

Effects of a major ice storm on the foliage of four New England conifers¹

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Abstract: The mechanical damage to forests caused by winter ice storms is well known. The January 1998 ice storm in the northeastern United States and adjacent regions of Canada caused major forest damage to the area. Here we report on the physiological effects on four conifers that did not show visible signs of damage after the January 1998 ice storm. Cuticular conductances normally increase during winter. In this winter, they were high immediately after the storm, then fell 17-74% in the following 30-45 days in hemlock, red pine, and red spruce. We hypothesize that this was caused by the loss of damaged foliage, with high cuticular conductances, over that period. Alternatively, damaged cuticles may have been repaired, although this seems less likely. Relative water contents were higher than normal in some species in the weeks after the storm, due either to an artifact of measurement introduced by the ice that coated needles or to short-term changes in the water-holding capacity of foliage. Water relations of white pine were least affected by this ice storm, whereas hemlock's were most affected. These ecophysiological results contrast with the structural effects of ice storms. Red pine is considered to be most sensitive to mechanical injury, while hemlock and red spruce are the least; white pine is intermediate. The order of sensitivity to physiological effects from a major ice storm appears to be hemlock and red spruce, followed by red pine, with white pine the least sensitive. Results from this study suggest that the physiological effects of ice storms can linger long after the ice melts from the canopy.

Keywords: conductance, conifers, foliage, ice storm, physiology, water relations, winter injury.

Résumé : Les dommages mécaniques causés aux forêts par les pluies verglaçantes sont bien connus. La tempête de verglas qui est survenue en janvier 1998 dans le nord-est des États-Unis et dans les régions adjacentes du Canada a causé d'importants dommages aux forêts. Nous présentons ici les effets de cette tempête de verglas sur la physiologie de quatre espèces de conifères qui ne semblaient pas avoir subi de dommage. Les conductances cuticulaires augmentent normalement au cours de l'hiver. Pendant l'hiver 1998, elles étaient élevées tout juste après la tempête. Par contre, au cours des 30 à 45 jours suivants, les valeurs ont connu une baisse de l'ordre de 17 à 74 % chez la pruche, le pin rouge et l'épinette rouge. Nous avons émis l'hypothèse que ce phénomène ait été causé par la perte du feuillage endommagé, feuillage ayant des conductances cuticulaires élevées. Il est aussi possible que les cuticules blessées aient été réparées, quoique cela semble peu probable. Les contenus hydriques relatifs étaient plus élevés qu'en temps normal chez certaines espèces pendant les semaines qui ont suivi la tempête. Ceci s'expliquerait soit par une anomalie introduite par la présence de glace autour des aiguilles pendant les mesures, soit par de rapides changements de la capacité du feuillage à retenir l'eau. C'est chez le pin blanc que la tempête de verglas a le moins affecté les relations hydriques. La pruche a été l'espèce la plus touchée à ce niveau. Ces résultats écophysologiques fournissent un éclairage très différent sur les impacts du verglas chez les conifères, surtout si on les compare aux impacts structuraux généralement observés chez les mêmes espèces à la suite de tempêtes de pluie verglaçante. En effet, le pin rouge est considéré comme l'espèce la plus sensible aux blessures mécaniques. La pruche et l'épinette rouge sont beaucoup moins sensibles, et le pin blanc a pour sa part un degré de sensibilité intermédiaire. Au niveau physiologique, la pruche et l'épinette rouge seraient les espèces les plus sensibles au verglas, suivies du pin rouge et du pin blanc. Les résultats de cette étude indiquent que les effets physiologiques des tempêtes de verglas peuvent se prolonger bien après la fonte de la glace recouvrant le feuillage.

Mots-clés : blessure hivernale, conductance, conifères, feuillage, physiologie, relations hydriques, tempête de verglas.

Nomenclature: Please give reference of nomenclature books for species cited in text.

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Introduction

Forest scientists have long appreciated the role of winter injury of various sorts on forest ecosystem struc-

ture and function. Damage at alpine or boreal treeline caused by winter desiccation, frost damage, cuticular abrasion or a combination of these stresses has been noted in many parts of the world (Baig & Tranquillini, 1976; Marchand & Chabot, 1978; Tranquillini, 1979; Hadley & Smith, 1983; 1986; 1987; 1990; Friedland *et al.*, 1984; McCracken *et al.*, 1985; Takahashi, 1985; Sakai &

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Larcher, 1987; Hadley *et al.*, 1991; Havranek & Tranquillini, 1995). Canopy damage at various elevations caused by snow, wind, and winter desiccation has been quantified by Grier (1988).

The mechanical damage to forests caused by winter ice storms is also well known (Grier, 1988; Irland, 2000). Ice storms break off twigs and branches, as well as entire crowns, of deciduous species. In addition, conifers also can lose significant amounts of foliage. The role of rime ice accumulation in the formation of "fir waves" has been well documented (Shimazu, 1959; Sprugel, 1976; Reiners & Lang, 1979; Sprugel & Bormann, 1981; Marchand, 1984; Boyce, 1988; Foster, 1988; Iwasa, Sato & Nakashima, 1991) and is another mechanical type of damage that can affect individual trees and entire stands.

