

Impact of the 1998 ice storm on the health and growth of sugar maple (*Acer saccharum* Marsh.) dominated forests in Gatineau Park, Quebec¹

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PISARIC, M. F. J. (Dept. of Geography and Environmental Studies, Carleton University, Ottawa, ON, Canada K1S 5B6), D.J. KING (Dept. of Geography and Environmental Studies, Carleton University, Ottawa, ON, Canada K1S 5B6), A. J. M. MACINTOSH (Institute of Environmental Science, Carleton University, Ottawa, ON, Canada K1S 5B6), AND R. BEMROSE (Dept. of Geography and Environmental Studies, Carleton University, Ottawa, ON, Canada K1S 5B6). Impact of the 1998 ice storm on tree health and growth in sugar maple (*Acer saccharum* Marsh.) dominated forests of Gatineau Park, Quebec. *J. Torrey Bot. Soc.* 135: 530–539. 2008.—The 1998 ice storm, which impacted many parts of eastern Canada and the northeastern United States, resulted in significant damage to forests. The intensity of the damage was quite variable both between stands and between individual trees. Using visual assessment of tree crown health and dendrochronological techniques we examined the response to the ice storm of sugar maple (*Acer saccharum* Marsh.) dominated forests in Gatineau Park, Quebec. Crown health assessment indicated that most of the heavily damaged trees showed some recovery in the years following the ice storm. However, dendrochronological analysis of the dominant sugar maples suggested that the most damaged individuals had still not returned to pre-ice storm stem growth levels six years following the ice storm. Combined, the crown health and dendrochronological analyses suggest that following the storm, in heavily damaged trees, resources were allocated to crown foliage production on remaining branches at the expense of stem growth.

Key words: dendrochronology, disturbance, forest health, ice storm.

Disturbance is an important factor in maintaining diversity and promoting succession in forest communities (DeSteven et al. 1991). In the mixed forests of eastern North America, disturbance is the result of a number of natural and anthropogenic factors (i.e., pathogen outbreaks, defoliating insects, hurricanes, ice storms, and acid rain) and occurs across a variety of spatial and temporal scales

(Burrows 1990, Irland 2000, Lafon 2006). For example, at local spatial scales senescence of individual trees produces small gaps in the canopy that could lead to localized changes in forest composition (Forcier 1975). At broader temporal and spatial scales, human induced and natural disturbances have also altered forest composition. European settlement produced fragmented landscapes in many regions and removed much of the old-growth forest stands. More recently, the impacts of acid rain have also been observed across broad portions of the mixed forests of eastern North America (Adams et al. 2000).

While ice storms are one of the most frequent forms of disturbance affecting the mixed forests of eastern North America (Lemon 1961), the ice storm of January 5–9, 1998 across eastern Canada and the northeastern United States was unique in both scale and intensity (Pellikka et al. 2000, Hooper et al. 2001). Up to 110 mm of freezing rain fell in

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parts of the region during the five-day storm (Coons 1999, Smith and Shortle 2003). Such extreme weather events are known to occur over small areas with return times of between 20 to 100 years, but widespread regional storms such as this may have return times of up to 500 years (Smith 1998).

Following the 1998 ice storm, a research study was established in sugar maple dominated forests of Gatineau Park, Quebec (Fig. 1) with the goal of monitoring forest structure and health changes in response to ice storm damage over the long term (10–20 years) using remote sensing data (King et al. 2005). The field data from that study showed dominant tree damage from the ice storm to be related to species (sugar maple and red oak (*Quercus rubra* L.) suffered lower damage compared to other species), tree size (damage increased with stem diameter and crown diameter), canopy structure (damage was greater for more open canopies with lower leaf area index and canopy closure), and topography (damage increased with elevation and slope aspects of east through southwest versus north facing slopes). In 2005, a dendrochronological investigation to quantify sugar maple growth trends before and after the ice storm was also initiated (MacIntosh 2006). Previous studies have investigated ice storm recurrence using dendrochronological techniques alone (Lafon and Speer 2002) and others have investigated forest dynamics using various post-event assessment techniques (Downs 1938, Whitney and Johnson 1984, DeSteven et al. 1991, Lafon et al. 1999, Warrillow and Mou 1999, Duguay et al. 2001, Hooper et al. 2001, Rhoads et al. 2002, Hopkin et al. 2003). This study combines the temporal aspects of the forest health and dendrochronological studies to provide new information regarding vegetation response, particularly of dominant trees, in a period of six years following a major ice storm event. Using this approach, we are able to hypothesize how trees re-allocate resources in their above ground biomass during the years following a severe ice storm event.

