NOTE / NOTE

Changes in understory light regime in a beech–maple forest after a severe ice storm

Ken Arii and Martin J. Lechowicz

Abstract: We assessed canopy openness (%) in an old-growth beech–maple forest immediately before and in the 3 years following a severe ice storm. We estimated canopy openness using hemispherical photographs taken at a height of 0.6 m above the soil surface in 101 permanent plots. Mean canopy openness increased from a prestorm value of 7.7% to 16.6% in the summer immediately following the storm. However, the mean canopy openness returned to prestorm levels within 3 years. The changes in canopy openness immediately after the storm were significantly influenced by canopy openness prior to the storm and also by species composition; plots with lower canopy openness prior to the storm and plots that consisted of more shade-tolerant species had greater canopy damage. While canopy gaps are often considered to promote the establishment of shade-intolerant species in the deciduous forests of eastern North America, gaps created by ice storms at our study site may not persist long enough to promote the establishment of these species.

Résumé : Nous avons évalué l'ouverture de la canopée (%) dans une vieille forêt d'érable et de hêtre immédiatement avant et durant les trois années qui ont suivi un verglas sévère. Nous avons estimé l'ouverture de la canopée à l'aide de photographies hémisphériques prises à une hauteur de 0,6 m au-dessus de la surface du sol dans 101 places-échantillons permanentes. L'ouverture moyenne de la canopée est passée de 7,7 % avant le verglas à 16,6 % à l'été qui a immédiatement suivi le verglas. Cependant, l'ouverture moyenne de la canopée est revenue à son niveau d'avant le verglas en 3 ans. Les changements dans l'ouverture de la canopée ont été significativement influencés par l'ouverture de la canopée avant le verglas et également par la composition en espèces. Les places-échantillons où l'ouverture avant le verglas était plus faible et qui étaient constituées de plus d'espèces tolérantes à l'ombre ont subi plus de dommages à la canopée. Bien que les trouées dans la canopée soient souvent considérées comme étant favorables à l'établissement d'espèces intolérantes à l'ombre dans les forêts feuillues de l'est de l'Amérique du Nord, les trouées créées par le verglas dans le site où a eu lieu notre étude pourraient ne pas persister assez longtemps pour promouvoir l'établissement de ces espèces.

[Traduit par la Rédaction]

Introduction

Ice storms are one of the important agents of natural disturbance in the deciduous forests of eastern North America (Lorimer 2001). In forested landscapes, ice accumulates on trees and results in bending and snapping of tree trunks, and twigs and branches are lost from the tree canopy (Duguay et al. 2001; Hooper et al. 2001; Proulx and Greene 2001). Previous studies examining the effects of ice storms on forest systems have mainly focused on damage inflicted on trees and (or) responses of trees following damage. For example, some studies have reported tree damage using arbitrarily chosen damage classes (e.g., Rebertus et al. 1997; Brisson et al. 2001; Duguay et al. 2001); some have quantified the number, the volume, and (or) the biomass of branch wood lost from the canopy (e.g., Bruederle and Stearns 1985; Melancon and Lechowicz 1987; Hooper et al. 2001); and others have measured the growth (Rhoads et al. 2002; Smith and Shortle 2003), mortality (Hopkin et al. 2003; Ryall and Smith 2005), and ecophysiological responses (Boyce et al. 2003) of trees following ice storms. Other studies have used simulation models to forecast the long-term effects of these damages on forest ecosystems (Jones et al. 2001; Lafon 2004; Tremblay et al. 2005). However, because ice storms are unpredictable disturbance events, very few studies have been able to compare the prestorm and poststorm conditions and quantify the extent of damage caused by the ice storm.

The damage on trees and their subsequent recovery following ice storms create substantial spatial and temporal variation in light availability in the forest understory, which is recognized as an important factor shaping the species composition, structure, and the development of forest stands (Bazzaz and Wayne 1994). For example, the extensive canopy removal due to ice storms may allow additional light to reach the understory, which can encourage the establishment and growth of shade-intolerant pioneer species (Abell 1934;

Received 24 June 2006. Accepted 25 January 2007. Published on the NRC Research Press Web site at cjfr.nrc.ca on 14 September 2007.

K. Arii[1,2] and M.J. Lechowicz. Department of Biology, McGill University, 1205 avenue Docteur Penfield, Montrèal, QC H3B 1A1, Canada.

