Effects of an intense ice storm on the structure of a northern hardwood forest[1]

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Abstract: A major ice storm in January 1998 provided an opportunity to study the effects of a rare, intense disturbance on the structure of the northern hardwood forest canopy. Canopy damage was assessed using visual damage classes within watersheds of different ages at the Hubbard Brook Experimental Forest (HBEF) and changes in leaf area index in two of these watersheds. Ice thickness was measured, and ice loads of trees were estimated using regression equations. In the 60- to 120-year-old forests (mean basal area 26 $m^2 \cdot ha^{-1}$), damage was greatest in trees >30 cm diameter at breast height and at elevations above 600 m. Of the dominant tree species, beech (*Fagus grandifolia* Ehrh.) was the most damaged, sugar maple (*Acer saccharum* Marsh.) was the most resistant, and yellow birch (*Betula alleghaniensis* Britt.) was intermediate. Trees with advanced beech bark disease experienced heavier ice damage. Little damage occurred in the 14-year-old forest, while the 24- to 28-year-old forest experienced intense damage. In the young stands of this forest, damage was greatest between 600 and 750 m, in trees on steep slopes and near streams, and among pin cherry (*Prunus pensylvanica* L.). Recovery of the canopy was tracked over three growing seasons, and root growth was monitored 1 year after the storm. Because of the high density of advance regeneration from beech bark disease and root sprouting potential in ice-damaged beech, HBEF will likely see an increase in beech abundance in older forests as a result of the storm. There will also be a more rapid change from pioneer species to mature northern hardwoods in the younger forests. These predictions illustrate the ability of rare disturbances to increase heterogeneity of forest structure and composition in this ecosystem, especially through interactions with other disturbances.

Résumé : En janvier 1998, une importante tempête de verglas a fourni une occasion d'étudier les effets d'une perturbation rare et sévère sur la structure du couvert dans une forêt de feuillus nordiques. Les dommages subis par le couvert ont été évalués visuellement à l'aide de classes de dommages dans des bassins d'âge différent situés à la forêt expérimentale de Hubbard Brook et des changements dans l'indice de surface foliaire dans deux de ces bassins. L'épaisseur de la glace a été mesurée et le poids de la glace sur les arbres a été estimé à l'aide d'équations de régression. Dans les forêts âgées de 60 à 120 ans (surface terrière moyenne de 26 $m^2 \cdot ha^{-1}$), les arbres de plus de 30 cm au diamètre à hauteur de poitrine et situés à une altitude de plus de 600 m étaient les plus sévèrement endommagés. Parmi les espèces dominantes, le hêtre à grandes feuilles (*Fagus grandifolia* Ehrh.) était le plus endommagé, l'érable à sucre (*Acer saccharum* Marsh.) était le plus résistant et le bouleau jaune (*Betula alleghaniensis* Britt.) se situait entre les deux. Les arbres sévèrement affectés par la maladie corticale du hêtre ont subi plus de dommages par le verglas. La forêt âgée de 14 ans a subi peu de dommages alors que les dommages étaient sévères dans la forêt âgée de 24 à 28 ans. Dans les jeunes peuplements de cette forêt, les dommages étaient les plus sévères à une altitude de 600 à 750 m, sur les arbres situés sur les pentes abruptes et près des cours d'eau ainsi que sur le cerisier d'Amérique (*Prunus pensylvanica* L.). La reconstruction du couvert a été suivie pendant trois saisons de croissance et la croissance des racines l'a été pendant 1 an après la tempête. À cause de la forte densité de la régénération préétablie due à la maladie corticale du hêtre et de la capacité de drageonnement des hêtres affectés par le verglas, la forêt expérimentale de Hubbard Brook connaîtra une augmentation de l'abondance du hêtre dans les vieilles forêts à la suite de la tempête. Dans les forêts plus jeunes, la transition des espèces pionnières vers les feuillus nordiques matures sera également plus rapide. Ces prédictions montrent que les perturbations rares ont la capacité d'augmenter l'hétérogénéité de la structure et de la composition de la forêt dans cet écosystème, particulièrement par le biais d'interactions avec d'autres perturbations.

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Introduction

Most of the northern hardwood forest is considered prone to moderate or heavy ice storms because of its geographical location and the potential susceptibilities of its dominant species (Lemon 1961; Melancon and Lechowicz 1987; Whitney and Johnson 1984). However, long-term studies of the effect of such storms on forest dynamics within this region are rare.

Ice storms occur when supercooled rain contacts solid surfaces. The resulting buildup of ice on trees can cause a 100-fold increase in canopy mass, leading to substantial branch loss and even tree death from bole breakage or tip-ups, especially when the precipitation is accompanied by high winds (Melancon and Lechowicz 1987; Rebertus et al. 1997). Ice storms influence forest community dynamics in the southern Appalachians of the United States, where they return every 2–4 years (Attiwill 1994; Carvell et al. 1957; Mou and Warrilow 2000). Still, the impacts of more rare ice storms like those occurring in the northern hardwood forest are unclear. Some aspects of the ecology of ice storm disturbance have been well studied, yet a more complete understanding is still lacking (Lemon 1961; Attiwill 1994). Tree susceptibility to crown damage by ice is determined by architecture (Bruederle and Stearns 1985; Boerner et al. 1988), size (Boerner et al. 1988; Rebertus et al. 1997), mechanical properties (Lemon 1961; Bruederle and Stearns 1985), age, and health (Lemon 1961; Bruederle and Stearns 1985; Seischab et al. 1993; Rebertus et al. 1997). Physiographic factors have also influenced the effects of ice storms on forests through their relationship with ice loading (i.e., elevation influences temperature and, therefore, ice formation) and through the effects of soils (i.e., texture and depth) and slope on stand-level susceptibility and damage responses (Whitney and Johnson 1984; Bruederle and Stearns 1985; Boerner et al. 1988; Rebertus et al. 1997; Warrilow and Mou 1999). The lack of agreement on the key determinants of ice storm susceptibility likely reflects differences in forest composition and structure, site characteristics, and storm conditions among sites and storms. To begin to address these variations across sites there is a need for long-term, quantitative studies at intensively studied forests, to compare pre- and post-storm forest conditions.

The study reported here documents forest canopy damage caused by a severe ice storm that impacted the northeastern United States and southeastern Canada from January 5–10, 1998 (Jones 2001). The storm left more than 8 cm of ice on trees and power lines in some areas (Irland 1998; Dobbs 1999). An estimated 7.1×10^6 ha in the United States (Dobbs 1999), and 427 011 forested ha in New Hampshire (Bofinger 2001) were impacted by the storm. Parts of the Hubbard Brook Experimental Forest (HBEF), New Hampshire, U.S.A., where detailed information on forest dynamics and ecosystem behavior has been collected for over 40 years (e.g., Bormann and Likens 1979*a*; Likens et al. 1996), were severely affected. The purpose of this study was twofold: (*i*) to document how forest conditions (age, structure, composition, and health) interact with physiographic factors (elevation, slope, soils) to influence both the magnitude and pattern of tree damage by an ice storm and (*ii*) to begin to understand the long-term recovery of the canopy in the northern hardwood forest. We predicted that: ice damage would differ among species based on mechanical properties of wood; damage would be size dependent, with large and very small trees being most vulnerable; there would be an elevational gradient in damage driven largely by freezing rain and wind; and topographic variation would result from microclimatic differences.

Methods

Study site

Located in Woodstock, N.H. (43°56′N, 71°45′W), HBEF encompasses 3160 ha in the White Mountain National Forest. It is managed by the USDA Forest Service Northeastern Research Station and has been a site for long-term ecological study since 1963. The climate of the region is cool, temperate, humid continental. The mean temperature in January is –9°C and in July is 19°C. The forest receives a mean of 123 cm of precipitation per year, one-third to one-quarter of which falls as snow. The bedrock of the area is Rangely formation and is overlain with unsorted basal till. Till depths range from 0 to 3 m and tend to increase at lower elevations (T.G. Siccama, unpublished data). The soils are primarily well-drained Spodosols (course, loamy, mixed, frigid, Typic Haplorthods) with sandy loam to loamy sand textures. The forest has a pit and mound topography resulting from boulders and fallen trees (Bormann et al. 1970).

The HBEF is considered a northern hardwood forest, with the highest elevations closely resembling a subalpine spruce–fir forest. Prior to 1900, the forest was characterized as a spruce–hardwood forest (Chittenden 1904; Braun 1950), but it has been greatly changed by human activity. The region was first settled in 1770, and the HBEF watershed was cleared of many merchantable trees from 1880 to 1917. The hurricane of 1938 further affected the forest, with some areas experiencing high levels of damage (Bormann and Likens 1979*b*). The stands of mature forest are now dominated by beech (*Fagus grandifolia* Ehrh.), sugar maple (*Acer saccharum* Marsh.), and yellow birch (*Betula alleghaniensis* Britt.), with spruce (*Picea rubens* Sarg.) and fir (*Abies balsamea* (L.) Mill.) primarily found on ridges and rocky areas (Bormann et al. 1970).