Materials and Methods. **SITE DESCRIPTION.** Gatineau Park is a 500 km² parcel of land whose southernmost boundary is located in the town of Gatineau, Quebec, just north of Ottawa, Canada (Fig. 1). The park is within

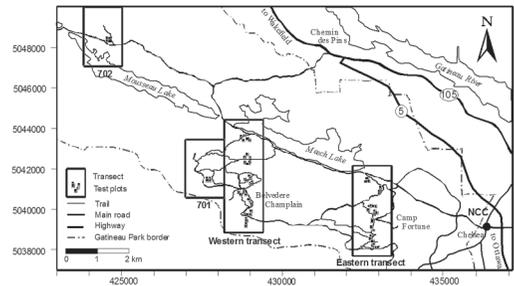


FIG. 1. Map of the study sites in Gatineau Park, Quebec (adapted from Pellikka et al. 2000). The health score and dendroecological studies were carried out within the 1998 plots along the Western and Eastern transects. Note: two Quebec Ministry of Natural Resources permanent plots (701, 702) that were used in other studies (e.g., Butson and King 2006) are also shown.

the Great Lakes St. Lawrence Forest Region of the Canadian Shield (Rowe 1972).

The forest examined in this study is dominated by sugar maple, which accounts for an average of 73% of the trees in the park. Small patches of American beech (*Fagus grandifolia* Ehrh.), quaking aspen (*Populus tremuloides* Michx), and red oak also occur. Other hardwood species that are present at much lower densities include red maple (*Acer rubrum* L.), ironwood (*Ostrya virginiana* (Mill.) K. Koch), black ash (*Fraxinus nigra* Marsh.), white ash (*Fraxinus americana* L.), paper birch (*Betula Papyrifera* Marsh.), and black cherry (*Prunus serotina* Ehrh.).

Following the 1998 ice storm, seventy 20 × 20 m plots were set up along two north-south transects in Gatineau Park (see Pellikka et al. 2000 for additional details) (Fig. 1). The plots and transects represent a range of elevations from 188 to 313 m above sea level (a.s.l.; mean = 285 m), as well as a range of slopes, aspects, and ice storm tree damage. Plots were deliberately selected to exclude conifers, which in general were not significantly impacted by the 1998 event. In 2000, and for subsequent sample years, the number of plots was reduced to 50 to improve field measurement efficiency and remove a plot from a given pair with nearly identical conditions that were spaced very close together.

ASSESSMENT OF INDIVIDUAL TREE HEALTH. In the spring of 1998 dominant trees in all plots were identified, marked with unique tags to facilitate tracking over time and assigned health scores. Intermediate trees were not

Table 1. Health score classifications for dominant sugar maple trees.

| Health score | Condition of tree |
|--------------|--|
| 0 | No visible crown damage or dieback |
| 1 | Slight damage with only branch ends being dead, or a single missing or dead major branch not in the upper portion of the crown |
| 2 | Moderate damage with greater than one upper crown dead or missing branch or up to half the crown missing or dead |
| 3 | Severe damage where the tree had only one or perhaps two remaining live branches |
| 4 | Dead |

tagged but each was assessed for health condition for plot-level analysis. A visually-based health score, based primarily on the relative amount of dead or broken branches, was assigned to each dominant and intermediate tree (Table 1). The advantage of using such a health score as opposed to estimations of crown loss is that it reflects only the current condition of a tree, and therefore does not rely on an estimate of pre-storm crown volume, which becomes more difficult as years pass. Although subjective, this health assessment methodology has been found to be repeatable between observers using random sampling on different days (Lévesque and King 1999). To test the precision of these health measurements, 30 trees were randomly selected and assessed by a second observer three times over a period of six weeks. The average of the standard deviations derived from these health measures was 0.238, which indicates good precision for this visually-based index (Lévesque and King 1999). Health scores were assigned to all dominant trees in 1998, 2000, 2003, 2004, and 2005, and to all intermediate trees in 1998, 2000, and 2003. For the purposes of this study, the dominant tree health scores up to 2004 are analyzed in detail as that year matches the most recent year of the dendro-chronological data. However, where relevant, comments are made that include the 2005 dominant health score data.