[1] Corresponding author (e-mail: ken.arii@mail.mcgill.ca).
[2] Present address: Faculty of Forestry, University of Toronto, 33 Willcocks Street, Toronto, ON M5S 3B3, Canada.

doi:10.1139/X07-024

Siccama et al. 1976; Boerner et al. 1988; DeSteven et al. 1991), as well as encourage the ground layer vegetation in the forest understory (Darwin et al. 2004). Thus, information on how light availability in the understory varies after an ice storm can enhance our understanding of how this disturbance may influence the patterns and the dynamics of species that occur in forest stands.

While measures of damage and recovery of trees reported in previous studies can provide an approximation of how light availability changes after ice storms, direct quantification of changes in the light regime will be most informative. However, this requires information on the light regime in the growing season prior to the ice storm, and such data are rare for eastern North American forests. We are aware of only two studies that have directly quantified the changes in light availability (i.e., gaps) resulting from an ice storm (Aarssen and Francq 2004; Darwin et al. 2004). Darwin et al. (2004) examined canopy gaps 1 year before and 4 years following a severe ice storm, using a method modified from James and Shugart (1970). The data set reported in Darwin et al. (2004) examined not only the immediate changes in light availability, but also showed the subsequent recovery. However, the method they applied to quantify the gaps uses a sight tube (5 cm × 30 cm length of PVC pipe with wire crosshairs affixed to one end of the tube), which only allows a rough approximation of canopy openness (CO) (for details see Darwin et al. 2004). Using this method, Darwin et al. (2004) found no significant differences in canopy gap index before and after one of the most severe ice storms on record. In contrast, Aarssen and Francq (2004) used hemispherical photographs to examine the changes in light availability following the same ice storm, and they found significant increases in gap openings after the storm. Aarssen and Francq (2004) took hemispherical photographs only in the summer before and immediately following the storm, so they were unable to provide any data on how light availability recovered in the subsequent years. Additionally, the height at which the photographs were taken varied between 1.5 and 4 m, and thus their data do not allow direct comparison among the sampled points.

In this study, we measured CO immediately prior to the 1998 ice storm (the same storm investigated by Aarssen and Francq (2004) and Darwin et al. (2004)) for 101 plots in an old-growth beech–maple forest near the northern margin of the deciduous forest biome in eastern North America. These CO values from the summer prior to the ice storm (1997) provide a benchmark against which damage and recovery from the ice storm can be gauged. The hemispherical photographs were taken at exactly the same locations in the 3 subsequent years following the storm. The main objective of this study is to report the changes in CO caused by the ice storm of 1998, as well as the subsequent gap closure. We also attempted to identify factors that could explain the variation in changes in CO immediately after the storm. Canopy gaps are often considered to account for the persistence of some shade-intolerant species in hardwood forests of eastern North America that are dominated by shade-tolerant species. However, ice storm disturbances have been suggested to enhance the turnover of the current canopy trees, and in younger forest stands, enhance the transition to later-successional stages (Abell 1934; Carvell et al. 1957; Lemon 1961). We discuss how the poststorm patterns of canopy gaps found in this study support or refute these previously suggested impacts of ice storms on forest dynamics.

Methods

Study site

We assessed the impact of the ice storm of January 1998 (Irland 1998) on a 10 km^2 tract of old-growth forest at Mont St. Hilaire, Quebec, Canada (45°31′N, 73°08′W), which lies within the region most hard hit by the storm. The forest at Mont St. Hilaire is the largest remaining remnant of the primeval forests of the St. Lawrence Valley; many of the trees exceed 150 years in age and a few are over 400 years old. Various forest communities occur at the site (Phillips 1972); *Acer saccharum* Marsh., *Fagus grandifolia* Ehrh., and *Quercus rubra* L. are the common canopy dominants (Arii et al. 2005). While canopy gaps at the site typically are created because of mortality of canopy trees (single-tree gaps), damage-causing ice storms, which have a return time of 10–20 years in our region (Proulx and Greene 2001), periodically lead to more extensive canopy opening.

Data collection and analysis

In summer 1997, we established 101 permanent plots (6 m radius, 113 m^2) with a metal rod at the center of each plot so that sequential photographs could be taken at exactly the same location. We recorded species and DBH of all trees and saplings (DBH ≥ 1 cm) in each plot.

