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Crown loss and subsequent branch sprouting of forest trees in response to a major ice storm[1]

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BROMMIT, A., N. CHARBONNEAU, T. A. CONTRERAS and L. FAHRIG (Department of Biology, Carleton University, Ottawa, Ontario, Canada, K1S 5B6). Crown loss and subsequent branch sprouting of forest trees in response to a major ice storm. J. Torrey Bot. Soc. 131: 169–176. 2004.—In January of 1998, a severe ice storm hit much of eastern Ontario, western Quebec, and the northeastern United States. The objective of this study was to determine whether this disturbance could result in short-term changes in canopy dominance by different tree species. We measured canopy loss in 1998 of 2,919 trees in 164 forest plots distributed across the Ottawa, Ontario region. In 2000, we measured branch sprouting in the same trees. We found a positive cross-species relationship between the proportion of stems damaged by the ice storm and the proportion of stems showing branch sprouting in response to damage ($r = 0.498$, $P = 0.01$). *Prunus serotina* and *Acer rubrum* showed exceptionally high sprouting-to-damage ratios, whereas *Fagus grandifolia* and *Populus tremuloides* showed exceptionally low ratios. Mean percent crown loss and mean number of branch sprouts on damaged stems were also correlated across species ($r = 0.404$, $P = 0.04$). *Prunus serotina* and *Quercus macrocarpa* showed exceptionally high mean number of branch sprouts and *Carpinus caroliniana* showed exceptionally low mean number of branch sprouts compared to other species. No conifer species showed any branch sprouting. We predict that due to these different sprouting-to-damage ratios, species such as *Prunus serotina*, *Acer rubrum*, and possibly *Quercus macrocarpa*, may become better represented in the forest canopy while *Fagus grandifolia*, *Populus tremuloides*, and conifer species may become less well represented in the canopy in the short-term. These changes in canopy dominance may be prolonged if ice storms become more common due to climate change.

Key words: canopy loss, sprouting, ice storm, forest disturbance, disturbance response, interspecies comparison, tree damage, tree recovery, glaze storm, succession, climate change, canopy composition, forest structure.

In January 1998 much of eastern Ontario, western Quebec, and the north-eastern United States was hit by a severe ice storm. This ice storm was one of the most extensive in North American history, affecting about 62 million hectares across Canada and the northeastern United States (Irland 1998). It was estimated that approximately 6 to 9 cm of ice was deposited in the Ottawa, Ontario region where the data for this study were collected (Schueler, unpublished data; see also Kerry et al. 1998).

Different tree species can sustain different levels of crown damage as the result of natural disturbances (Lemon 1961, Whitney and Johnson 1984, Zimmerman et al. 1994). It has been postulated that species differences in susceptibilities to ice storm-related crown damage are the result of differences in green wood strength and crown shape (Lemon 1961, Bruederle and Stearns 1985). Various studies in eastern North America on the effects of ice loading on tree crowns have suggested that: i) *Ulmus americana*, *Tilia americana*, *Populus tremuloides*, *Populus grandidentata*, and *Prunus serotina* are highly susceptible to crown damage, ii) *Acer saccharum* and *Acer rubrum* are only moderately damaged during ice storms, and iii) *Quercus rubra*, *Quercus alba*, *Ostrya virginiana*, and many *Pinus* spp. generally suffer low mean crown loss (Lemon 1961, Whitney and Johnson 1984, Bruederle and Stearns 1985, Rebertus et al. 1997). In addition, Lemon (1961) and Whitney and Johnson (1984) found that pioneer species of genera such as *Ulmus*, *Betula*, and *Populus* experienced more severe damage than species commonly associated with mature forests and they suggested that ice storms may therefore accelerate forest succession.