OTHER TREE AND PLOT MEASUREMENTS. In each plot, in the summer of 1998, elevation was measured using differential GPS, percent slope was measured using a clinometer, and aspect was measured using a compass. For dominant trees, diameter at breast height (DBH) and crown diameter were measured and stem density was calculated. Hemispherical photos were used to determine effective leaf area index and canopy closure (Pellikka et al. 2000). Ground vegetation abundance was measured in 1998 and 2000 by dropping a pin

through the vegetation from 0–2 m in height every 25 cm along a transect running from the NW to SE corner of each plot. Layers of 0–10 cm, 10–50 cm, 50 cm–1 m, 1–2 m, and > 2 m were assessed.

ANALYSIS OF TREE HEALTH AND STEM GROWTH CHANGES. Changes in individual dominant tree health scores between 1998 and each of the subsequent years were analyzed in terms of the following: 1) the magnitude of change with respect to damage incurred in 1998 was analyzed, including non-parametric Wilcoxon signed rank *t*-tests for ordinal data to determine if differences in health between years were significant. 2) The magnitude of change was analyzed with respect to tree species. 3) Bivariate correlation analysis was conducted of change in health versus damage incurred, dominant tree and canopy structural variables (listed above), and topographic variables (listed above; aspect being analyzed using non parametric *t*-tests). In conducting multiple bivariate correlations for the eight structural and topographic *x*-variables against a single *y*-variable (change in health score), the sequential Bonferroni criterion was applied (Holm 1979) using an initial significance (*P*) value of 0.00625 (i.e., 0.05/*n*, where *n* = 8, the number of *x*-variables). In consideration of critiques of this conservative procedure (e.g., Moran 2003), correlations that were significant at $P \leq 0.05$ but which failed the given Bonferroni *P*-value, are noted in the Results section below. 4) Once the post storm time period (1998–2000; 1998–2003; 1998–2004) that produced the best correlations between tree health change and forest variables was known, forward stepwise multiple regression was implemented to determine if multivariate models of health change could be produced. The probability of “F” to enter and exit was set at 0.05 and 0.10, respectively. Model residuals were verified to be uniform over the range of the *y*-variables. All *y*-

variables (change in health) were normally distributed. Testing of log transformation of some x-variables that deviated from normality did not improve models so those results are not reported here. Multicollinearity was checked and found to be negligible in the multivariate models.

The above correlation and regression analyses were repeated for change in plot average intermediate tree health. For change in ground vegetation cover, only the bivariate correlation analyses were conducted because few significant relationships were found. In addition to the above analyses, the magnitude of dominant tree DBH growth in these periods was analyzed by species and damage incurred for comparison with the dendrochronological results.

DENDROCHRONOLOGICAL METHODS. To examine the impact of the 1998 ice storm on sugar maple growth in Gatineau Park across longer temporal scales, increment cores were recovered from dominant trees in 16 of the 50 plots in 2005. The 16 plots were selected based on the following criteria: 1) each plot contained at least two trees with a 1998 health score of "3" and two trees with health scores of "0" or "1", 2) the plots represented the diversity of elevation, slope, and aspect in the study area [The diversity of topographic conditions was included in the samples because results from the health score analysis (see Results) found no relationship or only weak relationships of damage and topographic variables], and 3) each plot was sampled equally (i.e., four randomly selected trees per plot). For each tree, a Hagloff increment borer (internal diameter ~4.3 mm) was used to remove two cores at breast height (1.37 m) oriented at 90° to each other.

Preparation and analysis of the tree cores followed standard dendrochronological methods (Stokes and Smiley 1968, Fritts 1976) including visual cross-dating, measuring using a Velmex UniSlide measuring system with an accuracy of 0.001 mm, verification of the visual cross-dating using the program COFECHA (Holmes 1983), and chronology development using the program ARSTAN (Cook and Holmes 1986). Two standardized tree ring chronologies were developed. The first was comprised of trees with health scores "0" or "1" (RWI-0/1) and the second of trees with a health score of "3" (RWI-3). To measure the

strength of the common signal between trees at a given site, the series intercorrelation was determined by averaging the correlation of each individual series with a master chronology derived from all the other series (Holmes 1983). We also analysed the mean sensitivity for each chronology as the relative difference in ring width from one year to the next, which varies from 0 (no difference) to 2 (repeating pattern of alternating narrow and wide rings) (Fritts 1976).