This study focuses on watershed 1 (WS1), WS4, WS5, and WS6 at HBEF (Table 1). At the time of the storm, WS1 and WS6 were dominated by sugar maple, beech, and yellow birch based on basal area and density (Table 2). The dominant species on WS4 and WS5 were yellow birch, pin cherry, paper birch (*Betula papyrifera* Marsh.), American beech, sugar maple, and striped maple (*Acer pensylvanicum* L.) (Table 3). Together, these species made up over 90% of the forest basal area in 1997. The composition of the strips of different ages on WS4 was significantly different. Specifically, the younger strips had a much higher proportion of pin cherry (36% by basal area) and the older strips had more yellow birch (46% by basal area) than the mean for the watershed as a whole (Martin and Hornbeck 1989).

Ice measurements

Between January 5 and 11, 1998, >75 mm of melted precipitation fell in the Hubbard Brook valley. During the peak of the storm, maximum temperatures in the region ranged from –1 to 1°C. The mean daily temperature between Janu-

Table 1. Description of watersheds 1, 6, 4, and 5 at Hubbard Brook Experimental Forest, New Hampshire, U.S.A.

Watershed	Size (ha)	Age in 1998 (years)	Elevation (m)	Aspect (°)	Treatment history
1	11.8	Multiaged, 60–120*	488–747	15°, southeast	51 Mg of $CaSiO_3$ added in 1999
6	13.2	Multiaged, 60–120*	549–792	15°, southeast	None, biogeochemical reference
4	36.1	Even aged, 24, 26, 28	442–747	15°, southeast	Harvested in 1970, 1972, and 1974 using progressive strip cuts†
5	21.9	14	488–762	15°, southeast	Whole-tree harvested in the winter of 1983–1984

*Canopy trees of the watershed 1 and 6 forests were established following harvesting in the 1880s and 1910s and the 1938 hurricane.

†Forty-eight, 25 m wide strips were laid out along the contour, and every third strip was clearcut in 1970, 1972, and 1974.

Table 2. Relative basal area (%) and relative density (%) of the three dominant tree species, *Acer saccharum*, *Fagus grandifolia*, and *Betula alleghaniensis* in watersheds 1 (WS1) and 6 (WS6) at Hubbard Brook Experimental Forest, New Hampshire, U.S.A.

	Relative basal area (%)		Relative density (%)	
Species	WS1	WS6	WS1	WS6
Acer saccharum	41	36	31	28
Fagus grandifolia	26	31	31	39
Betula alleghaniensis	19	17	13	11

Note: The total relative basal areas for WS1 and WS6 were 26.3 and 26.1 m^2/ha, respectively, and the total densities were 567.6 and 557.8 stems/ha, respectively.

ary 8, 1998, the time of heaviest ice deposition, and the measurement of ice thickness on January 15, 1998 ranged from –5.9 to –7.9°C at the study site. During this time period, the air temperature was not above freezing in the zone of ice accumulation. The lack of icicle formation at the time ice thickness was measured further suggests limited melting. In addition, ice thickness on branches sequestered in the snowpack as a result of branch breakage was comparable with those exposed to the air.

Ice accretion was measured on 61 twigs (generally 3–6 mm diameter) among seven species at eight sites from 510 to 800 m on the western edge of WS6. Caliper measurements were taken of the twig diameter and the diameter of ice accumulated on the top and bottom surfaces of the twigs. All twigs sampled had been arrayed horizontally in the canopy or within openings near the ground. The twigs sampled were from fallen trees, broken branches on the ground, or smaller trees growing in the open. To interpolate among sites, a second-order polynomial regression model was developed between ice thickness and elevation ($y = -146.95 + 0.44x - 0.0003x^2$; $r^2 = 0.61$, $p = 0.0001$). This model was used to estimate ice thickness for each of the plots on WS6 where leaf area index (LAI) was measured. A second-order polynomial regression was then performed using ice thickness to predict July 1998 LAI values. To better understand this relationship, another second-order polynomial regression was performed using elevation to predict LAI.

Canopy ice damage and recovery assessment of the 60- to 120-year-old forests

Both WS1 and WS6 are subdivided into 25 × 25 m permanent plots. Prior to leafout in May 1998, all trees ≥20 cm diameter at breast height (DBH) in alternating rows of plots within the ice damage zone were tagged (49 plots above 560 m on WS1 and 77 plots above 624 m on WS6), DBHs were measured, and a damage assessment was made based on the percentage of crown damaged ((0) 0% damage; (1) 1–25%; (2) 26–50%; (3) 51–75%; (4) 76–100%; (5) crown gone; (6) uprooted or broken off at base). Weighted mean damage class was calculated for each plot by weighting the damage class of each tree by its individual basal area and finding the average for the plot.

Twenty-two damaged plots were selected for long-term LAI monitoring from middle and upper elevational plots impacted by the ice storm on WS1 (10 plots) and WS6 (12 plots) using a stratified random design. The plots were first stratified by weighted mean damage class (0 to <1, 1 to <2, and 2 to <3). Plots were selected from each damage category after they were stratified by elevation, making the plots representative of the elevational distribution in each damage class. Five plots below 560 m on WS1 and five below 624 m on WS6 were also established to serve as undamaged references.

In July of 1998, LAI measurements were taken in the 32 plots using a leaf area meter (LAI-2000, LI-COR Inc., Lincoln, Nebr.; Welles 1990; Welles and Norman 1991). A 15 × 15 m subplot was delineated within the centre of each preselected 25 × 25 m plot. Ten points were randomly chosen within each of these subplots, and a horizontal (sensor held at 0°) LAI reading of the canopy (2.5 m off the ground) was taken at each point. The LAI-2000's optical sensor was attached to a telescoping pole to maintain a consistent height between points. The readings of the two outer rings were eliminated, decreasing the area viewed by the optical sensor (from 0° to 43° of zenith) and reducing the influence of trees outside of the plots. Readings were taken at dawn and dusk to meet the diffuse light requirement of the LAI-2000. Measurements were repeated in July 1999 and 2000. In a related study, we found that the LAI-2000 yielded accurate results when compared with radiation estimates from hemispherical photographs and direct leaf area estimates from litterfall baskets. In July 1998, the number of branches, crown snap-offs, or tip-ups by species was recorded in 40 ice storm created gaps on WS6.

An additional census of the trees tagged in 1998 was conducted in the summer of 2000. Tree health was assessed using a qualitative four-scale rating system based on canopy

Table 3. Density and basal area of the major tree species and percent basal area damaged by the January 1998 ice storm on watershed 4 at Hubbard Brook Experimental Forest, New Hampshire, U.S.A.

			Basal area damaged (%)			
Species	Density (stems/ha)	Basal area (m^2/ha)	Bent	Snap	Tip-up	Total
Fagus grandifolia	1278	2.76	32	2	0	34
Betula payrifera	605	3.43	30	2	1	33
Prunus pensylvanica	595	6.86	17	29	12	58
Acer rubrum	94	0.46	13	8	1	22
Acer saccharum	623	1.94	31	2	0	33
Acer pensylvanicum	401	1.27	30	6	3	39
Fraxinus americana	70	0.71	9	3	0	12
Betula alleghaniensis	1422	9.14	37	6	1	43
Other species*	197	1.17	—	—	—	—
Total	5018	27.03				

*Includes *Prunus serotina*, *Abies balsamea*, and *Picea rubens*.

integrity and relative canopy position: (7) minimal damage, will live >10 years; (8) intermediate, will survive 5–10 years; (9) severe damage, will survive 2 or 3 years; (10) dead. This rating system has been developed for the HBEF after decades of observing the long-term fate of trees with crown damage (T.G. Siccama, unpublished data).

Assessment of root growth in the 60- to 120-year-old forest

Fine root growth was assessed in plots of differing damage in and near WS6 using an in situ root screen approach (Fahey and Hughes 1994; Tierney and Fahey 2001). In this approach, mesh screens are positioned horizontally at the top of the rooting zone in the Oe horizon, and the number of roots growing through each screen is quantified a few months later to provide an index of relative root growth (Battles and Fahey 2000). In early May 1999, 25 root screens (10 × 10 cm each) were placed in each of 16 plots chosen subjectively to represent the range of ice storm damage. Eight plots were in areas of high damage (>50% canopy damage; see above), five plots in areas of moderate damage (20–30%), and three plots in areas with no evidence of damage (reference plots). Out of necessity, the reference plots were located at lower elevations (520–580 m) than the damaged plots, which were intermingled in the elevation zone from 640–730 m. Sugar maple, beech, and yellow birch were dominant at all root sampling sites. Within each plot, screens were positioned in a stratified-random manner, avoiding large pits and mounds. In mid-August 1999 the root screens were assessed by measuring the number of fine roots (<2 mm diameter) growing through each screen. Various disruptions (e.g., small mammals) often reduced the sample size, such that 20–25 samples were available for each plot.

