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Response of forest understory vegetation to a major ice storm

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DARWIN, A.T., D. LADD, R. GALDINS, T. A. CONTRERAS AND L. FAHRIG (Dept. of Biol., Carleton University, Ottawa, ON, Canada K1S 5B6). Response of forest understory vegetation to a major ice storm. J. Torrey Bot. Soc. 131:45–52. 2004.—In January of 1998, Ottawa, Ontario was hit with a major ice storm. Detailed pre-storm vegetation data had been collected in 1997 in 164 forest interior sampling plots across a 3,000 km^2 region. These data included information on shrubs/saplings, woody seeds and seedlings, herbaceous seeds and ground cover, and canopy cover. For the four growing seasons following the ice storm (1998–2001), we resampled the same 164 plots. In addition, in 1998 we estimated an ice storm damage index for each plot, and the volume of downed coarse woody debris due to the ice storm in each plot. The objectives of this paper were to examine changes in shrubs/saplings and ground vegetation in response to ice storm damage over the four-year period following the storm. Contrary to our initial expectations, we found that woody seedlings showed a large decrease in density immediately following the storm (1998). Woody seedling density recovered to pre-storm levels by 2001. We hypothesize that the decrease in woody seedling density resulted from reduced seedling germination due to lower light availability on the forest floor, which resulted from the large amount of woody debris created by the storm. We also found that shrub/sapling counts showed a large increase in 1999, most likely due to increased light to the understory, due to opening of the upper canopy. Herbaceous cover increased from 1998 to 2000, but returned to pre-storm levels the following year (2001). The between-plot variation in these understory changes was positively correlated to plot damage from the ice storm, indicating that they resulted from the storm. Overall, it appears that the forest understory plant structure is rapidly returning to pre-ice storm conditions.

Key words: disturbance, forest ecology, ice storm, seed germination, seedling growth, shrubs, saplings, seed bank, forest structure, glaze storm, forest canopy.

Ice storms occur in southern Canada and in the United States each year (Bruederle and Stearns 1985) and, with a return time of 20–100 years, ice storms are more frequent than fires or windstorms in the deciduous forests of eastern Canada (Irland 1998; Zarnovican 2001). They are usually hard to predict but they do not often result in severe widespread damage to trees and shrubs. The severity and effect of the storm will depend on the topography of the area, the location within the storm track, the extent of the affected area, the duration and the total accumulation of ice, and site factors including elevation, slope, slope aspect, and species composition of trees and shrubs that differ in their susceptibility to damage (Bruederle and Stearns 1985; DeSteven et al. 1991; Rebertus et al. 1997).

Normally, the Ottawa area receives 12 to 17 days of freezing rain a year for an average of 45–65 hours (Regan 1998; Kerry et al. 1999). However, a single ice storm in January of 1998 lasted for six days, and in some areas, there was freezing rain for more than 80 hours, resulting in an accumulation of more than 85 mm of ice (Environment Canada 1998; Regan 1998). This storm affected much of eastern Ontario, western Quebec and the northeastern United States. There was widespread damage to woody vegetation and it was the most severe ice storm ever recorded in Canadian history (Anonymous 1999).

The primary source of ice storm damage to woody vegetation is from ice loading on branches which may result in the loss of branches, and snapped or bent stems (Lemon 1961). Twig weight can be increased as much as 30 times due to ice loading (Irland 1998). This damage may result in partial or total crown loss, which may create patchy gaps in the canopy. The degree of damage and stress to trees resulting from ice storms depends on several factors, including

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the species, size and location of the tree relative to forest edge (Bruederle and Stearns 1985; Boerner et al. 1988; Brommit et al. in press).

A number of studies have shown damage to woody vegetation by ice storms (Lemon 1961; White 1979; Whitney and Johnson 1984; Bruederle and Stearns 1985; Melancon and Lechowicz 1987; Seischab et al. 1993). However, many ice storm studies are not able to compare pre-existing forest conditions with post-ice storm conditions and must use control plots for comparison (Whitney and Johnson 1984; Van Dyke 1999). Others only examine data from one growing season and may miss important responses of the forest to ice storm damage that can only be observed over several years (Whitney and Johnston 1984; Rebertus et al. 1997). Our study examines data on understory plants in 164 forest vegetation sampling plots, collected in the year prior to the 1998 ice storm (1997) and during four growing seasons following the ice storm (1998–2001).

