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Effect of a major ice storm on understory light conditions in an old-growth *Acer–Fagus* forest: Pattern of recovery over seven years

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Abstract

We evaluated the effects of a major ice storm on understory light conditions (%PPFD, photosynthetic photon flux density) in an old-growth *Acer–Fagus* forest in Quebec, based on pre- and post-disturbance light measurements taken until the seventh growing season after the event (which occurred in January 1998). Before the ice storm, most microsites received between 2 and 4%PPFD. Following the ice storm, the stand-level mean %PPFD increased four- to five-fold, ranging from 13.8 to 20.5%PPFD, from 0.3 to 4 m aboveground. Despite its magnitude, the post-ice storm increase in light transmission was short-lived. By 1999 (2-year+), the mean light levels had decreased by half, and recovery to pre-storm conditions occurred within 3–7 years, depending on height. The decrease in light transmission during the post-disturbance years followed an inverse J-shape trend, indicating more dynamic changes early after disturbance. By 2004 (7-year+), light levels at ≤2 m had become slightly but significantly lower than before the ice storm, with most microsites receiving <2%PPFD. The ice storm led to a synchronized increase of the light levels at almost all understory locations, which might allow a high proportion of the advanced regeneration to experience a release. However, due to the rapid recovery of the light conditions to levels similar or lower than before the ice storm, this disturbance should be more advantageous to shade-tolerant species.

Keywords: Ice storm; Canopy disturbance; Understory light conditions; Post-disturbance recovery; Northern hardwoods

1. Introduction

Ice storms are a relatively common type of disturbance in northeastern North America, although severe ice storms that last several days and affect extensive geographic areas are much less frequent (Irland, 2000). In January of 1998, one of the most severe ice storm ever recorded in North American history affected much of southeastern Ontario, southern Quebec, New Brunswick and the northeastern United States (Irland, 1998). This ice storm caused widespread damage to forests and raised several questions about its short- and long-term ecological impacts (Irland, 2000; Bragg et al., 2003).

Most research efforts undertaken after ice storms aimed at evaluating levels of tree damage as a function of species, tree size, physiographic factors, ice storm severity and management practices (e.g., Duguay et al., 2001; Rhoads et al., 2002; Zarnovican, 2002; Hopkin et al., 2003; Nielsen et al., 2003; Morris and Ostrofsky, 2005). However, through their effects on forest canopy structure (Rhoads et al., 2002; Olthof et al., 2003), ice storms can also indirectly affect understory micro-environmental conditions, including light availability (Parker, 2003). Despite the importance of understory light for tree species regeneration and forest dynamics, only a few studies have evaluated how light conditions are modified by ice storms (e.g., Arii, 2002; Parker, 2003), and none that we know of has monitored the light conditions before and over more than 3 or 4 years after an ice storm.

The objective of this study was to assess the effects of a major ice storm on understory light conditions in an old-growth *Acer–Fagus* forest in Quebec (Canada), and describe their pattern of recovery during 7 years after the storm. Since pre-ice storm light conditions had been recorded at permanent sampling points at our study site (Beaudet et al., 1999), we were able to monitor the post-disturbance light conditions at the same locations starting the first summer after the ice storm, up until the seventh.

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2. Methods

2.1. Study site

The Boisé-des-Muir is a sugar maple (*Acer saccharum* Marsh.) – beech (*Fagus grandifolia* Ehrh.) old-growth forest located approximately 70 km southwest of Montréal, in southern Quebec (Canada). The forest has not been subjected to any major anthropogenic disturbance during the last 300 years (Brisson et al., 1992). The canopy height reaches 30 m, and the basal area (BA) and density of trees (with diameter at breast height [DBH] > 10 cm) in the area of the stand where the study was performed are 29.9 m^2/ha and 382 ha^{-1}, respectively. The overstory is dominated by sugar maple (59% BA), followed by beech (21%), basswood (*Tilia americana* L.) (10%), and hemlock (*Tsuga canadensis* [L.] Carr.) (4%). Sugar maple and beech dominate among seedlings and saplings (with an increasing proportion of beech with increasing size) (Beaudet et al., in press), but other tree and shrub species found in the understory include bitternut hickory (*Carya cordiformis* [Wangenh.] K. Koch.), basswood, white ash (*Fraxinus americana* L.), ironwood (*Ostrya virginiana* [Mill.] K. Koch.), and common prickly ash (*Zanthoxylum americanum* Mill.) (Brisson et al., 2001). Drainage varies from moderate to good, with slopes <5%. The humus is a Mull, and the soil a brown stony loam underlain with surface deposits of morainic origin. The region has a humid continental climate. The mean annual precipitation is 1102 mm, and the mean monthly temperature ranges from −9.1 °C in January to 21.3 °C in July (Huntingdon Meteorological Station, Environment Canada, 2004).