Ice damage assessment of the 24- and 28-year-old forest

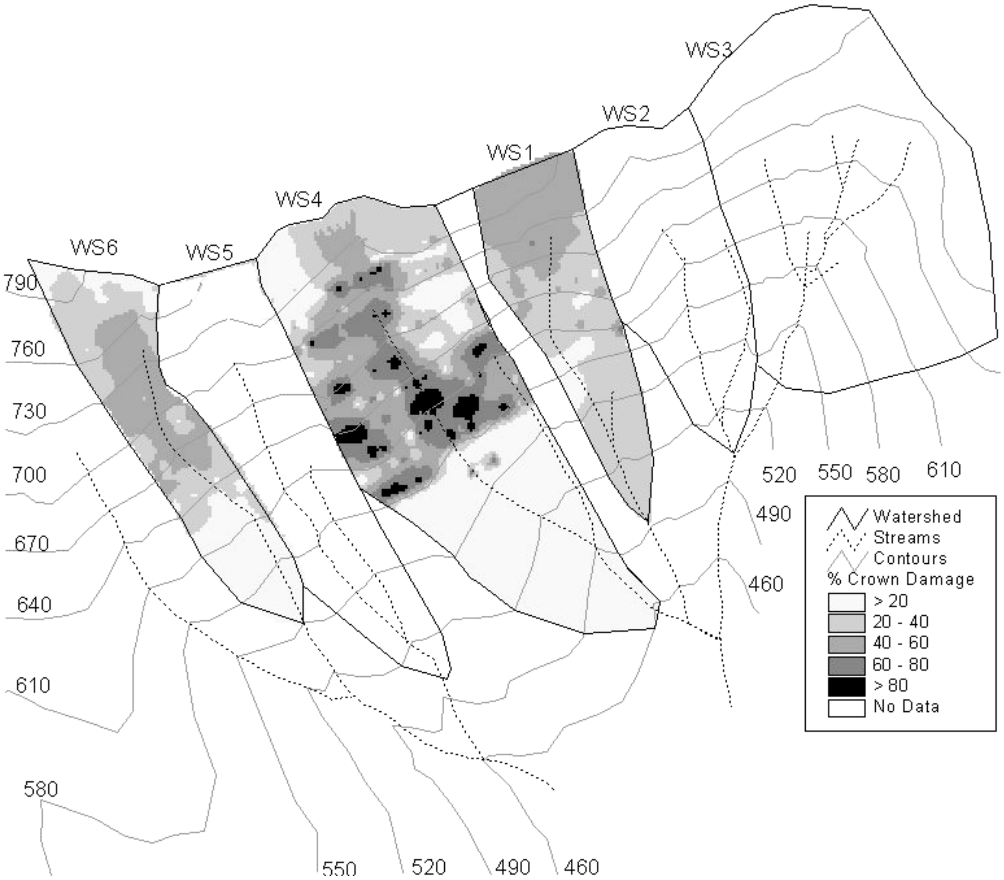
Ice damage to the 14-year-old forest of WS5 was visually assessed in summer 1998. Because virtually no damage, in the form of trees bent, broken, or tipped-up, was observed, it was deemed unnecessary to conduct plot-based measurements. Ice damage to trees growing on the WS4 strips cut in 1970 and 1974 was assessed using a 3 m wide belt transect centered on the mid-line along the length of each strip. Species identity, DBH, and damage class were determined for each tree with a DBH ≥2 cm. Four damage ratings were used: (1) no damage, (2) trees snapped off above ground level, (3) trees uprooted, (4) trees bent with their crowns horizontal to the slope. Although some loss of twigs and small branches occurred in WS4, this damage could not be assessed on an individual tree basis and constituted a minor source in comparison with whole-tree damage in the form of snapping, bending, and uprooting. A digital elevation model (DEM) of WS4 was developed from a 3-m topographic survey of HBEF (Schwarz 2001). By overlaying the DEM on the belt transect survey, the slope angle, slope aspect, and slope position of every 5 m long interval of the belt transects were estimated.

To estimate ice loads on individual trees on WS4 during the ice storm, we developed regression equations using standard dimension analysis techniques (Whittaker et al. 1974). For each of the eight dominant species, we harvested five to eight trees spanning the range of diameters encountered in the study area. These trees were selected from the lower one-third of WS4, where there was minimal ice damage (Fig. 1). Linear models using DBH to predict the total length of all twigs and branches were all highly significant (r^2 = 0.94–0.99, $p < 0.01$). These equations allowed us to estimate total ice loading for individual stems of each species on WS4.

Beech bark disease

In July 1998, using the rating scheme developed by Houston and O'Brien (1983), the severity of beech bark disease was noted for all tagged beech trees in 40 plots below 800 m on WS6 ((0) no damage; (1) small discrete lesions, cambial tissue affected in local areas only; (2) obvious necrotic bark, blocky, sunken lesions; (3) severe damage to vascular and cambial tissue, long vertical fissures, callus tissue). Fallen beech trees had not been tagged in the spring of 1998, so they were censused in July 1998. During the census in 2000

Fig. 1. Map of ice damage on watersheds 1, 4, and 6 at Hubbard Brook Experimental Forest, New Hampshire, U.S.A. Percent crown damage was based on visual damage class assessment in 1998. Values in the figure are elevations in metres (B. Houlton).



(see above), trees were re-evaluated for beech bark disease using the same 0–3 ranking system used in 1998.

Data analysis

LAI values of the WS1 and WS6 forest canopies prior to the ice storm were calculated using the 1997 forest inventory data (all trees with DBH ≥10 cm) and allometric equations developed at HBEF (Whittaker et al. 1974; Siccama et al. 1994). Because there were no significant differences in the patterns of damage within WS1 and WS6, data from the two watersheds were combined for all analyses.

Plot-level damage analysis of the 60- to 120-year-old forests

ANOVA was used to test for the effects of watershed, elevation, till depth, slope, aspect, mean DBH of trees ≥20 cm DBH in each plot, and species composition (percent biomass of sugar maple, beech, yellow birch, and conifer (balsam fir and red spruce)) on the post-storm LAI of the canopy and weighted damage class. ANOVA was also used to test for the effects of species (including all species) and DBH to predict damage class at the individual tree level.

To test for elevational trends in species composition on WS1 and WS6, plots were grouped into elevational bands (low, undamaged plots below 560 m on WS1 and below 624 m on WS6; middle, 625–709 m; high, 709–791 m; Whittaker et al. 1974), and an ANOVA was performed to test for the effects of elevation on canopy LAI in each of three elevational bands. It is important to note that the low-elevation band of Whittaker et al. (1974) includes elevations greater than the observed 600 m cutoff for ice damage, so only their distinction between mid- and high-elevation zones was used in evaluating canopy LAI. ANOVA was also used to examine differences in fine root growth among damage classes. Nominal logistic regression was used to test for the effects of beech bark disease score (BBD), DBH, elevation, and the interaction of BBD and DBH on ice damage class at HBEF. Linear regression analysis was used to examine the effect of ice thickness on canopy LAI values on WS6 in 1998.

Individual tree-level damage analysis of the 60- to 120-year-old forest

Chi-square analysis was used to examine differences in damage class among species across WS1 and WS6. For this analysis, all species were included, not just the dominant species. The effect of individual tree DBH on damage class was examined using ordinal logistic regression.

Damage analysis of the 24- and 28-year-old forest

Data analysis for variation in ice damage in the 24- and 28-year-old forests included three separate procedures. First, a two-way ANOVA was used to test for differences among the seven dominant species and between stand ages in the percentage of stems and basal area exhibiting the three types of damage (bent, snapped, tipped-up). Second, ANOVA was used to examine differences in basal area damage percentages of all three damage types among species in relation to stand age, slope angle, and elevation. In these tests, all factors were significant in the overall model ($p < 0.001$) and pairwise differences among species were determined using Tukey's 95% simultaneous confidence intervals. Third, the likelihood of stem failure (either bent, snapped, or tipped-up) was determined for every tree in the sample using logistic regression on an individual species basis. For this analysis we estimated an ice-loading factor for each stem on the basis of an allometric equation (see above). Other variables included in the logistic regression were slope angle, stand age, estimated ice thickness, stem DBH, and near-stream slope position (i.e., trees within 5 m of a perennial stream).

Recovery analysis for the 60- to 120-year-old forests

Changes in canopy LAI between 1998 and 2000 in WS1 and WS6 at HBEF were examined using ANOVA, and pairwise comparisons between years were made using Student's *t* test. Differences in changes in canopy LAI from 1998 to 2000 between the three elevational bands (Whittaker et al. 1974) were also examined using ANOVA, and pairwise comparisons between bands were again performed using Student's *t* test. Simple linear regression analyses were used to test for the effects of plot composition (percentage of biomass from sugar maple, beech, yellow birch, and spruce–fir combined), mean plot 1998 canopy LAI values, and 1998 mean weighted damage class on percent change in LAI values from 1998 to 2000. Ordinal logistic regression was used to test for the effects of size (DBH) and species on visual individual tree health score in 2000. A χ^2 test was performed to test for differences between 1998 and 2000 BBDs and to test for a relationship between 1998 ice damage scores and 2000 BBDs. All analyses used JMP version 3.2 (SAS Institute Inc. 1995).

