

Quantitative and qualitative effects of a severe ice storm on an old-growth beech–maple forest

Koichi Takahashi, Ken Ariei, and Martin J. Lechowicz

Abstract: Comparing permanent plots censused in 1997 and again in 2005, we quantified the impact of a severe ice storm on forest composition and dynamics in an old-growth beech–maple forest in eastern Canada. *Acer saccharum* Marsh. and *Fagus grandifolia* Ehrh. accounted for 78% of stand basal area immediately before the January 1998 ice storm. By 2005, eight growing seasons after the ice storm, stand basal area had dropped from 49.1 m²/ha to 31.5 m²/ha, and total tree density (>1 cm diameter at breast height (DBH)) decreased from 6350 stems/ha to 3875 stems/ha. However, *A. saccharum* and *F. grandifolia* remained dominant, accounting for 74% of stand basal area. Detrended correspondence analysis of relative dominance ratios at each plot in 1997 and 2005 showed that community composition did not change much during this period for either understory (1 cm ≤ DBH < 10 cm) or canopy trees (DBH ≥ 10 cm). The ice storm did not lead to significant recruitment of saplings (DBH ≥ 1 cm), but appears to have only contributed more to the growth of already-established saplings. We conclude that the ice storm of 1998 substantially decreased stand basal area and stem density but did not act to change the overall species composition or tree diversity in this old-growth beech–maple forest.

Résumé : En comparant les places-échantillons permanentes mesurées en 1997 et à nouveau en 2005, nous avons quantifié l'impact d'un verglas sévère sur la composition et la dynamique d'une forêt ancienne d'érable et de hêtre dans l'est du Canada. *Acer saccharum* Marsh. et *Fagus grandifolia* Ehrh. représentaient 78 % de la surface terrière immédiatement avant le verglas de janvier 1998. En 2005, huit saisons de croissance après le verglas, la surface terrière du peuplement était passée de 49,1 m²/ha à 31,5 m²/ha et la densité totale des arbres (>1 cm au DHP) de 6350 tiges/ha à 3875 tiges/ha. Représentant 74 % de la surface terrière du peuplement, *A. saccharum* et *F. grandifolia* étaient toujours les espèces dominantes. L'analyse des correspondances redressée des rapports de dominance relative dans chaque place-échantillon en 1997 et 2005 indique que la composition de la communauté n'a pas changé beaucoup durant cette période tant pour les arbres de sous-bois (1 cm ≤ DHP < 10 cm) que pour les arbres de la canopée (DHP ≥ 10 cm). Le verglas n'a pas entraîné de recrutement significatif de gaules (DHP ≥ 1 cm) mais semble seulement avoir davantage contribué à augmenter la croissance des gaules déjà établies. Nous concluons que le verglas de 1998 a diminué de façon importante la surface terrière du peuplement et la densité des tiges mais n'a pas modifié la composition globale en espèces ni la diversité des arbres dans cette forêt ancienne de hêtre et d'érable.

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Introduction

Ice storms are recurrent, often substantial disturbances in the forests of northeastern and central North America. Return times of ice glaze vary between several to as many as 100 years (Bragg et al. 2003; Cortinas et al. 2004), with ice accumulation sometimes exceeding several centimetres (Proulx and Greene 2001; Bragg et al. 2003). Ice accumulation on trees causes breakage of twigs, branches, or even trunks because of mass loading. Many researchers report large biomass loss from forest stands due to ice storms

(Bruederle and Stearns 1985; Boerner et al. 1988; Jacobs 2000; Hooper et al. 2001), but studies show that susceptibility to ice damage varies depending on the size of the tree (e.g., Proulx and Greene 2001; Lafon 2004), the species (e.g., Bruederle and Stearns 1985; Boerner et al. 1988; Rebertus et al. 1997; Hopkin et al. 2003), and landscape features (Millward and Kraft 2004). These differences in susceptibility to ice storm damage are believed to have significant impact on poststorm stand structure and species composition (Oliver and Larson 1996; Hooper et al. 2001; Greene et al. 2007).

Earlier studies investigating the impact of ice storms have reported contrasting views on how ice storms may affect species composition and diversity in forest stands. One view is based on the observation that early successional, shade-intolerant species are generally more susceptible to ice loading than late-successional species. The damage sustained by an intolerant overstory tree should allow the more tolerant, late-successional species to capture canopy gaps, thereby promoting stand dominance by later successional species (Carvell et al. 1957; Lemon 1961). A contrasting view is that extensive damage to the canopy creates large gaps allowing more light to reach the forest floor, which allows reproduction and establishment of early

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K. Takahashi,^{1,2} K. Ariei,³ and M.J. Lechowicz. Department of Biology, McGill University, 1205 Docteur Penfield, Montreal, QC H3A 1B1, Canada.

¹Corresponding author (e-mail: koichit@gipac.shinshu-u.ac.jp).

²Present address: Department of Biology, Faculty of Science, Shinshu University, Matsumoto, 390-8621, Japan.

³Present address: Ritsumeikan Asia Pacific University, College of Asia Pacific Studies, Health, Environment and Life Science Institute, 1-1 Jomonjibaru, Beppu, Oita, 874-8577, Japan.

successional species. The rapid reproduction and growth of shade-intolerant species then should effectively shift the forest to an earlier successional stage (Downs 1938; Siccama et al. 1976) and potentially increase species diversity. Available studies have shown that either scenario can occur, depending on stand structure, species composition, landscape features, as well as storm intensity (Siccama et al. 1976; Whitney and Johnson 1984; De Steven et al. 1991).

In this paper, we focus on the impact of a severe ice storm on an old-growth beech–maple forest. Forests dominated by *Acer saccharum* Marsh. (sugar maple) and *Fagus grandifolia* Ehrh. (American beech) are widely distributed in eastern North America (Braun 1950; Runkle 1996), a region where ice storms occur frequently (Chagnon 2003). Many researchers have examined the mechanisms giving rise to the development and dynamics of this forest type, with particular emphasis on the basis of beech–maple codominance (e.g., Fox 1977; Woods 1979, 1984; Brisson et al. 1994; Poulson and Platt 1996; Beaudet et al. 1999; Forrester and Runkle 2000; Arie and Lechowicz 2002). An influence of ice storms on the maintenance of beech–maple codominance has been suggested based on species differences in susceptibility to ice damage observed immediately after ice storms (e.g., Bruederle and Stearns 1985; Melancon and Lechowicz 1987; Duguay et al. 2001). This inference may be weakened by underestimation of mortality caused by the storm, because the susceptibility assessed immediately after the ice storm does not take longer term, storm-induced mortality into account. Only De Steven et al. (1991) examined changes in species composition in beech–maple forests many years after an ice storm. They found that, after 16 years, stands with less damage had an increase in dominance of *A. saccharum*, whereas forests with more damage had an increase in intolerant species. Given differences in stand composition and variation in the intensity of ice storms both within and among study sites, we cannot yet generalize conclusions about the impact of ice storms on the dynamics of beech–maple forests. Clearly more case studies are required to test competing perspectives and predictions.