If ice storms cause more damage to some species than to others, does this result in a short-term change in the species composition of the

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forest canopy? To answer this question one must examine the rate of regrowth of the canopy through vegetative sprouting from the trunk and from branches (hereafter termed "branch sprouting"), in response to ice storm-related damage. Branch sprouting in mature trees is an induced response to injury following damage. Epicormic buds, i.e., buds responsible for growth of new branches from the tree trunk or main branches, are found in or below the tree bark. These buds consist of primordial leaf and scale tissue. They are typically connected to interior vascular tissue and pith in the main stem by "traces" of vascular and cambium tissues, which are produced by the stem and keep the bud near the surface of the stem as it increases in diameter. In some species these buds can persist for years and even decades, but with damage or altered environmental conditions, hormonal changes can induce the development of the epicormic buds into new branches. Often, epicormic buds will produce axillary buds, particularly if the primary bud has died or been damaged, resulting in clusters of epicormic buds (Fink 1983, Fontaine 1998, del Tredici 2001).

The main question we address in this paper is: Did tree species that sustained more damage to their crowns during the 1998 ice storm also have higher rates of branch sprouting? If the answer is yes, then the composition of the forest canopy may not change much during the few years following the ice storm, since species whose crowns are heavily damaged by the disturbance quickly fill in their own canopy gaps.

This question has not been addressed in the context of vegetation response to ice storm damage. However, it is known that different species have different tendencies for sprouting in response to other disturbances; these differences may be related to stem and crown size and the successional stage of the species. Peterson (2000) found significant differences among three tree species in their tendencies to sprout after being damaged by tornadoes, with *Fagus grandifolia* and *Acer saccharum* most likely to sprout and *Tsuga canadensis* least likely. Peterson and Rebertus (1997) also found significant differences in post-tornado sprouting among species, but in their study *Liquidambar styraciflua* and *Ulmus* spp. were most likely to sprout and *Acer saccharum* and *Fraxinus* species least likely. They suggest that difference in sprouting may be associated with tree size in that larger trees were less likely to sprout. In addition, Zimmerman et al. (1994) studied vegetation recovery from hurricane winds in a subtropical wet forest and found that not only did pioneer species suffer greater crown damage, they also had a lower capacity to sprout new branches and stems than non-pioneer species. This again suggests that disturbances to forest canopy may accelerate forest succession.

The purpose of this study was to determine whether species that experienced high levels of canopy damage from the 1998 ice storm also had high rates of branch replacement, or sprouting. If so, then the overall effects of ice loading by an ice storm, even one as severe as the 1998 event, should have little effect on forest canopy composition in the short term. However, several studies have suggested that disturbances such as ice storms may accelerate changes in the species composition of some forest stands (Lemon 1961, Whitney and Johnson 1984, Zimmerman et al. 1994) by removing or reducing the crowns of early successional species from the forest canopy. These species appear to be 1) more susceptible to damage due to ice loading (weaker branches and/or a crown architecture conducive to ice accumulation) and 2) less likely to produce new branches in response to crown damage.

Materials and Methods. The study was conducted in 164 forest plots within 80 km of Ottawa, Ontario, Canada. The forest canopy in our study region is composed mainly of *A. saccharum*, *T. americana*, and *Fraxinus* spp. Mature *Pinus* spp. (particularly *P. strobus*) increases in prevalence in the more well-drained western sites in the study region, and *Fraxinus pennsylvanica* is a more important component of the forest canopy in the wetter sites in the eastern area of our study region. At all our study sites, the subcanopy is composed primarily of *T. americana*, *Fraxinus* spp., *O. virginiana*, and *U. americana*. The forests in our study region, including our study plots, are primarily second-growth; the original forests were cut between about 150 and 80 years ago.

