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Severe red spruce winter injury in 2003 creates unusual ecological event in the northeastern United States

Brynne E. Lazarus, Paul G. Schaberg, Donald H. DeHayes, and Gary J. Hawley

Abstract: Abundant winter injury to the current-year (2002) foliage of red spruce (*Picea rubens* Sarg.) became apparent in the northeastern United States in late winter of 2003. To assess the severity and extent of this damage, we measured foliar winter injury at 28 locations in Vermont and surrounding states and bud mortality at a subset of these sites. Ninety percent of all trees assessed showed some winter injury, and trees lost an average of 46% of all current-year foliage. An average of 32% of buds formed in 2002 were killed in association with winter injury. Both foliar and bud mortality increased with elevation and with crown dominance, and bud mortality increased with greater foliar injury. Foliar injury in 2003 at a plantation near Colebrook, New Hampshire, was more than five times the typical levels for 9 previous years of measurement and more than twice that measured for another high-injury year. Plantation data also indicated that bud mortality in 2003 was greater than previously documented and that persistent winter injury was associated with increased tree mortality. Comparisons of our data with past studies for two sites with native red spruce also indicated that damage in 2003 was greater than other recently reported, high-injury years. Because heavy foliar and bud losses can severely disrupt the carbon economies of trees, the 2003 winter injury event could lead to further spruce decline and mortality, particularly among dominant trees at higher elevations.

Résumé : Beaucoup de dommages causés par le froid ont été observés à la fin de l'hiver 2003 sur le feuillage de l'année (2002) de l'épinette rouge (*Picea rubens* Sarg.) dans le nord-est des États-Unis. Dans le but d'évaluer la sévérité et l'étendue de ces dommages, nous avons mesuré les dommages foliaires dus au froid à 28 endroits au Vermont et dans les États environnants ainsi que la mortalité des bourgeons dans un sous-ensemble de ces sites. Il y avait des dommages sur 90 % de tous les arbres examinés qui avaient perdu en moyenne 46 % de leur feuillage de l'année. Les dommages causés par le froid ont tué en moyenne 32 % des bourgeons formés en 2002. La mortalité du feuillage et des bourgeons augmentait avec l'altitude et la dominance de la cime; la mortalité des bourgeons augmentait avec la sévérité des dommages foliaires. Dans une plantation près de Colebrook au New Hampshire, les dommages foliaires de 2003 atteignaient plus de cinq fois le niveau typique de dommages mesurés depuis 9 ans et plus du double de ceux observés lors d'une autre année où les dommages avaient été sévères. Les données provenant de la plantation montrent que la mortalité des bourgeons a été plus importante en 2003 que celle qui a été observée précédemment et que la répétition des dommages causés par le froid est associée à une augmentation de la mortalité des arbres. La comparaison de nos données avec celles provenant d'études antérieures, réalisées dans deux sites où pousse naturellement l'épinette rouge, montre également que les dommages survenus en 2003 sont plus sévères que ceux qui ont été rapportés récemment pour d'autres années où il y a eu des dommages sévères. Parce que d'importantes pertes de feuillage et de bourgeons peuvent gravement perturber le bilan du carbone chez les arbres, les dommages causés par le froid durant l'hiver de 2003 pourraient entraîner une intensification du dépérissement et de la mortalité de l'épinette, particulièrement chez les arbres dominants situés à plus haute altitude.

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Introduction

Red spruce (*Picea rubens* Sarg.) winter injury — the distinctive late winter reddening and subsequent abscission of current-year foliage — is caused by freezing rather than by winter desiccation (Perkins et al. 1991; DeHayes 1992) and can be enhanced by southern exposure (Hadley et al. 1991; Boyce 1995), possibly through rapid freezing of foliage (Perkins and Adams 1995). Winter injury has been linked to the widespread decline of red spruce observed in the northeastern United States from the 1960s through the 1980s