Therefore, we assessed an 8 year trend in forest structure and species composition in an old-growth beech–maple forest following the extremely severe ice storm that occurred between 5 and 9 January 1998 (Kerry et al. 1999; Scarr et al. 2003). This storm was unprecedented not only in its duration and extent, but also in the amount of ice deposited. Glaze ice accumulation was up to 100 mm in the Montreal region (Kerry et al. 1999; Van Dyke 1999), more than double the amount recorded in any previous storms. In 1997, just prior to the storm, we had established 87 permanent plots (6 m radius) in an old-growth beech–maple forest at Mont St. Hilaire (MSH) to examine forest dynamics. We took advantage of this prestorm survey to assess the effects of the 1998 ice storm on the tree community in 2005, eight growing seasons after the disturbance event. We predicted that the ice storm of 1998 would reduce the relative dominance of *F. grandifolia* over this period for two reasons. First, previous studies at the site assessing the impact of the ice storm showed that *F. grandifolia* was more damaged in ice storms than *A. saccharum* (Melancon and Lechowicz

1987; Duguay et al. 2001). Second, *A. saccharum* has a higher growth rate than *F. grandifolia* under higher light conditions (Poulson and Platt 1996). Additionally, given the intensity of this storm and the results of De Steven et al. (1991), we also predicted that shade-intolerant species would increase their presence within the stand. More specifically, we attempted to answer the following questions. (i) Did the ice storm decrease stand basal area and tree density? If so, by how much? (ii) Was the susceptibility to longer term damage in this ice storm different between *A. saccharum* and *F. grandifolia*? (iii) Did species composition and diversity change after the ice storm?

Study site

Mont St. Hilaire, located approximately 32 km east of Montreal, in southern Quebec, eastern Canada (45°31'N, 73°08'W), is a rugged hill complex standing abruptly above the floor of the St. Lawrence River Valley; the 10 km² site is protected under provincial law as the Gault Nature Reserve. The monthly mean temperature in this region ranges between –10.2 °C (February) and 20.6 °C (August) with the annual mean temperature 5.9 °C. Annual precipitation is 1017 mm (Environment Canada 2002). All climatic data are for St. Hubert Airport (1928 – 1990), 45°31'N, 73°25'W, on the valley floor approximately 20 km west of MSH.

Forests in this region were cleared by European settlers beginning in the mid-18th century, but there were few human disturbances on MSH itself. Many of the trees exceed 150 years in age, and a few are over 400 years old (Cook 1971). The forests are dominated by deciduous broad-leaved trees such as *A. saccharum*, *F. grandifolia*, *Betula alleghaniensis* Britton, *Acer rubrum* L., *Tilia americana* L., *Fraxinus americana* L., *Populus grandidentata* Michx., and *Quercus rubra* L. and conifers such as *Pinus strobus* L. and *Tsuga canadensis* (L.) Carr. (Maycock 1961). Various tree communities occur in relation to local relief and aspect (Arie et al. 2005), but *A. saccharum* and *F. grandifolia* are the common canopy dominants in the reserve as a whole.

Materials and methods

We established 87 circular plots (6 m radius) along four transects in 1997 to examine forest dynamics (Arie and Lechowicz 2002), precisely recording the geographical coordinates of each plot using a GPS and permanently marking the plot centres. Elevation of the plots ranged between 126 m and 400 m a.s.l., their slopes ranged between 0° and 37°, and sampled aspects spanned all compass directions. At each plot, we identified species and measured diameter at breast height (DBH) for all trees greater than 1 cm DBH in 1997. We remeasured trees in late summer 2005. Individual trees were not tagged in the initial census of 1997, so we could calculate only aggregate mortality rates.

We considered the difference in susceptibility to the ice storm of 1998 between *A. saccharum* and *F. grandifolia* on the basis of the reduction of the basal area alone, not the density, because the recruitment of trees growing to >1 cm DBH after the ice storm of 1998 might have affected a change in tree density. Total basal area per plot is less affected by recruitment even if many trees recruited over 1 cm DBH. Thus, we used the change in basal area per plot

Table 1. Changes in basal area and density of trees (>1 cm DBH) between 1997 and 2005 at 87 circular plots (6 m radius, total 0.984 ha) in an old-growth beech–maple forest on Mont St. Hilaire, eastern Canada.

Species	Abbreviation	Basal area (m ² /ha)		Density (trees/ha)	
		1997	2005	1997	2005
<i>Acer pensylvanicum</i> L.	Apn	0.88 (1.68)	0.78 (1.24)	970 (1268)	680 (1016)
<i>Acer saccharum</i> Marsh.	Asa	26.54 (20.47)	17.06 (14.01)	3205 (2597)	1629 (1238)
<i>Acer spicatum</i> Lam.	Asp	0.26 (0.92)	0.10 (0.28)	195 (519)	159 (447)
<i>Amelanchier</i> spp.	Aml	0.04 (0.16)	0.03 (0.14)	56 (241)	44 (200)
<i>Betula alleghaniensis</i> Britton	Bal	1.26 (5.16)	0.80 (3.47)	47 (131)	53 (168)
<i>Betula papyrifera</i> Marsh.	Bpa	0.32 (1.38)	<0.01 (0.05)	5 (21)	1 (9)
<i>Fagus grandifolia</i> Ehrh.	Fgr	11.94 (15.19)	6.37 (4.46)	1531 (1852)	1114 (1487)
<i>Fraxinus americana</i> L.	Fam	1.35 (3.54)	1.24 (7.71)	52 (102)	36 (87)
<i>Ostrya virginiana</i> (Mill.) K. Koch	Ovg	0.45 (1.13)	0.26 (0.69)	147 (341)	81 (225)
<i>Pinus strobus</i> L.	Pst	0.40 (2.64)	0.26 (2.05)	4 (23)	2 (13)
<i>Prunus pensylvanica</i> L.f.	Ppn	<0.001 (0.02)	0 (0)	1 (9)	0 (0)
<i>Prunus serotina</i> Ehrh.	Pse	<0.001 (<0.01)	0 (0)	1 (9)	0 (0)
<i>Prunus virginiana</i> L.	Pvg	0.02 (0.11)	0.01 (0.04)	36 (269)	13 (99)
<i>Quercus rubra</i> L.	Qrb	4.50 (10.02)	4.20 (10.37)	46 (102)	40 (97)
<i>Tilia americana</i> L.	Tam	0.47 (2.28)	0.34 (1.51)	40 (90)	17 (46)
<i>Tsuga canadensis</i> (L.) Carr.	Tca	0.37 (2.97)	0.05 (0.31)	12 (59)	6 (35)
<i>Ulmus americana</i> L.	Uam	0.31 (2.89)	0 (0)	2 (13)	0 (0)
Total		49.11 (21.39)	31.50 (15.18)	6350 (1962)	3875 (1645)

Note: Values are means with SDs given in parentheses ($n = 87$ plots).

from 1997 to 2005 to compare the difference in susceptibility of *A. saccharum* and *F. grandifolia* to ice damage (stand-level susceptibility). We regressed total basal area per plot in 2005 against that in 1997 for *A. saccharum* and for *F. grandifolia* and compared the slope and intercept of regressions between the two species using *F* tests and analysis of covariance (ANCOVA), respectively (Sokal and Rohlf 1995).