The January 1998 ice storm of the northeastern U.S. and southeastern Ontario, Québec, and New Brunswick in Canada (Regan, 1998) caused major forest damage (Miller-Weeks & Eager, 1999; Irland, 2000; Hooper, Arie & Lechowicz, 2001; Proulx & Greene, 2001). The hardest hit areas received more than 100 mm of freezing rain within a 5-day period (Gyakum & Roebber, 2001). In the northeastern United States, 6.9 million hectares of forest were affected (Miller-Weeks & Eager, 1999), and an additional 1.6 million hectares were affected in Québec (Irland, 1998). Substantial areas in Ontario, Québec, and New Brunswick were also damaged to varying degrees (Irland, 1998; Jones *et al.*, 2001). Damage to hardwoods, particularly American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), red maple (*A. rubrum*), white birch (*Betula papyrifera*), and yellow birch (*B. alleghaniensis*), was extensive, including breakage of large limbs and even entire crowns (Miller-Weeks & Eager, 1999; Manion, Griffen & Rubin, 2001). Conifers were much less visibly damaged (Miller-Weeks & Eager, 1999). However, this does not mean that conifers escaped all adverse impacts of the ice storm. At the time of the January 1998 storm, we were conducting a study on the winter water relations of three low-elevation conifers at their upper elevational limits and one high-elevation conifer on Mt. Ascutney in east-central Vermont (Boyce, Vostral & Friedland, 2002; Vostral, Boyce & Friedland, 2002). Eastern hemlock (*Tsuga canadensis*), eastern white pine (*Pinus strobus*), and red pine (*Pinus resinosa*) were studied along with the higher-elevation conifer red spruce (*Picea rubens*). Mt. Ascutney received icing but sustained much less structural damage to trees than other nearby areas (Miller-Weeks & Eager, 1999; R. L. Boyce & A. J. Friedland, pers. observ.). Conifers at this site were affected in other ways, however. Winter water relations parameters of these species, especially cuticular conductance, were anomalous during the winter of 1998. Here we report on the effects of the January 1998 ice storm on conifer shoot winter water relations, focusing on differences among species. In particular, we report on trees that were not visibly damaged by the ice storm, but were adversely impacted by the storm in ways that manifested themselves in ecophysiological measurements over the succeeding three months.

Methods

STUDY AREA

Two sites were located on the north-facing slope of Mt. Ascutney (43° 27' N, 72° 27' W, 960 m elevation) in eastern Vermont. Eastern hemlock (*Tsuga canadensis*) and eastern white pine (*Pinus strobus*) data were collected from a lower study site, located at 640 m, near the upper elevational limit of these two species on this mountain (Boyce, 1998; R. L. Boyce, unpubl. data). Red pine (*P. resinosa*) and red spruce (*Picea rubens*) data were collected from an upper site at 715 m, which is near the upper elevational limit of red pine on this mountain (Boyce, 1998; R. L. Boyce, unpubl. data). These sites are further described elsewhere (Boyce, Vostral & Friedland, 2002; Vostral, Boyce & Friedland, 2002; Friedland *et al.*, 2003). Physiological data were collected during the winters of 1997, 1998 and 1999. Data from the first and last winter are reported elsewhere (Boyce, Vostral & Friedland, 2002; Vostral, Boyce & Friedland, 2002; Friedland *et al.*, 2003); only data from 1998 are reported here.

METEOROLOGICAL MEASUREMENTS

A meteorological tower was installed at each site and positioned so that instruments were placed within the canopy (7.2 m at lower site, 8.1 m at upper site). At both sites, the live canopy extended from the ground to approximately 20 m, but the maxima in foliar area were estimated to be in the range 7–13 m above the ground. Air and needle temperatures, relative humidity, and irradiance were measured as described in Vostral, Boyce, and Friedland (2002), Boyce, Vostral, and Friedland (2002), and Friedland *et al.* (2003).

WATER RELATIONS

Shoots were removed from four canopy trees of each species at midday on an approximately weekly basis from 3 January through 5 April in 1998. Collections were always made between 1100 and 1400 on each day of collection. Branches containing apparently undamaged sun-exposed foliage were removed with a 7.5-m telescoping pole pruner and kept in sealed plastic bags over ice and in darkness while being transported to the laboratory. Measurements were conducted within 6 hours after collection. Relative water contents (RWC), water potentials (Ψ), and cuticular conductances (g_c) were determined on current and previous-year foliage as described elsewhere (Boyce, Vostral & Friedland, 2002; Vostral, Boyce & Friedland, 2002). Cuticular conductances were measured on 11 January (Day of the Year [DOY] 11, just after the storm), 8 February (DOY 39), and 28 March (DOY 87).

