Impact of a major ice storm on an old-growth hardwood forest

Michael C. Hooper, Ken Arii, and Martin J. Lechowicz

Abstract: We quantified the amount of woody biomass and volume lost in an old-growth hardwood forest at Mont St. Hilaire, Quebec, as a consequence of a major ice storm. The storm of January 1998 brought down 19.9 (air-dried) metric tons or 33.6 m^3 of woody debris per hectare. This is about 7–10% of the total aboveground biomass in this forest before the storm and is about 10–20 times greater than the annual production of woody litter typical for temperate deciduous forests in northeastern North America. The woody biomass lost is the greatest recorded for any ice storm. The impact of this ice storm ranks among that of the most damaging windstorms and hurricanes recorded in forested landscapes anywhere.

Key words: glaze ice, forest disturbance, forest damage, tree biomechanics, forest dynamics, forest productivity.

Résumé : Les auteurs ont déterminé le poids et le volume de la biomasse ligneuse perdus dans une forêt décidue âgée, située au Mont St-Hilaire, Québec, suite à un verglas majeur. La tempête de janvier 1998 a jeté au sol 19,9 (séché à l'air) tonnes métriques ou 33,6 m^3 de débris ligneux par hectare. Il s'agit d'environ 7–10 % de la biomasse épigée totale de cette forêt avant la tempête, et représente de 10–20 fois la production annuelle moyenne de litière typique pour une forêt tempérée décidue, du nord-est de l'Amérique du Nord. La biomasse ligneuse perdue est la plus importante jamais enregistrée pour une tempête de verglas. L'impact de cet évènement se situe parmi les tempêtes de vent et les ouragans les plus dommageables enregistrés dans les paysages forestiers partout au monde.

Mots clés : verglas, perturbation forestière, dommage forestier, biomécanique des arbres, dynamique forestière, productivité forestière.

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Introduction

Ice storms are the most frequent form of major disturbance in the deciduous forests of northeastern North America, occurring every 20 to 100 years (Lemon 1961). Windstorms and fires, the other primary agents of disturbance in the region, occur with return times of 100 to 1000 years (Canham and Loucks 1984). As a recurring source of physical perturbation, ice storms are known to play a role in determining forest succession and are an important factor influencing the history and dynamics of the forests in this region (Bruederle and Stearns 1985; De Steven et al. 1991; Rebertus et al. 1997).

Ice storms develop when warm moist air passes over ground-level air masses at or near freezing temperature (Lemon 1961). Under these conditions, super-cooled rain freezes on contact with ground-level objects. In forested landscapes, ice accumulates on trees and results in the loss of branches and twigs from the forest canopy (Whitney and Johnson 1984; Bruederle and Stearns 1985). Ice storms redistribute living and dead biomass in forests, reduce canopy height and stratification, increase organic inputs to the soil, and expose mineral soil. The woody litter produced by ice storms is a substantial, yet little studied, pool of energy, carbon, and nutrients in forest ecosystems (Harmon et al. 1986).

Early studies of ice storms emphasized qualitative descriptions of damage (Harshberger 1904; Illick 1916; Deuber 1940). Most later studies have concentrated on assessments of tree-level damage using various, arbitrarily chosen damage classes (Croxton 1939; Whitney and Johnson 1984; Boerner et al. 1988; Nicholas and Zedaker 1989; Seischab et al. 1993; Rebertus et al. 1997; Siccama et al. 1976; Warrillow and Mou 1999). Only a few papers have quantified the number of fallen branches (Melancon and Lechowicz 1987) and the volume of litter (Bruederle and Stearns 1985; Rebertus et al. 1997). The objective of this paper is to quantify the effects of a major ice storm on both the standing biomass and volume of an old-growth hardwood forest near the northern edge of the eastern deciduous forest biome in North America.