During the summer of 1998, 164 interior forest plots across an area of approximately 3000 km^2 were sampled to assess crown damage to woody vegetation associated with the 1998 ice storm. Each plot was 12.5 × 25 m, and within each plot, in 1998, the species and percent crown loss were recorded for each woody stem that was at least 10 cm DBH. Percent crown loss was estimated by visually estimating the volume of the crown that was missing due to ice damage, using 10% increments (modified from Rebertus et al. 1997). Percent crown loss was estimated only for trees that exhibited ice damage. This damage was readily detected, due to the magnitude of the ice storm event. However, to decrease potential observer bias, wherever possible broken branches lying near damaged trees were used to verify estimates of missing crown volume as a result of the ice storm.

In 2000 the 164 plots sampled in 1998 were revisited and the number of branch sprouts that grew in response to damage caused by the ice storm was also recorded for each tree. Sprouts were only counted if found on trees that had clearly been damaged by the ice storm. They typically occurred on the branch or trunk immediately below the point where a previous branch had been broken by ice loading. We did not include sprouts arising from specialized underground stems, since the purpose of this study was to evaluate the short-term recovery of the canopy from the ice storm. Branch sprouts were easily identified by their green color, smooth surface, and their long, spindly growth form. We revisited the plots during the summer of 2001 to record any additional branch sprouting. However, almost no new sprouts were observed in 2001. Therefore, only sprouting data from 2000 were used in the analyses.

DATA ANALYSIS. We first tested to see whether species differed significantly in their ice storm damage and sprouting responses. For ice storm damage we conducted 1) a *G*-test of independence of species vs. damage, where damage was recorded qualitatively for each stem as "damaged" or "not damaged" and 2) an ANOVA of percent crown loss on species for damaged stems only. For the sprouting response, we conducted 1) a *G*-test of independence of species vs. sprouting, where sprouting was recorded qualitatively for each damaged stem as "sprouted" or "did not sprout" and 2) an ANOVA of number of sprouts on species (for sprouting stems only).

We conducted two cross-species regression analyses. In the first analysis we regressed the proportion of damaged stems that showed branch sprouting on the proportion of stems that sustained damage from the ice storm. In the second analysis we regressed the mean number of branch sprouts per stem (for stems that produced branch sprouts) on the mean percent crown loss, corrected for between-plot differences. In the second analysis we corrected for between-plot differences in crown loss to account for any differences between plots that could result in between-plot variation in ice storm damage (e.g., between-plot differences in ice deposition, stem density, slope, or aspect). We corrected for between-plot differences in damage by conducting a one-way ANOVA of percent crown loss (over all stems in the plot) on a class variable for plot identification. We then calculated residual mean percent crown loss for each species. These residual mean crown loss values were then used as the predictor variable in the second regression analysis (above). This correction effectively removed any between-plot variation in percent crown loss from the between-species analysis.

From the regression analyses, we identified species that exhibited exceptionally high or exceptionally low sprouting probabilities and number of sprouts, relative to damage. These species were identified as those with values of sprouting probability or mean number of sprouts above or below the 75 % confidence intervals for their expected values, based on the regression analyses. We also conducted within-species correlations between percent crown loss and number of sprouts for stems that sprouted.

Results. We sampled 2,919 trees of 26 tree species across the Ottawa-Carleton region. Sixty percent of trees showed crown loss from the ice storm in 1998. Average crown loss for all trees in our study plots was 23% $\pm$ 0.5 (S.E.). Canopy stems suffered the largest crown losses (emergent crowns, 19% $\pm$ 2; dominant crowns, 28% $\pm$ 2; codominant crowns, 36% $\pm$ 1). Subcanopy trees (intermediate and understory crown classes) suffered less crown loss than canopy trees (16% $\pm$ 1). The average crown loss of damaged trees was 54% $\pm$ 0.9. Twenty-five percent of damaged stems had branch sprouting in 2000. The mean number of sprouts per stem that sprouted was 13 $\pm$ 0.64.