Results. CHANGE IN TREE HEALTH AND DBH GROWTH IN RELATION TO DAMAGE INCURRED. The average health score of dominant trees improved from 1.84 in 1998 ($N = 603$; S.D. = 1.033) to 1.33 in 2003 ($N = 603$; S.D. = 1.207). Differences of both the 2003 and 2000 average scores with the 1998 average are significant ($P < 0.001$). In 2004, the average score had increased significantly from 2003 to 1.42 but in 2005, it had decreased to the same level as 2003. As expected, the proportions of trees with scores of moderate (2) or severe (3) damage were highest in 1998, the summer following the ice storm, but these scores have mostly decreased in frequency through time. In contrast, the proportion of trees that were found to be dead (4) in a given year steadily increased from 2.7% in 1998 to 12.5% by 2004. Many of the trees that died by 2004 had been severely damaged by the storm. For example, of the 155 trees given a score of 3 in 1998, 18.2% died in the six years following the storm and 78.0% recovered to varying degrees (score decreased to 2, 1, or 0). Of the 432 trees that were not severely damaged (0–2) in 1998, only 9.2% declined in health and scored a 3 or 4 in 2004. These data show that the mortality of severely damaged trees was twice the rate of decline and mortality of trees with moderate to no damage.

In assessment of individual species, for sugar maple, only 5.3% of the 434 trees assessed as 0, 1, or 2 in 1998 declined to a score of 3 or 4 in 2004. Conversely, 86% of the sugar maples assigned a 3 in 1998 recovered by at least one health score value over the six years. For other dominant species, resilience to ice storm damage appears to be lower (Table 2). For example, severely damaged white ash had a greater tendency to decline and die. Similar trends are evident for black and red ash (*Fraxinus Profunda* (Bush) Bush), and ironwood. The lower resilience of these

Table 2. Average health scores for dominant species examined in the four assessment years following the 1998 ice storm. The average percent change in diameter at breast height (DBH) for each species from 1998–2004 is also indicated.

| Species | Samples | Average health score | | | | % Change in DBH 1998–2004 |
|-------------------|---------|----------------------|------|------|------|---------------------------|
| | | 1998 | 2000 | 2003 | 2004 | |
| sugar maple | 434 | 1.67 | 1.22 | 1.09 | 1.17 | 7.99 |
| red maple | 7 | 2.14 | 1.43 | 1.29 | 1.43 | 4.21 |
| American beech | 20 | 2.50 | 1.55 | 1.80 | 1.65 | 4.93 |
| white ash | 39 | 2.79 | 2.54 | 2.69 | 2.77 | 1.62 |
| red ash | 11 | 2.00 | 1.64 | 2.18 | 2.55 | 0.42 |
| black ash | 8 | 2.00 | 1.75 | 2.00 | 2.38 | 2.20 |
| ironwood | 15 | 1.73 | 1.47 | 2.53 | 2.27 | –0.20 |
| black cherry | 11 | 2.73 | 1.36 | 1.18 | 2.00 | 4.23 |
| red oak | 41 | 1.68 | 1.46 | 1.24 | 1.63 | 7.26 |
| American basswood | 13 | 3.00 | 2.08 | 2.31 | 2.15 | 1.22 |

species is also supported by the relatively small percentage increase in DBH between 1998–2004 (Table 2). Overall, average DBH growth between 1998 and 2004 was only 4.3% for trees assigned a health score of 3 versus 9.1% for trees assigned scores of 0, 1, or 2 in 1998. More damaged trees have, on average, grown less in diameter in relation to healthier trees. These trends are also reflected in the dendrochronological results discussed later. Average DBH for iron wood actually declined from 1998–2004, highlighting the high proportion that died following the ice storm. However, many of these results are based on limited sample numbers that should be verified with additional field assessments directed at individual species in the coming years.

BIVARIATE CORRELATIONS BETWEEN CHANGE IN TREE HEALTH AND DAMAGE INCURRED, FOREST STRUCTURE, AND TOPOGRAPHY. *Change in Health vs. 1998 Damage.* Significant relationships were found for change in dominant tree health for the periods 1998 to 2000, 1998 to 2003, and 1998 to 2004 versus the 1998 dominant tree health score (e.g., $r = 0.73$, $P = 0.001$ for 1998–2004 health change vs. 1998 health score). Change in health was calculated by subtracting the later year health score from the 1998 score, which generally resulted in positive differences as 1998 health scores were most often greater (i.e., greater damage) than subsequent year scores. These results show that increasing damage is associated with a stronger crown response in dominant trees.