Before the ice storm, canopy gaps were generally rare and small, resulting from branch- and single tree-falls (Brisson et al., 1994). During the January 1998 ice storm, the Boisé-des-Muir received approximately 75 mm of icy rain (Milton and Bourque, 1998). In this forest, more than 83% of trees suffered some form of crown loss, and 37% had severe crown damage (>50% of crown loss) (Brisson et al., 2001). Less than 6% of the trees of the Boisé-des-Muir were broken off at mid-height, and these were almost all small-sized trees (DBH < 20 cm). More than 50% of the saplings incurred some damages, and >75% were bent due to ice accumulation and branch-fall from the overstory (Brisson et al., 2001).

2.2. Light measurements

Understory light conditions were characterized before the ice storm, in 1995 (Beaudet et al., 1999), and re-assessed after the storm in 1998 (1-year+), 1999 (2-year+), 2000 (3-year+), and 2004 (7-year+), at the same locations and using the same methodology as in 1995. On each measurement year, light measurements were taken between mid-June and mid-September, i.e. after complete canopy foliage emergence and before the onset of fall senescence (note that a within-year comparison of late June versus early September data, in 2000, did not show any significant difference in light transmission estimates (data not shown)).

Light measurements were taken at 44 permanent sampling points distributed every 10 m along four 100 m-long parallel transects, 20 m apart from each other. The transmission of above-canopy photosynthetic photon flux density (%PPFD) was determined at 0.3, 1, 2, and 4 m aboveground. Measurements were taken under completely overcast conditions, and are therefore representative of the mean daily %PPFD under both clear and overcast conditions (Gendron et al., 1998). One light sensor (LI-190SA point quantum sensor, LICOR, Lincoln, NE, USA) was installed in an open area <250 m from the study site, and linked to a datalogger (LI-1000, LICOR, Lincoln, NE, USA) programmed to record every minute the average of readings taken at 5 s intervals. The 1-min averages were used as estimates of above-canopy PPFD (Q_0). A second sensor was used to measure understory PPFD (Q_i), using a telescopic pole for measurements at 4 m. Percent PPFD was calculated as $(Q_i/Q_0) \times 100$, with Q_i and Q_0 being recorded at the same time (±1 min).

2.3. Statistical analysis

The variation of %PPFD as a function of time was investigated using an analysis of variance with repeated measurements (ANOVAR) with no between-subject factor, and time as the within-subject factor. A logarithmic transformation was required to meet the normality and homoscedasticity assumptions. The sphericity assumption was tested using Mauchly's criterion. When a departure from sphericity was detected, Huynh-Feldt's and Greenhouse-Geisser's corrected probabilities were calculated (Crowder and Hand, 1990) but are not presented since they never differed from the uncorrected values. When significant, the time effect was further investigated using contrasts among years.

The temporal pattern of variation of the stand-level mean %PPFD was described using linear and non-linear regression (logarithmic, exponential and power functions were investigated). We only present the functions that yielded the highest R^2. The latter statistic was considered adequate for model comparison since the models comprised the same number of parameters. Pearson correlation coefficients were calculated between %PPFD values from different years, and probabilities were Bonferroni corrected. Statistical analyses were performed using Systat (v. 10.0).

2.4. Results and discussion

Before the ice storm, light availability was low at the Boisé-des-Muir, ranging from 2.8 ± 0.2% (mean ± 1S.E.) at 0.3 m to 4.3 ± 0.5% at 4 m (Fig. 1). The frequency distribution of light levels was right-skewed, with most microsites (45–65%, depending on height) receiving between 2 and 4%PPFD (Fig. 2).

A four to five-fold increase in light transmission occurred after the ice storm, with mean light levels ranging from 13.8 ± 0.8% to 20.5 ± 1.0% in 1998 (1-year+), depending on height (Fig. 1). Values at all heights were significantly higher than in 1995 (ANOVAR Contrasts 1998-1995: $F_{1,172} > 260$,

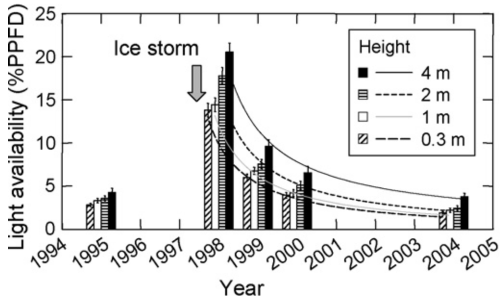

Fig. 1. Light availability (stand-level mean %PPFD ± 1S.E.) at four different heights in the understory of an old-growth *Acer–Fagus* forest measured before and at different times after a major ice storm. Fitted regressions describing the temporal pattern of variation in light after the ice storm are: at 0.3 m, $y = 13.73x^{-1.14}$, $R^2 = 0.997$; 1 m: $y = 14.39x^{-1.07}$, $R^2 = 0.997$; 2 m: $y = 17.68x^{-1.14}$, $R^2 = 0.996$; 4 m: $y = 20.36x^{-1.00}$, $R^2 = 0.993$ (where y is the stand-level mean and x is the number of years post-disturbance, with $x = 1$ for 1998).