Materials and methods

We assessed the impact of the ice storm of January 1998 (Irland 1998; Regan 1998) on a tract of old-growth forest at Mont St. Hilaire in southwestern Quebec, Canada (45°31′N, 73°08′W). This storm damaged about 1.62 million hectares of Quebec forest (Irland 1998). Mont St. Hilaire lies within the region most hard hit by the storm, with 78–110 mm of glaze ice accumulating over 5 days (Irland 1998; Regan 1998). Mont St. Hilaire itself is a rugged hill standing abruptly above the floor of the St. Lawrence River valley. The forest, approximately 10 km^2 in extent, is the

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largest remnant of primeval forests in this region; many of the trees exceed 150 years in age and a few are over 400 years old (Cook 1971). The last major ice storm at the site occurred in February 1983 (Melancon and Lechowicz 1987). Various tree communities occur in relation to local relief and aspect (Maycock 1961; Enright and Lewis 1985), but *Acer saccharum* and *Fagus grandifolia* are the common canopy dominants. To assess the impact of the January 1998 ice storm, we took advantage of seven transects that had been established in summer 1997 to monitor forest dynamics. We sampled 117 permanent plots located randomly along the seven transects; each plot is 113 m^2 (6-m radius).

We quantified biomass losses resulting from the ice storm using a sampling protocol based on the conserved relationship between branch diameter and mass (Whittaker and Marks 1975). We first determined regressions relating the air-dried biomass of a branch to its basal diameter and then used these regressions to estimate the total biomass of fallen material from measurements of the basal diameters of all fallen branches in our plots. Basal diameter in this context refers to the diameter of the branch at the point where it broke from the tree. The ice-encrusted branches falling onto deep snow in this storm did not break up, which made it possible to estimate total down biomass from the species-specific regressions on basal diameter.

To create the diameter–biomass regressions, we collected fallen branches from a representative range of sizes for each major tree species on Mont St. Hilaire. Between 20–70 branches for each species were gathered from at least three localities, and for the less frequent species from all over the mountain, to ensure the accuracy and precision of the regressions. Branches from 10 species were sampled: striped maple (*Acer pensylvanicum* L.), sugar maple (*Acer saccharum* Marshall.), paper birch (*Betula papyrifera* Marshall.), yellow birch (*Betula alleghaniensis* Britton.), white ash (*Fraxinus americana* L.), American beech (*Fagus grandifolia* Ehrh.), ironwood (*Ostrya virginiana* (Miller) K. Koch.), large-tooth aspen (*Populus grandidentata* Michx.), red oak (*Quercus rubra* L.), and basswood (*Tilia americana* L.). The primary criteria for selection of branches for determining the diameter–biomass regressions were that the branches (*i*) be essentially intact, (*ii*) be larger than 1 cm in diameter at their broken end, and (*iii*) in aggregate, provide a balanced sample over the full range of fallen branch sizes for a species. The 1-cm diameter cutoff was set by the 2-oz (1 oz = 28.349 g) resolution of the scale used to measure branch mass (Salter 235-10 angling scale, Salter-Weightronix, West Bromwich, West Midlands, England); smaller branches could not be accurately weighed. The diameter of the basal end of the broken branch was measured using a vernier caliper. To minimize changes in the moisture content of fallen material during the course of sampling, all branches were collected from 21 May to 10 June 1998. Because the storm occurred in January, well before sap flow began, the fallen material was essentially air-dried in early summer and provided highly repeatable estimates of the diameter–biomass relationship. Our values for woody biomass are on the order of 11–14% higher than they would be if reported on an oven-dried rather than air-dried basis (Winters 1951); note that we do not attempt to adjust our data for comparison with literature values for oven-dried material.

To use the regressions relating branch basal diameter to mass, we had to account for the bias in linear regressions after logarithmic transformation. The appropriate formula is $\mathrm{CF} = \exp(\mathrm{SEE}^2/2)$, where CF is the correction factor and SEE is the standard error of estimate with degrees of freedom $N - 2$ for a two variable equation (Sprugel 1983). Correction factors were calculated for the logarithmically transformed equation relating diameter and mass for each sampled species. To estimate the mass of a fallen branch, the ln(biomass) of the branch was first calculated from its ln(diameter), the ln(biomass) was then back-transformed to kilograms, and the back-transformed value was multiplied by the correction factor.

To estimate the areal loss of woody biomass in the forest as a whole, we recorded the basal diameter of every piece of woody debris greater than 1 cm in diameter in the 117 permanent plots. We identified material fallen in the ice storm according to position in the strata of downed branches, bark coloration, and wood fragility. Each newly fallen branch or branch fragment was identified to species. The total, air-dried biomass of fallen material in the 117 plots then was calculated by inputting the diameters of all fallen branches into the appropriate species-specific equations relating branch basal diameter to air-dried mass.

