. Such frequencies were similar to those observed over the last decade, and thus, we suggest that mortality of dominant trees can be effectively dated back 30–35 years. For this period, results seem reliable, since most trees die standing and decomposition rates are slow for portions of the trunk not touching the ground (Naesset 1999). Most dominant trees could thus be effectively dated.

White spruce, on the other hand, demonstrated a different pattern (Fig. 2). Unlike the wave form mortality observed for aspen, spruce showed a more sporadic pattern of mortality with distinct years of high mortality. Years with high levels of mortality can be identified as 1991, 1995, 1997, and 1999. We analyzed interyear daily variability in wind speed to see if there was any difference between years that could explain our observed yearly peaks in spruce mortality. No clear pattern was observed ($P < 0.938$) (data not shown).

Aspen and white spruce had contrasting patterns with respect to the age at which mortality occurred. Aspen tended to die at a younger age than spruce. The largest number of aspen died between 40 and 60 years of age. A second peak,

Fig. 2. Year of mortality for trembling aspen and white spruce. Relative frequencies reported on the y axis are based on the total number of dead trees by species. For a given species, the sum of dead trees for all years equals 100%.

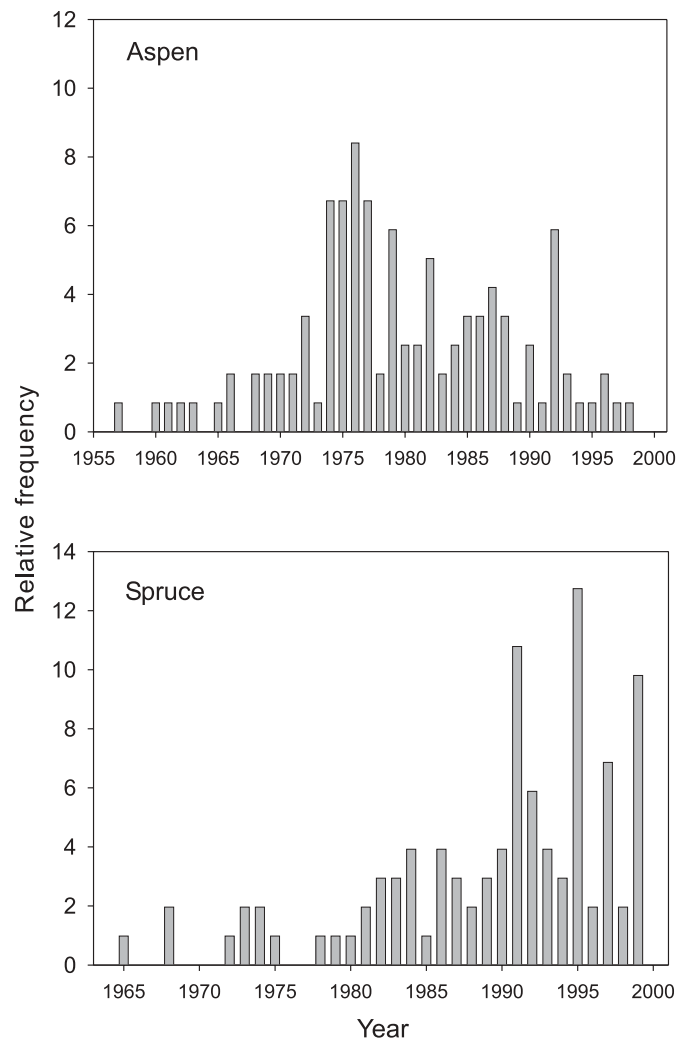
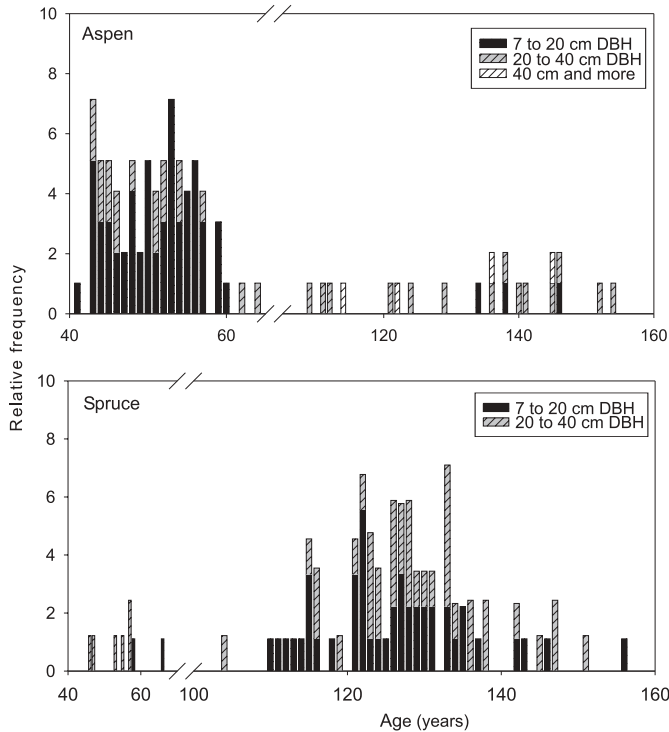


