

Assessment of weather-associated causes of red spruce winter injury and consequences to aboveground carbon sequestration

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Abstract: Despite considerable study, it remains uncertain what environmental factors contribute to red spruce (*Picea rubens* Sarg.) foliar winter injury and how much this injury influences tree C stores. We used a long-term record of winter injury in a plantation in New Hampshire and conducted stepwise linear regression analyses with local weather and regional pollution data to determine which parameters helped account for observed injury. Two types of weather phenomena were consistently associated with elevated injury: (i) measures of low-temperature stress that incite injury and (ii) factors that reduced the length of the growing season and predisposed trees to injury. At this plantation, there was a significant linear relationship between winter injury and growth reductions for 2 years after a severe winter injury event. Analysis using data from three New England states indicated that plantation data reflected a regional response. Using regional data, we estimated a reduction of 394 000 metric tons of C sequestered in living red spruce stems ≥ 20 cm in diameter growing in New York and northern New England during the 2 years following a severe winter injury event. This is a conservative estimate of reduced C sequestration because injury-induced mortality and other factors were not evaluated.

Abstract: Malgré le nombre considérable d'études, on ne sait toujours pas avec certitude quels facteurs environnementaux contribuent aux dommages foliaires qui surviennent durant l'hiver chez l'épinette rouge (*Picea rubens* Sarg.), ni à quel point ces dommages influencent les réservoirs de C dans l'arbre. Nous avons utilisé des relevés à long terme des dommages qui sont survenus durant l'hiver dans une plantation du New Hampshire et nous avons effectué des analyses de régression linéaire pas à pas avec les données météorologiques locales et les données régionales de pollution pour déterminer quels paramètres permettaient d'expliquer les dommages observés. Deux types de phénomène météorologique étaient invariablement associés à des dommages sévères : (i) des mesures de stress dû à de basses températures et (ii) des facteurs qui réduisent la durée de la saison de croissance et prédisposent les arbres aux dommages. Dans cette plantation, il y avait une relation linéaire significative entre les dommages survenus pendant l'hiver et les réductions de croissance pendant les deux années suivant un épisode de dommages sévères dus au froid. L'analyse des données provenant de trois États de la Nouvelle-Angleterre indiquent que les données de la plantation reflètent une réponse régionale. À l'aide de données régionales, nous avons estimé que la séquestration de C dans les tiges d'épinette rouge ≥ 20 cm de diamètre était réduite de 394 000 tonnes métriques dans l'État de New York et le nord de la Nouvelle-Angleterre au cours des années qui ont suivi un épisode de dommages sévères dus au froid. Il s'agit d'une estimation conservatrice de la réduction de la séquestration de C parce que la mortalité causée par les dommages dus au froid et les autres facteurs n'a pas été évaluée.

[Journal translation]

Introduction

Red spruce (*Picea rubens* Sarg.) winter injury is the reddening and mortality of foliage in late winter following freezing damage (DeHayes 1992). The current-year foliage of red spruce is less cold tolerant than older foliage or foliage from sympatric species such as balsam fir (*Abies balsamea* (L.) Mill.), and it is therefore more vulnerable to injury (DeHayes et al. 2001). Winter injury-induced foliar loss and potential bud mortality can lead to tree health declines and

eventual mortality (DeHayes 1992; Lazarus et al. 2004). Indeed, winter injury was linked to the widespread decline of red spruce in the northeastern United States from the 1960s through the 1980s (Friedland et al. 1984; Johnson et al. 1988; Johnson 1992), and recurring severe winter injury events have been documented (Lazarus et al. 2004).

Evidence from the laboratory (DeHayes et al. 1999; Schaberg et al. 2000) and the field (Hawley et al. 2006; Halman et al. 2008) has shown that acid deposition induced Ca depletion reduces the cold tolerance of red spruce foliage be-

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low already marginal levels and increases the likelihood of freezing injury and subsequent health declines. Although it is now clear that altered Ca nutrition is an important factor that predisposes red spruce to winter injury, altered nutrition is not a complete explanation for the considerable year-to-year variation in the severity of winter injury expression across the region. Indeed, severity of winter injury for trees growing on Ca-depleted soils can vary more than 10-fold from one year to the next (Lazarus et al. 2004).

Red spruce winter injury was severe region-wide in 1981, 1984, 1989, 1993, and 2003 (Friedland et al. 1984; Peart et al. 1991; Boyce 1995; Lazarus et al. 2004). However, the causes for this temporal pattern of extensive damage remain unknown. Both weather and pollutant stresses have been proposed as factors that predispose or incite red spruce winter injury (Johnson et al. 1992). Because freezing is the ultimate cause of injury, spatial and temporal fluctuations in winter temperature lows likely contribute to the patterns of injury in the field. Assessments of the relationship between winter conditions and yearly variations in foliar winter injury have been few and the results of these analyses inconclusive. Tobi et al. (1995) noted that two years (1981 and 1984) of broad-scale foliar injury of red spruce were associated with prolonged winter thaws and temperatures near or below -32°C . Two other years of regional injury (1989 and 1993) experienced no long thaws but did include significant temperature fluctuations and extreme cold (-30°C and lower; Tobi et al. 1995). However, winter temperature trends since the 1830s indicate that the coldest days and coldest winters on record occurred in the 1800s, the 1910s, and the 1930s, not in recent decades when red spruce winter injury has been most pervasive (Johnson 1992). Furthermore, because red spruce foliage can deharden as much as 14°C during winter thaws (Strimbeck et al. 1995), increases in the number or intensity of thaws that are projected to accompany climate change (Christensen et al. 2007) could increase the vulnerability of trees to winter injury at temperatures above those typically associated with injury. A more comprehensive analysis is needed to specifically analyze how climate may influence the occurrence and severity of red spruce winter injury. Moreover, because pollutant inputs can influence the cold tolerance of red spruce foliage (Schaberg and DeHayes 2000), a simultaneous evaluation of temporal patterns of pollutant loading may help further define the environmental factors that predispose or incite winter injury in the field.