To produce a second, independent measure of the amount of damage sustained at the stand level, the volume of downed macro-litter resulting from the ice storm was determined using a modified version of the Van Wagner (1968) method (Bruederle and Stearns 1985). Measurements were made along sample lines (12 m long) at each of the 117 study plots. The sample lines were established in a random compass bearing at each plot. We recorded the species and diameter of each piece of debris with a diameter greater than 1 cm at each point of intersection with the sampling lines. Guidelines for inclusion of macro-litter in the tally followed Van Wagner (1968). Litter volume was calculated according to the following equation (Van Wagner 1968; Bruederle and Stearns 1985):

$$[1] \qquad V = (\pi^2 \sum d^2/8L)\ (10\,000\ \mathrm{m}^2/\mathrm{ha})$$

where V is the volume of macro-litter in cubic metres per hectare, d is the diameter of litter at the point of intersection in metres, and L is the length of the sample line in metres. The 117 sampling lines provided an aggregate estimate of the total volume of downed woody material in our plots.

To estimate the amount of woody biomass in the forest canopy before the ice storm, we sampled forest composition in the 117 permanent plots in July 1998. We recorded the diameter at breast height (dbh) of all trees and saplings with dbh greater than 3 cm. Very few trees were broken at or near breast height. This provides a complete record of pre-storm composition in the permanent plots. We used these data in species-specific, allometric equations that predict aboveground biomass as a function of dbh on a tree by tree basis (Ter-Mikaelian and Korzukhin 1997; Hooper 1999). These allometric estimates were summed by species across all trees to estimate the proportionate losses of standing biomass in the ice storm of 1998.

Results

Strong relationships were found between branch basal diameter and air-dried biomass for each of the 10 species studied (Table 1). Coefficients of determination were above 0.94 in all cases, with $p < 0.001$; the scatter of sampling points around the fitted lines was tight and without outliers (Hooper 1999). In our census of the 117 permanent plots, we found and measured 17 534 pieces of woody debris greater than 1 cm in diameter at the broken end, somewhat more than one broken branch end in every square metre of the forest floor. Half the down branches were 1–2 cm in diameter, but in aggregate these small branches only accounted for 3.2% of the down biomass; the 4.2% of the down branches 10 cm or greater in diameter accounted for 72.4% of the down biomass. In other words, many trees lost small- to medium-sized branches and fewer lost major limbs. We used these sampled branches to estimate down biomass and volume across all plots and per hectare (Table 2). The 10 species for which we had determined diameter–biomass regressions account for 97% of all of the branches recorded

Table 1. Logarithmically transformed equations relating branch basal diameter (*d*, in cm) and air-dried woody biomass (BM, in kg) for 10 deciduous forest tree species at Mont St. Hilaire, Quebec.

Species	*N*	Slope	CF	r^2	*p*	Diameter range
Acer pensylvanicum	67	ln(BM) = 2.660 – 3.017ln(*d*)	1.027	0.945	<0.0001	1.04–5.00
Acer saccharum	39	ln(BM) = 2.771 – 2.942ln(*d*)	1.024	0.979	<0.0001	1.19–10.77
Betula alleghaniensis	59	ln(BM) = 2.520 – 2.575ln(*d*)	1.017	0.986	<0.0001	1.00–11.11
Betula papyrifera	21	ln(BM) = 2.770 – 2.998ln(*d*)	1.021	0.972	<0.0001	1.52–6.61
Fraxinus americana	58	ln(BM) = 2.607 – 2.644ln(*d*)	1.021	0.972	<0.0001	1.05–6.64
Fagus grandifolia	66	ln(BM) = 2.657 – 2.744ln(*d*)	1.023	0.983	<0.0001	1.00–17.13
Ostrya virginiana	39	ln(BM) = 2.709 – 2.799ln(*d*)	1.014	0.987	<0.0001	1.27–8.95
Populus grandidentata	22	ln(BM) = 2.921 – 3.325ln(*d*)	1.024	0.968	<0.0001	1.84–7.56
Quercus rubra	63	ln(BM) = 2.795 – 3.023ln(*d*)	1.019	0.973	<0.0001	1.70–11.05
Tilia americana	65	ln(BM) = 2.928 – 3.768ln(*d*)	1.051	0.937	<0.0001	1.28–7.70

and for 98% of the total basal area of trees in the study site; a few other species account for the balance of down branches. Considering only the 10 species that we studied, we estimate the storm of January 1998 brought down 19.9 metric tons (air-dried) or 33.6 m^3 of woody debris per hectare (Table 2).