Intermediate tree health improved over time in relation to 1998 dominant tree damage (e.g., $r = 0.56$, $P = 0.004$ for 1998–2003; $r = 0.39$, $P = 0.05$ (fails Bonferroni criterion) for 1998–2000) indicating that overstory damage was

associated with recovery of intermediate trees. Intermediate health change between 1998 and 2000 was also correlated to 1998 intermediate health ($r = 0.53$; $P = 0.002$). However, no relationship was found for 1998–2003 change versus 1998 intermediate tree health.

Change in Health vs. Forest and Tree Structure. For dominant trees, no significant relations were found for change in health versus dominant stem density or plot averaged dominant tree crown diameter. Dominant tree health change in the three periods (1998–2000, 1998–2003, 1998–2004) was significantly, but very weakly, related to 1998 dominant DBH (all $r \leq 0.32$; failed Bonferroni criterion).

For intermediate trees, significant relations were found between 1998–2003 change in health and 1998 dominant stem density ($r = -0.56$, $P = 0.004$) and dominant DBH ($r = 0.51$, $P = 0.009$; narrowly fails Bonferroni criterion), but no relations were found for 1998–2000. This shows that improved crown health of intermediate trees in the five years following the storm was associated with lower stem density and larger dominant trees.

Change in Health vs. Topography. For both dominant and intermediate trees, no significant relations were found for change in health versus elevation or slope. The only significant relation was for intermediate trees on southwest aspects versus all other aspects (non-parametric t -test, $P = 0.047$).

MULTIPLE REGRESSION MODELS OF CHANGE IN DOMINANT TREE HEALTH. Stepwise multiple regression models were created for the 1998–2004 change in dominant tree health and the 1998–2003 change in intermediate tree health because these time periods provided the

highest correlations with 1998 damage, forest structure, and topographic variables. The resulting model for change in dominant tree health included two predictor variables: 1998 dominant tree health (i.e., the damage incurred) and plot elevation (Adjusted $R^2 = 0.62$; $P < 0.001$; negative model coefficient). Although elevation was not by itself correlated significantly with change in health, it accounted for a small but very significant proportion of the remaining variance once 1998 damage had been entered into the model (contribution to adjusted $R^2 = 0.12$; $P = 0.009$). The negative relation indicates that improved crown health was greater at lower elevations. The model for change in intermediate tree health also included two predictor variables: 1998 dominant stem density and 1998 dominant tree health (adjusted $R^2 = 0.56$; $P < 0.001$), both contributing equally to the model.

CHANGE IN GROUND VEGETATION ABUNDANCE. Change in the canopy layer did not translate into predictable change in ground vegetation. From Fig. 2 it is apparent that between 1998 and 2000 the lowermost ground vegetation (0–10 cm) decreased in abundance while vegetation in all the higher layers increased in abundance. Correlation analysis of these changes against the tree health, structure, and topographic variables produced only three significant relationships: change in 0–10 cm ground vegetation versus 1998 dominant tree health score ($r = -0.59$, $P = 0.04$); change in 11–50 cm and 51–100 cm ground vegetation versus 1998 intermediate health ($r = -0.72$, $P = 0.01$; $r = -0.65$, $P = 0.02$, respectively), each failing the Bonferroni criterion but indicating trends of ground vegetation growth where dominant or intermediate tree damage was greater.

TREE RING CHRONOLOGIES. Two standardized tree ring chronologies were developed for dominant sugar maples sampled in this study, RWI-0/1 (trees with health scores of 0 or 1) and RWI-3 (trees with 1998 health scores of 3). The RWI-0/1 chronology was developed from 41 individual series and had a mean series intercorrelation of 0.408. RWI-3 was developed from 38 individual series and had a mean series intercorrelation of 0.481. Both chronologies contained a high degree of year-to-year variability in ring width as evidenced by the relatively high mean sensitivity of 0.387