Although we did not have direct estimates of ice accumulation for our study plots, we obtained an estimate for each plot from a trend surface analysis for the region in Ontario affected by the storm, based on measurements of ice lens thickness in snow profiles (Schueler, unpublished data; Lautenschlager and Nielsen 1999). The ice deposition estimates ranged from 5.9 to 9.3 cm of ice across our plots, and the trend surface model showed a slight increase in ice deposition from southwest to northeast across the study region (Schueler, unpublished data). There was a significant correlation across our study plots between the ice deposition estimates for the plots (from the trend surface model) and the average percent crown loss ($r = 0.63$, $P = 0.0003$).

Woody species differed in the crown damage sustained due to the ice storm, measured as both the number of stems that were damaged ($G = 400$, df = 25, $P < 0.0001$) and percent crown loss of damaged stems ($F = 6.79$, df = 25, $P < 0.0001$). Generally, the deciduous hardwoods showed a greater susceptibility to crown loss than the conifers (Table 1). *Quercus alba* was an exception in that relatively few *Q. alba* stems (34 %) of that species showed crown loss. *Pinus strobus*, on the other hand, was one conifer that showed a relatively high percentage of crown loss (57 % of stems damaged). In our sampling plots, more than 90 % of *Carpinus caroliniana*, *Populus tremuloides*, and *Acer saccharinum* stems were damaged, with all *C. caroliniana* stems exhibiting some degree of ice storm related damage.

Woody species also differed in their sprouting response to ice storm damage, measured as both the number of damaged stems that showed some branch sprouting ($G = 233$, df = 25, $P < 0.0001$) and the number of branch sprouts produced by stems that sprouted ($F = 3.89$, df = 25, $P < 0.0001$). About 50% of damaged stems of *Acer saccharinium*, *A. rubrum*, and *P. serotina* showed at least some sprouting, whereas less than 10% of damaged *F. grandifolia* and *Q. rubra* showed sprouting, and none of the conifer species sprouted (Table 1). Sprouting stems of *P. serotina* and *Quercus macrocarpa* produced particularly large numbers of sprouts (on average 41 and 39 sprouts per sprouting stem, respectively; Table 1).

Species that had higher proportions of stems damaged from the ice storm generally had higher proportions of damaged stems that sprouted (Fig. 1; $r = 0.498$, $P = 0.01$). There were some exceptions to this relationship. Based on the 75 % confidence intervals, *Prunus serotina* and *Acer rubrum* showed unusually high proportions of damaged stems that sprouted relative to the proportion of stems damaged while *Fagus grandifolia* and *P. tremuloides* showed unusually low proportions of damaged stems that sprouted relative to the proportion of stems damaged (Fig. 1). None of the conifer stems in our plots produced branch sprouts in response to crown loss. There was also a significant positive relationship between the mean number of branch sprouts per sprout producing stem and the residual mean crown loss (Fig. 2; $r = 0.404$, $P = 0.04$). Based on the 75% confidence intervals, *P. serotina* and *Q. macrocarpa* produced unusually high mean numbers of sprouts per sprouting stem, relative to crown loss, and *C. caroliniana* produced an unusually low number of sprouts per sprouting stem, relative to crown loss (Fig. 2).

Discussion. Sixty percent of all the trees in this study showed some crown loss attributable to the ice storm. Duguay et al. (2001) found that 97 % of the trees in an old-growth forest in southwestern Quebec were damaged after the same ice storm. The difference is likely due to the greater ice deposition in southwestern Quebec (8 to 10 cm) than in eastern Ontario (6 to 9 cm). Rebertus et al. (1997) found that in an old-growth oak-hickory forest in Missouri only 27 % of the trees were damaged with an ice deposition of 2.5 cm, which is considerably less than the ice deposition from the 1998 ice storm.