We assessed species diversity in each plot using both the Shannon–Wiener *H'* index and the Simpson *D* index. We calculated these indices for each plot in 1997 and in 2005 and compared the 1997 and 2005 values using paired *t* tests.

We examined changes in species composition of all the plots between 1997 and 2005 by detrended correspondence analysis (DCA) of the relative dominance ratio for each species at each plot. The relative dominance ratio (RDR_{*i*}) of species *i* was calculated as

$$[1] \quad \text{RDR}_i = \frac{\text{RD}_i + \text{RB}_i}{2}$$

where RD_{*i*} and RB_{*i*} are relative density and relative basal area of species *i*, respectively, at each plot. The RDR of each species was calculated separately for the canopy trees (DBH ≥ 10 cm) and the understory trees (1 cm ≤ DBH < 10 cm) in each of the 1997 and 2005 data set. Based on this calculation, we made DCAs separately for the canopy and understory trees, but both 1997 and 2005 data were included in each of these analyses. Therefore, the axes scores of each plot for both 1997 and 2005 can be shown in the same ordination diagram. Regression analysis was used to detect if species composition changed between 1997 (immediately prestorm) and 2005 (eight growing seasons post-storm). We regressed the DCA score of the axis 1 (or axis 2) in 2005 against that in 1997. If relative dominance of each species did not change much or in any consistent trend

during the 8 years, this regression should fall on a 1:1 line. We assessed the relationship between the axes score of 1997 and that of 2005 by reduced major axis regression using the program (S)MATR (Falster et al. 2003).

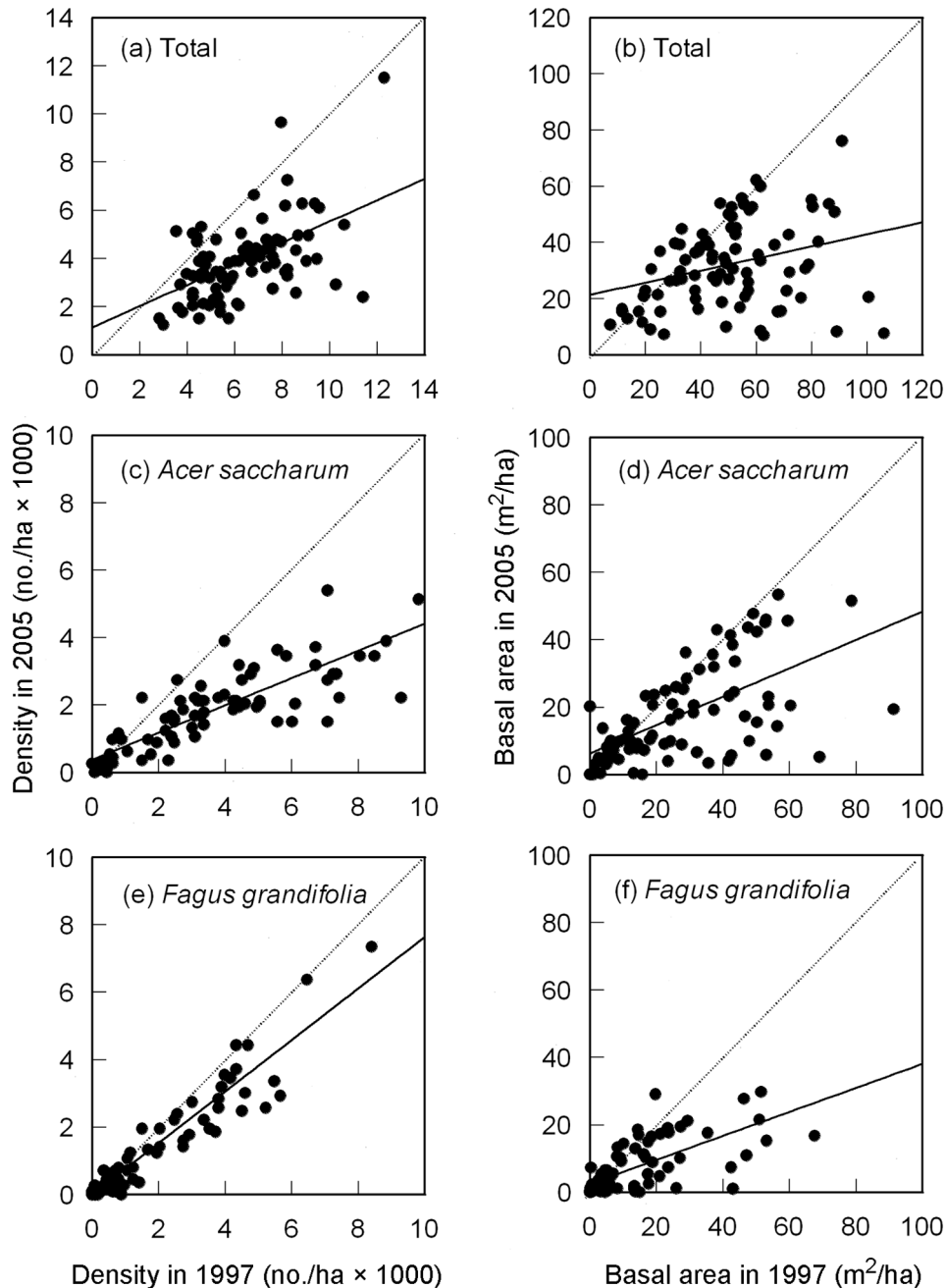
Results

A total of 17 tree species were recorded in 1997 (Table 1). *Acer saccharum* and *F. grandifolia* dominated the forest, accounting for 78% of the stand basal area and 75% of the total density in 1997. However, the standard deviation of basal area and density among the 87 plots was large for each species including *A. saccharum* and *F. grandifolia* (Table 1), indicating that each species was not distributed uniformly throughout the reserve.

The stand basal area decreased from 49.2 m²/ha to 31.5 m²/ha from 1997 to 2005 (36% reduction; Table 1). The total stem density decreased from 6350 trees/ha to 3875 trees/ha (39% reduction; Table 1). Total density and basal area decreased in most plots (Fig. 1). Reduction of basal area and density was observed in all species, except for the density of *B. alleghaniensis* (Table 1). The degree of reduction in stem density and basal area differed between the two dominant species (*A. saccharum* and *F. grandifolia*); reduction of stem density was much greater in *A. saccharum* than in *F. grandifolia* (49.2% vs. 27.2%; Table 1), but the reduction of basal area was greater in *F. grandifolia* than in *A. saccharum* (46.6% vs. 35.7%; Table 1). Total basal area per plot in 2005 at any basal area in 1997 was lower in *F. grandifolia* than in *A. saccharum*, i.e., the regression slope was not different between the two species (*F* test, $F_{[1,170]} = 0.72$, $P = 0.397$) and the intercept for *F. grandifolia* was significantly lower than that of *A. saccharum* (ANCOVA, $F_{[1,171]} = 11.8$, $P < 0.001$; Figs. 1d and 1f).