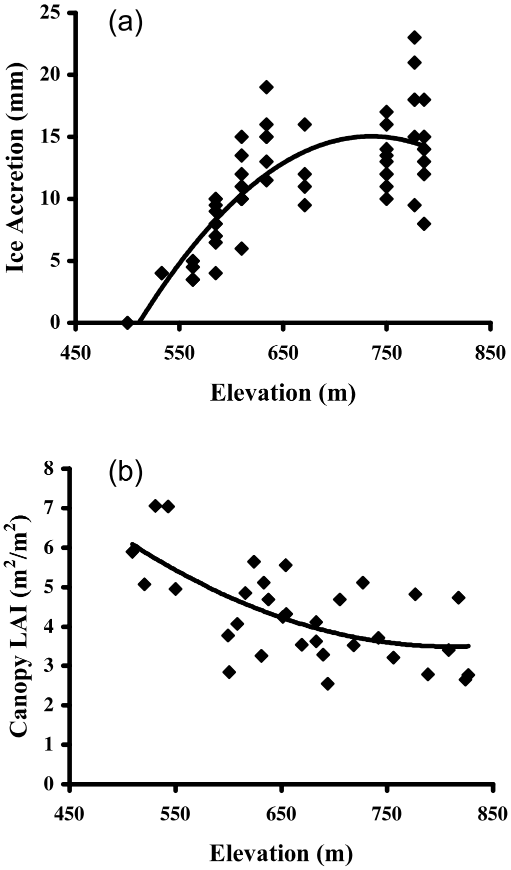


Fig. 2. Second-order polynomial regression of elevation predicting (*a*) ice thickness (mm) on watershed 6 ($y = –146.95 + 0.44x – 0.0003x^2$, $r^2 = 0.61$, $p = 0.0001$) and (*b*) canopy LAI (m^2/m^2) on watersheds 1 and 6 ($y = 6.17 + 4.27x – 0.69x^2$, $r^2 = 0.44$, $p = 0.0002$) at Hubbard Brook Experimental Forest, New Hampshire, U.S.A.

Results

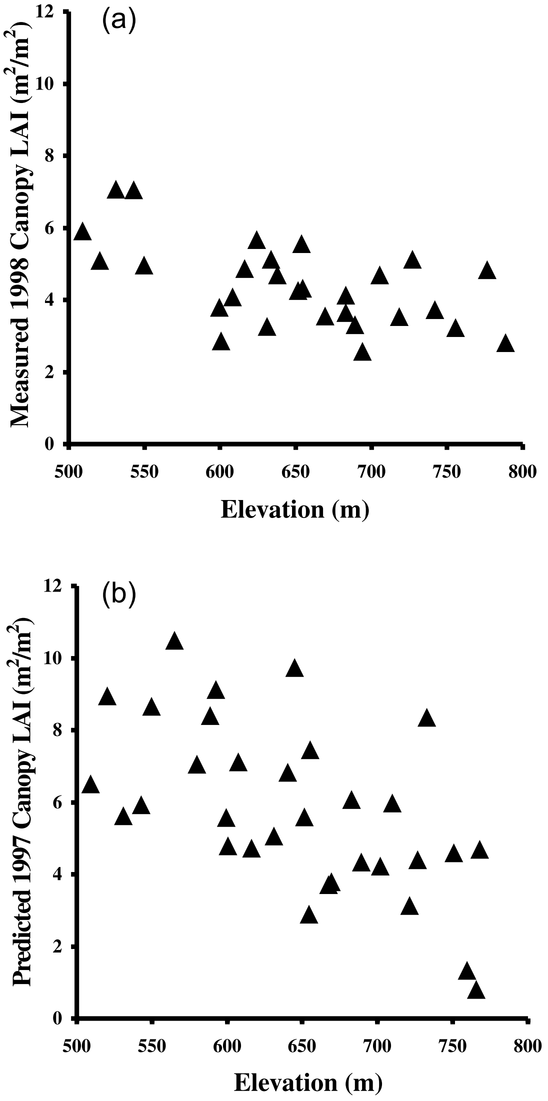
Damage to the 60- to 120-year-old forests

Across WS1 and WS6, 81% of the basal area of canopy trees (≥20 cm DBH) was damaged by this ice storm. Susceptibility to ice damage varied with elevation, species composition, and tree DBH. In particular, canopy damage increased significantly with elevation on both WS1 and WS6 (Fig. 1). Damage was limited to trees above 560 m on WS1 and 624 m on WS6. There was a highly significant relationship between elevation and ice thickness, with higher elevations having thicker ice deposits until about 725 m ($r^2 = 0.61$, $p = 0.0001$) (low elevation, 5.9 ± 0.66 mm (mean ± SE), mid-elevation, 12.3 ± 0.68 mm, high elevation, 14.4 ± 0.75 mm; elevational bands according to Whittaker et al. (1974)) (Fig. 2*a*). July 1998 canopy LAI decreased with increasing ice thickness ($r^2 = 0.44$, $p = 0.0002$). Ice thickness was a weaker predictor of weighted damage class ($r^2 = 0.07$, $p = 0.01$), but weighted damage class did increase with increasing ice thickness. Polynomial regression analysis showed that LAI decreased with increasing elevation, leveling off at about 725 m ($r^2 = 0.41$, $p = 0.0005$) (Fig. 2*b*). In fact, elevation was the only physiographic factor having a significant effect on canopy LAI following the storm (whole model, $p = 0.12$; elevation, $p = 0.02$; slope angle, $p = 0.8$; aspect, $p = 0.37$). Plots at higher elevations had lower LAI values (Fig. 3*a*). ANOVA by elevational band showed similar results, with low plots having significantly higher mean canopy LAI values than middle and high plots; LAI of mid- and high-elevation plots did not differ (low, 5.5 ± 0.3; middle, 3.7 ± 0.2; high, 3.7 ± 0.4) ($p < 0.0001$). Canopy LAI of the prestorm forest was also estimated to decrease with increasing elevation (low, 6.3 ± 0.8; middle, 3.7 ± 0.7; high, 3.2 ± 0.9) ($p = 0.03$) (Fig. 3*b*).

Ice storm damage patterns suggested that species composition played an important role in determining forest susceptibility to ice storm damage. Measurement of the number of branches, snap-offs, and tip-ups on the ground by species supported our canopy damage assessments, with the majority of litter being beech (73%), followed by yellow birch (25%) and finally sugar maple (2%).

Analysis of variance using watershed, mean plot DBH, elevation, and species composition to predict LAI of the canopy in 1998 showed significant effects of elevation (whole model, $p = 0.005$; elevation, $p < 0.001$), and the proportion of beech biomass ($p = 0.03$). Across WS1 and WS6, as elevation increased and as amount of beech increased, LAI decreased. There were no significant effects of any differences between WS1 and WS6 ($p = 0.07$); mean plot DBH ($p =$

Fig. 3. Elevation in metres versus (*a*) tree layer LAI (m^2/m^2) measured in 1998 across watersheds 1 and 6 at Hubbard Brook Experimental Forest, New Hampshire, U.S.A., and (*b*) predicted 1997 prestorm tree layer leaf area index (LAI) (m^2/m^2) using allometric equations (Whittaker et al. 1974).



0.08); or amount of sugar maple (p = 0.11), yellow birch (p = 0.24), or spruce–fir biomass (p = 0.2).

An analysis of variance of data from plots within the damaged area using mean DBH of trees by plot, elevation, and species composition to predict mean weighted damage class showed significant effects of species composition (whole model, p = 0.04). As the percentage of beech biomass increased, so did mean weighted damage class (p = 0.04). The same pattern was found for yellow birch (p = 0.04). There was no significant effect of the amount of sugar maple (p = 0.40) or spruce–fir (p = 0.78) on damage class. Mean tree size (DBH) also had no effect on the amount of damage within the damaged area (p = 0.87).

A nominal logistic regression using BBD, DBH (cm), elevation, and the interaction of BBD and DBH (BBD × DBH) to predict ice damage class showed the overall model to be significant ($p < 0.0001$). BBD, DBH, and BBD × DBH all had significant effects on ice damage class ($p < 0.0001$; p = 0.007; p = 0.003, respectively), while elevation on an individual tree level had no effect (p = 0.34).

Fig. 4. Proportion (%) of each visual ice damage class ((0) 0% damage; (1) 1–25%; (2) 26–50%; (3) 51–75%; (4) 76–100%; (5) crown gone; (6) uprooted or broken off at base) in 1998 made up of each of the three dominant tree species (sugar maple, beech, and yellow birch) within the damaged area of watersheds 1 and 6 at Hubbard Brook Experimental Forest, New Hampshire, U.S.A.