As we expected, there were species differences in the susceptibility of trees to ice damage. Direct comparisons with other studies are difficult due to differences in ice loads, forest compositions, and methods of assessing damage. However, in general, the differences we report in species susceptibility to ice damage are consistent with those reported from studies on the same ice storm (Duguay et al. 2001, Hooper et al. 2001, Manion et al. 2001, Proulx and Greene 2001, Zarnovican 2001). For example, similar to our study, Duguay et al. (2001) and Proulx and Greene (2001) found high crown damage to *F. grandifolia*, *Betula alleghaniensis*, and *P. tremuloides*, and low crown damage to *T. canadensis*. However, both these studies also found high crown damage to *A. saccharum*, which was only moderately damaged in our study.

Overall, 25 % of damaged trees in this study showed branch sprouting. Only one previous study has looked at sprouting in response to ice storms. Duguay et al. (2001) reported that 53 % of trees in a site near Montréal, Canada that were damaged by the 1998 ice storm sprouted new shoots and/or branch sprouts. We assume that this higher rate of sprouting was due to the greater damage sustained by trees due to greater ice-loading in the Quebec study. Like the Quebec study, we found that *P. serotina*, *A. rubrum*, *A. saccharinum*, *F. americana* and *F. pennsylvanica* were most likely to produce branch sprouts, while *F. grandifolia*, *Q. rubra* and *P. tremuloides* were least likely to sprout and generally had a low mean number of branch sprouts

Table 1. Damage statistics, sprouting statistics, and cross-stem correlations between percent crown loss and number of sprouts for damaged stems for each species.

Species	Number of stems sampled	Proportion of stems damaged	Mean percent crown loss of damaged stems (S.E.)	Proportion of damaged stems that sprouted	Mean number of sprouts per stem that sprouted (S.E.)	Cross-stem correlations (r) between percent crown loss and number of sprouts (P-value)**
Carpinus caroliniana Walt.	10	1.00	78.00 (10.93)	0.30	5.33 (0.88)	0.33 (0.338)
Populus tremuloides Michx.	118	0.94	66.00 (11.94)	0.11	10.25 (2.90)	0.14 (0.107)
Acer saccharinum L.	78	0.91	65.00 (4.33)	0.48	16.91 (3.22)	0.00 (0.588)
Fagus grandifolia Ehrh.	77	0.83	52.00 (4.70)	0.06	14.00 (8.09)	0.00 (0.743)
Carya cordiformis Wang.	50	0.80	57.00 (5.03)	0.30	19.42 (4.45)	0.32 (0.047)
Tilia americana L.	227	0.78	61.00 (8.01)	0.24	11.74 (2.13)	0.00 (0.498)
Ulmus americana L.	100	0.75	59.00 (39.94)	0.24	15.78 (5.46)	0.17 (0.130)
Populus grandidentata Michx.	12	0.75	54.00 (3.39)	0.22	12.50 (4.50)	−0.22 (0.552)
Fraxinus americana L.	158	0.73	64.00 (3.30)	0.41	14.91 (1.94)	0.17 (0.060)
Fraxinus pennsylvanica Marsh.	300	0.72	62.00 (2.65)	0.43	18.89 (1.41)	0.42 (<0.0001)
Betula alleghaniensis Britt.	23	0.70	59.00 (8.65)	0.31	12.40 (4.81)	0.32 (0.225)
Prunus serotina Ehrh.	13	0.69	72.00 (10.76)	0.56	41.20 (18.73)	0.37 (0.320)
Fraxinus nigra Marsh.	58	0.59	69.00 (6.16)	0.29	6.90 (1.68)	0.00 (0.788)
Pinus strobus L.	95	0.57	21.00 (6.14)	0.00	n.a.	n.a.
Acer saccharum Marsh.	596	0.57	41.00 (1.89)	0.22	9.29 (1.04)	0.3 (<0.0001)
Betula papyrifera Marsh.	38	0.50	57.00 (8.16)	0.21	4.75 (0.63)	0.33 (0.162)
Quercus macrocarpa Michx.	16	0.50	43.00 (5.56)	0.12	39.00*	0.62 (0.104)
Quercus rubra L.	94	0.49	36.00 (3.92)	0.09	3.50 (1.50)	0.00 (0.725)
Acer rubrum L.	162	0.45	54.00 (4.24)	0.45	11.18 (2.51)	0.17 (0.140)
Thuja occidentalis L.	162	0.43	46.00 (2.92)	0.00	n.a.	n.a.
Ostrya virginiana (Mill.) K. Koch	320	0.42	58.00 (3.40)	0.26	10.51 (1.37)	0.26 (0.002)
Pinus resinosa Ait.	17	0.41	57.00 (5.48)	0.00	n.a.	n.a.
Tsuga canadensis (L.) Carr.	50	0.38	41.00 (4.81)	0.00	n.a.	n.a.
Picea glauca (Moench) Voss	20	0.35	67.00 (14.09)	0.00	n.a.	n.a.
Quercus alba L.	41	0.34	35.00 (13.36)	0.14	14.00 (6.00)	0.37 (0.192)
Abies balsamea (L.) Mill.	84	0.19	62.00 (11.23)	0.00	n.a.	n.a.