In addition to determining how climate and pollutant inputs influence winter injury expression, researchers have long tried to quantify the influence of winter injury on the xylem growth reductions that precede tree decline and mortality. In their assessment of growth responses after known periods of winter injury, Tobi et al. (1995) found that stem basal area increment consistently decreased in the growing season immediately after foliar injury. In addition, Wilkinson (1990) found that sustained, multiyear winter injury could result in dramatic reductions in growth for some trees (e.g., up to 59% reduction in basal area growth in comparison with noninjury years). However, because these studies either did not specifically quantify winter injury prior to growth reduction assessments (Tobi et al. 1995) or were conducted for years of only moderate winter injury (e.g.,

over 55% of trees with <5% injury and only about 12% of trees with >30% injury; Wilkinson 1990), they only partially elucidate the influence of winter injury on growth.

Two of the most significant unresolved questions regarding the causes and consequences of red spruce winter injury are (i) which environmental factors incite or predispose trees to winter injury and (ii) what are the quantitative impacts of severe winter injury on tree growth and aboveground C sequestration? Here, we report the results of two companion assessments. In the first, we use long-term measurements of winter injury for red spruce trees in a Colebrook, New Hampshire, plantation to assess weather and pollution factors that may contribute to injury expression. In the second, we quantitatively assess the influence of winter injury on woody growth and C sequestration in this plantation and 23 native forest plots in northern New England.

Materials and methods

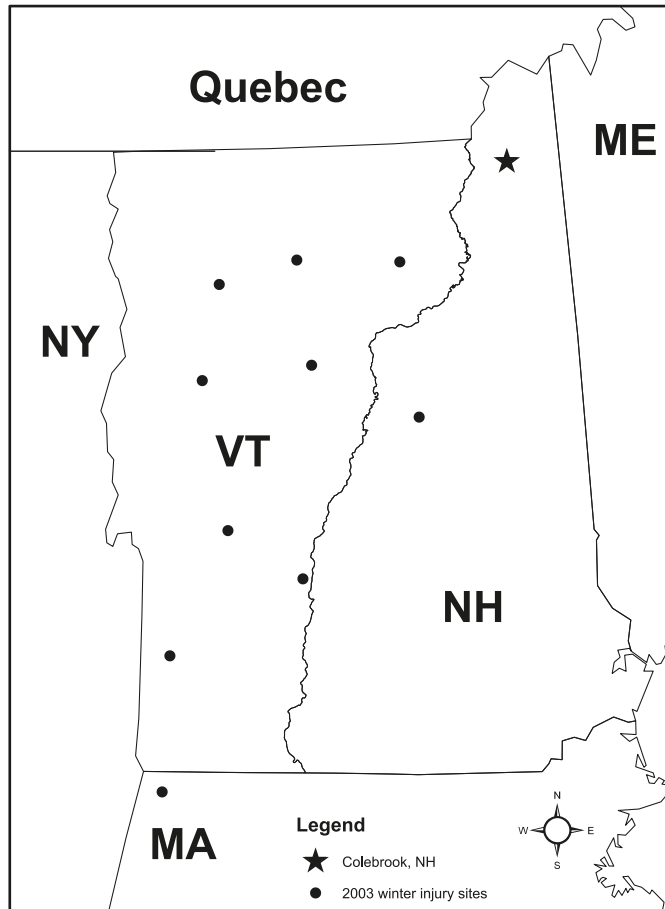
Winter injury assessments

Winter injury was assessed for red spruce trees growing under two circumstances: (i) in a plantation (elevation 715 m) established in 1960 near Colebrook, New Hampshire, and (ii) in 23 native forest plots from 10 locations in New Hampshire, Vermont, and Massachusetts (Fig. 1). The plantation contains 443 red spruce trees from 12 provenances, with seed sources extending from North Carolina to Quebec (Wilkinson 1990). Winter injury data were collected for all trees in this plantation by US Forest Service or University of Vermont researchers in the early spring of each year from 1986 to 1992 and from 2000 to 2004. Data were collected for a subset of 107 trees in 1993. Foliar damage was assessed for trees in the 23 native plots at 10 disparate locations in 2003 as part of a region-wide assessment of winter injury (Lazarus et al. 2004). For all locations, injury was scored by two observers as a visual estimate of the proportion of current-year foliage discolored on a 0–10 scale, with a score of 1 representing 1%–10% injury, a score of 2 representing 11%–20% injury, etc. (1988–1992 and 2000–2003) or on a 0–5 scale, with a score of 1 representing 1%–20%, a score of 2 representing 21%–40%, etc. (1986, 1987, and 1993) (Lazarus et al. 2004). Injury scores for each tree were converted into percentages using the midpoint of each class. Winter injury data for individual trees were used to calculate site-based yearly means.

Weather data

Daily and monthly weather data (minimum, maximum, and departures in monthly/seasonal temperature, precipitation, snowfall, snow depth, and associated measures) from 1980 to 2004 from the First Connecticut Lake weather station were obtained from the National Climatic Data Center (www.ncdc.noaa.gov). First Connecticut Lake is the closest station to the Colebrook plantation with a complete precipitation record. It is located approximately 16 km northwest of the plantation at an elevation of 506 m. The standardized precipitation index was calculated using First Connecticut Lake precipitation data with a program from the National Drought Mitigation Center at the University of Nebraska, Lincoln (http://www.drought.unl.edu/monitor/spi/program/spi_program.htm). We calculated 3-, 6-, and 12-month

Fig. 1. Map of the locations of the Colebrook, New Hampshire (NH), plantation (star) and 10 other native red spruce (*Picea rubens*) forests in NH, Vermont (VT), and Massachusetts (MA) (circles) where foliar winter injury was assessed in 2003 and woody cores for xylem growth analysis were collected in 2004 (Colebrook) and 2005 (all other sites). New York (NY), Maine (ME), and Quebec, Canada, are depicted to assist visual orientation.



standardized precipitation indices. We also obtained the Palmer drought severity index for New Hampshire Climate Division 1 (northern New Hampshire) from the National Climatic Data Center (<http://www.ncdc.noaa.gov/pub/data/cirs>).