Stem density decreased in most size classes, except for two size classes: 5–10 cm and 10–15 cm DBH (Fig. 2a).

Fig. 1. Changes in tree density and basal area per plot between 1997 and 2005 for all trees (a and b), *Acer saccharum* (c and d), and *Fagus grandifolia* (e and f) in an old-growth beech–maple forest on Mont St. Hilaire, eastern Canada. The dotted line indicates a 1:1 relationship.

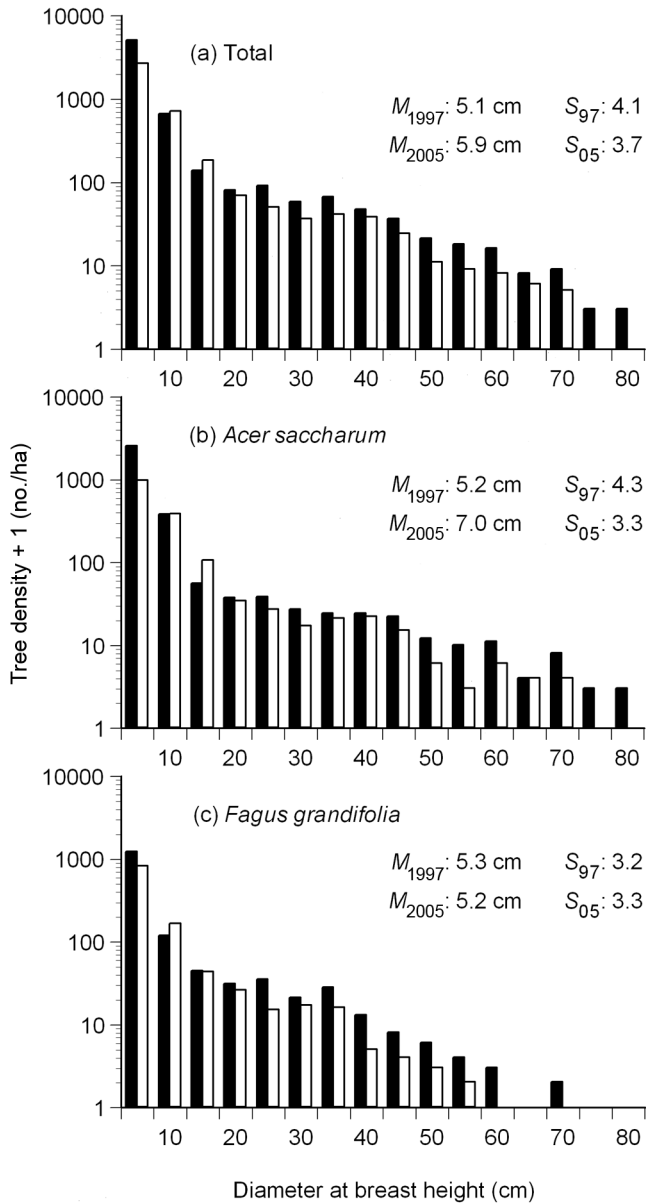


The largest reduction of stem density was observed at the smallest size class (1–5 cm DBH) for the two dominant species, and the absolute number of the reduction at this size class was four times greater in *A. saccharum* than in *F. grandifolia* (1543 trees/ha vs. 395 trees/ha; Figs. 2b and 2c). In contrast, the density of *A. saccharum* increased in the 10–15 cm DBH class, and that of *F. grandifolia* increased in the 5–10 cm DBH class (Figs. 2b and 2c). The shape of the DBH frequency distribution in 2005 differed significantly from that in 1997 for *A. saccharum* (Kolmogorov–Smirnov two-sample test, $P < 0.001$; Fig. 2b). Mean DBH increased and the skewness of the DBH frequency distribution decreased in *A. saccharum*

(Fig. 2b). Although the shape of the DBH frequency distribution of *F. grandifolia* also differed significantly between 1997 and 2005 (Kolmogorov–Smirnov two-sample test, $P < 0.001$), mean DBH and skewness were almost unchanged (Fig. 2c).

We examined change in species composition between 1997 and 2005 by DCA. The overall distribution of plot scores in the ordination diagram was similar between 1997 and 2005 for both the canopy (Figs. 3a and 3c) and understorey trees (Figs. 3b and 3d). In particular, plots dominated by *F. grandifolia* prior to the ice storm continued to be occupied by *F. grandifolia* after the storm, whereas plots dominated by *A. saccharum* also remained dominated by

Fig. 2. Frequency distribution of DBH for all trees (a), *Acer saccharum* (b), and *Fagus grandifolia* (c) in an old-growth beech–maple forest on Mont St. Hilaire, eastern Canada. Solid and open bars indicate the tree density in 1997 and in 2005, respectively. M_{1997} and M_{2005} , mean DBH in 1997 and 2005, respectively; S_{1997} and S_{2005} , skewness of the DBH frequency distribution in 1997 and in 2005, respectively.



A. saccharum poststorm, both in the canopy (Fig. 3c) and in the understory (Fig. 3d). We also analyzed the change in the relative dominance of species during 1997–2005 by regression analysis. In both the canopy and understory trees, the relationships between the axis 1 scores in 1997 and in 2005 and between the axis 2 scores in 1997 and in 2005 were close to a 1:1 line; the 95% confidence intervals included 1 for the slope and 0 for the intercept (Fig. 4; Table 2). Species diversity indices (Shannon–Wiener H' index and Simpson D index) were not significantly different between 1997 and 2005 (paired t test, $P > 0.05$; Fig. 5). These results

indicate that the species composition and diversity in the tree community did not change much or in any consistent trend over the first eight growing seasons after the 1998 ice storm.