Changes in CO

In late summer from 1997 through 2000, we took hemispherical (fisheye) photographs from the center of each plot. The camera was fixed on a tripod 0.6 m above the ground surface. Previous studies have used various camera heights to quantify CO (e.g., 1.5 m (Canham et al. 1990), 0.6 m (Walter and Himmler 1996), 0.5 m (Valverde and Silvertown 1997)), but height differences in this range are relatively insensitive in regard to CO estimation (Robinson and McCarthy 1999). We scanned each photograph and used the digital images to estimate CO (%) for each site and year with Gap Light Analyzer, version 2.0 (Frazer et al. 2000).

Because most of the sampling plots were placed on sloping terrain, some ground appeared on the periphery of many photographs. To avoid distorting the CO estimates, we limited the calculation to zenith angles between 0° and 60° (maximum slope angle in the sampling plots was 29°). While we lose some information by omitting zenith angles between 60° and 90°, the effect is minimal, as surrounding ground-layer vegetation obstructs most of the image areas near the horizon. Nevertheless, the CO obtained for zenith angles between 0° and 60° is highly correlated with CO obtained for angles between 0° and 90° ($r = 0.97$, $P < 0.001$).

Most of the hemispherical photographs were taken on an overcast day to reduce the overexposed region around the sun and the reflections on the leaves and bark, which could otherwise be construed as gap openings (Rich 1990). However, some photographs were unavoidably taken when there was direct sunlight, and for such photographs, recommendations described in the user's manual of Gap Light Analyzer

Fig. 1. Boxplots showing the percentile distribution of the canopy openness (CO) for each year ($n = 101$). The values at the bottom of the figure are means and standard deviations (SD) of the CO for the respective year. The extreme outliers found for years between 1998 and 2000 are values for a single plot where a canopy tree lost an entire crown because of the ice storm. The years represented by the same letter indicate that the values do not differ significantly based on repeated-measures ANOVA ($F = 145.4$, $P < 0.001$). Post hoc comparisons were performed using the Bonferroni adjustment for multiple comparisons.

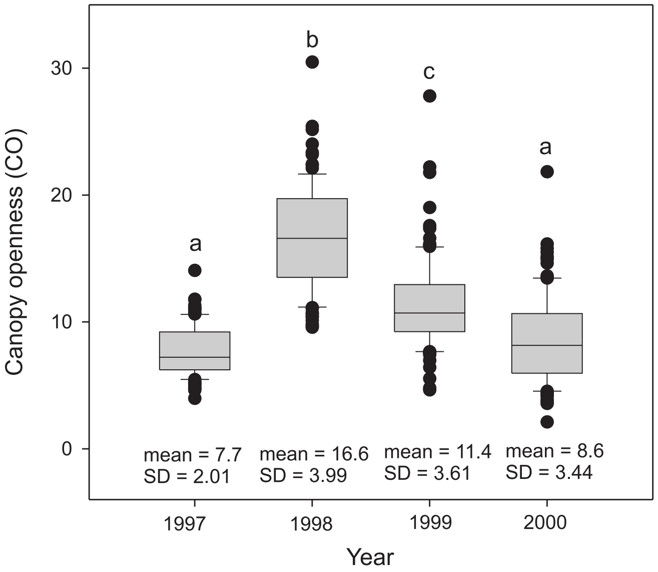
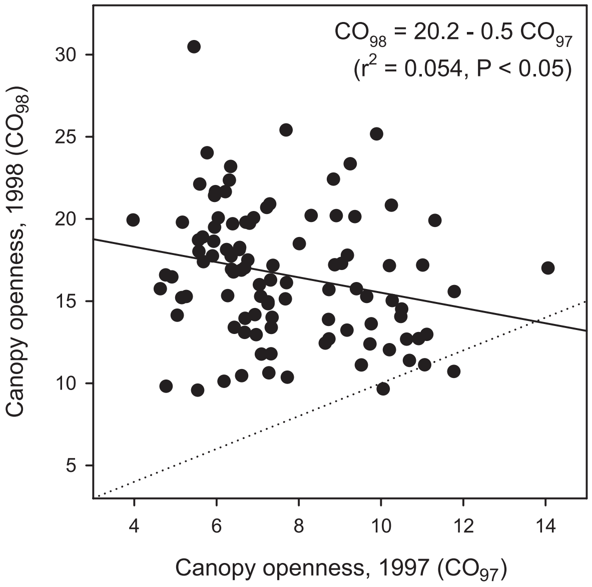


Fig. 2. Relationship between prestorm canopy openness (CO_{97}) and poststorm canopy openness (CO_{98}). Solid line indicates the regression line through the data points, while the dotted line indicates a 1:1 line (i.e., equal values of CO_{97} and CO_{98}).



were used to reduce the effects (e.g., separate RGB planes, selecting the region of interest).