CHLOROPHYLL FLUORESCENCE

Chlorophyll fluorescence parameters were determined on current-year foliage from all four species during the winter of 1998, following procedures described in Adams and Perkins (1993) and Perkins and Adams (1995). Shoots were collected from the same trees used for water relations measurements on 19 January (DOY 19), 17 February (DOY 48), and 15 April 1998 (DOY 105). They were stored at 4°C in the dark until the day after collection. They were then shipped over ice by overnight

express to the University of Vermont. Upon receipt, they were immediately placed into cold storage at 4°C in the dark. The following day, foliage was removed from twigs. Individual current-year needles were sliced into 2-mm-long segments and sieved to remove buds and woody shoot tissue. Needle segments were then placed into autosampler trays (5 replicate samples of needle segments/shoot), and fluorescence was measured after a 15-minute dark equilibration period, using a PK Morgan CF1000 fluorometer in the fast-kinetic measurement mode. Actinic light intensity was 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$, with a measurement interval of 5 s; this level is appropriate for winter-hardened foliage (T. D. Perkins, pers. observ.). The fluorometer was custom-programmed to accept the low fluorescence measurements typical of winter-hardened foliage. Measurements were conducted at approximately 20°C. Measured parameters included minimal, maximal, and variable fluorescence (F_o , F_m , F_v respectively) and the half-time rise ($t_{1/2}$); terminology follows Bolhär-Nordenkamp and Öquist (1993) and Mohammed, Binder, and Gillies (1995). Mean values of the ratio F_v/F_m and of $t_{1/2}$ for each species and date were calculated. Data were analyzed with a repeated-measures ANOVA using month and species as factors, with polynomial contrasts among dates (von Ende, 1993).

MODELING

The model WINWAT was used to determine how ice-storm-induced changes in g_c affected winter water relations in hemlock and white and red pines (foliar temperatures were not measured on red spruce, so that species was not included). WINWAT was developed by Boyce, Friedland, and Macdonald (1992); more recent modifications are described in Boyce and Saunders (2000) and Boyce, Vostrat, and Friedland (2002). Previous work has shown that the recharge parameter R_p of trees growing close to their upper elevational limits varies greatly from year to year (Boyce & Saunders, 2000), so WINWAT was recalibrated in 1998 for each species and foliar age class. Measured RWCs on 3 January 1998 were used to set initial values of WC during each model calibration run. WINWAT was run for the six combinations of species and foliar age classes each year. Runs were terminated on 22 March 1998, because measured values of temperatures and RWC after these dates indicated that stomates began opening. For each combination of species and foliar age class, the appropriate values of measured needle temperature, cuticular conductance, and initial measured water contents were input into the model. Only conductances from February and March were used, however, because of the anomalously high values measured in January. The model was run with variations of R_p until the following sum of squares between modeled and measured RWCs was minimized:

$$\chi^2 = \sum_i^n \frac{(\text{RWC}_{pi} - \text{RWC}_{mi})^2}{\sigma_{mi}^2} \quad [1]$$

where RWC_{pi} and RWC_{mi} are the i^{th} predicted and modeled RWC, respectively, and σ_{mi} is the standard deviation

of the i^{th} measured RWC (Omlin & Reichert, 1999). The 95% confidence interval of this minimum sum of squares and the upper and lower 95% confidence intervals of R_p were estimated as described in Boyce, Vostrat, and Friedland (2002). Goodness of fit, using the method of Parrish and Smith (1990), was applied to each model run from each age class and species and year as described in Boyce, Vostrat, and Friedland (2002). Bonferroni confidence intervals at a joint confidence level of 0.95 were calculated for each RWC measurement. A ratio R_j was calculated for each measurement as

$$\begin{aligned} R_j &= L_j/\mu_{pj}, & \text{if } \mu_{pj} < L_j \\ &= 1, & \text{if } L_j < \mu_{pj} < U_j \\ &= \mu_{pj}/U_j, & \text{if } \mu_{pj} > U_j, \end{aligned} \quad [2]$$

where L_j and U_j are, respectively, the lower and upper 95% confidence limits of the j^{th} measured mean, and μ_{pj} is the j^{th} mean predicted by the model. The calibration was considered acceptable if every value of R_j in a model run was less than or equal to 1.05, *i.e.*, the model predicted all RWCs in the run within a factor of 1.05 (Boyce, Vostrat & Friedland, 2002).