The objectives of this study were to examine systematic changes in shrubs/saplings and ground vegetation in response to ice storm damage and to observe changes and/or recovery seen over a four-year period after the storm. We predicted that growth of both shrub/saplings and ground vegetation would increase after the ice storm due to increased light available to the understory. We also predicted an increase in germination of woody and herbaceous seedlings, again due to increased light availability. This increase should be accompanied by a decrease in the size of the seed bank.

Our purpose was not to examine changes in species composition, but rather changes in overall cover or abundance of functional groups in the understory. However, to place the pre- and post-storm vegetation in successional context, we provide here a general description of changes in species composition of the understory over the five-year period of the study (Fahrig et al., in press). The most abundant species in the shrub/sapling layer before the ice storm—*Acer saccharum*, *Fraxinus pennsylvanica*, *Ostrya virginiana*, *Tilia americana*, *Ulmus americana*, and *Acer rubrum*—remained abundant in all four years following the ice storm. However, *Rhamnus cathartica*, an invasive shrub that was rare in our plots before the ice storm, was abundant in all four years following the ice storm. *Abies balsamea* and *Fagus grandifolia* also appeared to become more abundant in the shrub/sapling layer in the years following the ice storm than they were before the storm. Among woody seedlings, *Acer saccharum* was by far the most abundant in all five years. The other most common seedlings before the storm—*Fraxinus* spp., *Acer rubrum*, and *Ostrya virginiana*—remained abundant throughout the four years following the storm. However, seedlings of two vine species, *Rhus radicans* and *Parthenocissus quinquefolia*, were more abundant in the four years following the storm than before the storm. Similarly, the most prevalent species in the herbaceous layer (fern species, *Cyperaceae* species, *Viola* spp., *Maianthmum canadense*) did not change substantially over the five-year period. However, occurrence of *Trillium spp.*, which was common in 1997 (before the storm), declined over the four-year period following the storm. *Oxalis* spp. (ruderals) became quite common following the storm in 1998 and 1999, but then became rare again in 2000 and 2001. Another ruderal, *Taraxacum officinale*, also became more common following the storm, and was still widespread in 2001. Overall, the 1998 ice storm appears to have had a small effect on composition of the dominant species of understory vegetation in our plots.

Materials and Methods. SITE SAMPLING AND GREENHOUSE IDENTIFICATION. In the summer (June–August) of 1997, 164 interior forest plots located randomly in 29 1-km^2 landscapes distributed over a 3,000 km^2 area in the Ottawa (Ontario) area were sampled. The order of sampling was randomized. Following the ice storm of January 1998, the same plots were resampled in the summers of 1998, 1999, 2000 and 2001.

Trees, shrubs/saplings, woody seedlings and herbaceous vegetation were sampled using a nested plot design. All trees (defined as having a diameter at breast height (dbh) $\geq$ 10 cm) were identified and their dbh measured within 12.5 × 25 m tree plots. Nested within each tree plot was a 6.25 × 12.5 m shrub/sapling plot, where all shrubs/saplings (defined as stems over 1 m in height and having a dbh < 10 cm) were identified. The woody seedlings and herbaceous plants were sampled in two 1 m^2 quadrats within each shrub/sapling plot. Woody seedlings were defined as woody stems with cotyledons still present; i.e., woody stems that germinated in the year of sampling. In 1997, only the presence/absence of herbaceous plants was recorded by species. In 1998 and all subsequent years, percent cover by species was recorded as well. In

2000, shrubs/saplings were not sampled but they were sampled again in 2001.

In addition, 15 soil samples were taken at the same time as the vegetation sampling (June–August) in 1997, 1998, 1999, and 2000, at random locations from within the shrub/sapling plots with a soil corer (diameter 4.6 cm, depth 10 cm). The 15 soil samples from each plot were combined, transported to a greenhouse, dried and potted in trays. Soil was spread to a depth of 2–3 cm on 1–1.5 cm of vermiculite. As the seeds germinated, all seedlings were identified as soon as possible and then removed. After no more seedlings emerged the soil was mixed to allow further germination of seeds. This was repeated over a 3–4 month period. The soil was then allowed to dry and placed in cold storage (4 C) to simulate winter conditions, until the following summer. In the following summer, the soil was repotted and the process of identifying seedlings and removing them was repeated. This last step was to ensure that we obtained a sample of species that require a cold treatment (stratification) for germination (Baskin and Baskin 1998).