Fig. 3. Age of trembling aspen and white spruce mortality as a function of diameter at breast height (DBH). Relative frequency reported on the y axis is based on the total number of dead trees by species. For a given species, the sum of dead trees of all ages equals 100%.



although much less important in number, showed individuals dying between 110 and 155 years (Fig. 3). As expected, the younger dead individuals were in the smaller size classes; 59.1% of individuals that were under 60 years at their time of death were less than 20 cm DBH. The largest individuals (>40 cm DBH) accounted for 22.4% of the dead individuals greater than 100 years at time of death.

White spruce demonstrated the inverse pattern, with mortality being more important at an older stage (Fig. 3). The highest period of mortality occurred when white spruce trees were between 110 and 150 years, with a much lower number dying between 45 and 65 years. No trees that were dead were found to be larger than 40 cm, although most live trees were also below this size class. No clear relationship between age and DBH class was observed. Individuals from both classes (7–20 and 20–40 cm) were found across the full spectrum of ages at time of death. As an example, a tree with a DBH under 20 cm was found to have died at an age of 156 years.

Annual mortality rates of the studied species were clearly related to canopy position (Table 1). This was particularly true for aspen. Suppressed and codominant specimens had high average annual mortality rates, 15.5% and 11.5%, respectively. However, the mortality rate dropped to 3.2% for dominant aspen. For spruce, canopy position had a smaller impact on the annual rate of mortality. Although trees that were located beneath the canopy had a higher average annual mortality rate (6.6%) than larger individuals, the difference was small (5.5% for codominant spruce and 3.4% for dominant spruce) and no statistical differences were found.

Differences between the species were thus most important for the suppressed and codominant classes. Annual mortality rates for the dominant class were quite similar to the overall average annual mortality rates (4.0% for spruce and 5.9% for aspen). As with the annual mortality rate, the maximum likelihood analysis of Kobe and Coates (1997) demonstrated a lower shade tolerance for aspen (3.4) than for spruce (4.2) (significant at $P < 0.05$).

The relationship between canopy position and tree age was different between aspen and white spruce. For aspen, dominant individuals accounted for most of the dead trees that died between 110 and 155 years. Trees from no single canopy class were found to account for the mortality peak that was observed when aspen were 40–60 years of age. White spruce that died at an advanced age (110–150 years) were also principally composed of dominant trees; however, some codominants and a few suppressed trees were observed. Surprisingly, young dead spruce (55–65 years) did not come from the suppressed canopy class but rather were made up entirely of trees from codominant and dominant positions.

Discussion

Endogenous mortality

As with previous research that has identified seedling and sapling mortality to be related to periods of suppressed growth (Canham 1990; Kobe et al. 1995), our results show that growth-related mortality (which is a measure of shade tolerance) is also applicable to adult trees. The risk of mortality for smaller individuals of shade-intolerant trembling aspen was found to be higher than that for larger stems; these smaller individuals are presumably in the shade of the dominant trees. Aspen trees having not yet attained the canopy have a risk of mortality nearly two times that of white spruce. Our findings are also in general agreement with those of Yao et al. (2001) in Alberta. These authors found that a consistent mortality pattern was observed in all size classes such that large as well as small aspen have a greater probability of mortality than large white spruce. However, our study did not demonstrate any difference in spruce mortality by canopy class. Suppressed spruce had the same mortality rate as dominants. Unlike other studies, we found that there was a difference in size-dependent mortality between shade-tolerant and shade-intolerant trees. Shade-tolerant spruce did not show a size-related probability of mortality, whereas suppressed aspen had a higher probability of mortality than dominants. Moreover, we found surprisingly little difference in mortality between canopy trees of the two species. The lack of agreement between our study and that of Yao et al. (2001) may be related to stand structural, site, or age differences. The pattern of larger and old trees dying at a greater rate than small and young trees has also been questioned by Runkle (2000), and our data show clearly that the larger and older trees have a smaller (for aspen) or equal (for spruce) incidence of mortality.