Pollutant deposition data

Hydrogen ion, ammonium, and nitrate wet deposition data were obtained from the US Environmental Protection Agency National Atmospheric Deposition Program/National Trends Network (National Atmospheric Deposition Program 2004). Data were from the nearest measurement station, Hubbard Brook Experimental Forest, New Hampshire (elevation 250 m), approximately 115 km south-southwest of Colebrook.

Hourly ozone data from all stations in seven states (Vermont, New Hampshire, Massachusetts, New York, Maine, Rhode Island, and Connecticut) from 1980 through 2003 were obtained from the US Environmental Protection Agency (<http://www.epa.gov/ttn/airs/aqsdatamart/access.htm>). The hourly dose of ozone above 40 parts per billion

for May–September of each year was calculated using the methods of Ollinger et al. (1993). The hourly dose of ozone above 40 parts per billion for all stations with 75% or greater completeness for each month were averaged to obtain a single yearly value for the region as a whole. This approach relied on a large number of stations forming the mean rather than a single station or a constant set of stations forming the average, since the specific stations collecting these data varied greatly over the 24-year period for which data were available.

Radial stem growth

To provide a history of radial stem growth, xylem increment cores were collected for trees in the Colebrook plantation (November 2004) and the 23 regional winter injury assessment plots (October and November 2005). Colebrook plantation cores were collected on a subset of 88 trees. Two trees from each of four northern provenances in the plantation (New Hampshire, New York, and Maine, USA, and Quebec, Canada) were randomly chosen for sampling from each of the 11 winter injury classes (0–10). For the regional survey, a subset of 10 locations and 23 plots (from the 27 locations and 176 plots assessed by Lazarus et al. 2004) were chosen to include at least one and as many as three sites with average winter injury levels representing all but one of the 11 winter injury categories measured in 2003 (from 0 through 10). For logistical reasons, no plots representing 21%–30% injury (a rating of 3) were used to assess growth. Two cores positioned at 180° from each other were collected from trees parallel to the contours of plot slopes. Cores were mounted and sanded and annual xylem increments were microscopically measured (Stokes and Smiley 1968). Following measurement, cores were crossdated and basal area increment was calculated (Cook and Kairiukstis 1990). For all xylem cores from the regional assessment, the boundary between sapwood and heartwood was immediately marked in the field and then sapwood length (centimetres) was measured in the laboratory and linear measures were converted to an area basis (square millimetres) using stem diameter data. For coniferous species, sapwood area has long been used to provide a quantitative estimate of the foliar biomass supported by stem vasculature (e.g., Grier and Waring 1974).

Statistical approach

Our goal was to identify the environmental variables (weather and pollution, described above) that best explained the pattern of injury observed at the Colebrook plantation over the 12 years that these data were collected. We used the approach outlined by Teeri and Stowe (1976), performing stepwise linear regressions with JMP statistical software (SAS Institute Inc., Cary, North Carolina). To avoid overfitting, only one- and two-variable models were tested (Mickey et al. 2004). With injury as the dependent variable, we progressed systematically through a list of 144 environmental variables (temperature, precipitation, and pollutant deposition data summarized in Table 1), adding each to the model as the first variable and then allowing the program to choose the regressor that most improved the fit from among the other 143 variables. This second variable was then removed from the list of choices and the process repeated until no

Table 1. Number of environmental variables included in regression analysis to predict severe winter injury (total $n = 144$).

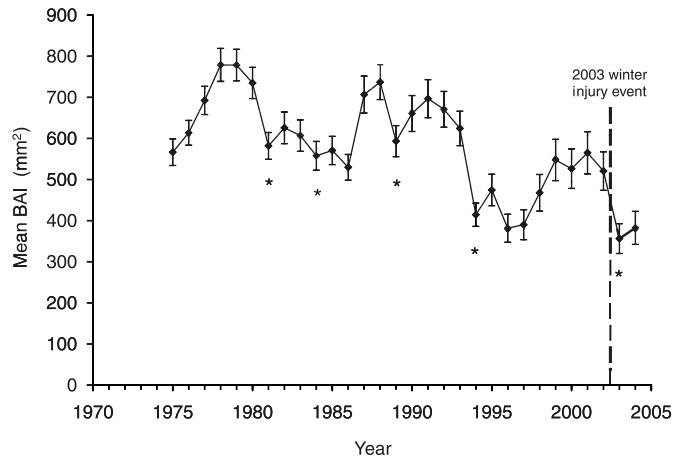
Variable categories	Regression variables analyzed		
	Monthly	Seasonal	Annual
Measures of heat/cold			
Departure from normal temperature	12	2	
Departure from normal temperature, lowest value		2	
Absolute departure from normal temperature	11	3	
Mean minimum temperature	11	2	
Mean minimum temperature, lowest value		2	
Mean maximum temperature	11		
Mean maximum temperature, highest value		1	
No. of days with maximum temperature <0 °F		1	
No. of days with maximum temperature <10 °F		1	
No. of days with maximum temperature <20 °F		1	
Depth and duration of cold			
Heating degree-days	6	2	
Consecutive days with maximum temperature <0 °F		1	
Consecutive days with maximum temperature <10 °F		1	
Consecutive days with maximum temperature <20 °F		1	
Temperature extremes and changes			
Extreme minimum temperature	6	1	
Largest temperature swing in 24 h	4	1	
Snowfall/precipitation			
Snowless days	4	2	
Total snowfall	6	1	
Maximum snow depth	4	1	
Total precipitation	12	4	1
Drought			
Standardized precipitation index		2	1
Palmer drought severity index	2		
Pollutant deposition			
Wet hydrogen ion deposition (Hubbard Brook Experimental Forest)		5	
Wet ammonium deposition (Hubbard Brook Experimental Forest)		5	
Wet nitrate deposition (Hubbard Brook Experimental Forest)		5	
Wet total N deposition (Hubbard Brook Experimental Forest)		4	
Ozone (region-wide)		2	

Note: Data were collected from First Connecticut Lake, New Hampshire, either monthly, seasonally, or annually unless otherwise noted. Seasonal measures of variables span either full seasons or portions thereof.

further significant combinations with the first variable were found. We screened the resulting set of statistically significant ($P \leq 0.05$) models by requiring that both variables contribute significantly to the model and that the two variables be independent (not significantly correlated with each other). We also used each model to predict injury for every year for which winter injury had been collected from 1980 to 2004. We then eliminated models that did not predict heavy injury ($\geq 15\%$) for 1981 and 1984, years for which no winter injury measurements were measured at Colebrook and were not used to build regression models but experienced heavy winter injury region-wide (Friedland et al. 1984). Colebrook plantation growth data, which show reductions in growth following heavy injury, demonstrate that the plantation followed the regional pattern and experienced reduced radial growth in 1981 and 1984 (Fig. 2).