Plot Canopy Index. The amount of overhead canopy in each plot, looking upward from a height of 2 m, was estimated in each of the five study years (1997, 1998, 1999, 2000 and 2001) during the vegetation sampling (June–August) using methods modified from James and Shugart (1970). The plot canopy index was estimated using a 'sight tube' (a 5 × 30 cm length of PVC pipe with wire cross-hairs affixed to one end of the tube). Starting at the center of the tree plot, the observer took two steps north and stopped. The sight tube was raised over the observer's head and held in a vertical position, i.e., the length of the tube was perpendicular to the ground. A '+' was recorded if the crosshairs were on branches or leaves and a '−' was recorded if the crosshairs were on sky. Two additional steps north were taken and another observation through the sight tube was taken. This was continued for a total of 10 observations and the whole process was then repeated for each of the other three cardinal directions (E, S, and W). The plot canopy index was the sum of the '+' readings for each plot (out of 40).

Coarse Woody Debris. For each tree plot, two randomly located coarse woody debris transects were run for the full length of the plot (25 m) during the vegetation sampling in 1998, the summer following the ice storm. The diameter, length and decomposition class (Hayden et al. 1995) were recorded for each downed branch with a diameter of greater than 2 cm that crossed the transect. A decomposition class of zero was recorded for branches that had fallen in 1998. The volume of coarse woody debris was calculated according to the following equation (Bruederle and Stearns 1985; Hooper et al. 2001):

$$V = (\pi^2 \sum d^2/8L)(10\,000)$$

where V is the volume of coarse woody debris in cubic meters per hectare, d is the diameter of the branch where it intersected the transect, and L is the length of the transect line.

Plot Damage Index. During the vegetation sampling in 1998, percent crown loss due to the ice storm was recorded for each tree in each plot. These were combined to give a damage index for each plot as the mean damage of trees in the plot, weighted by tree size (basal area). The index was calculated according to the following equation:

$$\text{Plot Damage Index} = \frac{\sum [\pi\, r^2\, (\%\ \text{crown loss})]}{100 \times \left[\sum \pi\, r^2\right]}$$

where r is ½ the diameter at breast height (dbh) of each tree, and the summations were over all trees in the plot.

Analyses. Six response variables were studied: i) the plot canopy index, ii) the number of shrub/sapling stems in the 6.25 × 12.5 m plots (1997–1999, 2001), iii) the number of woody seedlings in the two 1 m^2 quadrats in each plot (1997–2001), iv) the number of seedlings of woody species that germinated from the soil core samples (1997–2000), i.e., the woody seed bank, v) the total percent cover of herbaceous plants in the two 1 m^2 quadrats in each plot (1998–2001), and vi) the number of herbaceous seedlings that germinated in the greenhouse from the soil core samples (1997–2000), i.e., the herbaceous seed bank.

For each of the response variables, an ANOVA with an *a posteriori* Scheffé test was run to determine which consecutive years showed significant differences in mean values between years. In addition, we calculated differences in the values of each variable between consecutive years for each plot. We then calculated the correlations between these differences and the plot damage index, to determine whether any observed changes from year to year were related to ice storm damage.