$P < 0.001$). In comparison, following the same ice storm but at other sites and based on hemispherical photographs, Arii (2002) observed a 2.2-fold increase in canopy openness (at 0.6 m aboveground) in an old-growth forest in Quebec, and Aarssen and Francq (2004) reported a 2.7-fold increase in canopy openness (between 1.5 and 4 m) in a sugar maple stand in Ontario.

The variability in the light conditions was also modified by the ice storm. While both the range and standard deviation (S.D.) increased, the coefficient of variation (CV) decreased (since the increase in S.D. was comparatively smaller than for the mean) (Fig. 2). The frequency distribution of light levels became more symmetric (Fig. 2). Almost all understory locations experienced some increase in light transmission, but light conditions in 1998 (1-year+) were not correlated with pre-storm conditions, except at 4 m ($r = 0.395$, $P < 0.05$).

Despite its magnitude, the post-ice storm increase in understory light was relatively short-lived. By 1999 (2-year+), the light levels had decreased by half, and recovery to pre-storm conditions occurred within 3–7 years, depending on height (Fig. 1). Throughout the 7-year period during which light conditions were monitored, light levels remained strongly and positively correlated from year to year ($r = 0.545$–0.930, $P < 0.001$). The frequency distributions of light levels changed noticeably during the post-disturbance years, exhibiting an increasingly right-skewed shape (Fig. 2). In 2004 (7-year+), the mean light levels at 0.3, 1 and 2 m had become slightly but significantly lower than before the storm (Fig. 1; Contrasts 2004-1995: $F_{1,172} > 20$, $P < 0.001$), but no difference was observed at 4 m ($F_{1,172} = 3.5$, $P = 0.068$). The S.D. were similar to pre-storm values, but the CV remained slightly higher, especially at ≤2 m (Fig. 2). While before the ice storm most microsites received between 2 and 4%PPFD, in 2004, at ≤2 m, most microsites received <2%PPFD (Fig. 2). Light levels in 2004 were not correlated to pre-disturbance values, except at 0.3 m ($r = 0.534$, $P < 0.001$).

The rapid recovery of mean light conditions to pre-disturbance levels observed in this study is in general agreement with recovery periods reported in other studies about ice storm. For instance, Arii (2002) found that the mean gap fraction recovered within 3 years, and Olthof et al. (2003) that the LAI was stabilizing to pre-ice storm levels 4 years after the event. Our results however indicate that the time required for recovery of light conditions to pre-storm levels tends to be greater higher aboveground (e.g., at 4 m compared to lower heights).

The rapid decrease in understory light following the ice storm is likely a result of the recovery of both the overstory and understory vegetation (Parker, 2003), with more dynamic changes occurring early after canopy disturbance. The lateral expansion of overstory tree crowns was proposed by Arii (2002) and Rhoads et al. (2002) as a likely cause for the rapid recovery of canopy openness and LAI that they respectively observed after an ice storm. Other mechanisms involved in