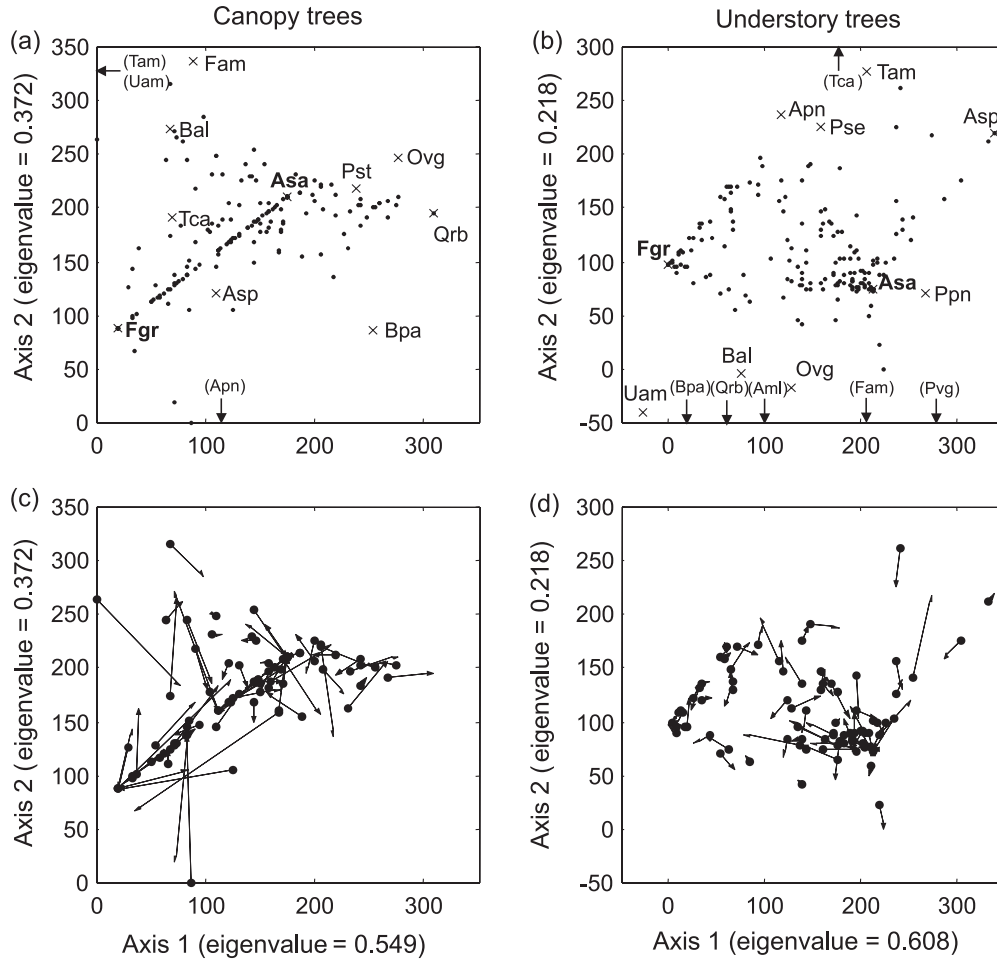
Discussion

The ice storm of 1998 had a significant impact on the total basal area and density, with 36% and 39% reductions in stand basal area and density, respectively, in the 8 years following the ice storm. At MSH, there was an immediate biomass loss of about 7%–10% resulting from the breakage of trunks and branches (Hooper et al. 2001). The probability of mortality of the trees that suffered such damage is likely to be higher after the storm because crown loss decreases photosynthetic production, which then leads to difficulties in maintaining carbon balance in individual trees. Additionally, the reduction in carbon gain lowers a tree's resistance to fungi and insects, which could also increase the probability of mortality (Rhoads et al. 2002). Hopkin et al. (2003) showed that individuals with severe crown damage (>75% of crown lost) had a 74% chance of dying within 3 years after the storm, with a significant mortality recorded in the first growing season after the storm. We believe the large reductions in stand basal area and density are evidence of the ongoing, deleterious impact of the ice storm on canopy trees.

Assuming that the reduction of the canopy-tree density (DBH > 10 cm) during 1997–2005 in this study was due to the death of trees, annual mortality is estimated to be 2.3%/year. In a sample of two 1 ha plots where individual trees were tagged at MSH, annual mortality was 3.2%/year from 1998 through 2000 for hardwood trees and conifers (DBH > 10 cm) (B.R. Hamel, McGill University, Montreal, Quebec, personal communication (2001)). If we assume that the mortality rate in the plots we studied was also 3.2%/year between 1998 and 2000, the mortality between 2001 and 2005 can be calculated as 1.7%/year. Annual mortality of deciduous hardwood trees and conifers (DBH > 10 cm) is usually ca. 1% in natural forests without the effects of large disturbances such as ice storms (Parker et al. 1985; Runkle 1990), which suggests that mortality rate remained high years after the ice storm of 1998. Annual mortality after the ice storm of 1998 was estimated as 7.2%/year during 1998–2001 in pine plantations (canopy height ranged from 15 m to 20 m) in eastern Ontario (Ryall and Smith 2005), and 1.3%/year during 1998–2002 for hardwood trees (23–46 cm DBH) in the northern United States (Shortle et al. 2003). The estimated mortality in this study falls within these reported values.

The reduction of the tree density at the smallest size class (1–5 cm DBH) indicates that newly recruited saplings grown to >1 cm DBH were infrequent after the ice storm. By contrast, tree densities at 5–10 and 10–15 cm DBH mostly increased, suggesting that the ice storm promoted the growth of saplings that were present in the understory prior to the storm (i.e., advance regeneration). This most likely occurred because larger canopy trees are generally more prone to ice storm damage (e.g., Rebertus et al. 1997; Duguay et al. 2001; Hopkin et al. 2003; Lafon 2004), which created gaps in the canopy favoring growth of saplings and small trees in

Fig. 3. Ordination of plots and species by detrended correspondence analysis for canopy trees and understory trees. Relative dominance ratio of each species at each plot was used for the analysis. (a and b) Species (crosses) and site scores (dots) for analysis based on canopy trees and understory trees. Species abbreviations are given in Table 1. (c and d) Changes in site scores before and after the ice storm (1997). The solid circles are the site scores prior to the ice storm (1997) and the arrowhead indicates the poststorm values (2005).



the 5–10 and 10–15 cm DBH size classes. The growth of these subcanopy trees appears to have created a closed, but lower, canopy relatively quickly. Arie and Lechowicz (2007) showed that, in these same permanent plots, gap fraction measured at 60 cm increased from 7.7% in 1997 to 16.6% in 1998 due to the damage caused by the ice storm but, by 2000, had returned to prestorm levels. This relatively quick closure of the recovering canopy may have limited the recruitment of seedlings and small saplings.

The degree of reduction in stem density and basal area differed between the two dominant species; the reduction of density was much greater in *A. saccharum* than in *F. grandifolia* (49.2% versus 27.2%), but the reduction of the basal area was greater in *F. grandifolia* (46.6% versus 35.7%). We believe this discrepancy arises primarily because of how understory saplings of *A. saccharum* and *F. grandifolia* are distributed at MSH. In general, *A. saccharum* understory saplings tend to occur densely under a relatively open canopy, whereas *F. grandifolia* understory saplings, which are mostly of sprout origin, are found close to a “parent tree.” Thus, although *F. grandifolia* understory saplings may have been sheltered from glaze deposition by parent trees, under-

story saplings of *A. saccharum* could have received considerable amounts of ice glaze. Because understory saplings of *Acer saccharum* are abundant, there could be a substantial reduction in the density of *Acer saccharum*, despite a relatively low reduction in basal area.