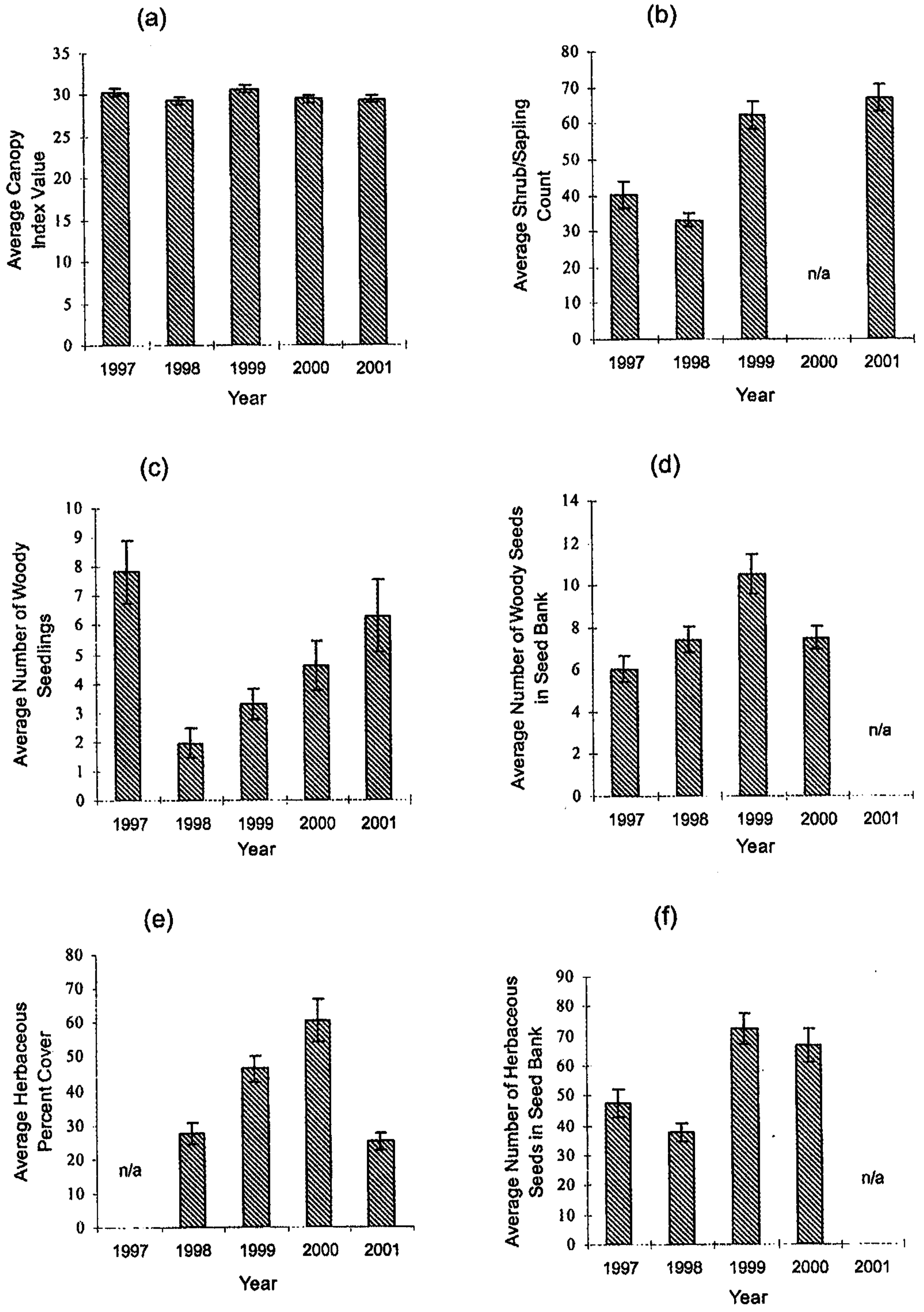

Fig. 1. Average values and standard errors for: (a) plot canopy index, (b) shrub/sapling count, (c) number of woody seedlings, (d) number of woody seeds in seed bank, (e) herbaceous percent cover, and (f) number of herbaceous seeds in seed bank.

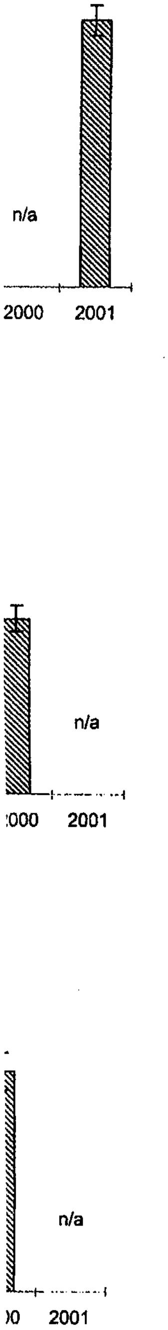

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Table 1. Correlations between year-to-year changes in the six response variables and plot damage index ($N = 164$ for all correlations). P-values are in parentheses. n/a indicates that there were no data available.

Response variable	1997 to 1998	1998 to 1999	1999 to 2000	2000 to 2001
Canopy index	−0.49 (<0.0001)	0.17 (0.03)	0.2 (0.01)	0.1 (0.17)
Shrubs/saplings	−0.1 (0.17)	0.42 (<0.0001)	n/a	n/a
Woody seedlings	−0.17 (0.03)	0.04 (0.58)	−0.01 (0.63)	−0.1 (0.17)
Woody seed bank	−0.04 (0.58)	0.04 (0.58)	−0.1 (0.17)	n/a
Herbaceous percent cover	n/a	0.24 (0.001)	0.001 (0.89)	−0.14 (0.05)
Herbaceous seed bank	0.1 (0.17)	−0.06 (0.42)	−0.09 (0.23)	n/a

Results. PLOT CANOPY INDEX. There was no overall significant difference among years in average plot canopy index (Figure 1a; $P = 0.127$). However, correlations between the change in plot canopy index between consecutive years and plot damage index were significant for all years except 2000 to 2001 (Table 1). From 1997 to 1998, plots with a higher plot damage index showed a larger decrease in canopy index. From 1998 to 1999 and 1999 to 2000, plots with higher plot damage index showed a larger increase in plot canopy index.