According to our allometric analyses, this is about 7–10% of the total aboveground biomass in this forest before the storm (Table 2). In comparing the aboveground woody biomass lost to pre-storm values for each species, we could not include either *A. pensylvanicum* or *O. virginiana* because allometric equations are not available for these species. Equations relating total aboveground biomass to dbh at a number of different sites existed for the other eight study species (Hooper 1999). We estimated the pre-storm, aboveground biomass for each species at Mont St. Hilaire using all the allometric equations available for each species; the range of predicted pre-storm biomass for each of the eight species is in Table 2. Based on our actual census of fallen debris, these eight species produced 19 404 kg·ha^{-1} of woody litter as a result of the ice storm. This is only slightly less than the 19 921 kg·ha^{-1} that includes the two species lacking allometric data. Since *A. pensylvanicum* and *O. virginiana* are both small trees with a negligible contribution to the total forest biomass at Mont St. Hilaire, the comparison of pre- and post-storm biomass is not greatly altered by their omission.

Discussion

The importance of natural disturbances in shaping forested landscapes and influencing the dynamics of forest ecosystems has gained wide recognition. Many studies concern large-scale fires in the boreal zone (Johnson 1992) or the creation of canopy gaps in mature deciduous forests (Pickett and White 1985). Natural perturbations that affect large areas and occur infrequently in deciduous forests of the north temperate zone remain poorly studied. We can describe in detail the consequences of small canopy gaps caused by the death of one or a few trees, but the far more extensive damage that is occasionally caused by wind and ice storms is less well known. Our results quantify the very substantial and species-specific impacts that a severe ice storm can have in an old-growth forest in northeastern North America and point to the necessity of assessing tree and forest responses in the aftermath of such large-scale disturbances.

The 19.9 tons·ha^{-1} of air-dried, woody litter brought down by the ice storm of 1998 at Mont St. Hilaire substantially exceeds the annual total aboveground litter fall in undisturbed temperate deciduous forests. At the Hubbard Brook forest nearby in New Hampshire, the annual fall of aboveground litter (wood and foliage) for a similar beech–maple forest is 5.7 tons·ha^{-1} (Gosz et al. 1972; Whittaker et al. 1979). This value falls within the range of 4–7 tons·ha^{-1} reported by Rodin and Bazilevich (1967) in their summary of world litter production. Since we have reported only the amount of woody litter, not total litter, the losses observed at Mont St. Hilaire in the ice storm of 1998 are all the more exceptional. In most undisturbed forests, woody material constitutes the smallest component of annual litter fall and thus the comparison underestimates the impact of the ice storm in terms of loss of aboveground woody structure. Two reviews of the global literature on litter production reported annual values of woody litter production in cool temperate, deciduous forests to be 1.3 tons·ha^{-1} (Bray and Gorham 1964) or 1.0 tons·ha^{-1} (Vogt et al. 1986). In the northern, deciduous forests of New Hampshire, Gosz et al. (1972) reported a slightly higher value of 2.1 tons·ha^{-1} of woody litter annually (Table 3). The 19.9 kg·ha^{-1} of air-dried, woody litter brought down by the ice storm at Mont St. Hilaire is thus approximately 10–20 times more than the normal annual production of woody litter in temperate deciduous forests.

Among climatic events causing the greatest damage in forested landscapes, the ice storm of 1998 approaches some of the largest hurricanes (Table 3). In terms of litter production, Hurricane Gilbert stands as the single most powerful climatic disturbance on record (Whigham et al. 1991). Hurricane Gilbert felled 16.0 tons·ha^{-1} of coarse woody debris (>10 cm diameter) in the dry, tropical forests of the Yucatan Peninsula of Mexico (Whigham et al. 1991); the comparable figure owing to the 1998 ice storm at Mont St. Hilaire was 8.9 tons·ha^{-1}. Hurricane Hugo brought down 18.1 tons·ha^{-1} of woody biomass and foliage in a tropical, broad-leaved forest in the Luquillo Mountains of Puerto Rico (Frangi and Lugo 1991). This reduced the standing biomass of the forest by 10% (Frangi and Lugo 1991); the comparable figure is 7–10% for the 1998 ice storm at Mont St. Hilaire. The actual biological impact of the ice storm is greater than it first appears because the loss of the potential to produce foliage in the next season is not accounted for in the fallen woody biomass at Mont St. Hilaire.