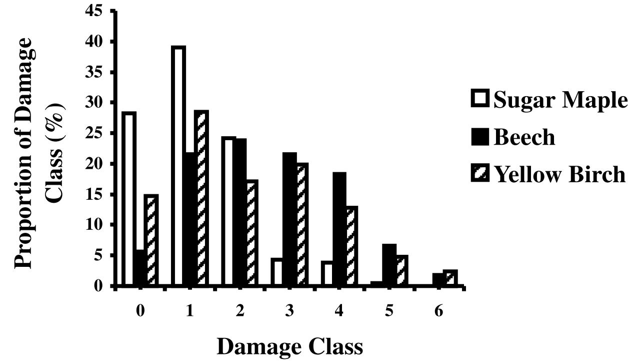
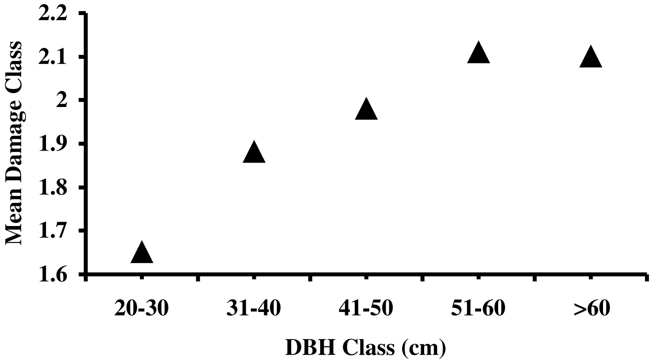


Fig. 5. Mean visual ice damage class of trees in five diameter (DBH in cm) classes. Ordinal logistic regression was performed using DBH (cm) of individual trees to predict damage class on watersheds 1 and 6 at Hubbard Brook Experimental Forest, New Hampshire, U.S.A.



At the individual tree level, species had a significant effect on visual damage class within the severely damaged area (above 600 m) ($p < 0.0001$) with beech and yellow birch being the most damaged and red spruce, sugar maple, red maple, and fir being less damaged (Fig. 4). Also, at the individual tree level, trees with larger diameters were found to have a higher probability of being in higher damage classes, than those with smaller diameters ($p < 0.0001$) (Fig. 5). There was a significant relationship between beech DBH and damage class (p = 0.03), sugar maple DBH and damage class (p = 0.02), and yellow birch DBH and damage class ($p < 0.0001$). On an individual tree level, ANOVA showed that species and DBH were significant predictors of damage class (whole model, $p < 0.0001$; species, $p < 0.0001$; and DBH, p = 0.01). Trees with larger diameters were more damaged, with trees over 30 cm DBH being most damaged (Fig. 5). Of the dominant species, beech was most damaged, yellow birch was intermediate, and sugar maple was the least damaged.

Differences in tree species composition at low, middle, and high elevations were examined to see if this could explain the relationship between elevation and damage patterns. Neither the percentage of beech nor yellow birch biomass varied with elevation (p = 0.73 and 0.40, respectively). Sugar maple biomass did vary with elevation (p = 0.01), with plots at high elevations having a significantly lower biomass than at low- and mid-elevation plots, which did not differ from each other.

Damage to the 14-, 24-, 26-, and 28-year-old forests

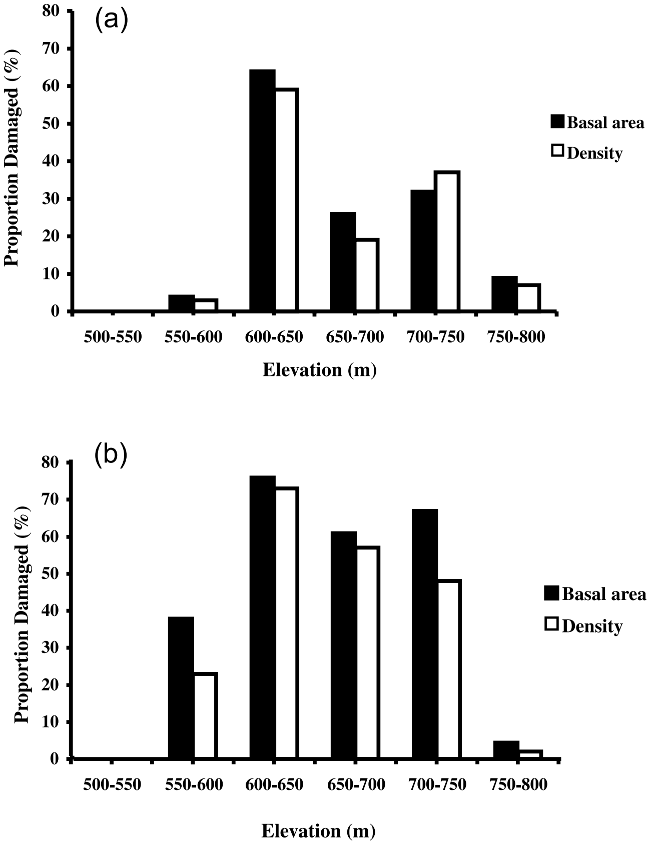
On a whole watershed basis, 36% of the stems (≥2 cm DBH) and 29% of the forest basal area on WS4 exhibited ice damage as severe bending, snap-off, or tip-up. Within the severe damage zone, the percentage of basal area damaged was variable, and the pattern was very patchy (Fig. 1). In striking contrast, ice damage in the adjacent 14-year-old forest on WS5 was minimal. A few bent stems were observed along skid road openings in mid-elevations of WS5, but no severe bending or breakage occurred within the closed forest.

Across all species, the majority of ice damage in the 24- and 28-year-old stands was in the form of severely bent trees (78% of damaged stems), with smaller numbers of snap-offs (17%) and tip-ups (5%). These proportions varied significantly among species and stand age-classes ($p < 0.01$). In particular, pin cherry experienced much higher damage in the form of snap-offs (50% on a density basis) and tip-ups (21%) as compared with other species, and the overall proportion of snap-offs was higher in the older than the younger stands.

The percentage of basal area damaged (Table 3) varied significantly with stand age, elevation, slope angle, and slope position ($p < 0.001$). Damage was significantly higher in the 24-year-old strips (45% basal area damage) than in the 28-year-old strips (29%). This difference was largely the consequence of the much higher proportion of basal area of pin cherry in the younger (38% of total) than the older (12%) stands and the high susceptibility of pin cherry to ice damage. Pairwise species comparisons indicated that percentage basal area damage was significantly higher ($p < 0.01$) for pin cherry than the other dominant species for which interspecific differences were not statistically significant (Table 3). The severity of damage varied markedly with elevation, and peak damage was seen between 600 and 750 m (Fig. 6). Unlike in the 60- to 120-year-old forests, percent damage increased with increasing slope in these stands, peaking at 64% on steep slopes (>24°) in the younger strips. Plots located along perennial streams also had significantly higher ($p < 0.01$) percent basal area damage than those further away from streams.

The probability of stem failure for each species in the 24- and 28-year-old stands was modeled as a function of site and individual tree factors using logistic regressions. These regressions reflected the ANOVA results as the best models generally included stand age, slope angle, and proximity to streams as highly significant predictors. For pin cherry and yellow birch, estimated ice thickness was also a significant predictor, and tree DBH was a significant factor for every species except paper birch, with larger trees being more susceptible to stem failure. An ice loading factor, calculated as the ratio of estimated ice load to stem cross-sectional area was not significant in any of the final models. A separate assessment of ice loading as a predictor of the probability of failure using a simple logistic regression showed that pin cherry differed from the other dominant species. In effect, pin cherry stem failure occurred at a significantly lower value of the ice loading factor than for the other species.

Fig. 6. Percentage of stems damaged by the January 1998 ice storm in strips of two different ages cut in (*a*) 1970 and (*b*) 1974 along the elevation gradient on watershed 4, Hubbard Brook Experimental Forest, New Hampshire, U.S.A., expressed in terms of basal area and density.



Changes since 1998 in the 60- to 120-year-old forests

Canopy LAI did not change significantly between 1998 and 1999 but increased markedly (35%, 4.3–5.8) from 1998 to 2000 ($p < 0.0001$) (Fig. 7). Not surprisingly, plots with higher 1998 LAI values showed lower percentage increases in LAI of the canopy between 1998 and 2000 ($r^2 = 0.35$, $p < 0.0001$, $y = -21.6x + 134.9$). Plots with higher mean weighted damage classes in 1998 showed greater percentage increases in LAI of the canopy from 1998 to 2000 ($r^2 = 0.24$, $p = 0.005$, $y = 18.4x + 15.5$). Plots with a greater percentage of beech biomass prior to the storm also showed a greater percentage change in canopy LAI ($r^2 = 0.16$, $p = 0.02$, $y = 0.85x + 16.9$), reflecting the high damage of beech-dominated plots. There were no significant effects of percentage of sugar maple ($r^2 = 0.001$, $p = 0.8$), yellow birch ($r^2 = 0.01$, $p = 0.6$), or spruce–fir ($r^2 = 0.02$, $p = 0.4$) biomass on percent change in canopy LAI.

Mid-elevation plots showed the greatest increase in canopy LAI between 1998 and 2000 (61.1%). Plots at high elevations showed an intermediate increase (48.5%), while

Fig. 7. LAI (m^2/m^2) of the canopy layer (>2.5 m from ground) on watersheds 1 and 6 at Hubbard Brook Experimental Forest, New Hampshire, U.S.A., in July of 1998, 1999, and 2000 as measured by the LI-COR LAI-2000.