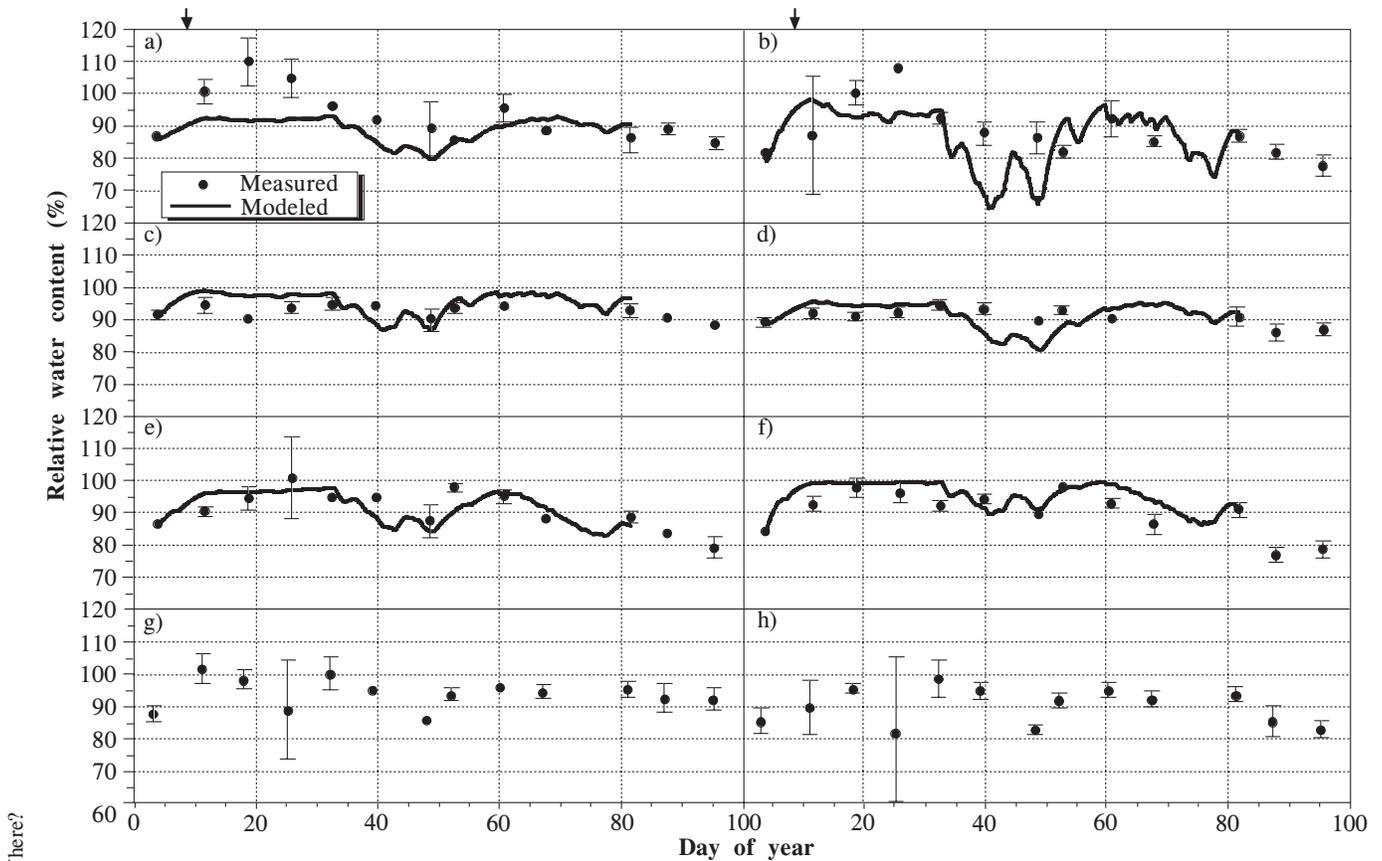
Results

Relative water contents (RWCs) are shown in Figure 1. Hemlock, red pine, and red spruce all responded to the ice storm, which occurred on DOY 8-9 at this site, with RWCs that were both highly variable and occasionally above 100% (this was especially true of hemlock). Shoots remained coated with ice until after DOY 25, when increased temperatures and lower relative humidities (data not shown) caused canopies to dry out. After this date, RWCs of both foliar age classes of these three species generally remained at a typical normal range of 85% to 95% until the end of the winter, when stomatal opening occurred. White pine RWC, however, did not appear to be affected by the ice storm and maintained relatively constant RWCs throughout the winter. The two foliar age classes sampled were highly correlated in all four species (Table I).

Responses of water potentials (Figure 2) were more variable. Red pine and red spruce had much lower and more variable values of Ψ on DOY 11 than was generally observed later in the winter. Hemlock showed no initial response on DOY 11, but dropped to $\Psi < -1.0$ MPa between days 35 and 55. White pine showed no obvious response and maintained values above -1.0 MPa throughout the winter. Only in hemlock were RWC and Ψ significantly ($P < 0.05$) correlated (Table I).

In hemlock, red pine 1-year-old foliage, and red spruce, values of g_c fell from high values in January, collected immediately after the ice storm, to much lower values in February (Table II). Red spruce, in particular, had January values of g_c that were ~ 2 -3.5 times greater than February values. March g_c values were generally about the same as, or slightly larger than, February's. White pine and red pine 1-year-old foliage was little affected, however.

RWC modeling results are shown in Figure 1 and Table III for hemlock, white pine, and red pine. Even



Asterisk? Where?

FIGURE 1. Measured and modeled relative water contents in winter 1998. a) hemlock current-year, b) hemlock 1-year-old, c) white pine current-year, d) white pine one-year-old, e) red pine current-year, f) red pine 1-year-old, g) red spruce current-year, and h) red spruce 1-year-old. Model runs are shown for the first three species. **Measured values marked with an asterisk were not used for model calibration.** Error bars are standard deviations ($n=4$ trees). Arrows show date of 8-9 January ice storm.

though dates that were obviously affected by the ice storm were excluded, model fits were poor compared to 1997 and 1999 (Boyce, Vostral & Friedland, 2002). Except for red pine 1-year-old foliage, mean square errors of the model fits (Table III) were at least two times the 1997 and 1999 values (Boyce, Vostral & Friedland, 2002). Thus, it is not surprising that the approximate 95% confidence intervals of R_p in 1998 usually overlapped those from 1997 and 1999 (Boyce, Vostral & Friedland, 2002). R_j values exceeded 1.05 on two dates for 1-year-old hemlock and on one date for 1-year-old white pine, resulting in unacceptable calibrations for those foliar age classes. By comparison, R_j never exceeded 1 for any species or age class in 1999 (Boyce, Vostral & Friedland, 2002). In 1997, we had less-extensive measurements of g_c ; nonetheless, R_j exceeded 1 on only two occasions each in 1-year-old hemlock and white pine, and it still remained less than 1.05 on all dates (Boyce, Vostral & Friedland, 2002).