Table 2. Forest composition (basal area per species) at Mont St. Hilaire, total estimated standing biomass of forest trees, and the losses of air-dried biomass and volume owing to the ice storm of 1998.

Species	Standing biomass (Mg·ha^{-1})	Biomass losses (kg·ha^{-1})	% biomass lost	Volume of litter per hectare (m^3·ha^{-1})	No. of pieces of litter	Basal area in study plots (m^2)
Acer pensylvanicum	—	313.7	—	0.92	617	0.72
Acer saccharum	96.8–146.0	8284.7	5.7–8.6	14.26	8 747	19.16
Betula alleghaniensis	3.4–4.9	122.3	2.5–3.6	0.05	105	0.63
Betula papyrifera	2.6–3.7	60.3	1.9–2.4	0.26	177	0.88
Fagus grandifolia	30.9–48.8	590.4	9.4–14.8	3.97	3 434	2.09
Fraxinus americana	9.4–11.3	4585.2	5.2–6.3	0.51	1 058	7.08
Ostrya virginiana	—	203.3	—	1.40	163	1.18
Populus grandidentata	2.0–2.3	49.4	21.7–24.7	0.01	32	0.07
Quercus rubra	45.4–54.5	5614.6	10.3–12.4	11.94	3 071	7.92
Tilia americana	1.0–1.3	97.0	7.5–9.3	0.01	133	0.42
Other*	—	NA†	—	0.22	471	0.64
Total	189.7–270.6	19920.9	7.2–10.2	33.55	17 534	40.79

Note: Based on a sample of 117 plots, each with a 6-m radius.

*Other species include *Acer spicatum* L., *Amelanchier laevis* Wieg., *Cornus alternifolia* L.f., *Pinus resinosa* Ait., *Pinus strobus* L., *Prunus pensylvanica* L.f., *Prunus serotina Ehrh.*, *Prunus virginiana* L., and *Tsuga canadensis* (L.) Carriére.

†NA, not available.

Table 3. Comparison of biomass losses resulting from the ice storm of January 1998 at Mont St. Hilaire with normal biomass losses and those resulting from other disturbance events. The Mont St. Hilaire data are for air-dried biomass, on the order of 10–15% heavier than oven-dried biomass estimates.

Study	Forest type, location	Reference	Debris, size range	Biomass lost	Comparable losses at MSH* (kg·ha^{-1})
This study	Old-growth northern hardwood, Quebec	Hooper 1999	Woody litter >1 cm	19 921 kg·ha^{-1}	—
Generalised woody litterfall	Cool temperate forests	Bray and Gorham 1964	Woody litter	1 325 kg·ha^{-1}·year^{-1}	19 921
Generalised woody litterfall	Hardwood forests, New Hampshire	Gosz et al. 1972	Woody litter	2 072 kg·ha^{-1}·year^{-1}	19 921
Generalised woody litterfall	Cold temperate, broadleaf deciduous forest	Vogt et al. 1986	Woody litter	1 046 kg·ha^{-1}·year^{-1}	19 921
Woody litterfall in Hurricane Gilbert	Tropical dry forest, Yucatan	Whigham et al. 1991	Coarse woody debris >10 cm	16 000 kg·ha^{-1}	8 868
Woody litterfall in Hurricane Hugo	Tropical broad-leaved forest, Puerto Rico	Scatena et al. 1993	Woody litter >2.5 cm	10 460 kg·ha^{-1}	17 970
Macro-litter in Hurricane Hugo	Tropical broad-leaved forest, Puerto Rico	Frangi and Lugo 1991	>1 cm	18 100 kg·ha^{-1}	19 921
Woody litterfall in Hurricane Iniki	*Acacia* forests, Hawaii	Harrington et al. 1997	Woody litter	1 200 – 4 400 kg·ha^{-1}	19 921

*MSH, Mont St. Hilaire.

Table 4. Comparison of volume losses resulting from the ice storm of January 1998 at Mont St. Hilaire with volume losses in other disturbances.

