and ambient acid deposition (DeHayes et al. 1991; Vann et al. 1992) in seedlings and mature trees. These reductions in cold tolerance occur following the leaching of calcium (Ca) associated with foliar cell membranes (DeHayes et al. 1999; Jiang and Jagels 1999; Schaberg et al. 2000), which leads to membrane destabilization and the possible disruption of cellular stress response systems (DeHayes et al. 1999; Schaberg et al. 2000). Low levels of protracted N deposition may also impact Ca availability by decreasing Ca:Al (Al, aluminum) ratios (Aber et al. 1998), which can interfere with Ca uptake by fine roots (Clarkson and Sanderson 1971). Indeed, protracted N fertilization has been shown to deplete cell membrane associated Ca, destabilize cells, reduce cold tolerance, and lead to higher levels of winter injury in mature spruce trees (Schaberg et al. 2002). Based on this evidence from controlled studies, it is predicted that winter injury should be greatest in locations where red spruce experience both high pollution loading and elevated freezing stress. However, field verification of this is currently lacking.

In the northeastern United States, a small amount of winter injury occurs on red spruce foliage almost every year, particularly at exposed high-elevation locations (Curry and Church 1952). Severe, widespread injury has been observed in certain years, including 1981, 1984 (Friedland et al. 1984), 1989 (Peart et al. 1991), and 1993 (Boyce 1995), with 2003 being the most recent and extreme example of region-wide damage (Lazarus et al. 2004). Severe or repeated winter injury has been associated with reduced radial growth (Wilkinson 1990; Tobi et al. 1995) and increased mortality (Lazarus et al. 2004) and has been implicated as an "important initiating and synchronizing factor in the decline of red spruce" observed between the mid 1960s and the mid 1980s (Johnson et al. 1988).

Previous studies have characterized some spatial patterns in winter injury during years when damage was severe. Peart et al. (1991) assessed winter injury on Mount Moosilauke, New Hampshire, in 1989 and found that injury increased with elevation and that sapling injury was greater on a western slope than on an eastern slope (no north or south slope assessment was included). They also found that injury increased with height in the canopy at high elevations and decreased with height in the canopy at low elevations. Boyce (1995) assessed winter injury on Whiteface Mountain, New York, in 1993 and found that injury increased with height in the canopy and was greatest on the southern followed by the western crown aspect. Hadley et al. (1991) examined the orientation (but not the severity) of winter injury on vertical shoots on red spruce saplings growing on five different mountains in the northeastern United States in 1989. They found that needle death on these shoots was centered in a south to southeast orientation, though needles were sometimes killed on all sides of the shoot. Curry and Church (1952) also observed that injury was worst on the south and southwest sides of trees during the severe injury event they closer to negative one. While it would have been possible to calculate a single orientation value such as relative northeast versus southwest orientation (sine of compass bearing plus 45°; Beers et al. 1966), this was not done because the hypotheses associated with winter injury variation along a north versus south slope orientation gradient are related to insolation, while the hypotheses associated with winter injury variation along an east versus west slope orientation gradient are related to pollutant deposition. Using a single variable would have simplified the models but would have made it impossible to separately address the two hypotheses.

Data presented here are a subset of the 176 plots at 27 locations reported by Lazarus et al. (2004). Some of those plots and locations were not included in the analyses that follow because they did not contain any dominant or codominant trees or because they had no perceptible slope and thus no clear orientation.

Statistical analyses

An ordinary least squares full factorial regression model (Table 1, model 1) was used to evaluate overall landscape patterns. This model was constructed with average plot injury as the dependent variable and the following set of independent variables (all measured or calculated at the plot level): latitude, longitude, elevation, slope, relative N–S orientation, and relative E–W orientation. Assumptions of normality, homogeneity of variance, and linearity were satisfied, and residuals showed no spatial autocorrelation. This analysis resulted in many complex interactions involving latitude and longitude, suggesting the presence of spatial nonstationarity. Spatial nonstationarity is the variation of model parameters software, was the one that minimized the Akaike information criterion (AIC; Akaike 1974). The AIC provides a measure of relative model performance that is more accurate than other measures of model fit, such as the coefficient of determination (R^2), because it takes into account the number of degrees of freedom (level of complexity) of the model and identifies an appropriate trade-off between model fit and complexity. The 79 km bandwidth provided a good balance between these factors and allowed for local regressions over areas that were small enough to be meaningful and yet contained a sufficient number of plots to be statistically viable. Figure 1 provides an indication of which points were weighted most heavily in each local regression using this bandwidth.

GWR software generated Student's t values at each plot for every parameter in the local regression models. Because each local regression had a different number of degrees of freedom, each t value was compared to a t distribution with degrees of freedom equal to the sum of the weights of all points for that regression minus the effective number of parameters (Fotheringham et al. 2002), to determine the probability that the parameter differed significantly from zero for that individual local regression. While this test was statistically rigorous for any single local regression, group-wise error rate was not controlled. As a result, the probabilities obtained by this method were used only to provide a general idea of the geographic area for which a particular parameter helped account for injury levels (i.e., was not equal to zero).

Results

Broad patterns across the landscape

Patterns of winter injury detected with ordinary least squares regression (model 1, R^2 = 0.83) included increases in injury with increasing elevation, with plot location from east to west across the study region, and with the degree to which plots faced west (Table 2). However, results also indicated that more complex spatial patterns were present. In addition to the significant main effects, there were numerous significant interactions, many as high as fourth order (Table 2). Two-way interactions are not interpreted here because their interpretations were complicated by higher order interactions. All these significant higher order effects included latitude and (or) longitude as interaction components, demonstrating the potential for variability across the landscape (spatial nonstationarity) for some model parameters.