The half-time rise $t_{1/2}$ showed significant differences between species ($F_{3,11}=132.19$; $P=0.0002$) and months ($F_{2,22}=100.69$; Huynh-Feldt adjusted $P<0.0001$), and there was a significant species \times month interaction ($F_{6,22}=14.18$; Huynh-Feldt adjusted $P<0.0001$) (Figure 3). Polynomial contrasts showed that when all species were considered together, there were significant ($P<0.025$) quadratic and linear trends across months; however, the strength of the linear component varied

TABLE I. Spearman rank correlations between relative water content (RWC) and water potential (Ψ) of current-year and 1-year-old shoots. Statistically significant coefficients ($P \leq 0.05$) are shown in bold. The P -values are listed below the coefficients, and n is given in parenthesis.

| Correlation | Hemlock | White pine | Red pine | Red spruce |
|------------------------------------|-------------------------------|-------------------------------|-------------------------------|-------------------------------|
| Current-year versus 1-year-old RWC | 0.86 0.0001 (13) | 0.76 0.0045 (12) | 0.91 0.0001 (13) | 0.79 0.0013 (13) |
| Current-year RWC versus Ψ | 0.72 0.0298 (9) | 0.33 0.3466 (10) | 0.35 0.3538 (9) | 0.41 0.2115 (11) |
| One-year-old RWC versus Ψ | 0.68 0.0424 (9) | 0.44 0.2004 (10) | 0.38 0.3085 (9) | 0.53 0.0947 (11) |

among species ($F_{3,11}=18.32$; $P<0.0001$). Hemlock had the lowest overall values, but it and the pines all responded by increasing $t_{1/2}$ from January to April. Red spruce, however, remained fairly constant. By April, red pine had the longest $t_{1/2}$. Increases in half-time rises of conifers during spring indicate recovery of electron transport by photosystem II (Lindgren & Hällgren, 1993). When time was not accounted for, F_v/F_m did not vary among species ($F_{3,11}=1.42$; $P=0.29$). However, there were differences