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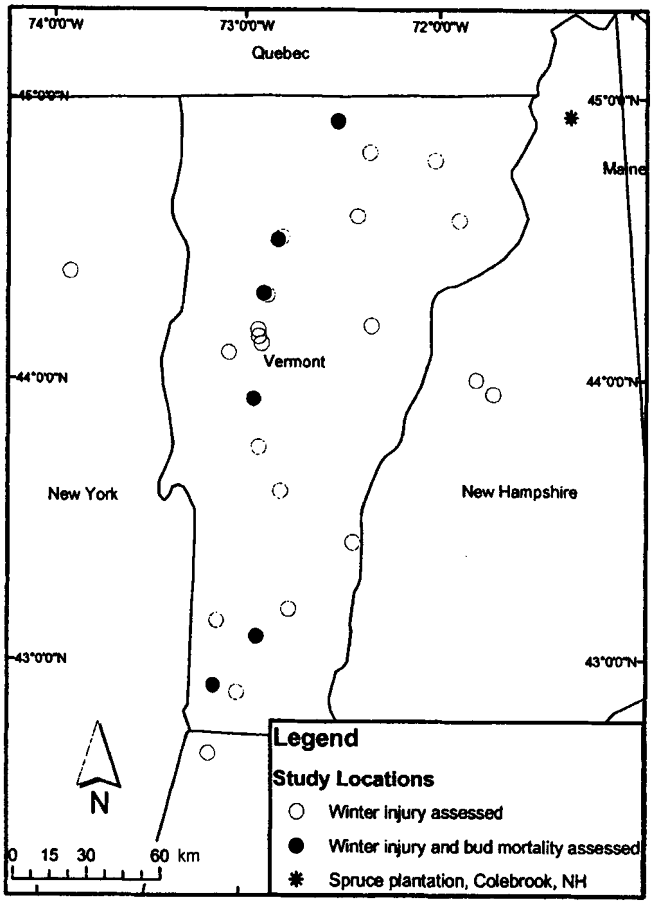
Fig. 1. Locations of the red spruce plantation near Colebrook, New Hampshire, and the 27 native forest sites in the northeastern United States where red spruce were assessed for winter injury and, in some cases, bud mortality in 2003.



(Friedland et al. 1984; Johnson 1992). The minimal cold tolerance of red spruce, combined with reductions in cold hardiness due to acidic deposition and other anthropogenic factors, contribute to winter injury episodes — some mild, others severe — when trees are exposed to various freezing stresses (e.g., low minimum temperatures, freeze–thaw cycles, rapid freezing) (see review by Schaberg and DeHayes 2000). Bud mortality can accompany winter injury (Peart et al. 1991; DeHayes 1992; Hadley et al. 1993), although historically, few winter injury studies have included bud mortality observations.

Abundant winter injury became apparent throughout Vermont and adjacent states in late winter of 2003, and we conducted a survey to document its extent and severity in that region. In this paper, we present the results of that survey and describe the potential influence of the 2003 winter injury event on the health, productivity, and composition of red spruce forests in the northeastern United States.

Materials and methods

Foliar winter injury

Winter injury was assessed between April and June of 2003 on native red spruce at 27 locations in Vermont, New Hampshire, Massachusetts, and New York, and at a mature red spruce plantation near Colebrook, New Hampshire (Fig. 1). These locations were chosen to represent a broad geographic area. An average of two to three 1/10-ha circular plots containing dominant or codominant red spruce were chosen randomly within 100 m of access trails at elevations representing the differing forest cover types in which red spruce are found. A total of 1419 trees in 176 plots were assessed at elevations ranging from 255 to 1415 m. All spruce trees in each plot were visually examined for the reddening of current-year (elongated in 2002) foliage and rated on a scale from 0 to 10 by two observers. A score of 1 represented 1%–10% injury, a score of 2 represented 11%–20% injury, etc. Obvious patterns of injury concentration within crowns (e.g., top vs. bottom, aspect) were noted, though not quantified. The relative dominance of tree crowns (dominant, codominant, intermediate, suppressed, or understory) was also recorded. Trees shorter than breast height were not examined except in high-elevation krummholz forests.

Winter injury was also assessed at a red spruce provenance plantation established in 1960 near Colebrook, New Hampshire (elevation 715 m). This plantation contains trees from 12 provenances, with seed sources extending from North Carolina to Quebec (Wilkinson 1990). Winter injury was measured yearly in this plantation from 1986 to 1992 and from 2000 to 2003.