* Only one stem had sprouts.
** Correlations were conducted across all damaged stems; sample size for each correlation is the number of stems sampled times the proportion of stems damaged.

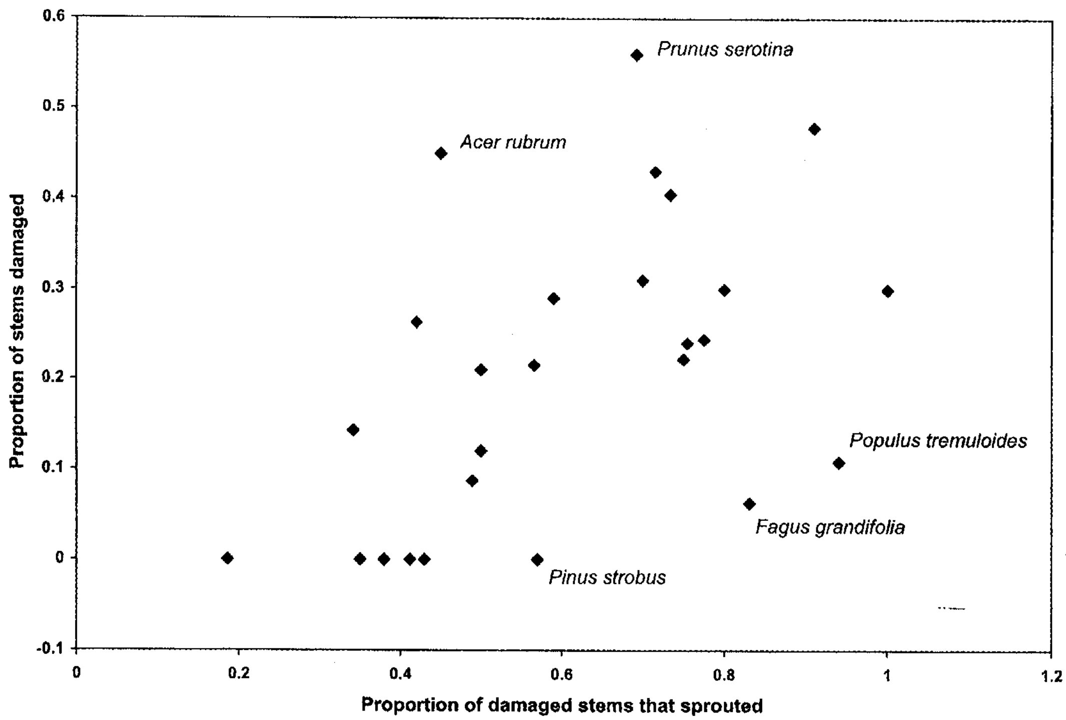

Fig. 1. Proportion of damaged stems that sprouted vs. proportion of stems damaged following a severe ice storm in 1998 (r = 0.498, P = 0.04). Each data point represents a species (see Table 1). Data are from 164 study plots across the region surrounding Ottawa, Ontario, Canada.

per damaged stem (Table 1). None of the damaged conifers in our study produced sprouts, which is also consistent with other studies (Peterson 2000, Zimmerman et al. 1994).