We conducted separate regression analyses to quantify the linear relationships between xylem growth and foliar winter injury. For the Colebrook plantation, average changes in radial growth in 2003 and 2004 (after winter injury) calculated as a percentage of growth in 2002 (before winter injury) were assessed against the midpoints of winter injury classes (expressed as a percent). Growth in 2002 was representative of levels before the 2003 winter injury event (Fig. 2) but was slightly lower than the 4-year average prior to 2003, providing a conservative measure of estimated growth reductions. Regression analyses for the regional assessment were similar to those conducted for data from the Colebrook plantation except that growth means were often calculated using data from more than one forest plot. A regression between winter injury and sapwood area measures was also conducted using regional plot means.

Fig. 2. Mean (\pm SE) basal area increment (BAI) for red spruce (*Picea rubens*) trees growing in the Colebrook, New Hampshire, plantation ($n = 88$). Asterisks denote reductions in growth either the year of (1981, 1984, 1989, and 2003) or following (1993) region-wide winter injury events (winter injury events were observed in early spring of each year) (Peart et al. 1991; Boyce 1995; Tobi et al. 1995; Lazarus et al. 2004).



Results and discussion

Exploring the causes of winter injury: regression analyses with environmental data

We found no one-variable regression model that met pre-identified screening criteria. In contrast, we identified 15 two-variable models that fit the pattern of measured injury and also predicted heavy injury in 1981 and 1984, years that are known to have experienced region-wide severe injury (Friedland et al. 1984) but for which no data were available from the Colebrook plantation (Table 2). Common themes within this set of models included greater injury with cold winter temperatures (averages and extremes), long winter cold spells, cold or snowy conditions in March of the year that injury occurred (which were correlated with each other), aberrant temperatures in January or February (extreme cold and winter thaws), cold May and October temperatures during the growing season prior to injury, and drought. Values of R^2 for these models ranged from 0.52 to 0.79 (Table 2). Overall, weather data associated with an increased level of winter injury can be classified into two thematic groups: (i) factors that can incite freezing injury (various measures of low temperature stress) and (ii) factors that may predispose red spruce to winter injury (winter thaws that can induce foliar dehardening or measures of a shorter growing season). Greater expression of injury in years with various forms of cold exposure is consistent with the observation that red spruce current-year foliage is vulnerable to damage from a variety of freezing stresses (Schaberg and DeHayes 2000; DeHayes et al. 2001). It is also recognized that winter thaws can cause significant dehardening of red spruce foliage, increasing the risk of winter injury (Strimbeck et al. 1995). In addition, a shorter growing season could (i) decrease the production and storage of sugars that help enhance foliar cold tolerance (Strimbeck and Schaberg 2009) and (ii) diminish the uptake of Ca via transpiration, which is also known to support the development of

elevated cold tolerance in red spruce (DeHayes et al. 1999; Halman et al. 2008).

No pollutant deposition data contributed to the fit of the models listed in Table 2. Pollutant data may not have contributed to modeled estimates of winter injury for many reasons, including (i) that they lacked the necessary spatial resolution (some pollutant data were regionally based, whereas weather data were from a site adjacent to the Colebrook plantation), (ii) that they lacked the necessary temporal resolution (only seasonal values were available for many parameters, so acute events at a finer scale could have been missed), or (iii) that their effects may be cumulative over many years rather than acute.

One potential critique of our analytical approach is that the likelihood of type I errors (models incorrectly identified as influencing injury expression) increases with the number of regression models evaluated. However, the conclusions presented here do not rely on the significance or fit of any single model but rely on the commonalities among the group of significant models, thus highlighting general categories of environmental variables that most likely influence winter injury. Another limitation of our approach is the fact that all models, in addition to predicting heavy injury for years in which it is known to have occurred, also predicted heavy injury for one or more years in which heavy injury was not observed; we classified these as “false positives.” It is possible that false positives occurred because there were simply too few years of winter injury data to better isolate specific environmental factors that predispose trees to or incite injury. It is also plausible that false positives represented years when winter injury was substantial at the Colebrook plantation but injury was not high throughout the region (our metric for corroboration of likely injury). However, it is also possible that factors other than the inciting and predisposing weather phenomena that we identified also influence injury expression. For example, compensating factors that help mitigate inciting or predisposing factors (e.g., a mild or extended fall following early-season drought conditions) could reduce injury expression.

Although the issue of false positives highlights the need for further data collection and analysis, our findings that winter cold, winter thaws, and a shorter growing season are associated with an increased risk for red spruce winter injury are consistent with the physiology of red spruce winter injury (Schaberg and DeHayes 2000; DeHayes et al. 2001). These findings are also consistent with the results of past studies on woody growth (Johnson et al. 1986, 1988) that found significant reductions in red spruce xylem ring widths associated with warm late summers (potentially associated with drought and stomatal closure) and cold winters. Our regression results are also consistent with patterns of radial growth data collected at the Colebrook plantation (Fig. 2).

Xylem growth and inferences on the causes and consequences of winter injury

The additive role of environmental factors in winter injury expression is supported by the relationship of basal area growth to winter injury at the Colebrook plantation. Overall, there was a noted drop in basal area increment for all trees at Colebrook following the 2003 winter injury event (Fig. 2). A greater understanding of the growth reductions

Table 2. Significant models used to predict heavy winter injury ($\geq 15\%$) in 1981 and 1984.