SHRUB/SAPLING COUNT. There was a significant difference among years in the average number of shrubs/saplings per plot (Figure 1b; $P < 0.0001$). The results of the Scheffé analysis showed that this was due to an 87.5% increase in shrub/sapling count from 1998 to 1999. Correlations between the change in shrub/sapling numbers per plot and the plot damage index were only significant for the increase in shrubs/saplings from 1998 to 1999 (Table 1; Figure 2a). Plots with a higher plot damage index showed a larger increase in the number of shrubs/saplings per plot from 1998 to 1999.

WOODY SEEDLINGS. There was a significant difference among years in average number of seedlings of woody species germinating (per 2 m^2) (Figure 1c; $P < 0.0001$). A significant decrease of 75% was seen in the number of woody seedlings from 1997 to 1998. Significant increases were seen from 1998 to 1999, 1999 to 2000 and 2000 to 2001; these represented increases of 68.4%, 39.7% and 36.7%, respectively. The difference in the abundance of woody seedlings between 1997 and 1998 was significantly correlated to the plot damage index; plots with more damage showed a larger decrease in the number of woody seedlings germinating from 1997 to 1998 (Table 1; Figure 2b).

WOODY SEED BANK. There was a significant difference among years in the average number of seeds of woody species in the seed bank (Figure 1d; $P < 0.0001$). A significant overall increase of 42.2% was seen in the average number of woody seeds present in the seed bank from 1998 to 1999 and a significant overall decrease of 28.8 % from 1999 to 2000. No significant correlations were found between the difference in number of woody seeds per plot between consecutive years and plot damage index (Table 1).

HERBACEOUS PERCENT COVER. There was a significant difference among years in the average herbaceous percent cover (Figure 1e; $P < 0.0001$). This was due to significant increases in the average herbaceous cover from 1998 to 1999 (increase of 68.7%), and to a significant decrease from 2000 to 2001 (58.6%). The change in herbaceous cover from 1998 to 1999 was significantly correlated to the plot damage index; plots sustaining more damage showed a larger increase in herbaceous cover from 1998 to 1999 (Table 1; Figure 2c).

HERBACEOUS SEED BANK. There was a significant difference between years in the average number of herbaceous seeds in the seed bank (Figure 1f; $P < 0.0001$). This resulted from a significant increase in the average number of seeds in the seed bank from 1998 to 1999 (an increase of 92.6%). No significant correlations were seen between the differences in the number of herbaceous seeds between consecutive years and the plot damage index (Table 1).

Discussion. Based on the method we used to observe changes in the forest canopy, there was