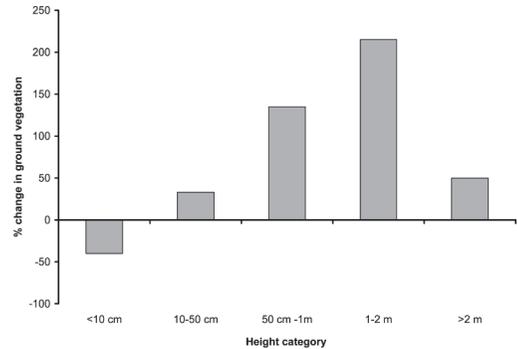


FIG. 2. Changes in ground vegetation abundance between 1998 and 2000 as a percent of 1998 abundance.

and 0.396 for RWI-0/1 and RWI-3, respectively. RWI-3 was the longer of the two chronologies, covering the period 1885–2004; RWI-0/1 spanned the period 1925–2004 (Fig. 3a). However, sample depth was low in the early portions of each chronology (Fig. 3a); only after approximately 1950 was sample depth sufficiently high to confidently interpret the ring width series. Regardless, the ring width chronologies for RWI-0/1 and RWI-3 are remarkably similar to one another during most of the period of overlap. In general, low growth occurred from the late 1800's to 1925 in RWI-3 and between 1960–1970 in both tree ring chronologies. Above average growth typified much of the 1970s. After 1998 the similarity between the two chronologies is lost. While growth in the most damaged sugar maples (RWI-3) declined, in the least damaged trees (RWI-0/1) it remained relatively high (Fig. 3b). By approximately 2003 the two series again exhibited similar growth trends. First differences indicate that the two chronologies were most different prior to 1950 and after 1998 (Fig. 3c). After 1998 the two chronologies rapidly diverged from one another and the growth rates of the RWI-0/1 trees began to exceed the more heavily damaged RWI-3 series as indicated by the negative first differences (Fig. 3c).

When comparing pre- and post-ice storm growth levels for the least and most damaged trees, it is apparent that individuals that experienced little damage are doing significantly better than the most damaged individuals, even seven years following the ice storm. For the RWI-0/1 trees, growth rates are higher than prior to the ice storm (Table 3). The

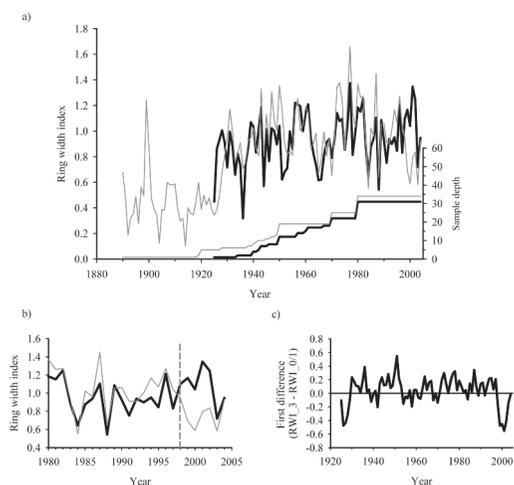


FIG. 3. a) Standardized ring width chronologies for RWI-0/1 (thick black line) and RWI-3 (thin grey line). Sample depth for each chronology is also indicated. b) Same as 3a, but for 1980 to 2004. Vertical dashed grey line indicates 1998, the year of the ice storm. c) First differences between the standardized ring width chronologies RWI-0/1 and RWI-3 through time.

greatest increases in growth rate with respect to pre-storm rates occurred five years after the ice storm. For the most heavily damaged trees, post-ice storm growth as a percentage of pre-ice storm growth decreased significantly (Table 3). Generally, growth rates were approximately 28–30% lower after the ice storm for the most damaged trees (Table 3). In comparison, the least damaged trees experienced increased growth rates that were approximately 16–27% higher than prior to the ice-storm.