Interpretation	Stepwise regression output			
	Variable 1	Variable 2	R^2	P
Cold winter, snowy March	Maximum snow depth, March (+)	No. of days with maximum temperature $< 0^\circ\text{F}$, winter (+)	0.79	0.0009
Long cold spell, cold March	Minimum temperature, March (-)	Consecutive days with maximum temperature $< 0^\circ\text{F}$, winter (+)	0.74	0.0022
Long cold spell, cold March	Heating degree-days, March (+)	Consecutive days with maximum temperature $< 0^\circ\text{F}$, winter (+)	0.69	0.0056
Cold winter, drought	Standardized precipitation index, May–October (-)	No. of days with maximum temperature $< 0^\circ\text{F}$, winter (+)	0.68	0.0056
Long cold spell, cold March	Departure from normal temperature, March (-)	Consecutive days with maximum temperature $< 0^\circ\text{F}$, winter (+)	0.68	0.0057
Long cold spell, snowy March	Total snow, March (+)	Consecutive days with maximum temperature $< 0^\circ\text{F}$, winter (+)	0.68	0.0062
Cold winter, aberrant February temperature	Absolute departure from normal temperature, February (+)	No. of days with maximum temperature $< 0^\circ\text{F}$, winter (+)	0.66	0.0074
Cold October, cold May	Heating degree-days, previous October (+)	Departure from normal temperature, previous May (-)	0.65	0.0090
Cold October, cold May	Departure from normal temperature, previous May (-)	Departure from normal temperature, previous October (-)	0.63	0.0118
Cold October, cold May	Departure from normal temperature, previous May (-)	Minimum temperature, previous October (-)	0.59	0.0176
Aberrant October temperature, cold May	Absolute departure from normal temperature, previous October (+)	Maximum temperature, previous May (-)	0.58	0.0211
Aberrant January temperature, extreme January cold	Absolute departure from normal temperature, January (+)	Extreme minimum temperature, January (-)	0.55	0.0266
Cold winter, aberrant February temperature	Absolute departure from normal temperature, February (+)	Minimum temperature, winter (-)	0.54	0.0295
Cold October, cold May	Minimum temperature, previous October (-)	Maximum temperature, previous May (-)	0.52	0.0376
Cold May, extreme cold in winter	Departure from normal temperature, previous May (-)	Extreme minimum temperature, winter (-)	0.52	0.0382

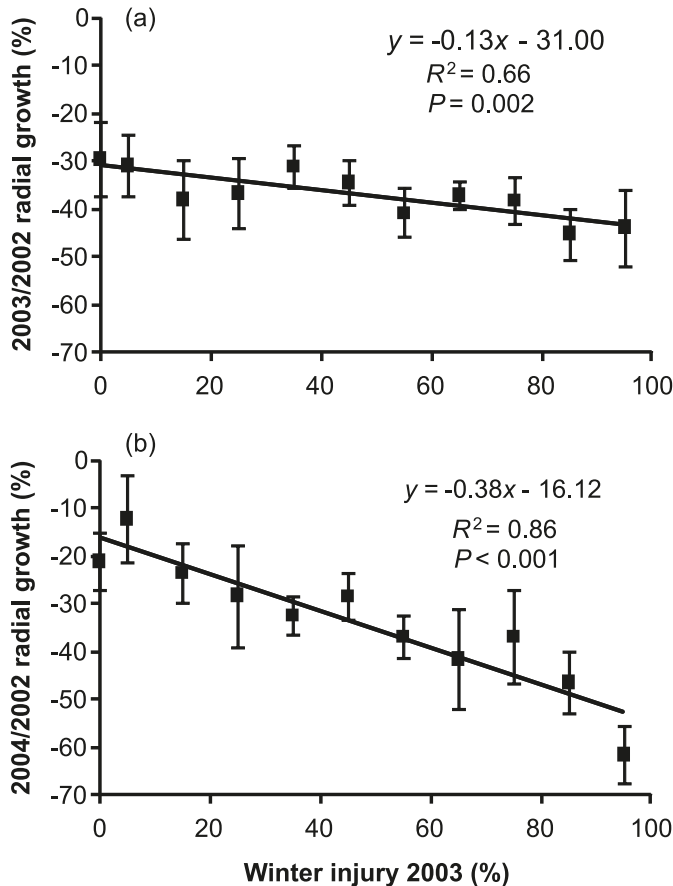
Note: These two years (1981 and 1984) of known regionally severe winter injury were not used in regression analysis because specific winter injury data were not available. They are thus used here for model verification. The direction of each relationship (+ or -) is indicated in parentheses after each variable. All maximum or minimum measures are means unless noted as "extreme", which indicates a single low or high measurement for that time period. HDD, heating degree-days; SPI, standardized precipitation index; DPNT, departure from normal temperature.

that occur with winter injury is obtained when 2003 growth (after winter injury) relative to 2002 growth (before winter injury) is plotted for trees representing the full range of injury levels (0%–100% damage to current-year foliage in 2003) (Fig. 3a). These data exhibit a significant linear reduction in growth with increasing winter injury and show a 31% reduction in 2003 growth relative to 2002 even for trees with no apparent winter injury (y -intercept = -31.00) (Fig. 3a). Reduced growth in the absence of winter injury could reflect the influence of some sublethal (nonvisible or repairable) winter injury. However, considering the results of our regression analyses, this reduction might better reflect the influence of suboptimal growing season conditions that reduced growth and predisposed trees to injury but did not incite freezing damage. Results of regression analyses that suggest some predisposing influence of growing season conditions on the increased risk of foliar winter injury (Table 2), combined with dendrochronological evidence of a reduction in woody growth even for trees with no measured winter injury (Fig. 3a), highlight the previously underrecognized influence of nonwinter climate on winter freezing injury.