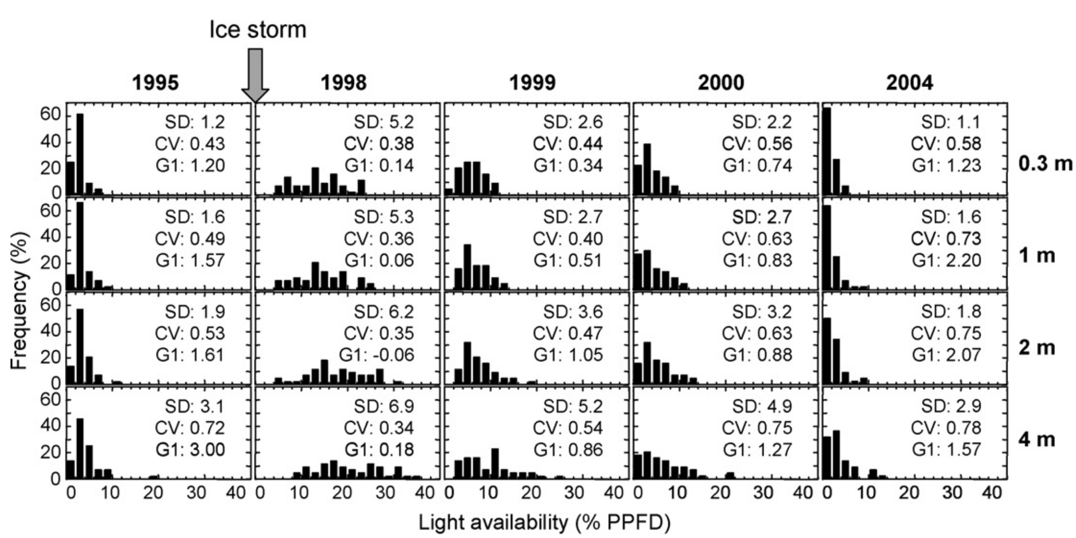

Fig. 2. Frequency distributions of understory light levels before (1995) and at different times after a major ice storm. Measurements were performed at different heights (from first to last row: 0.3, 1, 2, and 4 m), at 44 locations in the understory of an old-growth *Acer–Fagus* forest (S.D.: standard deviation, CV: coefficient of variation, *G*1: skewness coefficient).

causing the rapid decrease in understory light might include branch sprouting (Duguay et al., 2001; Brommit et al., 2004) and the development of a sub-canopy layer of foliage resulting from the growth of released saplings (Brisson et al., 2001; Olthof et al., 2003; Darwin et al., 2004). At our study site, a three to five-fold increase in height growth was observed among pre-established sugar maple and beech saplings following the storm (Beaudet et al., in press). The development of a sub-canopy foliage layer was reported by Olthof et al. (2003), who observed a nearly three-fold increase in LAI between 2 and 7 m in sugar maple stands, following the 1998 ice storm.

The time required for the recovery of light conditions to pre-disturbance levels following an ice storm might be shorter than following other disturbances which involve the formation of single- or multiple-tree gaps. Beaudet et al. (2004), for example, reported that understory light conditions took 8–13 years to recover to pre-disturbance levels following selection cutting. We are not aware of any monitoring of the light conditions following natural tree fall gap formation in northern hardwood forests. However, reports of mean release duration (i.e., positive growth release of advanced regeneration) ranging from 11 to 24 years for sugar maple and beech following gap formation (Canham, 1985, 1990) provide indirect evidence suggesting that tree fall gaps might lead to more prolonged modifications of understory light regimes than ice storms.

The brief modification of the understory light conditions that followed the ice storm provided a relatively narrow window of opportunity for the response of the understory vegetation. At our site, after an initial three to five-fold increase, the radial and height growth rates of sugar maple and beech saplings had already decreased noticeably 7 years after the storm (Beaudet et al., in press). In Ontario woodlands, Darwin et al. (2004) observed an initially strong response of shrubs and saplings following the 1998 ice storm, which stabilized within 4 years of the event. A transient increase in understory light following an ice storm, such as observed in this study, should be more advantageous for shade-tolerant species, which are able to cope with low light and sustain several periods of growth suppression (Canham, 1985, 1990).

Apart from its transient nature, another characteristic of the ice storm' impact on the light conditions was that it led to an increase of the light levels at almost all locations in the understory. This type of effect is characteristic of diffuse disturbances (*sensu* DiGregorio et al., 1999) which lead to widespread canopy thinning, such as insect defoliation (Krasny and DiGregorio, 2001), dieback episodes (Houle, 1990; Shimizu, 2005), and hurricanes of low to moderate intensities (Bellingham et al., 1996; Sherman et al., 2001; Shimizu, 2005). Since canopy openings affect understory light levels beyond gap boundaries (Canham et al., 1990; Tryon et al., 1992), the synchronized formation of several, often interconnected gaps following diffuse canopy disturbances may leave very few areas in the understory where light conditions are not affected by nearby canopy openings (DiGregorio et al., 1999). The impact of ice storms and other diffuse canopy disturbances on understory dynamics might therefore differ from that of discrete tree fall gaps in that a higher proportion of the advanced regeneration may simultaneously experience a release (although the duration and magnitude of the release might be lower). At our site for instance, approximately 70% of sugar maple and beech individuals 5–15 cm in DBH showed a significant growth response following the ice storm (Beaudet et al., in press).

Further research is required to better characterize the effect of various types of disturbances on forest understory light regimes. While pre-disturbance versus post-disturbance comparisons can be useful, longer-term surveys are required to describe the temporal variation of light conditions and assess the time required for their recovery to pre-disturbance levels. Moreover, while light regimes have often been compared between gap and non-gap areas, it is now generally recognized that the gap versus non-gap dichotomy is an oversimplification of reality, and that forest light environments should be described as continuum of light conditions (Lieberman et al., 1989). Frequency distributions of understory light levels can therefore be useful to describe the complexity of forest light regimes (e.g., Nicotra et al., 1999) and assess the impact extent of various types of canopy disturbances on understory light conditions. Detailed descriptions of the effects of canopy disturbance on the characteristics of understory light regimes, including their pattern of heterogeneity and how it evolves through time, are therefore useful to differentiate disturbances and anticipate their impact on forest dynamics.

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