We found a positive correlation across species between the proportion of stems that were damaged by the ice storm and the proportion of those damaged stems that sprouted (Fig. 1; r = 0.498, P = 0.01). We also found a positive cross-species correlation between the mean number of sprouts per stem that sprouted and the mean percent crown loss, after controlling for between-site effects (Fig. 2; r = 0.404, P = 0.04). The latter indicates that the between-species relationship was not confounded by possible correlations between species distribution and site factors such as ice deposition, stem density, drainage, etc. The within-species correlations between number of sprouts and percent crown loss (Table 1) were generally low and only four were statistically significant. However, lack of statistical significance for several of these species is likely due to small sample sizes. For the species showing highly significant relationships, sample sizes were well over 100 stems. Taken together, these results suggest that while most species showed some branch sprouting in response to damage, the number of branch sprouts produced was rather weakly correlated to the amount of damage sustained.

We are unaware of any other studies that have conducted cross-species comparisons between crown damage and branch sprouting following an ice storm. However, Zimmerman et al. (1994) reported a correlation of 0.528 between the frequency of disturbance-related branch damage and sprouting following a hurricane in Puerto Rico, which is similar to the correlation of 0.498 in our study.

Species with the highest proportion of sprouting stems did not necessarily produce the largest number of branch sprouts per stem in this study. For example, *Q. macrocarpa* had the second highest mean number of branch sprouts despite having a low probability of sprouting (12%; Table 1), and although 45, 48, and 41 % of damaged stems of *A. rubrum*, *A. saccharinum* and *F. americana* sprouted (respectively), their mean numbers of branch sprouts were moderate (11,17, and 15 respectively; Table 1).

Several studies suggest that ice storms may accelerate forest succession because pioneer

