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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: (

low already marginal levels and increases the likelihood of standardized precipitaion indices. We also obtained the Palmer drought severity index for New Hampshire Climate Division 1 (northern New Hampshire) from the National

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

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 ($<$ 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.

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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 vulthat 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 dendrochonological 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 reduction in growth with increasing winter injury loss (slope = –0.13, P 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 comprehensive 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 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 km^2 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 numlent 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 CO_2) 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.

(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 dendrochonological 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 CO_2 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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