Factors influencing the variation in changes in CO after the ice storm

For each plot, the changes in canopy openness (CO_{change}) are calculated as $CO_{change} = CO_{98} - CO_{97}$, where CO_{98} is canopy openness in 1998, and CO_{97} is canopy openness in 1997. To explain spatial variation in CO_{change}, we examined the relationships between CO_{change} and various factors, including slope, aspect, total basal area, total density, and species composition of canopy trees (DBH $\geq$ 10 cm) and saplings (1 cm $\leq$ DBH $<$ 10 cm) within the sampling plot. We used detrended correspondence analysis (DCA, basal area used as response variable) to differentiate the species composition among the plots (CANOCO ver. 4.0); the analyses were done separately for the two size classes (i.e., saplings and canopy trees). The first DCA axis site scores were used to numerically rank the differences in species composition among the sampled plots. While we examined the relationships between CO_{change} and various other factors, we only report the results that showed significant relationship with CO_{change} ($\alpha = 0.05$).

Results

The ice storm of 1998 caused pronounced changes in CO values between 1997 and 2000. The CO increased significantly immediately after the ice storm; however, the mean CO value returned to the prestorm levels within three growing seasons after the storm (Fig. 1). The CO immediately following the storm (CO_{98}) had a significant negative relationship with prestorm canopy openness (CO_{97}) (Fig. 2). The regression line through these two variables (Fig. 2, solid line) deviated significantly from a line that assumes CO_{97} and CO_{98} are equal (Fig. 2, dotted line). This deviation is particularly more pronounced in plots with low CO_{97}, indicating that plots with lower CO prior to the storm suffered more ice damage. Sapling and canopy species composition in the sampled plots, which were ranked numerically by the first DCA axis, also explained a major portion of the variation in CO_{change} (species scores are given in Table 1). These DCA axes based on basal area of saplings and canopy trees, which will be referred to as sapling composition index (SCI) and canopy composition index (CCI), respectively, can be considered a gradient from plots that consists mainly of individuals with low to moderate shade tolerance (e.g., *Ostrya virginiana* (P. Mill.) K. Koch, *Fraxinus americana* L., *Quercus rubra*, *Betula papyrifera* Marsh. — low SCI, CCI) to plots with individuals of high shade tolerance (e.g., *Fagus grandifolia*, *Acer pensylvanicum* L. — high SCI, CCI) (Table 1). The significant relationships between SCI and CO_{change} (Fig. 3*a*) and CCI and CO_{change} (Fig. 3*b*) suggest that plots that consisted of shade-tolerant species suffered more canopy damage. Note that CO_{97} and SCI showed a high negative correlation ($r = -0.59$, $P < 0.001$), as did CO_{97} and CCI ($r = -0.51$, $P < 0.001$). This indicates that plots primarily occupied by the shade-tolerant species had lower CO values prior to the storm. Additionally, SCI and CCI are positively correlated ($r = 0.72$, $P < 0.001$), which suggests that the understory of the canopy dominated by shade-tolerant species is primarily occupied by saplings of the shade-tolerant species (more detailed analyses in Arii and Lechowicz 2002). Other factors that were considered (e.g., slope, elevation, canopy tree species composition, stem basal area, stem density) did not show any significant relationship with CO_{change}, alone or in combination.

Table 1. Axis 1 species scores of detrended correspondence analysis (DCA) based on basal area of saplings and canopy trees in the sampling plots.