If we examine only the larger sized trees, we find that *F. grandifolia* was damaged more. This agrees with previous studies (Melancon and Lechowicz 1987; Duguay et al. 2001; Rhoads et al. 2002; Hopkin et al. 2003), but it is not clear why the susceptibility to ice damage is higher in *F. grandifolia* than in *A. saccharum*. Rebertus et al. (1997) reported more damage to trees on lower slopes, probably because cold-air drainage allows ice to persist longer there. At MSH, *F. grandifolia* is distributed predominantly on lower slopes, whereas *A. saccharum* is predominant on the upper slopes or hilltops (Arie et al. 2005). This difference in elevational distribution might account for the greater damage to *F. grandifolia*, but we found no significant difference in percent reduction of basal area per plot between high elevations (>280 m a.s.l.) and low elevations (<280 m a.s.l.) for either *A. saccharum* or *F. grandifolia* (data not shown). Thus, plot elevation is unlikely to have brought about the species dif-

Fig. 4. Relationships between the axes scores of 1997 and 2005 for canopy trees (*a* and *b*) and understory trees (*c* and *d*). Regression statistics are given in Table 2.

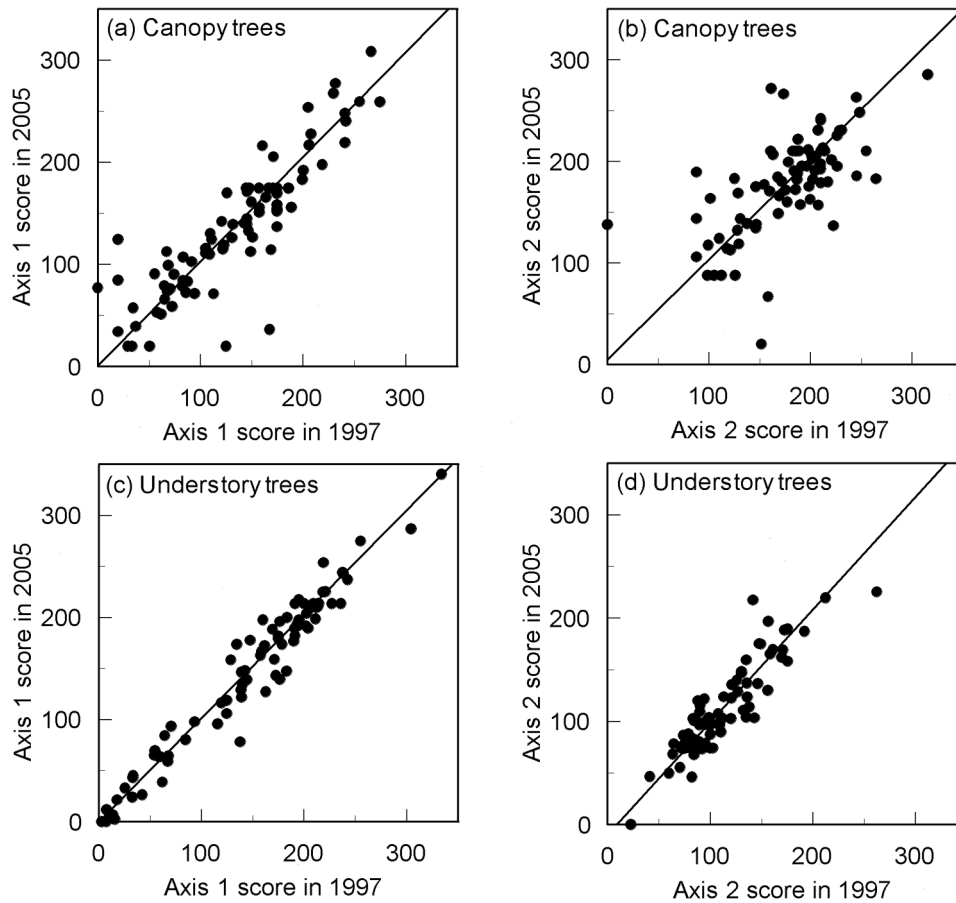


Table 2. Regression equation of the relationship between the DCA axis scores in 2005 and those in 1997 for canopy trees (DBH ≥ 10 cm) and understory trees ($1 \leq$ DBH < 10 cm).

Size class	y	x	Slope	Intercept	R^2	n
Canopy	A1 ₂₀₀₅	A1 ₁₉₉₇	1.026 (0.885 to 1.167)	1.1 (-22.1 to 19.9)	0.77	87
Canopy	A2 ₂₀₀₅	A2 ₁₉₉₇	0.971 (0.762 to 1.181)	6.2 (-32.6 to 45.0)	0.43	87
Understory	A1 ₂₀₀₅	A1 ₁₉₉₇	1.025 (0.963 to 1.087)	-4.1 (-14.4 to 6.3)	0.96	87
Understory	A2 ₂₀₀₅	A2 ₁₉₉₇	1.101 (0.970 to 1.233)	-11.6 (-26.7 to 3.6)	0.83	87

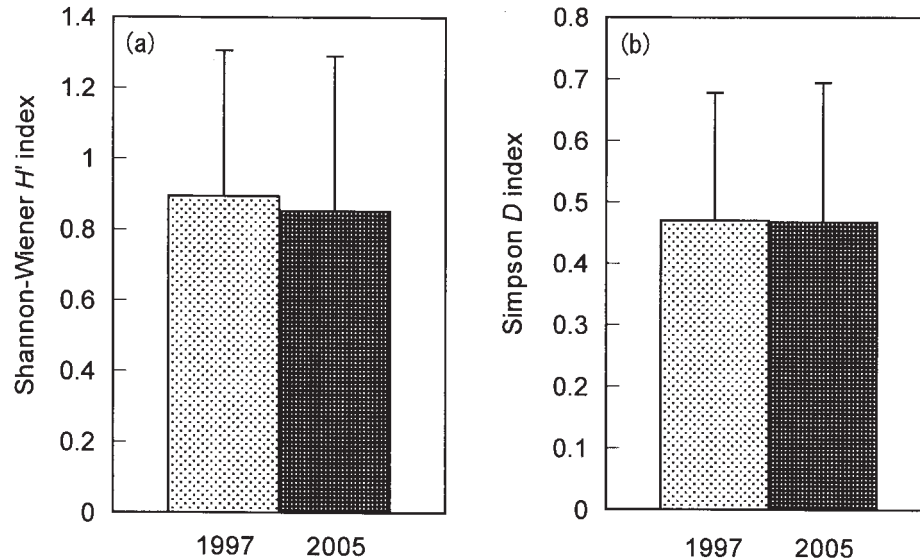
Note: Values in parenthesis are the 95% CIs. A reduced major axis regression was used for the calculation. All regressions are significant at the 1% level. A1₂₀₀₅, axis 1 score in 2005; A1₁₉₉₇, axis 1 score in 1997; A2₂₀₀₅, axis 2 score in 2005; A2₁₉₉₇, axis 2 score.

ference in the susceptibility at this site. Alternatively, infection by beech bark disease might have weakened *F. grandifolia* (Rhoads et al. 2002) and led to its greater susceptibility to ice damage, but the disease only recently reached MSH. Finally, another possible explanation for the greater ice damage to beech over time may be that branch sprouting is more common in *A. saccharum* than in *F. grandifolia* after ice storms (Duguay et al. 2001; Brommit et al. 2004). The ability of *A. saccharum* to branch sprout may have allowed individuals to fix enough carbon to maintain a positive carbon balance, reducing poststorm rates of mortality compared with beech.