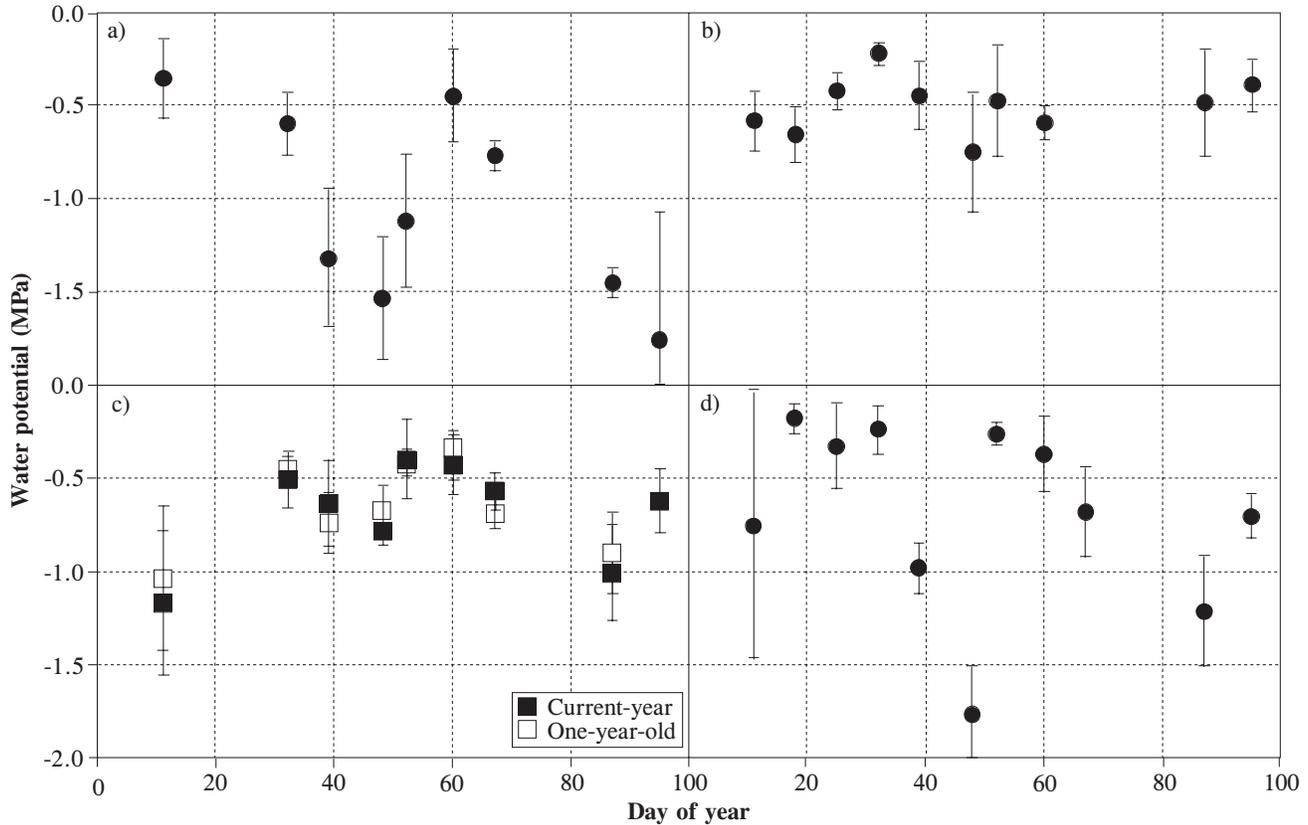


FIGURE 2. Water potentials of a) hemlock, b) white pine, c) red pine, and d) red spruce shoots versus day of year (1998). Water potential was measured separately on red pine age classes. Error bars are standard deviations ($n=4$ trees).

among months ($F_{2,22}=40.67$; Huynh-Feldt adjusted $P<0.0001$), and the response across months varied among species ($F_{6,22}=10.64$; Huynh-Feldt adjusted $P<0.0001$). There was an overall linear change across months ($F_{1,11}=65.81$; $P<0.0001$), but individual species varied in how they changed across months ($F_{3,11}=16.22$; $P=0.0002$), especially red spruce. Hemlock and the pines behaved fairly similarly, with initial values of approximately 0.600, then climbing steadily to 0.700 by April. Red spruce, however, maintained a fairly steady value of 0.650, so by April F_v/F_m was considerably lower than the other three species. F_v/F_m indicates the level of recovery of whole photosystem II function (Bolh ar-Nordenkampf &  quist, 1993).

Discussion

Cuticular conductance behaved in a manner very different from what was observed in the other two years of this study (Vostral, Boyce & Friedland, 2002). In 1999, cuticular conductances either remained stable or rose slightly through the winter (Vostral, Boyce & Friedland, 2002). Similar trends were observed during the winter by McCracken *et al.* (1985), and Hadley and Smith (1986; 1990) found consistent increases in g_c over the course of the winter in Rocky Mountain conifers. In 1998, however, g_c for many species was very high immediately after the ice storm, then fell to lower levels in February and

TABLE II. Mean cuticular conductances (g_c) of current and 1-year-old shoots of hemlock, white pine, red pine, and red spruce by month.

| Species | Foliar Age Class | g_c ($m\ ks^{-1}$) | | |
|------------|------------------|------------------------|----------|-------|
| | | January | February | March |
| Hemlock | Current | 0.115 | 0.039 | 0.041 |
| | One-Year-Old | 0.201 | 0.167 | 0.197 |
| White pine | Current | 0.032 | 0.031 | 0.037 |
| | One-Year-Old | 0.028 | 0.021 | 0.031 |
| Red pine | Current | 0.097 | 0.101 | 0.089 |
| | One-Year-Old | 0.142 | 0.099 | 0.132 |
| Red spruce | Current | 0.031 | 0.009 | 0.008 |
| | One-Year-Old | 0.060 | 0.032 | 0.029 |

March. We interpret this to mean that foliage with ice-damaged cuticles was present on twigs in January, contributing to the high g_c values measured then. By February, however, damaged foliage would have desiccated to the point where death had resulted, and it had fallen off the twigs. Undamaged or only slightly damaged foliage would remain, resulting in lower conductance values. Unfortunately, we did not collect litterfall after the storm, which would have established whether this hypothesis is correct. However, our interpretation is supported by the results of a WINWAT run, shown in Figure 4, for hemlock current-year foliage, which predicts what would have happened had the conductance measured for current-year hemlock foliage in January 1998 been used with the

TABLE III. Values of calibrated recharge coefficient R_p by species and foliar age class. Approximate 95% confidence intervals are shown in parentheses. Mean square errors are shown beneath in bold.

| Age class | Hemlock | White pine | Red pine |
|--------------|------------------------------|-----------------------------|-------------------------------|
| Current-year | 25 (17, 42) 9.69 | 60 (21, ∞) 12.66 | 85 (53, 201) 9.48 |
| One-year-old | 70 (40, 175) 11.03 | 20 (12, 51) 13.36 | 205 (105, 738) 8.24 |