Table 3. Post-storm radial growth expressed as a percentage of pre-storm growth of standardized ring width chronologies RWI 0/1 and RWI 3 (bold values) following the 1998 ice storm. Percent growth increase/decrease following the ice storm are given in parentheses.

| Pre-ice storm growth | Post-ice storm growth | | |
|----------------------|----------------------------------|----------------------------------|----------------------------------|
| | 3-year (1998–2000) | 5-year (1998–2002) | 7-year (1998–2004) |
| 3-year (1995–1997) | 114% (+14%) 66% (–34%) | 123% (+23%) 68% (–32%) | 112% (+12%) 68% (–32%) |
| 5-year (1993–1997) | 116% (+16%) 67% (–33%) | 124% (+24%) 69% (–31%) | 114% (+14%) 69% (–31%) |
| 7-year (1991–1997) | 120% (+20%) 70% (–30%) | 128% (+28%) 73% (–27%) | 118% (+18%) 73% (–27%) |
| 10-year (1987–1997) | 123% (+23%) 73% (–27%) | 129% (+29%) 73% (–27%) | 120% (+20%) 76% (–24%) |
| 15-year (1982–1997) | 120% (+20%) 73% (–27%) | 129% (+29%) 76% (–24%) | 118% (+18%) 75% (–25%) |
| Average | 119% (+19%) 70% (–30%) | 127% (+27%) 72% (–28%) | 116% (+16%) 72% (–28%) |

Discussion. The 1998 ice storm that affected large portions of eastern Ontario, Quebec, the Atlantic Provinces, and the northeast United States is considered a rare event given its magnitude and areal extent (Smith 1998). Forests across these regions experienced a wide range of damage from very little to, in some locations, complete devastation. In Gatineau Park, Quebec, sugar maple dominated forests received upwards of 80 mm ice accretion. This level of glazing caused significant damage and could lead to successional change in these forests over time.

This study has combined temporal tree crown health assessment and dendrochronological analyses to evaluate tree response in the six years following the storm and relationships of response with species, forest and tree structure, and topography. Overall, the average crown health score of dominant trees improved significantly between 1998 and 2004. This was also reflected in field observations noting that many damaged trees produced new foliage in often vertically thick but horizontally narrow crowns. Of the dominant trees that were severely damaged from the storm, about 80% recovered to some degree during this period. However, almost 20% of these trees died, a mortality rate twice that of trees that were moderately, lightly, or not damaged. These results agree with previous literature stating that trees with more than 50% crown loss would be expected to decline in subsequent years (Irland 1998, Coons 1999, QMNR 2000).

Different species of canopy dominant trees were impacted to varying degrees by the ice storm. For example, white ash, black ash, red

ash, and ironwood, which were significantly damaged, had a greater tendency to decline and die as indicated by a general trend of increasing health scores from 1998–2004. The lower resilience for these species is also supported by their relatively small increase in DBH over the same period. In contrast, sugar maple, the dominant species of the study area forests and a species that is largely believed to be relatively resilient to ice storm damage (Duguay et al. 2001), was generally less damaged by the storm and recovered well in the six years following the storm.

When relationships were examined between change in health following the storm and initial damage, tree and forest structure, and topography, interesting findings emerged. Initial damage incurred was the strongest and most consistent predictor of post storm change in health for both dominant and intermediate trees. Greater damage generally resulted in greater recovery, although as stated above, a significant proportion of severely damaged dominant trees did die. Changes in intermediate tree health and ground vegetation abundance were also associated with greater dominant (overhead) tree damage, indicating that where canopy openness increased, smaller trees and vegetation profited from the increased light and moisture. For all dominant trees, no significant relations were found between change in health and several forest and tree structural variables with the exception of weak relations with DBH, indicating that larger trees may have recovered better than smaller trees during the six year period. For intermediate trees, 1998–2004 change in health was found to be (negatively) related to dominant stem density. Thus, in locations where dominant tree size was greater (and stem density typically lower), ice storm damage to dominant trees was greater (King et al. 2005) resulting in greater recovery of intermediate tree crown health as found here. No significant bivariate relationships were found for change in health versus topographic variables, but elevation was included as the second of two variables in a stepwise regression for dominant trees. It indicates that recovery from ice storm damage may be greater at lower elevations but the association is not as strong as that previously found showing damage incurred to increase with elevation (Irland 2000, Duguay et al. 2001, Lafon 2004, King et al. 2005).

In terms of stem growth, both the DBH measurements and the dendrochronological data show that less damaged trees grew more in the subsequent years. The dendrochronological data indicate that prior to the 1998 ice storm sugar maple trees in Gatineau Park had growth trends that were similar across large spatial scales. Following the ice storm, growth trends began to diverge in response to the degree of damage experienced by individual trees. While growth differences in the two tree ring chronologies prior to 1950 likely reflect low sample depth, the large differences after 1998 are most likely attributable to the degree of damage resulting from the ice storm.