Study	Forest type, location	Reference	Debris, lower size limit	Volume lost	Comparable losses at MSH* (m^3·ha^{-1})
This study	Old-growth northern hardwood, Quebec	Hooper 1999	Woody litter >1 cm	34 kg·ha^{-1}	—
Woody litterfall in an ice storm	Old-growth oak-hickory forest, Missouri	Rebertus et al. 1997	Woody litter	5 m^3·ha^{-1}	34
Woody litterfall in an ice storm	Mesic forest, Wisconsin	Bruederle and Stearns 1985	Woody litter >1.3 cm	19 m^3·ha^{-1}	32
Woody litterfall in a major wind storm	Survey of British forests	Kirby et al. 1998	Woody litter	13 m^3·ha^{-1}	34

*MSH, Mont St. Hilaire.

Although information on downed wood volume caused by major climatic disturbances is limited, the volume loss caused by the 1998 ice storm (33.6 $m^3 \cdot ha^{-1}$ of woody litter) is greater than that reported for any other non-fire disturbance. The volume of woody litter (in comparable size ranges) produced by the ice storm at Mont St. Hilaire is 1.7 times greater than that of the Wisconsin ice storm (Bruederle and Sterns 1985), 6.6 times greater than that of the 1994 Missouri ice storm (Rebertus et al. 1997), and 2.6 times greater than that of a major wind storm in England (Kirby et al. 1998) (Table 4).

We have shown that the ice storm of 1998 had effects on the scale of some of the most powerful climatic disturbances on record, including Hurricane Hugo (Frangi and Lugo 1991) and Hurricane Gilbert (Whigham et al. 1991). While it is recognized that hurricane-induced wind damage is largely responsible for the structural patterning and dynamics of the natural forests of central New England (Foster 1988; Henry and Swan 1974), the role of ice storms has generally not been considered in studies of forest dynamics. Since major ice storms have been shown to occur more frequently in the forests of northeastern North America than either large-scale wind storms or fires (Lemon 1961), it is likely that ice damage has played a fundamental role in the dynamics and history of these forests. Despite this, the role of ice storms in the dynamics, history, and structure of the forests of the northeastern United States and adjacent Canada remains largely unstudied. Results from studies of other disturbance types and from experimental disturbances indicate that the effects of ice storms on nutrient cycling and hydrology may be limited. On the other hand, the scale of biomass transfers to the forest floor in ice storms indicates a significant role in structuring forests and driving forest succession. Changes in the frequency and intensity of ice storms, e.g., as a result of global climate change, could have important implications for the forests of the region. The effects of ice storms on forest ecology merit greater attention.

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References

Boerner, R.E., Runge, J.S.D., Cho, D.S., and Kooser, J.G. 1988. Localized ice storm damage in an Appalachian Plateau watershed. Am. Midland Nat. **119**: 199–208.

Bray, R.J., and Gorham, E. 1964. Litter production in forests of the world. Adv. Ecol. Res. **2**: 101–157.

Bruederle, L.P., and Stearns, F.W. 1985. Ice storm damage to a southern Wisconsin mesic forest. Bull. Torrey Bot. Club, **112**: 167–175.

Canham, C.D., and Loucks, O.L. 1984. Catastrophic windthrow in the presettlement forests of Wisconsin. Ecology, **65**: 803–809.

Cook, B.D. 1971. Tree-age distribution in a northern hardwood forest. M.Sc. thesis, Department of Geography, McGill University, Montréal, Quebec.

Croxton, W.C. 1939. Study of the tolerance of trees to breakage by ice accumulation. Ecology, **20**: 71–73.

De Steven, D., Kline, J., and Matthiae, P.E. 1991. Long-term changes in a Wisconsin *Fagus-Acer* forest in relation to glaze storm disturbance. J. Veg. Sci. **2**: 201–208.

Deuber, C.G. 1940. Glaze storm of 1940. Am. For. **46**: 210.

Enright, N.J., and Lewis, J.E. 1985. Aspect related vegetation patterns and climate at Mont St. Hilaire, Quebec. Can. Geogr. **29**: 249–256.

Foster, D.R. 1988. Species and stand response to catastrophic wind in central New England, U.S.A. J. Ecol. **76**: 135–151.

Frangi J.L., and Lugo, A.E. 1991. A flood plain forest in the Luquillo Mountains of Puerto Rico five years after Hurricane Hugo. Biotropica, **30**: 339–348.

Gosz, J.R., Likens, G.E., and Bormann, F.H. 1972. Nutrient content on the Hubbard Brook experimental forest, New Hampshire. Ecology, **53**:769–784.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K., Jr., and Cummins, K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res. **15**: 133–302.