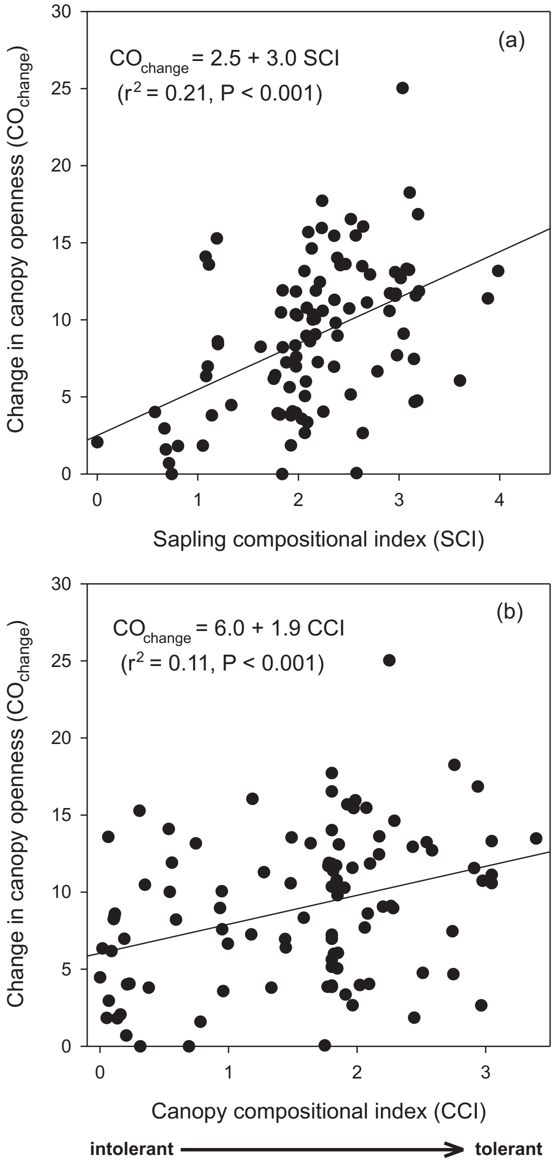
	Axis 1 species scores	
Species	Saplings	Canopy trees
Betula papyrifera Marsh.	–0.72	0.54
Quercus rubra L.	0.03	0.00
Fraxinus americana L.	0.32	0.87
Ostrya virginiana (P. Mill.) K. Koch	0.65	0.55
Tilia americana L.	0.96	1.16
Betula alleghaniensis Britt.	1.39	1.50
Prunus virginia L.	1.62	NA
Acer saccharum Marsh.	1.92	1.80
Acer pensylvanicum L.	2.71	3.99
Fagus grandifolia Ehrh.	3.20	3.05
Acer spicatum Lam.	4.08	3.60

Note: The eigenvalues of the first axes are 0.611 and 0.70 for the analyses based on saplings and canopy trees, respectively. For both axes, shade-intolerant species such as *Betula papyrifera* and *Fraxinus americana* are found to have low species scores, while shade-tolerant species such as *Acer saccharum* and *Fagus grandifolia* have higher scores. This implies that plots that have low axis 1 scores (site scores) mainly consist of shade-intolerant species, while those that have high axis 1 scores consist of shade-tolerant species. Using these characteristics, we used the DCA axes to numerically rank sampling plots by species composition, from plots with mainly shade-intolerant species to those dominated by shade-tolerant species. See the text for details on sapling composition index (SCI) and canopy composition index (CCI).

Discussion

The substantial increases in CO in the summer immediately following the ice storm are not surprising given the amount of damage inflicted on the trees during the ice storm of 1998 at our study site (Duguay et al. 2001; Hooper et al. 2001). Aarssen and Francq (2004) report similar changes in CO following the same ice storm in stands dominated by *Acer saccharum*; in their study, the prestorm CO values ranged approximately between 6% and 12%, while poststorm values ranged between 10% and 40%. The poststorm CO values in their study tended to be slightly higher than our measurements, which is likely due to the fact that their canopy photographs were taken at a higher point above the ground (ranging between 1.5 and 4 m).

Fig. 3. (*a*) Relationship between sapling composition index (SCI) and the changes in canopy openness (CO_{change}). (*b*) Relationship between canopy composition index (CCI) and the changes in canopy openness (CO_{change}).



At our study site, greater changes in canopy openness (CO_{change}) were found on sites that had lower prestorm canopy openness (CO_{97}) and on sites where shade-tolerant species primarily occupied the plot (i.e., sites that have high SCI and CCI values). Generally, we would expect branching patterns to be formed to reduce leaf overlap and competition for light (Givnish 1984), as the ability to do so will have substantial consequences for the survival of a tree in a forest community (Kuuluvainen 1992). It has been suggested that light-demanding species are less efficient in filling new space than late-successional, shade-tolerant species (Küpper 1994), which may be partly explained by the light-demanding species' orthotropic shoots (Givnish 1984; Poorter et al. 2006) and decreased bifurcation of stems in low to mid-light environments (Kull and Tulva 2002). Whatever the mechanisms, the ability of shade-tolerant species to fill space will often rely on increased investment in stem tissue (Givnish 1995), which will result in creation of a more extensive network of branches and twigs. This, however, results in greater surface area that will come in contact with freezing rain, which is likely to have had a major influence on the degree of damage caused by the ice storm (i.e., more damage in plots with shade-tolerant species). The ability of shade-tolerant species to fill space also explains why there is a negative correlation between CO_{97} and species composition indices, SCI and CCI (i.e., more light transmission in stands dominated by less shade-tolerant species prior to the storm).