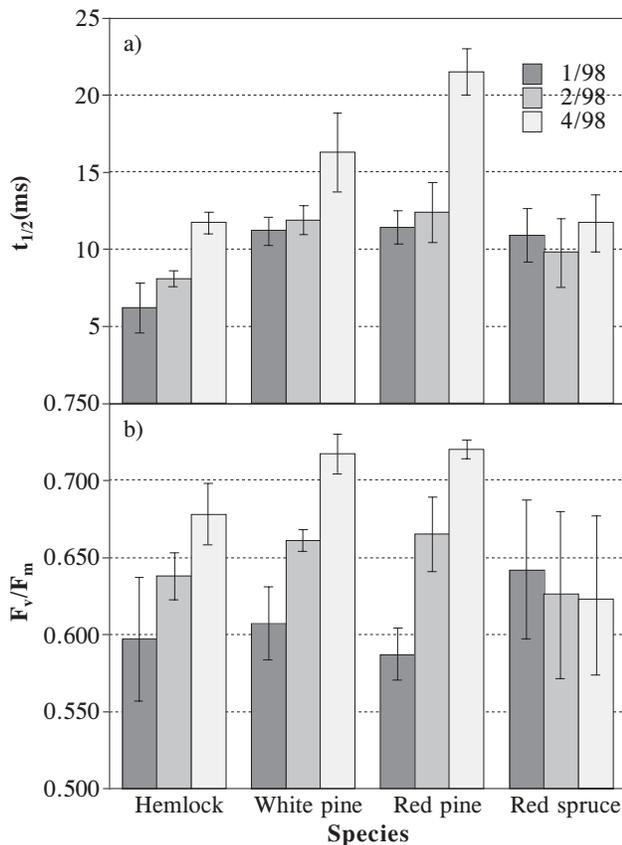


FIGURE 3. Chlorophyll fluorescence parameters measured on the four species during the winter of 1998 in January, February, and April. A) Half-time rise ($t_{1/2}$); B) F_v/F_m . Error bars are standard deviations ($n=4$ trees).

Should this be months? OK? value of R_p from calibration with the other month's conductances. Foliage desiccates to RWCs < 50%, well below levels considered damaging (Boyce, Vostral & Friedland, 2002), in approximately a month, well before the next conductance sampling occurred. Note that the conductance value is conservative. The actual value of g_c used was the mean of damaged and undamaged foliage, so conductance of damaged foliage would have been considerably higher, leading to desiccation well before the time shown in Figure 4. The resulting rapid changes in g_c may be responsible for the poor fit of WINWAT during 1998, especially relative to its very good performance in 1999. Alternatively, the ice storm could have temporarily increased g_c , followed by a recovery. Since g_c cannot be measured on the same shoots, due to the destructive nature of the measurements, this could not easily be determined. Furthermore, the only study of which we are

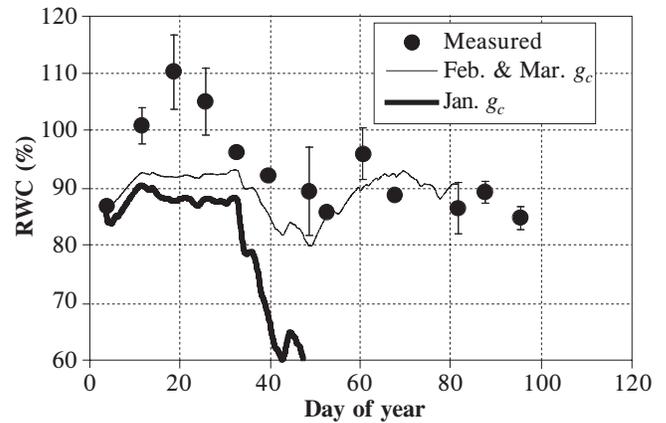


FIGURE 4. Measured and modeled RWC for hemlock current-year foliage in 1998. Light line shows modeled RWC using g_c calculated from February and March measurements (Table II). Dark line shows modeled RWC using R_p from Table III and g_c measured in January immediately after the ice storm (Table II).

aware that demonstrated a decrease in g_c showed that it occurred in current-year conifer foliage during the late summer and early fall (Hadley & Smith, 1994). While that study did not follow changes in g_c over the winter, it did note that g_c was higher in 1-year-old foliage in all species examined. Studies which have examined changes in g_c over the winter show that it usually remains constant or increases (McCracken *et al.*, 1985; Hadley & Smith, 1986; 1990; Vostral, Boyce & Friedland, 2002), so we think that a recovery of g_c during the winter is unlikely. If, as we suggest, damaged foliage was lost during this winter, growth in subsequent years would be adversely affected. Foliar loss due to winter desiccation is thought to cause treeline in the Alps (Tranquillini, 1979; Havranek & Tranquillini, 1995). Freezing injury to red spruce foliage has also been implicated in that species' decline (Johnson *et al.*, 1992). Winter foliar loss is also thought to be one of the factors responsible for the decline of trees at the leading edge of fir waves (Sprugel, 1976; Sprugel & Bormann, 1981; Marchand, 1984). Thus, any stress that causes winter foliar death has the potential to decrease growth of that species in subsequent years. While the ice storm of early January 1998 did not cause significant structural damage to forests in this area (Miller-Weeks & Eager, 1999; R. L. Boyce, pers. observ.), we believe that this forest did sustain damage that was less apparent to visual observation. Furthermore, this damage has the potential to decrease growth in the species most affected.

By definition, RWC is not supposed to exceed 100%, yet such values were measured in many species on dates after the ice storm, until foliage was no longer encased in ice (R. L. Boyce, pers. observ.). Ice had to be removed from foliage before fresh weights could be measured, and it was not possible to avoid melting during that process. We speculate that shoots became supersaturated while ice was melting, such that measured fresh weights were well above true fresh weights. It is also possible that a temporary change in epidermal and/or cuticular structure occurred in the field as a result of the ice storm, allowing foliage to absorb more water in the field or during trans-

port to the laboratory. It is difficult to determine when exactly the artifacts of the measurement process or a storm-induced surface change became unimportant following the ice storm. Accordingly, it is not possible to use RWC as a useful indication of ice storm damage to foliage.