In addition to the generalized reduction in growth in 2003/2002, Fig. 3a also shows a small but significant reduc-

tion in growth with increasing winter injury loss (slope = -0.13, $P = 0.002$). Beyond any predisposing influence of environmental factors on radial growth, the more foliage that was lost in 2003 due to winter injury, the greater the overall reduction in radial growth. Gradual decreases in growth for trees with increasing levels of winter injury may better reflect tree-to-tree differences in tolerance to environmental factors that actually incite freezing injury. Among other factors, variations in winter injury expression among trees in a high-injury year may reflect differences in Ca nutrition among trees. We know that trees in the Colebrook plantation differ in Ca nutrition and that these differences are correlated with differences in cold tolerance and winter injury expression (Borer et al. 2004). Furthermore, we know that increasing the Ca content of red spruce foliage can significantly reduce foliar winter injury in a high-injury year (Hawley et al. 2006). Ultimately, winter injury expression likely reflects differences in predisposing, inciting, and other factors (such as inherent site and tree differences in Ca nutrition) that integrate to influence injury expression. Spatial patterns of winter injury across the region in 2003 (Lazarus et al. 2006) are consistent with this conclusion. Patterns reflect both spatial differences in inciting factors (cold and so-

Fig. 3. Results of regression analyses showing the association between increasing average winter injury foliar loss in 2003 and radial woody growth in (a) 2003 and (b) 2004 relative to growth levels in 2002 (before injury) for red spruce (*Picea rubens*) trees in the Colebrook, New Hampshire, plantation. Means (\pm SE) are for 10 trees for each of the 11 winter injury categories from an average 0%–95% loss of current-year foliage.



lar radiation) and site-to-site differences in factors that alter Ca nutrition (pollutant H and N inputs) (Lazarus et al. 2006).

Radial growth data for 2004/2002 (Fig. 3b) show a diminished influence of nonwinter injury associated growth reductions (growth at zero winter injury), suggesting that trees were rebounding from any predisposing environmental deficits that reduced baseline growth in 2003. Perhaps because the influence of other factors influencing growth appears to be more removed (i.e., the y -intercept is closer to 0), data from 2004 may better highlight the specific influence of foliar winter injury on growth. Even two growing seasons after the 2003 winter injury event, trees that had averaged near 100% loss of current-year foliage during 2003 still experienced an approximate 60% reduction in radial growth (Fig. 3b). Evidence that winter injury can result in a protracted reduction in woody growth is consistent with the findings of Wilkinson (1990) who noted that reductions in woody growth following winter injury can be considerable and that reduced growth may persist for at least 2 years following foliar loss. However, the current data set includes trees with a far broader range of injury levels (from 0% to 100% loss of current-year foliage) to provide a more com-

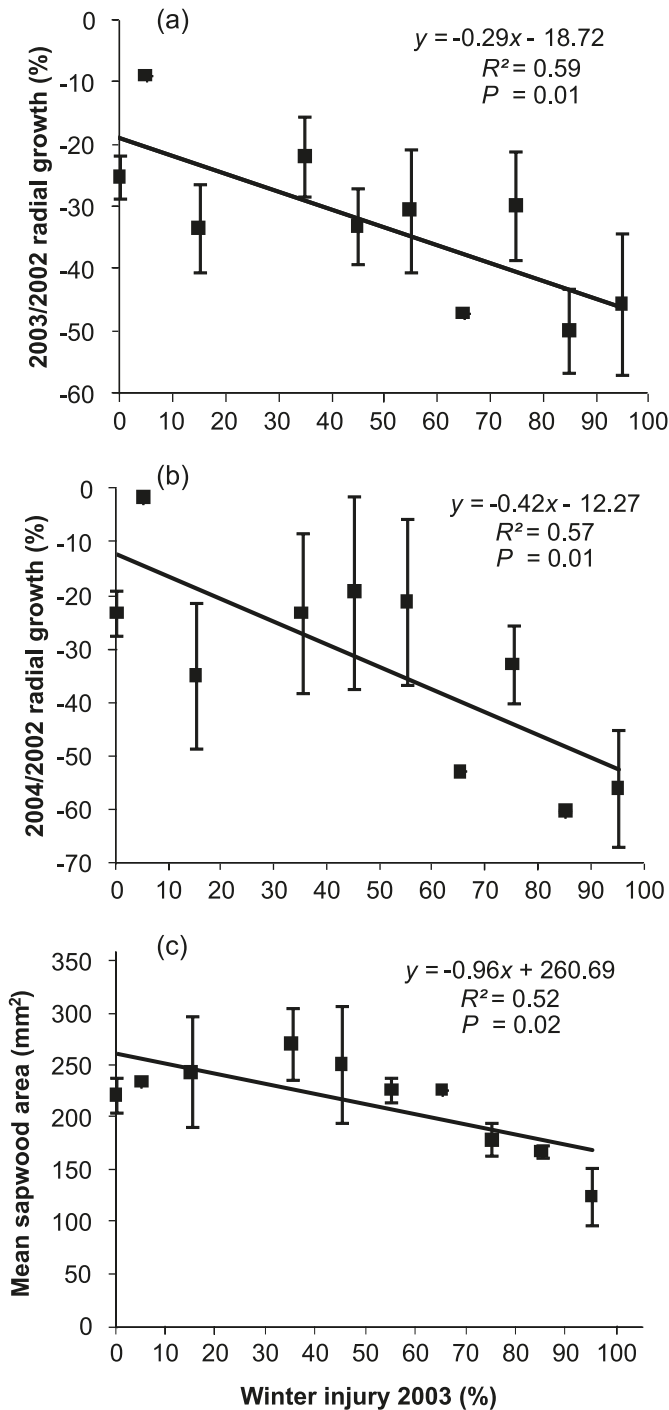
prehensive quantitative assessment of the influence of winter injury on xylem growth.