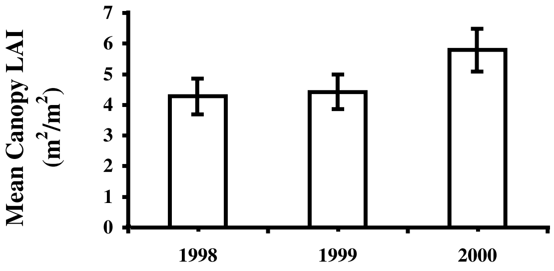


Table 4. Canopy LAI (m^2/m^2) in 1998, 1999, and 2000 and the changes between 1998 and 2000 at low, middle, and high elevations (low, undamaged plots <560 m on WS1, <624 m on WS6; middle, 625–709 m; high, 709–791 m) (middle and high elevation according to Whittaker et al. (1974)) on watersheds 1 and 6 at Hubbard Brook Experimental Forest, New Hampshire, U.S.A.

	LAI			
Elevational band	1998	1999	2000	Mean % change in LAI 1998–2000
Low	5.5 (0.3)	5.3 (0.21)	6.0 (1.6)	11
Middle	3.7 (0.20)	4.3 (0.28)	5.9 (1.1)	61.1
High	3.7 (0.4)	3.5 (0.34)	5.3 (0.17)	48.5

Note: Values are means with SEs given in parentheses.

plots at low elevations experienced a smaller increase (11%) (Table 4). Pairwise comparisons showed that the difference between middle and low plots was significant, but those between low and high or middle and high plots were not.

The 2000 tree census revealed significant differences in rates of recovery among species, with sugar maple having generally better health 2 years after the storm, beech being more unhealthy, and yellow birch being intermediate ($p < 0.0001$) (Fig. 8). Additionally, significant differences were found between 1998 and 2000 BBDs ($p < 0.0001$). The percentage of trees found in the lower beech bark disease classes decreased (0, –31%; 1, –23%), while the percentage of trees in the higher damage classes increased (2, 12%; 3, 42%). There was a significant effect of 1998 ice damage score on the change in BBDs of individual trees from 1998 to 2000 ($p = 0.0081$) (Fig. 9).

Fine root growth during the second growing season (May–August 1999) after the ice storm differed significantly among three damage classes. The root growth index (RGI = no. of roots/cm^2 screen area) was highest in moderately damaged plots (RGI = 0.39 ± 0.04, $n = 5$ plots with 125 screens and 4875 roots); intermediate in severely damaged plots (RGI = 0.26 ± 0.03, $n = 7$ with 4108 roots); and lowest in undamaged plots (RGI = 0.19 ± 0.02, $n = 3$ with 1380 roots).

Fig. 8. Percentage of total trees in each visual health class ((7) healthy, will live >10 years; (8) intermediate, will survive 5–10 years; (9) sick, will survive 2 or 3 years; (10) dead) from each of the three dominant species (sugar maple, yellow birch, American beech) on watersheds 1 and 6 at Hubbard Brook Experimental Forest, New Hampshire, U.S.A.

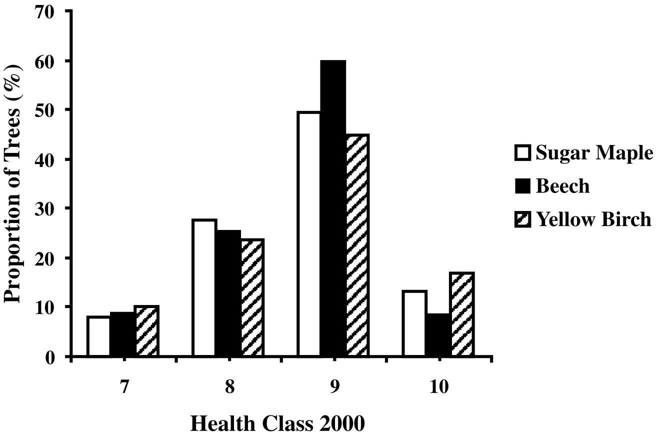
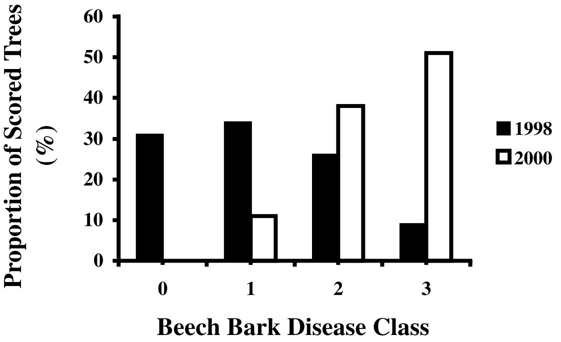


Fig. 9. Percentage of scored trees in each of three beech bark disease classes in 1998 and 2000 ((0) no damage; (1) small discrete lesions, cambial tissue affected in local areas only; (2) obvious necrotic bark, blocky, sunken lesions; (3) severe damage to vascular and cambial tissue, long vertical fissures, callus tissue). Data collected on watershed 6 at Hubbard Brook Experimental Forest, New Hampshire, U.S.A.



Discussion

The January 1998 ice storm severely damaged forests in an elevation band from 600 to 800 m on the south-facing slope of HBEF (Fig. 1). However, within this heavily damaged zone the pattern of ice storm damage varied as a result of a variety of factors, and the dominant influences on damage pattern differed markedly across forests of different ages.

Ice damage in mature forests

In WS1 and WS6, the oldest forests at HBEF, elevation, tree diameter, and species composition had the greatest influence on susceptibility to the ice storm. Damage increased with elevation, with damage only occurring above about 600 m. Prior to the storm, low and middle elevations at HBEF had similar LAIs, and following the storm, mid-elevational plots suffered the greatest decline in LAI. Trees at higher elevations can be more damaged in ice storms than those at lower elevations because they are exposed to higher winds and typically grow in shallow soils. Both of these factors can lead to trees being more easily uprooted by heavy ice loads. Our study, however, showed no effect of till depth on damage at HBEF, suggesting that elevational effects were the result of climatic conditions. Our measurements of ice thickness indicated peak damage in the elevational zone where ice loading also peaked.

Elevational trends in ice damage can result in part from changes in species composition with elevation. However, this was not the case at HBEF, since plots in the undamaged low elevations did not differ from the damaged middle and high elevations in percentage of beech biomass, the most susceptible species. Also, although low elevation plots had a higher percentage of damage-resistant sugar maple than damaged, upper elevational plots, percentage of biomass made up of sugar maple did not differ between the undamaged low-elevation plots and the highly damaged mid-elevation plots.

As was found in other studies (Boerner et al. 1988; Whitney and Johnson 1984; Rebertus et al. 1997), tree diameter was important in determining susceptibility at HBEF, with larger trees being more damaged than smaller trees. This was found at both the individual tree and plot levels, although the latter was not statistically significant. Tree health may partly explain the differential susceptibility between large and small diameter trees. Since size is usually a function of age, larger trees are more likely to be partially decayed and more susceptible to other stresses, such as insect and pathogen attack due to decreased mechanical and chemical resistance. Decay can then weaken the mechanical properties of the wood, increasing susceptibility to damage from ice and wind (Bruederle and Stearns 1985). Trees with larger diameters also tend to have larger crowns and, therefore, more surface area available for ice accumulation and wind action (Bruederle and Stearns 1985; Seischab et al. 1993).

We found beech to be the most ice damaged of the dominant species and sugar maple to be the least damaged at both the plot and individual tree level. Yellow birch experienced intermediate levels of damage, but patterns more closely resemble those of beech (Fig. 4). Interspecific damage patterns at HBEF differed from those found in other studies (Lemon 1961; Siccama et al. 1976; Bruederle and Stearns 1985; Melancon and Lechowicz 1987; Boerner et al. 1988). Variations across studies are likely due to a multitude of factors including differences in tree and root architecture, size, age, health, and ice load.

Tree architecture has been used to explain differential ice damage among species (Lemon 1961; Zimmermann and Brown 1971; Rebertus et al. 1997) and would suggest that at HBEF, conifers should have experienced more ice damage than hardwood species. This did not occur. Crown architecture alone cannot, therefore, explain interspecific differences in ice storm damage at HBEF. When the inherent mechanical properties of the trees' wood (modulus of elasticity and modulus of rupture) are also considered, the pattern of ice damage becomes more clear (Bruederle and Stearns 1985; Lemon 1961; Rebertus et al. 1997). Of the three dominant species at HBEF, disease-free beech has the lowest modulus of elasticity (9.515 GPa) and a low modulus of rupture (59.297 MPa); beech bark disease probably lowers the value of both moduli. Yellow birch has a higher modulus of elasticity (10.342 GPa) but a lower modulus of rupture (57.229 MPa) compared with beech. Sugar maple has the highest modulus of elasticity (10.687 GPa) and modulus of rupture (64.813 MPa) (Alden 1995). Other studies have found these moduli to be poor predictors of ice damage (e.g., Lemon 1961). In our study, although these values do not completely predict the observed patterns, they do suggest that in this ice storm, it was advantageous to resist bending while holding a load of ice and to be able to hold that load over time.