Assuming that the spatial distributions of *A. saccharum* and *F. grandifolia* in the reserve were random, we would expect species-specific differences in susceptibility to ice

damage to shift the pattern of codominance in this forest. Given that *F. grandifolia* suffered more damage at our study site, we can expect *A. saccharum* to become more dominant over time (De Steven et al. 1991; Lafon 2004). However, our study showed that plots dominated by *A. saccharum* prior to the storm continue to be dominated by *A. saccharum* after the storm in both the canopy and understory; the same outcome prevailed in plots dominated by *F. grandifolia*. This pattern of persistent local dominance arises in a degree of spatial segregation of *F. grandifolia* and *A. saccharum* at our study site, which is brought about primarily by edaphic factors (Arii and Lechowicz 2002). If the two species are spatially segregated to some degree, the differences in susceptibility will not yield significant changes in species dominance; the damaged trees will simply be re-

Fig. 5. Shannon–Wiener H' index (a) and Simpson D index (b) in 1997 and 2005. Error bars are SDs.



placed by the same locally favored species, preserving the reserve-wide pattern of codominance.

Although the ice storm of 1998 caused significant damage to the trees and opened up the canopy (Hooper et al. 2001), we did not detect any significant increase in the shade-intolerant species; all species showed a decrease in both basal area and density. The only exception is *B. alleghaniensis*, which showed an increase in stem density; however, the difference is minimal, and it is not expected to influence species composition. In a beech–maple forest studied by De Steven et al. (1991), shade-intolerant species increased in abundance, particularly at locations hard hit by the storm. This is contrary to our finding; their study site reported many shade-intolerant species in the canopy prior to the storm, which may have provided seed sources for recruitment under the storm-damaged canopy (De Steven et al. 1991). At our site, beech and sugar maple dominated the canopy prior to the storm, and this may have limited the successful colonization and establishment of shade-intolerant species after the storm.

In conclusion, we found that (i) the severe ice storm of 1998 substantially decreased stand basal area and total density in this old-growth forest, (ii) the susceptibility to the ice storm was higher in *F. grandifolia* than in *A. saccharum* (large-sized trees), and (iii) the ice storm had little influence on species composition and diversity. The dominance of *A. saccharum* and *F. grandifolia* was maintained after the ice storm, most likely because of a degree of spatial segregation between the two species. Thus, our working hypothesis that the severe ice storm of 1998 might reduce the relative dominance of *F. grandifolia*, was rejected. Although some earlier studies suggested that increases in shade intolerant species effectively shifted the forest into an earlier successional stage after an ice storm (Downs 1938; Siccama et al. 1976), we did not observe this pattern. Rather, the ice storm appeared to accelerate the turnover of the canopy trees, which remain dominated by *F. grandifolia* and *A. saccharum*.

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References

- Arii, K., and Lechowicz, M.J. 2002. The influence of overstory trees and abiotic factors on the sapling community in an old-growth *Fagus–Acer* forest. *Ecoscience*, **9**: 386–396.
- Arii, K., and Lechowicz, M.J. 2007. Changes in understory light regime in a beech–maple forest after a severe ice storm. *Can. J. For. Res.* **37**. In press.
- Arii, K., Hamel, B.R., and Lechowicz, M.J. 2005. Environmental correlates of canopy composition at Mont St. Hilaire, Quebec, Canada. *J. Torrey Bot. Soc.* **132**: 90–102.
- Beaudet, M., Messier, C., Pa, D., Brisson, J., and Bergeron, Y. 1999. Possible mechanisms of sugar maple regeneration failure and replacement by beech in the Boisk-des-Muir old growth forest, Quebec. *Ecoscience*, **6**: 264–271.
- Boerner, R.E.J., Runge, S.D., Cho, D.-S., and Kooser, J.G. 1988. Localized ice storm damage in an Appalachian Plateau watershed. *Am. Midl. Nat.* **119**: 199–208. doi:10.2307/2426069.
- Bragg, D.C., Shelton, M.G., and Zeide, B. 2003. Impacts and management implications of ice storms on forests in the southern United States. *For. Ecol. Manage.* **186**: 99–123. doi:10.1016/S0378-1127(03)00230-5.
- Braun, E.L. 1950. *Deciduous forests of eastern North America*. The Blakiston Co., Philadelphia, Penn.
- Brisson, J., Bergeron, Y., Bouchard, A., and Leduc, A. 1994. Beech–maple dynamics in an old-growth forest in southern Quebec, Canada. *Ecoscience*, **1**: 40–46.
- Brommit, A.G., Charbonneau, N., Contreras, T.A., and Fahrig, L. 2004. Crown loss and subsequent branch sprouting of forest trees in response to a major ice storm. *J. Torrey Bot. Soc.* **131**: 169–176.