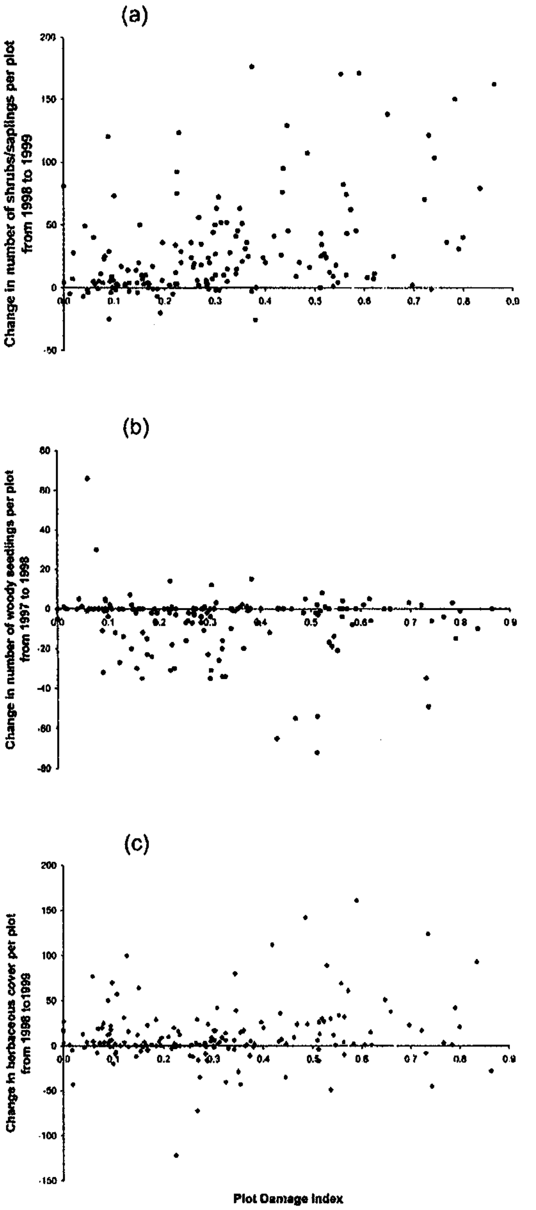

Fig. 2. (a) Change in the number of shrubs/saplings from 1998 to 1999 vs. plot damage index. [$r = 0.42$, $P < 0.0001$]. (b) Change in number of woody seedlings from 1997 to 1998 vs. plot damage index [$r = -0.17$, $P = 0.03$]. (c) Change in herbaceous cover from 1998 to 1999 vs. plot damage index [$r = 0.23$, $P = 0.003$].

no significant overall change in overhead canopy after the ice storm. However, we did find that the plot canopy index was significantly correlated to the plot damage index. The plots with higher damage had larger decreases in canopy immediately following the ice storm. This indicates that although average plot canopy index values were similar between years, damage to the canopy layer through broken branches and snapped stems was significant. Since our plot canopy index measures were observed from a height of 2 m, it is likely that although there was extensive damage to the upper canopy (32% crown loss per canopy tree on average; Brommit et al. in press), the subcanopy layer was not significantly damaged. This interpretation is supported by our results showing no significant decline in the number of shrubs/saplings following the storm (Figure 1b).

In the second year following the ice storm (1999), plots with higher damage had a larger increase in plot canopy cover. This suggests vigorous growth in terms of sprouting in the canopy layer and growth in the upper shrub/sapling layer. In the same study area, Brommit et al. (in press) found that 25% of damaged trees showed aboveground sprouting. This would greatly contribute to the filling in or expansion of the upper canopy layer.

The response in the shrub/sapling layer was not seen until 1999 (2 growing seasons following the storm) when there was a significant increase in shrub/sapling count. This increase had a significant positive relationship with the plot damage index; plots that had the highest damage showed the greatest increase in number of shrubs/saplings. This suggests that removal of a large fraction of the upper canopy (Brommit et al. in press) caused increased growth of stems in the seedling layer. Growth is known to be stimulated in gaps, as understory vegetation receives more light and the soil has higher moisture content (Mladenoff 1990). As a result, we observed an increase in stem density in the shrub/sapling layer two summers following the storm. No increase was seen in 1998 most likely because small seedlings and root sprouts may not have attained the necessary 1 m height to be counted as shrubs/saplings using our sampling scheme, during the first growing season following the ice storm. The growth rate of many shrub and tree seedlings is about 0.5 to 1.0 m/year (see Runkle 1985).

Higher shrub/sapling counts persisted into 2001 but did not increase past levels observed in 1999, indicating that growth was no longer being stimulated. The shrubs/saplings that had grown since the ice storm may have intercepted most of the available light, creating a sub-canopy that may be suppressing other new growth. The lateral growth of tree crowns may also have