Hemlock water potential fell below -1.5 MPa on two occasions in 1998 (Figure 2), on the same two dates that 1-year-old foliage R_j values exceeded 1.05, whereas it never fell that low in 1997 or 1999 (Vostral, Boyce & Friedland, 2002). White pine water potentials, however, fluctuated around -0.5 MPa in all three years (Figure 2, Vostral, Boyce & Friedland, 2002). Water potential of red pine remained above -1.0 MPa in 1998, except on DOY 11, immediately after the ice storm (Figure 2); it also remained above -1.0 MPa in 1997 and **1998** (Vostral, Boyce & Friedland, 2002). Although the mean value of Ψ for red spruce immediately after the ice storm was above -1.0 MPa, there was a great deal of variation among trees (Figure 2). Red spruce water potential also fell below -1.5 MPa later in the winter (Figure 2), whereas such low values had not been measured in either 1997 or 1999 (Vostral, Boyce & Friedland, 2002). Thus, Ψ was most affected in hemlock and red spruce and may be a better indicator of stress than RWC.

Interpretation of the chlorophyll fluorescence results is complicated by the imposition of a major ice storm on normal winter responses. However, the pattern of change in F_v/F_m in hemlock and white and red pines is similar to that seen for other conifers recovering from the winter (Lundmark, Hällgren & Hedén, 1988; Adams & Demmig-Adams, 1994). By April, white and red pines had the highest values of the half-time rise $t_{1/2}$, indicating good recovery of electron transport by photosystem II (Lindgren & Hällgren, 1993). They also had high values of F_v/F_m by April, indicating recovery of whole photosystem II function (Leverenz & Öquist, 1987; Bolhår-Nordenkamp & Öquist, 1993; Verhoeven, Adams & Demmig-Adams, 1996; 1999). April values were still below those considered optimum (~ 0.83 ; Björkman & Demmig, 1987), but full recovery in conifers often is incomplete until summer (Lundmark, Hällgren & Hedén, 1988; Adams & Demmig-Adams, 1994). Thus, recovery of photosynthetic activity in these two species did not appear to be affected by the ice storm.

The pattern of red spruce chlorophyll fluorescence differed from the other species in this study. Red spruce did not show the recovery of F_v/F_m seen in the other species but maintained a fairly constant ratio in the range 0.600-0.650. This was higher than the other species in January but lower by April, when the other species had ratios in the range 0.650-0.750. This suggests that red spruce may have been photosynthesizing at this site during the winter, which has been observed in other studies in Vermont (Schaberg *et al.*, 1995; 1996; 1998). Also, $t_{1/2}$ did not recover during the winter in this species. The half-time rise has been shown to decrease in autumn, indicating that electron transport is blocked at the reducing side of photosystem II (Lindgren & Hällgren, 1993). Hemlock and the two pines in this study show an increase in $t_{1/2}$ over the winter, presumably indicating recovery of

electron transport, whereas red spruce does not. It is unclear whether this behaviour of F_v/F_m and $t_{1/2}$ represents a typical pattern for red spruce or indicates stress induced by the ice storm. If this pattern is typical, it may indicate that although red spruce is considered a subalpine conifer, it recovers full photosynthetic activity more slowly in spring than low-elevation conifers. Red spruce extends in elevation well above our site, but this species appears to suffer more winter stress than might be expected for a subalpine conifer (Friedland *et al.*, 1984; DeHayes *et al.*, 1990; Hadley *et al.*, 1991).

Recovery of hemlock chlorophyll fluorescence parameters lagged the pine species. The half-time rise was well below the pines in all months. This parameter is considered to be proportional to the plastoquinone pool (Bolhår-Nordenkamp & Öquist, 1993) and is affected by shade tolerance. Hemlock, which is quite shade-tolerant, thus would be expected to have a consistently lower value than the shade-intolerant pines. However, hemlock $t_{1/2}$ did not reach the January values of red spruce, which is similar in shade tolerance, until April. Since red spruce $t_{1/2}$ did not behave like that of the other species, care must be taken with this comparison, but hemlock did appear to have slower recovery than the pines. Recovery of F_v/F_m also lagged the pines, with values < 0.700 in April. Again, it is difficult to determine whether this is a typical winter pattern or was induced by the ice storm. It does appear, however, that hemlock is more susceptible to photoinhibition induced by winter stresses than its conifer competitors.

Water relations of white pine were least affected by this ice storm, whereas hemlock's were most affected. These ecophysiological results contrast sharply with the structural effects of ice storms. Red pine is considered to be most sensitive to injury, while hemlock and red spruce are the least; white pine is intermediate (Irland, 2000). The order of sensitivity to physiological effects from a major ice storm appears to be hemlock and red spruce, followed by red pine, with white pine the least sensitive. Overall, these findings suggest that the physiological **effects** of ice storms can linger long after the ice melts from the canopy. The less apparent cuticular damage appears to be severe enough to cause foliar losses to occur long after the initial loss caused by the ice deposition itself. Furthermore, species that are less likely to sustain crown damage, such as hemlock and red spruce, are the ones most likely to undergo long-term water stress and foliar loss. Hemlock has long been considered particularly susceptible to winter injury (Curry & Church, 1952; Hadley, 2000); our data suggest it is equally vulnerable to winter damage induced by ice storms.

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Should be 1999?

What do you mean more specifically? stresses?

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