Bud mortality

Bud mortality accompanying winter injury was visually estimated using binoculars in October and November of 2003 at the plantation near Colebrook, New Hampshire, and at 6 of the 27 locations where foliar injury was assessed (Fig. 1). Because plots were located with GPS units and not permanently marked, we were able to return to the same general areas, though not to precisely the same trees. The same 0–10 injury scale used for foliar assessments was used for bud mortality measurements. Two assessments were made for each tree: (*i*) the proportion of current-year (2002) shoots affected by foliar winter injury in 2003, and (*ii*) the proportion of these shoots that failed to break bud. These two measurements were multiplied to estimate the proportion of all buds produced in 2002 that were lost in association with winter injury.

$$[1] \qquad \%\ 2002\ \text{bud mortality} = \text{Fol}_{WI} \times \text{Bud}_{WI}$$

where Fol_{WI} is the proportion of current-year foliage that was winter-injured, and Bud_{WI} is the proportion of winter-injured shoots that failed to break bud. Bud failure not associated with winter injury was not measured.

Statistical analyses

All reported statistics were calculated with tree as the unit of analysis unless otherwise noted. Foliar injury and bud mortality means were calculated from damage class percent midpoints. Data were treated as continuous because damage class ranges were small and of equal size and because the 11 damage classes represented steadily increasing levels of injury. ANOVA and Tukey–Kramer comparisons were used to compare winter injury and bud mortality means among canopy classes. Because elevation was measured at the plot level, Spearman's rank correlations with plot injury means were used to assess relationships between elevation and in-

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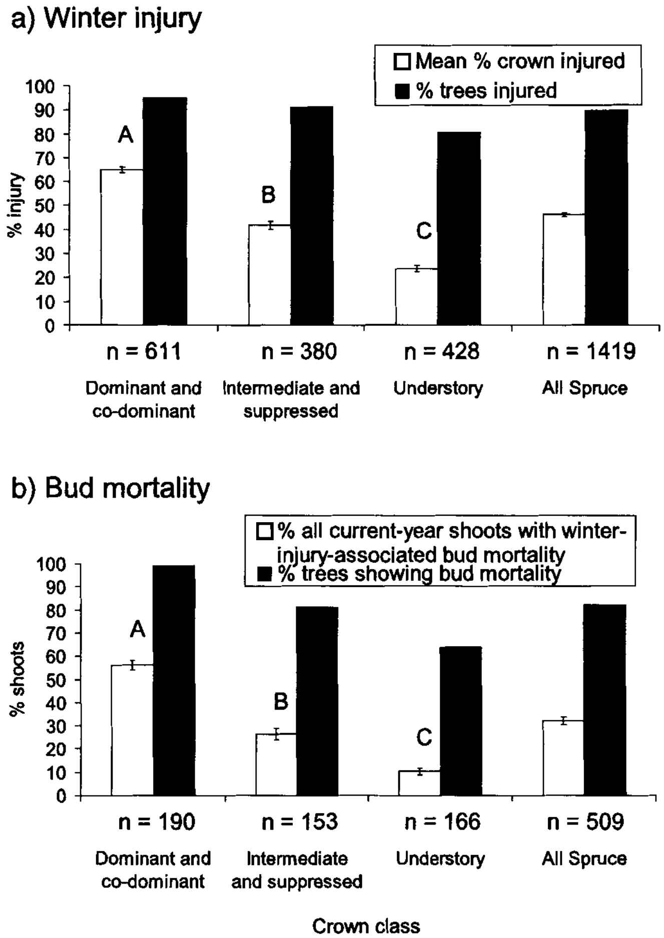
Fig. 2. Winter injury and bud mortality assessed in the northeastern United States in 2003: (*a*) mean (±SE) winter injury and % trees injured, measured on current-year red spruce foliage in early spring, at 27 locations; and (*b*) mean (±SE) bud mortality and % trees showing bud mortality, measured at 6 locations in late fall. Crown class means with different letters are significantly different (Tukey–Kramer comparisons, $P < 0.05$). Means were based on damage class percent midpoints from an 11-class injury scale.



jury. Spearman's rank correlation was also used to relate foliar winter injury and bud mortality. *t* tests for unequal variances were used to compare injury levels between groups of trees at the Colebrook plantation.

Results and discussion

Foliar injury in native stands

Ninety percent of the 1419 red spruce trees assessed showed some winter injury (Fig. 2). An average of 46% of current-year foliage was injured, and significant differences in injury were evident among crown classes. Injury was greatest for dominant and codominant crown classes and increased with the level of crown exposure (Fig. 2). Injury also increased with elevation ($r = 0.69$, $P < 0.0001$). When injury was light, it was often concentrated at the top of the crown, and injury did not appear to be concentrated on any crown aspect.