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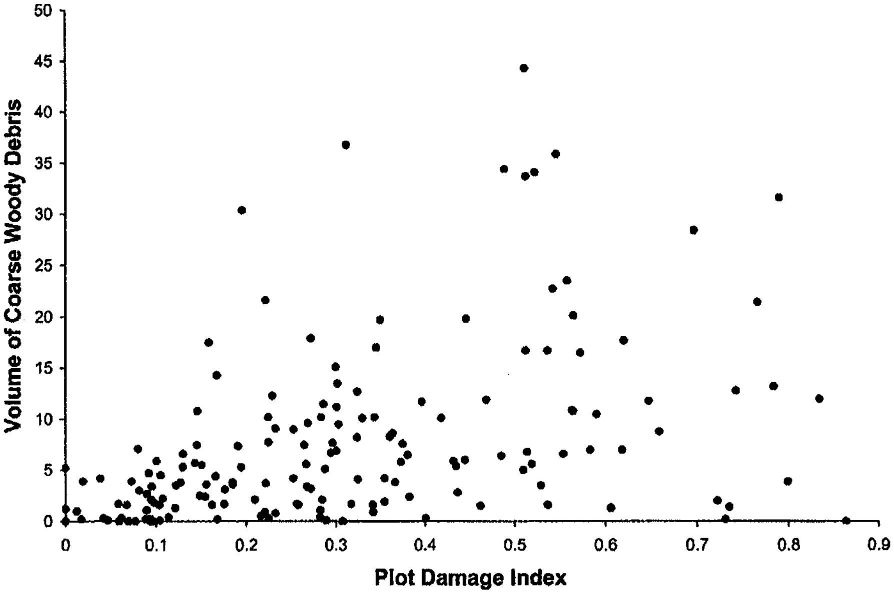

Fig. 3. Relationship between volume of coarse woody debris (m^3/ha) and plot damage index [$r = 0.43$, $P < 0.0001$].

decreased the gap openings (Brommit et al. in press). This would result in a more dense sub-canopy level than what was seen prior to the ice storm.

The number of woody seedlings decreased from 1997 (pre-storm) to 1998 (post-storm). This decrease was negatively correlated to the plot damage index. Subsequent years showed increases and, in 2001, woody seedling counts were not significantly different from those seen before the ice storm in 1997. The observed decrease in woody seedling germination immediately following the ice storm was not what we had predicted, and is opposite to the results of Whitney and Johnson (1984) who found a greater seedling and root sprout density (woody stems < 1 m height) in ice storm affected plots. We had assumed that with such a large scale disturbance and damage to the canopy, there would be increased light levels at the forest floor which would trigger germination. The average plot damage index value for this study area was 31% (range 0 to 86%) with 60% of trees showing some crown loss due to the storm (Brommit et al. in press). However, following the ice storm, there was a very large increase in the volume of coarse woody debris on the forest floor due to newly fallen trees, logs and branches (personal observations). Plots with more damage contained more coarse woody debris (Figure 3). In a study performed at Mont St. Hilaire, Quebec, the amount of litter fall following the same ice storm was 10 to 20 times higher than the mean annual litter fall in temperate deciduous forests (Hooper et al. 2001). In the long term, greater amounts of woody debris may help to stimulate germination, as these sites will have greater nutrient availability upon decomposition of the fallen woody debris. However, in the short term, the presence of large amounts of new debris on the forest floor may have created a micro canopy at the forest floor which may have impeded germination. Large quantities of woody debris falling from trees after the ice storm may also have killed some of the seedlings. The volume of downed woody debris most likely countered any increase in light availability from canopy opening.

There are several possible explanations for the increase in the number of seeds of woody plants in the seed bank in 1999. It may have resulted from an accumulation of seeds due to the lower seed germination levels in 1998. Alternatively, there may have been increased seed production in 1998, possibly due to the stress to trees caused by the ice storm. However, there was no evidence that the increase in woody seeds in 1999 was actually due to the ice storm, since there was no relationship between the difference in number of woody seeds per plot between consecutive years and the plot damage index. Therefore, the increase in woody seeds in 1999 may have been related to environmental conditions other than the ice storm.

We observed an increase in average herbaceous cover from 1998 to 1999, which was positively correlated to ice storm damage. Since woody seedling mortality/lack of germination was higher in this same time frame, we postulate that the herbaceous plants were better able to take advantage of overstory changes related to the ice storm and had increased germination and growth. The peak in herbaceous cover seen in 2000 was not related to ice storm damage (no correlation to plot damage index), and may be related to the higher count in the herbaceous seed bank seen in 1999. This peak in the herbaceous seed bank was also not correlated to ice storm damage. The high level of herbaceous cover in 2000 may also be related to good overall conditions for herbaceous growth in that year (Environment Canada 2000).

The ice storm of 1998 was the largest ice storm in Canadian history (Anonymous 1999). It raised questions about forest resiliency, or the degree to which forests could withstand such high levels of damage. Overall, it appears that the forest understory plant community is returning to pre-ice storm conditions. Initial suppression of woody seedlings was seen but there appears to be a full recovery 4 years later. The middle layer of the forest showed the greatest response with an increase in shrubs/saplings, most likely as a response to the opening of the upper canopy. However, this increase has now stabilized.

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