Harrington, R.A., Fownes, J.H., Scowcroft, P.G., and Vann, C.S. 1997. Impact of Hurricane Iniki on native Hawaiian *Acacia kao* forests: damage and two-year recovery. J. Trop. Ecol. **13**: 539–558.

Harshberger, J.W. 1904. The relation of ice storms to trees. Con. Bot. Lab. Univ. Penn. II: 345–349.

Henry, J.D., and Swan, J.M.A. 1974. Reconstructing forest history from live and dead plant material – an approach to the study of forest succession in S. W. New Hampshire. Ecology, **55**: 772–783.

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

Illick, J.S. 1916. A destructive snow and ice storm. For. Leaves, **15**: 103–107.

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

Johnson, E.A. 1992. Fire and vegetation dynamics: studies from the North American boreal forest. Cambridge University Press, Cambridge.

Kirby, K.J., Reid, C.M., Thomas, R.C., and Goldsmith, F.B. 1998. Preliminary estimates of fallen wood and standing dead trees in managed and unmanaged forests of Britain. J. Ecol. **35**: 148–155.

Lemon, P.C. 1961. Forest ecology of ice storms. Bull. Torrey Bot. Club, **88**: 21–29.

Maycock, P.F. 1961. Botanical studies on Mont St. Hilaire, Rouville County, Quebec: general description of the area and a floristic survey. Can. J. Bot. **39**: 1293–1325.

Melancon, S., and Lechowicz, M.J. 1987. Differences in the damage caused by glaze ice on codominant *Acer saccharum* and *Fagus grandifolia*. Can. J. Bot. **65**: 1157–1159.

Nicholas, N. S., and Zedaker, S.M. 1989. Ice damage in spruce-fir forests of the Black Mountains, North Carolina. Can. J. For. Res. **19**: 1487–1491.

Pickett, S.T.A., and White, P.S. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, London.

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. Midland Nat. **137**: 48–61.

Regan, M. 1998. Canadian ice storm 1998. Bull. World Met. Org. **47**: 250–256

Rodin, L.E., and Bazilevich, N.I. 1967. Production and mineral cycling in terrestrial vegetation. Oliver and Boyd. Edinburgh, Scotland.

Scatena, F.N., Silver, W., Siccama, T., Johnson, A., and Sachez, M.J. 1993. Biomass and nutrient content of the Bisley Experimental watersheds, Luquillo experimental forest, Puerto Rico, before and after Hurricane Hugo, 1989. Biotropica, **25**: 15–27.

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.

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.

Sprugel, D.G. 1983. Correcting for bias in log-transformed allometric equations. Ecology, **64**: 209–210.

Ter-Mikaelian, M.T., and Korzukhin, M.D. 1997. Biomass equations for sixty-five North American tree species. For. Ecol. Manag. **97**: 1–24.

Van Wagner, C.E. 1968. The line intersect method in forest sampling. For Sci. **14**: 20–26.

Vogt, K.A., Grier, C.C., and Vogt, D.J. 1986. Production, turnover, and nutrient dynamics of above- and belowground detritus of world forests. Adv. Ecol. Res. **15**: 302–377.

Warrillow, M., and Mau, P. 1999. Ice storm damage to forest trees in the ridge and valley region of southwestern Virginia. J. Torrey Bot. Soc. **126**: 147–158.

Whigham, D.F., Olmsted, I., and Harmon, M.E. 1991. The impact of hurricane Gilbert on trees, litterfall, and woody debris in a dry tropical forest in the Northeastern Yucatan Peninsula. Biotropica, **23**: 434–441.

Whitney, H.E., and Johnson, W.C. 1984. Ice storms and forest succession in southwestern Virginia. Bull. Torrey Bot. Club, **111**: 429–437.

Whittaker, R.H., and Marks, P.L. 1975. Methods of assessing primary productivity. *In* Primary productivity of the biosphere. *Edited by* H. Leith and R.H. Whittaker. Springer-Verlag, New York.

Whittaker, R.H., Likens, G.E., Bormann, F.H., Easton, J.S., and Siccama, T.G. 1979. The Hubbard brook ecosystem study: Forest nutrient cycling and element behaviour. Ecology, **60**: 203–220.

Winters, R.H. 1951. Canadian woods. Their properties and uses. Forestry Branch, Ministry of Resources and Development, Ottawa.