Bud mortality

At the six sites sampled for bud mortality, 32% of all buds produced in 2002 were killed in association with foliar winter injury. Significant differences in bud mortality were detected among crown classes, and bud mortality was greatest for trees with more dominant and exposed crowns (Fig. 2). Bud mortality also increased with elevation ($r = 0.71$, $P < 0.0001$). In addition, bud mortality increased with foliar injury; the proportion of winter-injured shoots that failed to break bud increased as foliar injury increased ($r = 0.66$, $P < 0.0001$). As a result, approximately half of the 190 dominant and codominant trees included in this study fell into the highest two foliar injury classes (81%–100%), and on average, these trees lost more than three quarters of all the buds they produced in 2002. This pattern of increasing bud failure with increasing foliar injury is consistent with the findings of Peart et al. (1991).

Temporal context of 2003 winter injury

Winter injury has been quantified 11 times since 1986 at the red spruce plantation near Colebrook, New Hampshire, providing some historical context for the magnitude of the 2003 winter injury event. In contrast with typical injury levels of about 7%, 51% of current-year foliage was damaged at Colebrook in 2003 (Fig. 3). In 1989, a year of heavy injury throughout the region (Peart et al. 1991), only 18% of current-year foliage was injured at the Colebrook plantation — less than half of what occurred in 2003. Ninety-five percent of the 443 living trees in this plantation showed some foliar winter injury in 2003, a substantially higher proportion than is typical (32%–58%) and exceeding levels of the next highest year, 1989 (66%). Even trees of a particularly hardy Quebec provenance, which previously showed a maximum average of 6% injury to current-year foliage (in 1987), averaged 46% injury in 2003. In 2003, 96% of these trees showed some winter injury, while no more than 55% (in 2000) of trees from this provenance had been injured previously.

Bud mortality was also extensive in this plantation in 2003. Approximately 35% of all buds produced in 2002 were killed in association with foliar winter injury. This is much greater bud mortality than has been previously reported at this location. For example, in 1989, a year of heavy foliar injury for the plantation and the region, DeHayes et al. (1990) estimated bud mortality to be about 15.3% on trees showing 60%–100% injury to current-year foliage. In contrast, we measured 59% bud mortality for similarly injured trees in 2003.

While precise comparisons across studies are difficult to make because of differences in methods and plot locations, two sites in our regional survey were also assessed in past years of heavy winter injury. This made it possible to estimate temporal trends across the region (Fig. 3). For example, Peart et al. (1991) reported 29% of current-year foliage was winter injured on Mt. Moosilauke, New Hampshire, in 1989, whereas we found 56% injury on trees of similar sizes at comparable elevations in 2003. In addition, Boyce (1995) reported 21% injury to current-year red spruce foliage at Whiteface Mountain, New York, in 1993, whereas we measured 83% in 2003. These data reinforce results from the

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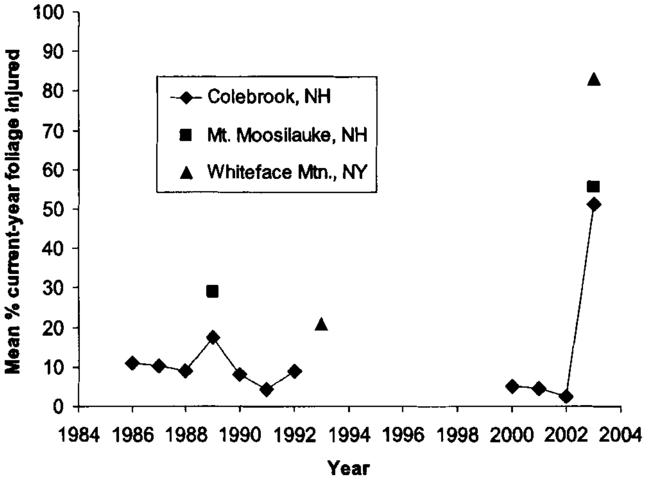
Fig. 3. Winter injury at a red spruce plantation near Colebrook, New Hampshire, and at Mt. Moosilauke, New Hampshire, and Whiteface Mountain, New York. Injury measurements at Mt. Moosilauke in 1989 are from Peart et al. (1991), while 1993 measurements at Whiteface Mountain are from Boyce (1995). Moosilauke and Whiteface injury measurements for 2003 include trees that were of comparable size and growing at elevations similar to those of the previous reports.