Exogenous mortality

We hypothesized that mortality of white spruce would be related to the distance to the lake edge, whereas aspen would be much less influenced. Although the total number of dead

spruce and aspen was higher near the lake, because of a greater total density of these species close to the lake, the ratio number of dead trees/total number of trees was positively related to the proximity of the lake edge for spruce and somewhat negatively related for aspen between 0 and 150 m. The difference between this research and earlier research, in which spruce had a greater probability of being killed by wind near edges (Stacey et al. 1994; Gardiner et al. 1997), may be explained by the permanence of the edge opening or the time since the opening was created. Earlier research has focused on proximity to edge in recently opened forests, e.g., following burns or clear-cutting (Huggard et al. 1999; Ruel et al. 2001). In such situations, trees are not wind firm and are thus more susceptible to the effects of being exposed to wind. Alternatively, in the situation where there is a permanent open edge, trees are wind trained and thus less at risk to damage or mortality (Peterson and Pickett 1991; Dyer and Baird 1997). In forest interiors, canopy trees have been found to be more susceptible to strong winds than subcanopy (protected) or supercanopy (wind-trained) trees (Peterson and Pickett 1991). Our results may thus reflect the lack of wind training of interior canopy trees and their infrequent exposure to strong winds. However, the overall low number of trees dying from windthrow cannot alone explain the higher mortality found in the stand interior. Neither is lower soil fertility likely to explain higher mortality in the stand interior because all transects were located on rich clay soil. Moisture stress differences between the interior and lake edge may help to explain the higher mortality found in the interior. Proximity to the lake could contribute to prevent drought in summer months when evapotranspiration is greater than precipitation.

Therefore, contrary to our hypothesis for white spruce, windthrow does not seem to be a major cause of mortality, since most spruce and aspen died standing. From visual characterizations of dead trees, three main causes of mortality stand out. First, wood-boring insects are responsible for a minor portion of mortality of spruce and aspen. Contrary to the high mortality that occurs during spruce budworm (*Choristoneura fumiferana* Clem.) (Blais 1981) or forest tent caterpillar (*Malacosoma disstria* Hbn.) (Hogg et al. 2002) outbreaks, insect impact is low in non-outbreak periods. Second, fungus and disease were observed on a very small proportion of the snags. White spruce was observed to have more external signs of fungus than aspen, but this may not reflect the overall abundance of fungus, as canker-type fungi are not always visible externally, and thus, wood dissection is often necessary. Third, lengthwise cracks were more frequently observed on spruce snags than on aspen. Wood splits, largely resulting from frost- and wind-crack, increase susceptibility to disease (Silva et al. 1998). A lower frequency of observed aspen cracks may be linked to its higher wood density.

Temporal patterns in mortality

Annual mortality rates have not been calculated or reported for most adult boreal tree species in intact forests. To date, several studies have focused on a specific agent of mortality, such as the spruce budworm (Blais 1981; Morin 1994; Bergeron et al. 1995; Maclean and Mackinnon 1997), wind (Dyer and Baird 1997; Peltola et al. 1999; Ruel et al.

2001), drought (Elliott and Swank 1994; Condit et al. 1995; Jenkins and Pallardy 1995), or disease (James et al. 1984; Lewis and Lindgren 2002). Other studies such as Yao et al. (2001) developed models based on tree growth, tree diameter at breast height, etc. In our study, aspen had a higher overall mortality rate than spruce. However, when broken down by size class or canopy class, the highest mortality rate for aspen was found in the codominant and suppressed positions. Such an observation may reflect aspen's intolerance of shade and thus the difficulty in surviving beneath other individuals. Earlier work (Kobe 1996; Kobe and Coates 1997) has shown that probability of mortality explained by recent growth is directly related to shade tolerance ranking. Results from a maximum likelihood analysis showed that aspen has a much lower value of C (estimates of the generalized mortality function based on likelihood ratio test) than spruce, suggesting that it is indeed less shade tolerant even as individuals increase in size. For adult trees, the difference between aspen and spruce was found to be less than many authors have suggested for seedlings and saplings. Such decreasing differences in the probability of mortality at low growth rates with increasing size are believed to be common in adult trees (Clark and Clark 1999), and this may be in part due to the ability of larger trees to store large amounts of carbon reserves (Canham et al. 1999), making them less susceptible to mortality induced by low light availability.