The gaps created by the ice storm closed quickly, returning to prestorm levels within 3 years after the storm. Two factors can account for this quick gap closure. The first is the height in which the photographs were taken (0.6 m above the ground). Old-growth stands in northern hardwood forests typically have an irregular, uneven-aged canopy with trees in various stages of development (Lorimer and Frelich 1994). A qualitative assessment of damage inflicted by the storm of 1998 at our study site found that trees suffered severe damage, but a high number of stems in the sapling stratum (4 cm ≤ DBH < 10 cm) were unscathed (Duguay et al. 2001). These relatively undamaged saplings have grown substantially after the storm, taking advantage of the heightened light availability due to canopy damage. Darwin et al. (2004) also found a considerable increase in the number of saplings–shrubs (stems over 1 m in height and DBH < 10 cm) following the ice storm of 1998, suggesting substantial growth of individuals in this size class. This rapid growth of individuals in the subcanopy may have led to the rapid development of a relatively closed, but low, canopy after the storm (Brisson et al. 2001; Rhoads et al. 2002). Another important factor that can contribute to rapid gap closure is the way in which ice storms damage trees. Although an ice storm with a magnitude of the 1998 storm may occasionally remove an entire crown (Duguay et al. 2001), most gaps arise from loss of branches <10 cm in diameter (Melancon and Lechowicz 1987; Seischab et al. 1993; Hooper 1999). Thus, gaps created by ice storms may be relatively small compared with single treefall gaps and can be occupied readily by the lateral extension of intact branches. These two factors combined could explain the quick closure of gaps after the storm.

This rapid closure of gaps after the ice storm has important implications for the role that ice storms may play in determining the patterns and the dynamics of forest understory vegetation. It is generally accepted that forest gaps enhance light conditions in the understory, allowing trees of less shade-tolerant species to establish, which in turn helps maintain the species diversity in old-growth forests (Denslow 1985). Our results that gaps created by an ice storm recover to the prestorm levels very rapidly indicates that the duration of increased light levels may not always be sufficient to allow successful dispersal and establishment of seedlings of less shade-tolerant species. If the ice storm gaps do provide a window of opportunity for shade-intolerant species to establish, and considering that the return time of damage-causing ice storms in our region is about 10–20 years (Proulx and Greene 2001), we would expect shade-intolerant species to be more abundant at our study site. However, two of the most shade-tolerant species in the temperate deciduous forests, *Acer saccharum* and *Fagus grandifolia*, dominate the canopy at the site, while less shade-tolerant species, such as *Betula papyrifera*, *Fraxinus americana* and *Betula alleghaniensis*, are infrequent (Phillips 1972; Arii and Lechowicz 2002). Darwin et al. (2004) found reduced woody seedling density following an ice storm, which also is contrary to the idea that ice storm gaps promote the establishment and the recruitment of the less shade-tolerant tree species. On the other hand, De Steven et al. (1991) reported that sapling densities (2.5–10 cm DBH) of less shade-tolerant species increased following an ice storm, but we cannot know if the ice storm promoted the recruitment of new individuals or merely enhanced the growth of individuals <2.5 cm DBH that were already present prior to the storm. Further studies are required to fully resolve the role of ice storms in maintaining the balance of shade-intolerant and shade-tolerant trees in northern hardwood forests.

It should be noted that the creation of canopy gaps does not only influence tree seedlings and saplings, but also shrubs and herbaceous species in the understory. In the forest stands of eastern Ontario, Canada, Darwin et al. (2004) found that herbaceous vegetation cover increased significantly immediately after the ice storm of 1998, but that it returned to prestorm levels 4 years after the storm. This rapid increase and subsequent decline in herbaceous species cover coincide well with the opening and the closure of gaps that we found and with our own observations of herbaceous plant cover at our study site (not reported here). This burst of herbaceous growth leads to increased seed production, substantially enriching the soil seed bank; Darwin et al. (2004) found a 93% increase in the number of seeds in the seed bank two summers after the ice storm. The frequent occurrence of ice storms, which allows these species to reproduce aggressively during the brief gap phase, may contribute to the maintenance of a diverse, viable seed bank of herbaceous species and may allow them to germinate and establish in future canopy openings. This brief increase in herbaceous vegetation cover could also affect the establishment and the growth of tree seedlings during the gap phase as they compete for resources (e.g., light, water, and nutrients). The decline in woody seedling density following an ice storm reported in Darwin et al. (2004) may be due to this competitive interaction.