Colebrook plantation, which indicate that the 2003 winter injury event was unusually severe.

Ecological implications

In addition to highlighting the unusual severity of the 2003 winter injury event, data from the Colebrook plantation show that repeated or severe winter injury was associated with increased tree mortality. Eighty-nine trees in the plantation (16%) died between 1992 and 2000. In comparison with the 469 that remained alive, these 89 trees showed significantly more winter injury each year from 1986 to 1992 (t tests for unequal variances, $P < 0.001$ in all cases). Trees that died averaged 18% injury to current-year foliage between 1986 and 1992, while trees that survived averaged 8% injury during the same period. Average maximum injury between 1986 and 1992 was also greater for trees that died (42%) than for trees that lived (24%). As far as we know, this tree mortality occurred without significant bud injury. While it is possible that repeated winter injury was the direct cause of mortality for these trees, it is also possible that their health was first compromised through some other mechanism, and winter injury occurred as a result of their weakened state.

Although the precise effects of winter injury on red spruce carbon budgets have not been fully quantified, it is logical that repeated or severe episodes of winter injury might be associated with tree decline and mortality. Current-year foliage, the age class preferentially injured, generally comprises a fourth to a fifth of a tree's total foliage (Andersen et al. 1991; Hadley et al. 1993). It has higher photosynthetic capacity than older foliage classes (Andersen et al. 1991) and is less shaded than older foliage. Foliage can also be a significant carbohydrate reservoir in red spruce (Schaberg et al. 2000); thus, defoliation would deplete an important pool of stored carbon. Foliar mortality from winter injury builds upon natural losses of older foliage to thin a crown from its periphery as well as its interior. Furthermore, bud mortality exacerbates the consequences of foliar loss by reducing a tree's potential for future growth, photosynthetic capture, and carbohydrate storage. While there is some evidence that "stress" shoots and older buds within the canopy may help compensate for winter injury losses (Liedeker et al. 1988; Hadley et al. 1993), it is likely that some injury threshold exists, beyond which the remaining foliage is incapable of producing enough carbon to support continued respiration and growth.

A disruption in the carbon balance following crown damage to red spruce may result in reduced growth. Although Peart et al. (1992) found no effect on growth in the 2 years following a heavy winter injury event at Mt. Moosilauke, New Hampshire, Tobi et al. (1995) showed radial growth reductions in the years following major winter injury events at Whiteface Mountain, New York, and Wilkinson (1990) documented radial and height growth reductions following winter injury. Analysis of tree mortality at the Colebrook plantation indicates that winter injury can also be accompanied by increased death rates.

Given this connection among severe and (or) repeated winter injury, growth decline, and mortality, we propose that the extensive freezing injury of foliage and buds documented for 2003 could disrupt the carbon balance of red spruce trees and precipitate further decline and mortality in this species, particularly among dominant and codominant trees at high elevations. Indeed, it is possible that the broad-scale decline of red spruce observed within the region from the 1960s through the 1980s was initiated by earlier winter injury events of a similar magnitude (e.g., the one described by Curry and Church (1952)).

While less injury on intermediate, suppressed, and understory trees may ensure that red spruce remains a component of these forest ecosystems in the long term, it seems clear that many stands currently dominated by red spruce are likely to undergo near term changes in composition. Investigations following the declines observed in the 1960s through the 1980s led some to conclude that, at least initially, other species often emerged where dead and dying red spruce created gaps in the canopy (Perkins et al. 1992; Battles and Fahey 2000). In addition, the near synchronous death of many dominant spruce trees might disrupt ecosystem services (e.g., optimal net primary productivity, controlled nutrient cycling, seed production, habitat) that support forest community productivity and stability.

We are now examining an extensive climate and pollution data set to better describe the environmental conditions that led to the 2003 winter injury event. There is no doubt that the 2002–2003 winter was very cold (e.g., average departures from normal temperature for Mt. Mansfield, Vermont, were −11.7 °C in January and −8.3 °C in February; Northeast Regional Climate Center 2003), but evidence suggests that other predisposing factors are also needed in order for significant winter injury to occur (Schaberg and DeHayes 2000). Whatever the cause, we believe that the 2003 winter injury event has the potential to initiate dramatic changes within mature red spruce forests of the northeastern United States in the years ahead.

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