Wood strength cannot be the sole explanation of susceptibility (Bruederle and Stearns 1985; Lemon 1961; Rebertus et al. 1997), because differences in wood moisture, growing conditions, health, age (Bruederle and Stearns 1985), and the presence of insects and pathogens can complicate the relationship between wood mechanical properties and ice damage. Beech susceptibility to ice damage in other studies has varied greatly from slight (Siccama et al. 1976) to moderate (Bruederle et al. 1985; Lemon 1961) to high (Downs 1938; Melancon and Lechowicz 1987), and this is most likely the result of the presence or absence of beech bark disease. In our study, beech bark disease likely reduced the predictive power of mechanical properties. Beech's ice damage levels were likely increased by a decreased modulus of rupture resulting from rot caused directly by the disease and by other fungi attracted to the weakened trees (Snyder 1998). In our study, trees with more severe beech bark disease experienced more ice damage, and there was a significant interaction of beech bark disease severity and DBH, with larger trees being more damaged by beech bark disease. Trees with more severe beech bark disease were also less healthy 2 years following the ice storm (Fig. 9) indicating that the disease is interfering with recovery from storm damage.

Ice damage in young forests

Few studies (but see Lemon 1961) have reported the susceptibility of young, even-aged forest stands to damage by ice storms. Foster (1988) noted that damage by catastrophic windstorms increased when stands of hardwood forests reached about 20 years, an observation consistent with our ice storm results that showed stem failure reaching high levels in stands 24 years old but virtually no damage occurring in 14-year-old stands.

The pattern of ice damage within the 24- and 28-year-old forests was more heterogeneous than that within the 60- to 120-year-old forest (Fig. 1). Damage reflected variations in elevation (and consequent ice loads), topography, and forest age and composition. Within the zone of highest damage (600–750 m), the intensity of damage was highly patchy, with some areas experiencing no damage and others extreme damage. In the patches of extreme damage, virtually every stem failed (snapping in pin cherry or bending in other species). It appears that this pattern was the result of large pin cherry and paper birch stems falling and initiating a domino effect, as dozens of stems on the downslope side all failed together. Unlike our results from the 60- to 120-year-old forests, the young forests on steeper slopes were much more prone to damage, independent of the age effect. This effect of slope angle has been found elsewhere in mature hardwood forests (Seischab et al. 1993) and is likely the result of trees leaning downhill and having greater crown development on their downslope sides. As in the older forests, forest species composition influenced ice damage intensity on WS4; in fact, the highly significant effect of stand age on damage intensity was explained by differences in species composition. Young stands in northern hardwoods in this region have a higher abundance of pin cherry, and by stand age 24 years, pin cherry is declining, as high mortality results from the inability of this species to compete (Mou et al. 1993). Moreover, on WS4, pin cherry basal area was especially low in the 28-year-old strips in part because of the soil scarification associated with the harvest (Martin and Hornbeck 1989). The high level of damage to other dominant species in these young stands was partly the result of collateral damage caused by the falling pin cherry stems. However, unmeasured differences in stem or canopy properties also might have contributed to the age-related patterns. For example, canopy height was slightly greater in the 28- than the 24-year-old strips, leading to a discontinuity at the interface between adjacent strips.

The role of unmeasured spatial variation in ice loading or possible differences in wind patterns immediately following the ice storm was suggested by the significantly higher damage intensity in near-stream areas. In the severe damage zone on WS4, three perennial streams have cut small channels and ice damage within 5 m of these streams was about 17% higher (in terms of basal area damaged) than in nonstream areas. Higher damage near streams may be the result of small-scale differences in ice accumulation resulting from within-canopy inversions (Devito and Miller 1983). Air movement was apparently very limited during and immediately following the January 1998 ice storm (S. Bailey, USDA Forest Service, personal communication); therefore, elevational and synoptic patterns of ice deposition are robust.

Our attempts to develop empirical models of stem failure probability on the basis of topographic, ice loading, and individual tree factors were not very successful. Several complications and sources of error probably limited the predictive power of our logistic regression models: (*i*) the likelihood that failure of many stems was actually collateral damage from neighboring stems; (*ii*) errors in ice thickness estimated from elevation; (*iii*) variation in ice thickness with microtopography (e.g., stream channels); and (*iv*) error in the allometric relationships between stem DBH and total stem and branch lengths.

Recovery patterns

Following ice damage to a forest canopy, surviving trees surrounding gaps undergo lateral growth (Runkle 1985). Initially regrowth of the HBEF canopy was slow, but by 2000, two years after the storm, LAI values had increased considerably (Fig. 7). The initial delay in regrowth may reflect the physiological shock of growing under the altered conditions caused by damage to neighboring trees (Oliver and Larson 1996). Once trees acclimate to the new conditions, lateral extension growth can occur at a mean rate of 4–14 cm/year (Runkle 1985). Delayed LAI recovery in 1999 also may be explained in part by the effects of a severe hailstorm in August 1998 that removed many twigs and buds across several stands in this study area (1.0–1.5 LAI units were knocked down; T.J. Fahey, unpublished data). The significant increase in LAI at HBEF between 1998 and 2000 was also the product of an unusually good growing season in 2000, when warm and moist conditions led to increases in the LAI of trees in both ice-damaged and undamaged plots. As expected, tree regrowth was most intense in the most severely damaged plots. The combination of good growing conditions and significant increases in nutrient availability following the storm (B. Houlton, personal communication) led to tree LAI values rising above the calculated prestorm values (B. Houlton, Princeton University, Department of Ecology and Evolutionary Biology, personal communication).

It is likely that the greater root growth in damaged versus undamaged plots during the second growing season following the ice storm also contributed to the ability of the forest to regrow rapidly. Few observations of root growth responses to forest canopy damage have been reported, but our results concur with those of Battles and Fahey (2000), where root growth was higher in canopy gaps than in reference plots in the hardwood–conifer transition zone in the Adirondack Mountains, New York. Significant increases in nutrient concentration in soil solutions and streams draining the ice damaged areas at HBEF (B. Houlton personal communication) suggest that root growth responded to nutrient availability. The possibility that the high carbon demands of the expanding root systems constrained canopy expansion during 1999 deserves further study.

Ice damage and long-term forest change

At HBEF and throughout most of the region impacted by the 1998 ice storm, this disturbance event has been superimposed on a forest landscape variously affected by previous large-scale disturbances that have resulted in a patchwork of even- and multi-aged stands. Our results indicate that the even-aged northern hardwood forest is not very susceptible to ice storm damage until it reaches 15–20 years of age, but thereafter, it is exceedingly vulnerable. The fact that the 14-year-old forested watershed (WS5) at HBEF suffered virtually no ice damage across a wide range of ice loading, forest composition, and physiography, whereas the adjacent 24- to 28-year-old watershed was severely impacted, suggests that susceptibility to ice damage in even-aged northern hardwoods is age related. The selective destruction of pin cherry by ice damage should accelerate the transition in dominance from this pioneer species to mature northern hardwoods that normally occurs from age 20 to 35 years old (Mou et al. 1993). However, the severe bending that occurred either independently or by collateral damage probably will have long-term effects on the structure and possibly the composition of these forests. No studies have quantified the fate of severely bent stems; epicormic branches were flourishing on many bent stems in 2002, while considerable mortality (25%), defined by a lack of live foliage, was also observed (T.J. Fahey, personal observation). Quantifying the risk to even-aged silvicultural management associated with ice storm damage will require quantitative data on these responses as well as information on the upper age limit at which even-aged stands are susceptible to severe stem bending.

In the mature forest, interspecific variability in susceptibility to ice damage may alter competitive interactions between and among woody and herbaceous vegetation, changing the composition and structure of the forest and, ultimately, successional patterns over the long-term (Lemon 1961; Whitney and Johnson 1984; Rebertus et al. 1997). Our study found that beech bark disease severity was intensified following the ice storm, with fewer undamaged and more highly damaged trees in 2000 as compared with 1998. Despite injury from ice damage and beech bark disease and a decline in health status from 1998 to 2000 because of these two stresses, it is likely that beech will actually increase in importance at HBEF. Because small-diameter beech trees have increased nearly fivefold since the appearance of beech bark disease (E. Denny and T.G. Siccama, unpublished data), gaps formed in the January 1998 ice storm were dominated by beech root sprouts (72% of saplings). Increased resources in the new ice storm gaps may allow beech in the 2- to 5-cm class to grow into the next size class (E. Denny and T.G. Siccama, unpublished data), but the future effects of beech bark disease on this regeneration are not yet clear.

Conversely, sugar maple, the most resistant to ice damage of the dominant species, may actually decline in the future as an indirect result of the storm. Following the removal of the canopy layer of red spruce through logging, the importance of sugar maple increased, but in the past 34 years smaller sugar maples (2–10 cm) in the 60- to 120-year-old forest have declined by 80% (E. Denny and T.G. Siccama, unpublished data). This trend is likely to be the result of competition with vigorous beech root sprouts produced as a response to beech bark disease and is unlikely to be affected by the ice storm (Hane 2000). Although sugar maple is known to grow well in small gaps (Canham 1985; Runkle 1990) and to have a greater growth response in gaps compared with beech (Brisson et al. 1994), it only represented 4% of the regeneration in the newly formed gaps in 1998. Adult sugar maples represented the highest percentage of trees in the healthiest class in 2000 (sugar maple, 42%; yellow birch, 16%; beech, 22%). However, they also made up a greater percentage of trees in the least healthy classes as compared with yellow birch, a species less damaged by ice. This unhealthy status is likely the result of interactions of several factors: climate change (Davis and Zabinski 1992; Spear et al. 1994), nutrient deficiencies associated with acid rain, and air pollution (Bernier and Brazeau 1988; Bernier et al. 1989; Kolb and McCormick 1993; Wilmot et al. 1995). It is likely, then, that the high levels of beech saplings in the canopy gaps and adult sugar maple dieback, will equate to further increases in beech dominance.