Conclusions

While previous studies have suggested rapid return of understory light availability to prestorm levels following an ice storm (e.g., Brisson et al. 2001; Rhoads et al. 2002), our study provides direct quantification of changes in light availability (i.e., canopy gaps). Based on our measurement of changes in CO following one of the most severe ice storms on record (Irland 1998), we observed that gaps created by an ice storm did not persist, at least at heights close to the ground. Thus, these gaps may not promote new establishment of less shade-tolerant species, but instead may favor species that can establish under forest cover (advanced regeneration) and take advantage of episodic canopy opening (release episodes). In the shade-tolerant hardwoods, this may enhance the turnover of current canopy trees, and in younger forest stands, this may enhance the transition to later-successional stages (Abell 1934; Carvell et al. 1957; Lemon 1961). While further studies are required, ice storms should be recognized as a disturbance agent that can accelerate rather than reinitiate forest succession (Abrams and Scott 1989).

Acknowledgements

This work was supported by grants from Natural Sciences and Engineering Research Council of Canada (NSERC) and Fonds pour la Formation de Chercheurs et l'Aide à la Recherche (FCAR) to MJL and Government of Canada Awards (Department of Foreign Affairs and International Trade) to KA. We thank McGill University for access to the Gault Nature Reserve. Comments by Dr. Richard Kobe and two anonymous reviewers helped improve the manuscript.

References

Aarssen, L.W., and Francq, A.E. 2004. Effects of ice storm canopy gaps on shoot architecture in young sugar maple (*Acer saccharum*). Ecoscience, **11**: 201–208.

Abell, C.A. 1934. Influence of glaze storms upon hardwood forests in southern Appalachians. J. For. **32**: 35–37.

Abrams, M.D., and Scott, M.L. 1989. Disturbance-mediated accelerated succession in two Michigan forest types. For. Sci. **35**: 42–49.

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., Hamel, B., and Lechowicz, M.J. 2005. Environmental correlates of canopy composition at Mont St. Hilaire, Quebec, Canada. J. Torrey Bot. Soc. **132**: 90–102.

Bazzaz, F.A., and Wayne, P.M. 1994. Coping with environmental heterogeneity: the physiological ecology of tree seedling regeneration across the gap–understory continuum. *In* Exploitation of environmental heterogeneity by plants: ecophysiological processes above and below ground. *Edited by* M.M. Caldwell and R.W. Pearcy. Academic Press, San Diego. pp. 349–390.

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.

Boyce, R.L., Friedland, A.J., Vostral, C.B., and Perkins, T.D. 2003. Effects of a major ice storm on the foliage of four New England conifers. Ecoscience, **10**: 342–350.

Brisson, J., Lareau, C., Millet, J., and Bouchard, A. 2001. Rétablissement des arbres ayant subi des dommages dus au verglas de janvier 1998, dans une forêt ancienne de l'est de l'Amérique du Nord. *In* Colloque international sur l'arbre (4^{e} : 2000 : Montréal, Que.). *Edited by* M. Labrecque. Institut de recherche en biologie végétale et Isabelle Quintin. pp. 307–313.

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.

Canham, C.D., Denslow, J.S., Platt, W.J., Runkle, J.R., Spies, T.A., and White, P.S. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. Can. J. For. Res. **20**: 620–631.

Carvell, K.L., Tyron, E.H., and True, R.P. 1957. Effects of glaze on the development of Appalachian hardwoods. J. For. **55**: 130–132.

Darwin, A.T., Ladd, D., Galdins, R., Contreras, T.A., and Fahrig, L. 2004. Response of forest understory vegetation to a major ice storm. J. Torrey Bot. Soc. **131**: 45–52.

Denslow, J.S. 1985. Disturbance-mediated coexistence of species. *In* The ecology of natural disturbances and patch dynamics. *Edited by* S.T.A. Pickett and P.S. White. Academic Press, New York. pp. 307–321.

DeSteven, 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.

Duguay, S.M., Arii, 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.