Our assessment of 10 sites from Vermont, New Hampshire, and Massachusetts (Fig. 4) shows a greater variation in growth response means within injury categories than in those at the Colebrook site (Fig. 3), a response that is expected when comparing stands of variable ages (the Colebrook stand is an even-aged plantation) across a range of site conditions (soils, elevations, aspects, etc.). Despite this added variation, data from this broader scale help expand the findings from the Colebrook plantation in two important ways. First, these data show that factors that are not associated with the induction of winter injury appear to have a muted influence when evaluated at this broader spatial scale (i.e., y -intercept = -18.72% growth reduction in Fig. 4a compared with -31.00% in Fig. 3a). A more negative y -intercept would be expected for data at a specific site if localized environmental factors during the growing season contributed to reduced xylem increment when winter injury was low. Second, analysis at a broader scale shows that the influence of winter injury on growth is a generalized phenomenon and is not site specific. Indeed, despite the numerous factors (differences in local soils and climate, different stand ages and densities, etc.) that can alter tree growth for any one stand, the influence of winter injury on xylem growth reductions during the year of winter injury (Fig. 4a) and the year after (Fig. 4b) can be consistent and strong. Indeed, the similarities of the slopes and intercepts of the regression lines for growth data from 2004 (Figs. 3b and 4b) suggest a robust relationship between winter injury losses and reduced growth potential, regardless of location and site-specific variations in weather and radial growth. In addition, reductions in sapwood area associated with increasing winter injury for the regional data (Fig. 4c) highlight the cumulative impact of winter injury on total foliar biomass, which is highly correlated with the area of supporting sapwood (e.g., $R^2 = 0.96$ or greater; Grier and Waring 1974). Reductions in foliar biomass have implications for the future energy relationships of trees because foliage is both a source of continued C capture and an important site for transient C stores that support growth and the production of plant defense compounds that promote foliar function despite biotic or abiotic stress (e.g., Apel and Hirt 2004).

Estimating impacts on C sequestration

To more completely assess the influence of winter injury on C sequestration, we used the linear associations between winter injury and growth depicted in Fig. 4 and combined this information with past analyses of aboveground biomass, woody biomass, and measures of C in wood (Jenkins et al. 2003; Bertaud and Holmbom 2004) to estimate how increases in winter injury alter the C relationships of a hypothetical 30 cm diameter at breast height (DBH) (1.3 m above ground level) red spruce tree (Table 3). The relationship between winter injury in 2003 and growth in 2004 for stands throughout Vermont (Fig. 4b) was used to estimate the influence of winter injury on growth because (i) it appeared less affected by other predisposing influences on tree growth (i.e., the y -intercept was closer to 0 than other linear assessments made) and (ii) it provided a broader geographic

Fig. 4. Results of regression analyses showing the association between increasing winter injury in 2003 and radial woody growth in (a) 2003 and (b) 2004, both relative to growth levels in 2002 (before injury), and (c) mean sapwood area for red spruce (*Picea rubens*) trees at 23 plots at 10 locations in Vermont, New Hampshire, and Massachusetts assessed for winter injury in 2003 (Lazarus et al. 2004). Means (\pm SE) are for 10 trees at each of one to three plots from each of the 10 winter injury categories from an average 0%–95% loss of current-year foliage. No plots for the 35% winter injury class were assessed, and plot means with no visible SE represent either the average of only one plot (5% and 65% injury classes) or error bars that are smaller than symbols for injury means (85% injury class).



perspective than estimates from the Colebrook plantation (Fig. 3).

The data in Table 3 highlight the toll that winter injury can have on woody aboveground C stores. These reductions in C sequestration seem minor when expressed as a one-time influence on a single 30 cm DBH tree. For example, even with near 100% loss of current-year foliage, the tree depicted in Table 3 contains only about 1.5 kg less aboveground woody biomass than a similar tree that experienced no winter injury. This number increases to about 3.0 kg of biomass if a second year of growth reduction is included (Fig. 4b). However, for some sites, winter injury occurs almost every year, and moderate to heavy injury occurs as frequently as one in five years (Lazarus et al. 2004). Therefore, the example of damage from only one winter injury event on a mature tree (Table 3) provides a muted estimate of the potential impacts of foliar loss. Nonetheless, especially when winter injury levels are high and occur on a regional scale, the single tree reductions in C storage depicted in Table 3 can be multiplied several hundred million times over (it is estimated that there are about 387 400 000 red spruce trees that are 17.8 cm (7 in.) DBH or greater in New York and northern New England; USDA Forest Service 2009). In 2003 during one region-wide event, Lazarus et al. (2004) measured winter injury severity for 1419 trees in 176 plots at 28 locations in four northeastern states (Vermont, New York, New Hampshire, and Massachusetts). They found that 90% of all trees showed some winter injury and lost an average of 46% of all current-year foliage (Lazarus et al. 2004). Winter injury levels exceeded regional averages for dominant and codominant trees (Lazarus et al. 2004) and in stands at higher elevations, in western longitudes, and western aspects (Lazarus et al. 2006). Indeed, because red spruce occurs on over 100 000 km² in the northeastern United States and adjacent Canada (Gordon 1985), possibilities for winter injury-induced reductions in C sequestration during a region-wide event are abundant.

To explore the influence of a region-wide winter injury event on the C sequestration of red spruce trees, we applied the relationships between winter injury and C storage depicted in Table 3 to data from the USDA Forest Service Forest Inventory and Analysis Program regarding the number and size of red spruce trees in New York and northern New England (USDA Forest Service 2009). Field-based Forest Inventory and Analysis data were used to estimate state-specific inventories of red spruce trees in size classes ranging from saplings (about 5 cm DBH) to large trees (>76 cm DBH). Following the example depicted in Table 3, we used the midpoints of tree diameter size classes from the Forest Inventory and Analysis database to estimate the impacts of a 65% loss of current-year foliage (the region-wide average for dominant and codominant red spruce in 2003; Lazarus et al. 2004) for an average tree from each diameter class. We then multiplied C estimates for each typical tree per diameter class by Forest Inventory and Analysis estimates of the number of red spruce in that class for the region overall (New York, Vermont, New Hampshire, Massachusetts, and Maine). Results of this analysis indicate that the 2003 winter injury event reduced the regional C sequestration of aboveground woody portions of red spruce trees 20 cm DBH and larger by about 197 000 metric tons (t), with a CO₂ equiva-

Table 3. Estimates of the influence of 1 year of winter injury on 1 year's growth, aboveground biomass accumulation, woody biomass, C gain, and CO₂ equivalents for a 30 cm DBH (1.3 m above ground level) red spruce (*Picea rubens*) tree.