We also expect the ice storm to reinforce the trend in declining importance of yellow birch since measurements at HBEF began in 1965. Yellow birch saplings made up only 6% of regeneration in ice storm gaps at HBEF, and these young birch will likely be outcompeted by beech root sprouts. Further, the lack of new areas of bare mineral soil will reduce regeneration (Godman and Krefting 1960).

Acknowledgments

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References

Alden, H.A. 1995. Hardwoods of North America. USDA Gen. Tech. Rep. FPL-GTR-83.

Attiwill, P.M. 1994. The disturbance of forest ecosystems: the ecological basis for conservative management. For. Ecol. Manage. **63**: 247–300.

Battles, J.J., and Fahey, T.J. 2000. Gap dynamics following forest decline: a case study of red spruce forests. Ecol. Appl. **10**: 760–774.

Bernier, B., and Brazeau, M. 1988. Foliar nutrient status in relation to sugar maple dieback and decline in the Quebec Appalachians. Can. J. For. Res. **18**: 754–761.

Bernier, B., Paré, D., and Brazeau, M. 1989. Natural stresses, nutrient imbalances and forest decline in southeastern Quebec. Water Air Soil Pollut. **48**: 239–250.

Boerner, R.J., Runge, S.D., Cho, D., and Kooser, J.G. 1988. Localized ice storm damage in an Appalachian plateau watershed. Am. Midl. Nat. **119**: 9–208.

Bofinger, J. 2001. New Hampshire ice storm damage assessment and response. *In* New York Society of American Foresters Ice Storm Symposium. USDA Forest Service, Cortland, N.Y. Publ. NA-TP-03-01. pp. 73–76.

Bormann, F.H., and Likens, G.E. 1979*a*. Catastrophic disturbance and the steady-state in northern hardwood forests. Am. Sci. **67**: 660–669.

Bormann, F.H., and Likens, G.E. 1979*b*. Pattern and process in a forested ecosystem. Springer-Verlag, New York.

Bormann, F.H., Siccama, T.G., Likens, G.E., and Whittaker, R.H. 1970. The Hubbard Brook ecosystem study: composition and dynamics of the tree stratum. Ecol. Monogr. **40**: 377–388.

Braun, E.L. 1950. Deciduous forests of eastern North America. The Blakiston Co., Philadelphia, Pa.

Brisson, J., Bergeron, Y., Bouchard, A., and Leduc, A. 1994. Beech–maple dynamics in an old-growth forest in southern Quebec, Canada. Écoscience, **1**: 40–46.

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

Burns, R.M., and Honkala, B.H. (*Technical coordinators*).1990. Silvics of North America. Vol. 2. Hardwoods. U.S. Dep. Agric. Agric. Handb. 654.

Canham, C.D. 1985. Suppression and release during canopy recruitment in *Acer saccharum*. Bull. Torrey Bot. Club, **112**: 134–145.

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

Chittenden, A.K. 1904. Forest conditions of northern New Hampshire. State of New Hampshire, Concord, N.H. Biennial Rep. For. Comm. pp. 1903–1904.

Davis, M.B., and Zabinski, C. 1992. Changes in geographic range resulting from greenhouse warming: effects on biodiversity in forests. *In* Global warming and biological diversity. *Edited by* R.L. Peters and T.E. Lovejoy. Yale University Press, New Haven, Conn. pp. 298–308.

Devito, A.S., and Miller, D.R. 1983. Some effects of corn and oak forest canopies on cold air drainage. Agric. Meteorol. **29**: 39–55.

Dobbs, D. 1999. Disaster or disturbance? North. Woodlands, Winter: 33–36.

Downs, A.A. 1938. Glaze damage in the birch–beech–maple–hemlock type of Pennsylvania and New York. J. For. **36**: 63–70.

Fahey, T.J., and Hughes, J.W. 1994. Fine root dynamics in a northern hardwood forest ecosystem at Hubbard Brook Experimental Forest, NH. J. Ecol. **82**: 533–548.

Fahey, T.J., Hughes, J.W., Pu, M., and Arthur, M.A. 1988. Root decomposition and nutrient flux following whole-tree harvest of northern hardwood forest. For. Sci. **34**: 744–768.

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

Godman, R.M., and Krefting, L.W. 1960. Factors important to yellow birch establishment in upper Michigan. Ecology, **41**: 18–28.

Hane, E.N. 2000. Multi-factor interactions in the decline of *Acer saccharum* regeneration in the White Mountains of New Hampshire. Ph.D. dissertation, Brown University, Providence, R.I.

Houston, D.R., and O'Brien, J.T. 1983. Beech bark disease. USDA For. Serv. For. Insect Dis. Leafl. 75.

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

Jones, K.F. 2001. The physics of ice formation: ice on trees. *In* New York Society of American Foresters Ice Storm Symposium. USDA Forest Service, Cortland, N.Y. Publ. NA-TP-03-01. pp. 1–10.

Kolb, T.E., and McCormick, L.H. 1993. Etiology of sugar maple decline in four Pennsylvania stands. Can. J. For. Res. **23**: 2395–2407.

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

Likens, G.E., Driscoll, C.T., and Buso, D.C. 1996. Long-term effects of acidic deposition: response and recovery of a forest ecosystem. Science (Washington, D.C.), **272**: 244–246.

Martin, C.W., and Hornbeck, J.W. 1989. Revegetation after stripcutting and block clearcutting in northern hardwoods: a ten-year history. USDA For. Serv. Res. Pap. NE-625.

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.

Mou, P., and Warrillow, M.P. 2000. Ice storm damage to a mixed hardwood forest and its impacts on forest regeneration in the ridge and valley region of southwestern Virginia. J. Torrey Bot. Soc. **127**: 66–82.

Mou, P., Fahey, T.J., and Hughes, J.W. 1993. Effects of soil disturbance on vegetation recovery and nutrient accumulation following whole tree harvest of a northern hardwood ecosystem. J. Appl. Ecol. **30**: 661–675.

Oliver, C.D., and Larson, B.C. 1996. Forest stand dynamics. John Wiley & Sons, Inc., New York.

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.

Runkle, J.R. 1985. Disturbance regimes in temperate forests. *In* The ecology of natural disturbance. *Edited by* S.A. Pickett and P.S. White. Academic Press Inc., Orlando, Fla. pp. 17–33.

Runkle, J.R. 1990. Gap dynamics in an Ohio *Acer–Fagus* forest and speculations on the geography of disturbance. Can. J. For. Res. **20**: 632–641.

SAS Institute Inc. 1995. JMP, version 3.2 ed. SAS Institute Inc., Cary, N.C.

Schwarz, P.A., Fahey, T.J., Martin, C.W., Siccama, T.G., and Bailey, A. 2001. Structure and composition of three northern hardwood–conifer forests with differing disturbance histories. For. Ecol. Manage. **144**: 201–212.

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.

Siccama, T.G., Hamburg, S.P., Arthur, M.A., Yanai, R.D., Bormann, F.H., and Likens, G.E. 1994. Corrections to allometric equations and plant tissue chemistry for Hubbard Brook Experimental Forest. Ecology, **75**: 246–248.

Snyder, M. 1998. The resilient beech. Vt. Woodland's Mag. **5**: 26–29.

Spear, R.W., Davis, M.B., and Shane, L.C.K. 1994. Late Quaternary history of low- and mid-elevation vegetation in the White Mountains of New Hampshire. Ecol. Monogr. **64**: 85–109.

Tierney, G.L., and Fahey, T.J. 2001. Evaluating minirhizotron estimates of fine root dynamics in a northern hardwood forest. Plant Soil, **229**: 167–176.

Warrilow, M., and Mou, P. 1999. Ice storm damage to forest tree species in the Ridge and Valley region of southwestern Virginia. J. Torrey Bot. Soc. **126**: 147–158.

Welles, J.M. 1990. Some indirect methods of estimating canopy structure. Remote Sens. Rev. **5**: 31–43.

Welles, J.M., and Norman, J.M. 1991. Instrument for indirect measurement of canopy architecture. Agron. J. **83**: 818–825.

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., Bormann, F.H., Likens, G.E., and Siccama, T.G. 1974. The Hubbard Brook ecosystem study: forest biomass and production. Ecol. Monogr. **44**: 233–252.

Wilmot, T.R., Ellsworth, D.S., and Tyree, M.T. 1995. Relationships among crown condition, growth and stand nutrition in seven northern Vermont sugarbushes. Can. J. For. Res. **25**: 386–397.

Zimmermann, M.H., and Brown, C.L. 1971. Trees structure and function. Springer-Verlag, New York.