Frazer, G.W., Canham, C.D., and Lertzman, K.P. 2000. Technological tools. Gap Light Analyzer. Version 2.0. Bull. Ecol. Soc. Am. **81**: 191–197.

Givnish, T.J. 1984. Leaf canopy adaptations in tropical forests. *In* Physiological ecology of plants of the wet tropics. *Edited by* E. Medina, H.A. Mooney, and C. Vasquez-Yánes. Dr. Junk, The Hague, the Netherlands. pp. 51–84.

Givnish, T.J. 1995. Plant stems: biomechanical adaptation for energy capture and influence on species distributions. *In* Plant stems: physiology and functional morphology. *Edited by* B.L. Gartner. Academic Press, San Diego. pp. 3–49.

Hooper, M.C. 1999. Impacts of a catastrophic ice storm on an old-growth, hardwood forest. M.Sc. thesis, Department of Biology, McGill University, Montrèal, Que.

Hooper, M.C., Arii, 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.

Irland, L.C. 1998. Ice storm of 1998 and the forests of the northeast: a preliminary assessment. J. For. **96**: 32–40.

James, F.C., and Shugart, H.H. 1970. A quantitative method of habitat description. Audubon Field Notes, **24**: 727–736.

Jones, J., Pither, J., DeBruyn, D., and Robertson, R.J. 2001. Modeling ice storm damage to a mature, mixed-species hardwood forest in eastern Ontario. Ecoscience, **8**: 513–521.

Kull, O., and Tulva, I. 2002. Shoot structure and growth along a vertical profile within a *Populus–Tilia* canopy. Tree Physiol. **22**: 1167–1175. PMID:12414376.

Küpper, M. 1994. Canopy gaps: competitive light interception and economic space filling — a matter of whole-plant allocation. *In* Exploitation of environmental heterogeneity by plants. Ecological processes above- and belowground. *Edited by* M.M. Caldwell and R.W. Pearcy. Academic Press, San Diego. pp. 111–144.

Kuuluvainen, T. 1992. Tree architectures adapted to efficient light utilization: is there a basis for latitudinal gradients? Oikos, **65**: 275–284. doi:10.2307/3545019.

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.

Lorimer, C.G. 2001. Historical and ecological roles of disturbance in eastern North American forests: 9,000 years of change. Wildl. Soc. Bull. **29**: 425–439.

Lorimer, C.G., and Frelich, L.E. 1994. Natural disturbance regimes in old-growth northern hardwoods: implications for restoration efforts. J. For. **92**: 33–38.

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.

Phillips, W.J. 1972. An evaluation of the relative importance index to the study of forest vegetation on Mont St. Hilaire, Quebec. M.Sc. thesis, Department of Geography, McGill University, Montrèal, Que.

Poorter, L., Bongers, L., and Bongers, F. 2006. Architecture of 54 moist-forest tree species: traits, trade-offs, and functional groups. Ecology, **87**: 1289–1301. PMID:16761607.

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.J., Shifley, S.R., Richards, R.H., and Roovers, L.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.

Rich, P.M. 1990. Characterizing plant canopies with hemispherical photographs. Remote Sens. Rev. **5**: 13–29.

Robinson, S.A., and McCarthy, B.C. 1999. Potential factors affecting the estimation of light availability using hemispherical photography in oak forest understories. J. Torrey Bot. Soc. **126**: 344–349.

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.

Seischab, F.K., Bernard, J.M., and Eberle, M.D. 1993. Glaze storm damage to western New York forest communities. Bull. Torrey Bot. Club, **120**: 64–72. doi:10.2307/2996665.

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.

Smith, K.T., and Shortle, W.C. 2003. Radial growth of hardwoods following the 1998 ice storm in New Hampshire and Maine. Can. J. For. Res. **33**: 325–329. doi:10.1139/x02-185.

Tremblay, M., Messier, C., and Marceau, D.J. 2005. Analysis of deciduous tree species dynamics after a severe ice storm using SORTIE model simulations. Ecol. Model. **187**: 297–313. doi:10.1016/j.ecolmodel.2005.01.038.

Valverde, T., and Silvertown, J. 1997. Canopy closure and forest structure. Ecology, **78**: 1555–1562. doi:10.2307/2266148.

Walter, J.M.N., and Himmler, C.G. 1996. Canopy structure measurement by gap fraction analysis using commercial instrumentation. Can. J. For. Res. **26**: 1610–1619.