Although these dendrochronological data cannot provide explicit proof, it is hypothesized the ice storm and the subsequent damage to sugar maples likely induced physiological responses in the most heavily damaged trees that re-directed carbohydrate reserves within the trees. While most carbohydrates formed by photosynthesis are oxidized in respiration, a large portion is also used in growth, being translocated to the stem (Kozłowski and Pallardy 1997). Another fraction of the carbohydrate pool is accumulated as reserve foods that can eventually be used in metabolism and growth (Kozłowski and Pallardy 1997). Reserve carbohydrates have been shown to be important for re-growth following pruning and disturbance events such as early-season frost (Kozłowski et al. 1991). Often, trees with lower carbohydrate reserves will experience lower tree vigor and ultimately have fewer accumulated reserves to heal injuries and maintain physiological processes at levels required to sustain the tree when damaged by a disturbance event (Waring 1987, Kozłowski and Pallardy 1997). Following the 1998 ice storm, it is believed that the most heavily damaged sugar maples made use of these carbohydrate reserves from undamaged portions of the tree. For example, nutrient reserves stored in tree roots during previous growing seasons are typically used for early season growth in trees (Tromp 1983). This early season growth, or earlywood, normally accounts for much of the increase in annual stem increment. For trees that were severely damaged by the ice storm, these resources may have been allocated to generating new sprouts from damaged branches in the years following the ice storm instead of being translocated to the stem for growth purposes,

resulting in less radial growth and smaller growth rings (Duguay et al. 2001, Lafon and Speer 2002). This was evident in the field during subsequent assessments of tree health as new sprouts had developed throughout the upper crown of most of the damaged trees in the years immediately following the ice storm. The growth trends observed for RWI-0/1 and RWI-3 following the ice storm mirror the results of the health score analysis which noted that the change in diameter growth from 1998 to 2004 for trees with 1998 health class "3" was significantly less than for trees with 1998 health classes "0" and "1".

In contrast, the post-storm increase in growth for trees with 1998 health scores of "0" and "1" (RWI-0/1) is likely attributed to canopy release. These trees had little crown damage and thus would not have to draw upon reserves of carbohydrates for re-growth, while also benefitting from thinning of the canopy layer (Lafon and Speer 2002). Greater light, nutrient and water availability may all have contributed to increased growth for RWI-0/1 trees following the ice storm.

The analysis of pre- and post-ice storm growth rates suggests that the impacts of the 1998 ice storm were still apparent in the 2004 growing season. Lafon and Speer (2002) found that the disturbance signal in the tree ring record caused by a glaze event in 1979 persisted for 14 years, while the signal from an ice storm in 1921 was still visible 13 years later. While the radial growth record of sugar maples in Gatineau Park indicates that growth of severely damaged trees was significantly lower than that for less damaged trees following the storm, the analysis of visual health scores based on crown characteristics indicates that 86% of sugar maples in health class "3" had improved their scores by 2004. This suggests that severely damaged sugar maples must have allocated carbohydrate reserves towards canopy restoration at the expense of stem growth. It is possible that the consequence of this strategy is reflected in the observation that severely damaged trees had twice the mortality rate in subsequent years as that for moderate to undamaged trees.

Conclusions. The mixed forests of eastern North America have a long history of disturbance due to natural and anthropogenic factors. These processes have shaped the composition and development of current

forests and will likely continue to shape them for many years to come. Therefore, understanding the response of forests to infrequent and severe disturbance events like the 1998 ice storm is important from ecological and economic perspectives.

By examining tree health change and incremental tree growth records, we believe we have documented physiological changes within a temperate hardwood forest damaged to varying degrees by the 1998 ice storm. The visual health score analysis based on tree crown characteristics suggested an initial overall improvement in tree health following the ice storm. However, DBH growth and dendrochronological analyses indicate that the growth of the most heavily damaged sugar maple trees was considerably lower in the six years following the storm than prior to the storm. Trees that experienced little or no damage exhibited a pattern of increased growth, attributed to canopy release. This dual pattern of growth was still apparent in 2004 indicating the persistence of sugar maple response to the ice storm through time, and confirming the broad temporal response of forests to ice storm damage noted by other researchers. The discrepancy between the health scores and the dendroecological analysis suggests that sugar maples that were severely damaged by the ice storm must have re-allocated carbohydrate reserves to crown restoration at the expense of stem growth.

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