Winter injury (%)	Annual radial growth reduction ^a (%)	Basal area increment (mm ²)	Aboveground biomass (kg) ^b	Woody biomass (kg) ^b	C content of wood (kg) ^c	CO ₂ sequestration of woody growth (kg) ^d
0	0	520.7	352.6	228.5	114.3	418.7
10	4.2	498.7	351.9	228.1	114.0	417.8
20	8.5	476.6	351.6	227.9	113.9	417.4
30	12.7	454.5	351.3	227.7	113.9	417.2
40	16.9	432.5	351.1	227.6	113.8	416.9
50	21.2	410.4	351.0	227.5	113.7	416.7
60	25.4	388.4	350.8	227.4	113.7	416.5
70	29.7	366.3	350.7	227.3	113.6	416.4
80	33.9	344.3	350.5	227.2	113.6	416.2
90	38.1	322.2	350.4	227.1	113.5	416.0
100	42.4	300.1	350.3	227.0	113.5	415.9

^aBased on the equation in Fig. 4b.

^bBased on biomass equations for spruce in Jenkins et al. (2003).

^cBased on measures of the chemical composition of Norway spruce (*Picea abies* (L.) Karst.) wood by Bertaud and Holmbom (2004).

^dAssuming a 1:1 conversion of sequestered C to CO₂.

lent of about 719 000 t if a 1-year reduction in growth is considered. This increases to about 394 000 t of C (over 1.4×10^6 t of CO₂) when a 2-year growth reduction (as depicted in Fig. 4b) is calculated. This 2-year estimate represents a 1.2% reduction in aboveground C sequestration.

As evident at the Colebrook plantation (Lazarus et al. 2004), repeated past winter injury events have resulted in substantial mortality that has selectively retained hardy trees. Although this selection should reduce the vulnerability of residual trees to winter injury over time, it also suggests that C losses associated with past winter injury events probably exceeded C losses estimated for 2003 because in the past, more trees with high sensitivity to freezing injury existed across the landscape. Regardless of past C losses, the calculated reduction in C sequestration following the 2003 injury event is likely highly conservative because it (i) does not include the influence of repeated winter injury events over the life of the tree, (ii) excludes C losses associated with winter injury on smaller trees that are less likely to be injured (Lazarus et al. 2004) but are more numerous across the landscape (USDA Forest Service 2009), (iii) does not include increased turnover of C and further reductions in C uptake associated with foliar loss due to winter injury (estimated reduction inferred from Fig. 4c), (iv) does not include winter injury induced mortality (DeHayes 1992; Johnson 1992; Lazarus et al. 2004), and (v) ignores likely reductions in belowground biomass of red spruce trees that may accompany aboveground decline. These broader measures were not part of the current study. However, recognizing their likely influence helps underscore the importance of winter injury in reducing red spruce C sequestration and altering C cycling in associated forests. Some of these alterations likely include the increased presence and growth of noninjured species (Beckage et al. 2008), a factor that would help offset the short-term consequences of winter injury on forest C storage. Beyond its direct influence on C budgets, winter injury associated reductions in C sequestration could have broader ecological impacts, potentially altering nutrient and water cycling, and other ecosystem services that are influ-

enced by C uptake, storage, and conversion (e.g., Jackson et al. 2005; Sohngen and Brown 2006). Indeed, some of the ecological consequences of winter injury have long been recognized. Winter injury was identified as a primary causal agent in the decline of montane red spruce in the northeastern United States during the late twentieth century (DeHayes 1992; Johnson 1992). This widespread mortality reduced the diversity of tree species at higher elevations and sped the conversion of mixed conifer stands to hardwood-dominated forests at midelevations (Beckage et al. 2008). Among its impacts, the loss of high-elevation red spruce reduced critical habitat for a regionally threatened bird, Bicknell's thrush (*Catharus bicknelli* (Ridgway, 1882)) (Atwood et al. 1996), and likely altered food and habitat resources for other biota within these sensitive ecosystems. The changes in forest structure and function that begin with foliar winter injury, result in reduced woody growth and biomass accretion, and contribute to the decline and mortality of trees and forest stands also have the potential to alter a wide range of dependent ecological processes.

Winter injury and possible connections to climate change

Climate change is predicted to increase the nature and extent of weather extremes and variability (Christensen et al. 2007) that our regression analyses indicate are associated with an increased risk of red spruce winter injury (Table 2). For example, generally warmer temperatures may not provoke red spruce trees to develop maximum hardiness levels (deep cold tolerance is induced by exposure to low temperatures; Bigras et al. 2001), thereby predisposing foliage to damage when low winter temperatures periodically occur. Furthermore, although climate change is predicted to generally increase air temperatures, especially in the winter and at northern latitudes, extreme winter lows may persist, while freeze-thaw cycles may increase in number, duration, or magnitude (Christensen et al. 2007). Current-year red spruce foliage can deharden significantly (up to 14 °C) during winter thaw events, resulting in an increased risk of freezing injury when more characteristic winter temperatures return

(Strimbeck et al. 1995). In addition, cycles of freeze–thaw activity can directly induce damage (Lund and Livingston 1998). Although probably less directly important to winter injury expression, both our regression and dendrochronological data suggest that changes in growing season conditions (e.g., warmer summer temperatures or reduced precipitation levels that may increase in frequency or intensity with climate change; Christensen et al. 2007) could also increase the risk of winter injury and decline. These combined influences of a changing climate on red spruce physiology across all seasons suggest that winter injury will remain a significant factor affecting forest ecosystem health and productivity even with generally warmer temperatures. Indeed, despite a multidecade trend toward warmer winter temperatures in the northeastern United States (Northeast Climate Impacts Assessment 2006), the most severe winter injury event on record occurred quite recently (Lazarus et al. 2004). It is important that winter injury reduces C uptake from the atmosphere (as foliar losses reduce crown volume; Fig. 4c) and decreases C sequestration in long-term woody stores (Figs. 3 and 4; Table 3). Winter injury is also associated with an increased risk of tree mortality (Lazarus et al. 2004), which turns a net C sink into a C source as dead foliage and trees decay. Thus, even as climate change may induce conditions that are more likely to predispose or incite winter injury, the reductions in C sequestration and increases in CO₂ evolution that follow winter injury, decline, and mortality may further propel climate change. As such, climate change and the consequences of red spruce winter injury could interact to promote further disruptions of climate and forest systems.

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