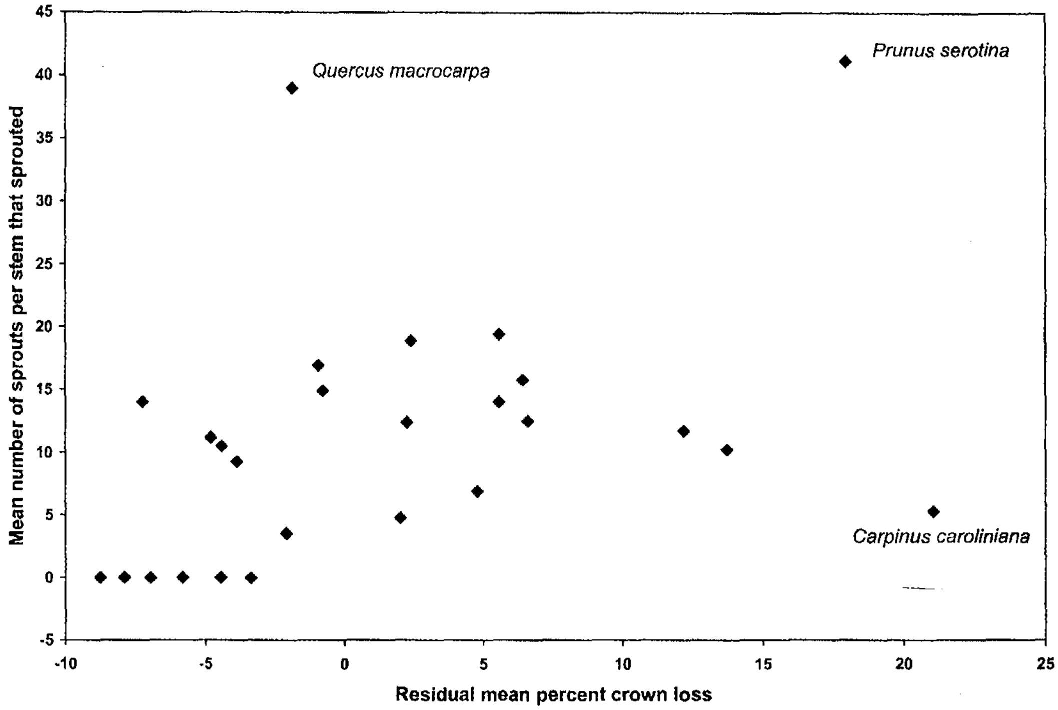

Fig. 2. Mean number of sprouts per stem that sprouted vs. residual mean percent crown loss (i.e., corrected for between-plot differences; see Methods) following a severe ice storm in 1998 (r = 0.404, P = 0.04). Each data point represents a species (see Table 1). Data are from 164 study plots across the region surrounding Ottawa, Ontario, Canada.

species generally sustain greater damage than climax species and have a lower capacity for producing new branches (Lemon 1961, Whitney and Johnson 1984, Zimmerman et al. 1994). Overall our results support this hypothesis. We found that many early successional species (e.g., *B. alleghaniensis*, *P. tremuloides*, *P. grandidentata*, and *U. americana*) had a relatively large proportion of their stems damaged by ice-loading but the number of branch sprouts produced in response to the damage was comparable to species that had fewer stems damaged (e.g., *A. saccharum*; see Table 1). Conversely, many later successional species (e.g., *A. saccharum*, *Q. alba*, and *O. virginiana*) had a lower proportion of stems damaged by the storm but generally had a comparable proportion of damaged stems that exhibited branch sprouting. There were two notable exceptions. *Fagus grandifolia*, a late-successional species, whose stems suffered moderate to high ice storm related damage (on average 83% of stems were damaged with an average of 52% crown loss; see Table 1) showed a very weak branch sprouting response. Also, *A. rubrum*, an early successional species, had a low proportion of stems damaged but a high proportion of damaged stems that exhibited branch sprouting (Table 1).

This study focuses on short-term changes in the composition of forest canopies affected by the 1998 ice storm. It could be argued that in the long-term, replacement of individuals through recruitment should be more important for canopy composition than changes in the canopy due to damage and branch sprouting. However, a study of the understory vegetation in the same plots found that germination of woody seeds did not increase, but was actually suppressed in the year following the storm, and then rebounded to pre-storm levels three years following the storm (Darwin et al. 2004). In addition, vigorous branch sprouting following the ice storm appears to have caused a very rapid closing of the canopy, within two years following the storm (Darwin et al. 2004). Although Darwin et al. (2004) did not look at germination by species, the lack of an increase in germination following the storm makes it unlikely that the storm had an effect on species composition through differential germination.

We suggest that the responses we observed in the canopy could result in long-term changes in canopy composition. It has been predicted that the rate and magnitude of extreme weather disturbances will increase as a result of climate change (Dale et al. 2001). Researchers generally agree that climate change will cause an increase in conditions favoring ice storms in eastern Ontario (Regan 1998). If large, severe ice storms become frequent in our region, our results suggest that *Q. alba*, *A. rubrum* and *A. saccharum* will be more prevalent in the forest canopy and *P. tremuloides*, *F. grandifolia*, and *P. strobus* will be less prevalent in the forest canopy than in the recent past. In addition, early successional tree species (e.g., *Betula alleghaniensis*, *P. tremuloides*, *P. grandidentata*, and *U. americana*) may disappear from the canopy at a higher rate with more frequent ice storms, and a greater susceptibility to damage from ice loading for some later successional species (e.g., *F. grandifolia*, *P. strobus*) may reduce the prevalence of those species in the forest canopy. Ultimately these changes in the forest canopy could even be reflected in the seed and seedling banks, since more common canopy species will produce relatively more seeds.

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