- Bruederle, L.P., and Stearns, F.W. 1985. Ice storm damage to a southern Wisconsin mesic forest. *Bull. Torrey Bot. Club*, **112**: 167–175. doi:10.2307/2996413.
- Carvell, K.L., Tryon, E.H., and True, R.P. 1957. Effects of glaze on the development of Appalachian hardwoods. *J. For.* **55**: 130–132.
- Chagnon, S.A. 2003. Characteristics of ice storms in the United States. *J. Appl. Meteorol.* **42**: 630–639.
- Cook, B.D. 1971. Tree-age distribution in a northern hardwood forest. M.Sc. thesis, Department of Geography, McGill University, Montréal, Que.
- Cortinas, J.V., Bernstein, B.C., Robbins, C.C., and Strapp, J.W. 2004. An analysis of freezing rain, freezing drizzle, and ice pellets across the United States and Canada: 1976–90. *Weather Forecast.* **19**: 377–390. doi:10.1175/1520-0434(2004)019<0377:AAOFRF>2.0.CO;2.
- De Steven, D., Kline, J., and Matthiae, P.E. 1991. Long-term changes in a Wisconsin *Fagus-Acer* forest in relation to glaze storm disturbance. *J. Veg. Sci.* **2**: 201–208. doi:10.2307/3235952.
- Downs, A.A. 1938. Glaze damage in the birch-beech-maple-hemlock type of Pennsylvania and New York. *J. For.* **36**: 63–70.
- Duguay, S.M., Arie, K., Hooper, M., and Lechowicz, M.J. 2001. Ice storm damage and early recovery in an old-growth forest. *Environ. Monit. Assess.* **67**: 97–108. doi:10.1023/A:1006464511158. PMID:11339708.
- Environment Canada. 2002. Canadian climate normals, St. Hubert A., Quebec (1928–1990) [online]. Meteorological Service of Canada, Downsview, Ont. Available from http://www.msc.ec.gc.ca/climate/climate_normals/show_normals/show_normals_e.cfm [Updated 13 March 2002; accessed 22 April 2002].
- Falster, D.S., Warton, D.I., and Wright, I.J. 2003. (S)MATR: standardised major axis tests and routines, version 1.0. Department of Biology, Macquarie University, North Ryde, NSW, Australia. [<http://www.bio.mq.edu.au/ecology/SMATR>].
- Forrester, J.A., and Runkle, J.R. 2000. Mortality and replacement patterns of an old-growth *Acer-Fagus* woods in the Holden Arboretum, northeastern Ohio. *Am. Midl. Nat.* **144**: 227–242. doi:10.1674/0003-0031(2000)144[0227:MARPOA]2.0.CO;2.
- Fox, J.F. 1977. Alternation and coexistence of tree species. *Am. Nat.* **111**: 69–89. doi:10.1086/283138.
- Greene, D.F., Proulx, O.J., and Jones, K.F. 2007. The effect of icing events on the death and regeneration of North American trees. *In* *Plant disturbance ecology: the process and the response*. Edited by E.A. Johnson and K. Miyanishi. Elsevier, San Diego, Calif. In press.
- Hooper, M.C., Arie, K., and Lechowicz, M.J. 2001. Impact of a major ice storm on an old-growth hardwood forest. *Can. J. Bot.* **79**: 70–75. doi:10.1139/cjb-79-1-70.
- Hopkin, A., Williams, T., Sajan, R., Pedlar, J., and Nielsen, C. 2003. Ice storm damage to eastern Ontario forests: 1998–2001. *For. Chron.* **79**: 47–53.
- Jacobs, D.M. 2000. February 1994 ice storm: forest resource damage assessment in northern Mississippi. USDA For. Serv. Res. Bull. SRS-54.
- Kerry, M., Kelk, G., Etkin, D., and Kalkok, S. 1999. The ice storm of 1998. *Environment*, **41**: 7–33.
- Lafon, C.W. 2004. Ice-storm disturbance and long-term forest dynamics in the Adirondack Mountains. *J. Veg. Sci.* **15**: 267–276. doi:10.1658/1100-9233(2004)015[0267:IDALFD]2.0.CO;2.
- Lemon, P.C. 1961. Forest ecology of ice storms. *Bull. Torrey Bot. Club*, **88**: 21–29. doi:10.2307/2482410.
- Maycock, P.F. 1961. Botanical studies on Mont St. Hilaire, Rouville County, Quebec: general description of the area and a floristic survey. *Can. J. Bot.* **39**: 1293–1325.
- Melancon, S., and Lechowicz, M.J. 1987. Differences in the damage caused by glaze ice on codominant *Acer saccharum* and *Fagus grandifolia*. *Can. J. Bot.* **65**: 1157–1159.
- Millward, A.A., and Kraft, C.E. 2004. Physical influences of landscape on a large-extent ecological disturbance: the northeastern North American ice storm of 1998. *Landscape Ecol.* **19**: 99–111. doi:10.1023/B:LAND.0000018369.41798.2f.
- Oliver, C.D., and Larson, B.C. 1996. *Forest stand dynamics*. John Wiley & Sons, New York.
- Parker, G.R., Leopold, D.J., and Eichenberger, J.K. 1985. Tree dynamics in an old-growth, deciduous forest. *For. Ecol. Manage.* **11**: 31–57. doi:10.1016/0378-1127(85)90057-X.
- Poulson, T.L., and Platt, W.J. 1996. Replacement patterns of beech and sugar maple in Warren Woods, Michigan. *Ecology*, **77**: 1234–1253. doi:10.2307/2265592.
- Proulx, O.J., and Greene, D.F. 2001. The relationship between ice thickness and northern hardwood tree damage during ice storms. *Can. J. For. Res.* **31**: 1758–1767. doi:10.1139/cjfr-31-10-1758.
- Rebertus, A.E., Shirley, S.F., Richards, R.H., and Roofers, K.M. 1997. Ice storm damage to an old-growth oak-hickory forest in Missouri. *Am. Midl. Nat.* **137**: 48–61. doi:10.2307/2426754.
- Rhoads, A.G., Hamburg, S.P., Fahey, T.J., Siccama, T.G., Hane, E.N., Battles, J., Cogbill, C., Randall, J., and Wilson, G. 2002. Effects of an intense ice storm on the structure of a northern hardwood forest. *Can. J. For. Res.* **32**: 1763–1775. doi:10.1139/x02-089.
- Runkle, J.R. 1990. Eight years change in an old *Tsuga canadensis* woods affected by beech bark disease. *Bull. Torrey Bot. Club*, **117**: 409–419. doi:10.2307/2996838.
- Runkle, J.R. 1996. Central mesophytic forests. *In* *Eastern old-growth forests: prospects for rediscovery and recovery*. Edited by M.B. Davis. Island Press, Washington, D.C. pp. 161–177.
- Ryall, K.L., and Smith, S.M. 2005. Patterns of damage and mortality in red pine plantations following a major ice storm. *Can. J. For. Res.* **35**: 487–493. doi:10.1139/x04-180.
- Scarr, T.A., Hopkin, A.A., and Howse, G.M. 2003. Aerial sketch-mapping of the 1998 ice storm in eastern Ontario. *For. Chron.* **79**: 91–98.
- Shortle, W.C., Smith, K.T., and Dudzik, K.R. 2003. Tree survival and growth following ice storm injury. USDA For. Serv. Northeast. Res. Stn. Rep. NE-723.
- Siccama, T.G., Weir, G., and Wallace, K. 1976. Ice damage in a mixed hardwood forest in Connecticut in relation to *Vitis* infestation. *Bull. Torrey Bot. Club*, **103**: 180–183. doi:10.2307/2484493.
- Sokal, R.R., and Rohlf, F.J. 1995. *Biometry*. 3rd ed. Freeman, New York.
- Van Dyke, O. 1999. A literature review of ice storm impacts on forests in eastern North America. Ontario Ministry of Natural Resources, Southcentral Sciences Section, Pembroke, Ont. Tech. Rep. No. 112.
- Whitney, H.E., and Johnson, W.C. 1984. Ice storms and forest succession in southwestern Virginia. *Bull. Torrey Bot. Club*, **111**: 429–437. doi:10.2307/2995892.
- Woods, K.D. 1979. Reciprocal replacement and the maintenance of codominance in a beech-maple forest. *Oikos*, **33**: 31–39. doi:10.2307/3544508.
- Woods, K.D. 1984. Patterns of tree replacement: canopy effects on understory pattern in hemlock-northern hardwood forests. *Vegetatio*, **56**: 87–107.