We hypothesized that aspen mortality would be the greatest in the period associated with senescence of the stand, i.e., at the average longevity of the species, which is expected to be between 80 and 120 years (Nienstaedt and Zasada 1990). Both Bergeron (2000) and Cumming et al. (2000) suggested that stand breakup may be responsible for creating open patches that are large enough to lead to the recruitment of a second aspen cohort. Our data only indirectly and partially support this hypothesis. The peak in aspen mortality occurred in the 40- to 60-year age category. This peak in mortality may be related to the fact that aspen is a shade-intolerant species and that these relatively young aspen were mainly codominant and suppressed trees. Self-thinning of aspen may have occurred earlier in smaller trees (Lee 1998), but it is more likely that this peak in mortality is related to the canopy position of this young aspen cohort. Originating from root sprouts, a high frequency of aspen is often found growing in large gaps following the death of dominant trees. Furthermore, our results show a break in the period of mortality from about 65 years until almost 110 years, with a secondary peak in mortality occurring in old aspen, around 140 years. The hypothesized period of sudden stand breakup between 80 and 120 years is therefore not observed in our stands, perhaps because many of the trees have already died and decayed. For aspen, we were able to reconstruct mortality for a period of up to 30 years, which means that we should be at the limit of the hypothesized period of stand breakup in the studied 153-year-old stands.

A stand breakup period may be deduced from the high mortality of aspen that recruited 40–60 years earlier. This recruitment would have occurred while the stand was 90–110 years old and may have been due to an important period of canopy opening. This cohort may thus be due to a stand

breakup period that occurred across a period of more than 20 years. This relatively gradual stand breakup period resulting from senescence may help explain why researchers have had difficulty in locating stands that are breaking up in large numbers over a short time frame. Our data also show that some individuals survive the period of breakup and live up to 173 years. These old trees represent a minor part of the forest but may contain genetic traits for longevity.

Temporally, we also observed a peak in aspen mortality from 1974 to 1979. This peak coincides with a forest tent caterpillar outbreak that was reported to have occurred in the area between 1971 and 1973 (Camiré 1997). Researchers have noted that repeated deforestation by forest tent caterpillars is an important agent of mortality for aspen. After successive defoliation, stands continue to have higher mortality rates many years following the outbreak (Hogg et al. 2002).

A spruce budworm outbreak was also reported in the area between 1970 and 1987 (Morin et al. 1993). Bergeron et al. (1995) observed little white spruce mortality in their data set. This concurs well with our observations that spruce did not sustain a higher than normal mortality in the 1980s. The higher relative frequency of mortality in spruce after the spruce budworm outbreak, but it is unlikely that these high mortality peaks occurring so many years after the end of the outbreak were directly caused by it. Our initial hypothesis was that these peaks were related to single-year wind events, but this hypothesis is rejected because our data show that most of the trees died standing in these years. Furthermore, we did not find any evidence from the meteorological data (Environment Canada 2002) that these yearly peaks in mortality are related to years of unusual high winds. Further studies are therefore required to explain these single-year high peaks in spruce mortality. The peak in spruce mortality found in 110- to 150-year-old trees may be explained by senescence. Although it is known that spruce may live until 350 years of age, we very rarely observed such old spruce in our region.

Ecological implications for modelling

Our results can be used to validate and parameterize various simulation models of stand dynamics. Sortie (Pacala et al. 1994), for example, is a spatially explicit simulation model that is mainly driven by single-tree mortality that causes changes in light availability to understory trees. Currently, Sortie uses a constant mortality rate for trees greater than 10 cm. Our data clearly show that while this might be correct for shade-tolerant species such as white spruce, it is not adequate for shade-intolerant species such as aspen. Data such as those presented in this study can therefore be used to better fine tune adult tree mortality in such models.

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