Localized patterns — GWR

GWR software was used to explore whether these higher order interactions were related to localized influences of the parameters measured. This analysis employed both global and local models to distinguish broad patterns of variability (similar to those identified using model 1) from more localized patterns of injury expression.

Least squares global model

The ordinary least squares global model (model 2, R^2 = 0.55, AIC = –65.18) was identical to model 1, except that it did not include latitude, longitude, or any of the accompanying interactions. As such, this 16-parameter model contained no locational component, but evaluated the average effect of each parameter across the entire study region. With this model, injury increased significantly with elevation and with the degree to which plots faced south and west (Table 3). There were also significant interactions between elevation and relative E–W orientation and between elevation and slope (Table 3). The interaction between elevation and relative E–W orientation indicated that west-facing slopes were more damaged than east-facing slopes except at the highest elevations, where damage appeared to be uniformly severe regardless of orientation (Fig. 2). The interaction between elevation and slope (Fig. 3) showed an increase in injury with increasing slope steepness at higher elevations and a decrease in injury with increasing slope steepness at lower elevations.

Geographically weighted local models

Geographically weighted regresion (model 3, R^2 = 0.66, AIC = –75.36) was a significant improvement (P = 0.0004) over the ordinary least squares global regression model (model 2), indicating that a significant amount of variability in injury was accounted for by taking the local variation of parameters into consideration. Only one parameter, the interaction between elevation and relative N–S orientation, was significantly nonstationary (varied from one location to another) based on a Monte Carlo significance test (Table 4), and this result was stable over a wide range of bandwidths. In fact, the same result (i.e., that only this one interaction was significantly nonstationary) was obtained with fixed bandwidths uniquely comprehensive analysis of spatial patterns in 2003 winter injury. These combined results indicated that, in general, injury increased

(1) with elevation,
(2) from east to west across the study region,

environmental factors that may contribute to injury expression. Although numerous environmental factors vary across the landscape, and although many of these factors have been tested to determine whether they reduce red spruce foliar cold tolerance, only a few of these have been shown to significantly increase the risk of winter injury in controlled experiments (see review by Schaberg and DeHayes 2000). The following analysis focuses on those parameters with documented links to altered cold tolerance and (or) increased winter injury in controlled experiments or localized field studies to evaluate the possibility that they influence injury expression at the landscape level.

In addition to its inherently marginal cold tolerance, red spruce is thought to require the influence of one or more anthropogenic environmental factors (e.g., acidic deposition) to lower foliar cold tolerance levels further as well as exposure to some form of freezing stress (e.g., low ambient temperatures) to induce significant winter injury (Schaberg and DeHayes 2000). Unfortunately, environmental data with the spatial resolution appropriate to compare with our winter injury data were not available. However, limited comparisons of landscape-level injury and environmental gradients revealed consistencies with numerous factors specifically associated with altered winter injury expression in controlled experiments or more localized field studies.

Elevation

Greater winter injury at higher elevations has been documented previously (Peart et al. 1991), and this association is consistent with well-established patterns of factors known to exacerbate winter injury. For example, air temperatures generally decrease with increasing elevation (Blair 1942), thereby increasing the potential for freezing injury. In addition, high-elevation forests in the northeastern United States are frequently immersed in orographic clouds, from which they intercept moisture with very high pollutant concentrations (Mohnen 1992). Of the various pollutants disproportionately deposited at high elevations, only the elevated exposure to hydrogen ions (H^+) and protracted additions of N have consistently been shown to reduce the cold tolerance of current-year red spruce foliage (Schaberg and DeHayes 2000). One mechanism by which this occurs involves depletion in mesophyll cell membrane associated Ca, which reduces foliar membrane stability and leads to lower cold tolerance, increasing the risk of freezing injury (DeHayes et al. 1999, Schaberg et al. 2000, 2002). Ozone (O_3) concentrations also increase with elevation (Mohnen 1992), but there is very little evidence indicating that O_3 impacts cold tolerance or leads to winter injury in red spruce. In an O_3 fumigation experiment, Fincher et al. (1989) found a small but significant effect of O_3 treatment on visible winter injury when only the subset of trees showing some degree of winter injury was considered. Other O_3 fumigation experiments have found no effect of O_3 treatment on cold tolerance (Amundson et al. 1990–1991; DeHayes et al. 1991) or winter injury (Fincher and Alscher 1992), and one recorded a slight increase in cold tolerance with greater O_3 exposure (Waite et al. 1994). However, all these O_3 experiments were conducted on seedlings and none lasted longer than two growing seasons, leaving some uncertainty as to whether the same results would have been obtained with mature trees exposed over longer periods of time.

In addition to low temperatures and high pollutant loading, montane sites also tend to have thin, nutrient-poor soils (Fernandez 1992) and more intense solar radiation (Blair 1942). Both soil nutrient limitations (especially Ca deficiencies; Schaberg et al. 2001, 2002) and intense solar radiation (see southern exposure discussion, later section) have been shown to increase the expression of winter injury.

Western longitudes and slopes

The tendency for greater injury on west-facing slopes coincides with the findings of Peart et al. (1991), who in 1989 measured greater bud failure and foliar injury on saplings on a western slope of Mount Moosilauke than on an eastern slope. The tendency for greater injury in the western part of the study region and on west-facing slopes also corresponds with findings of Vogelmann and Rock (1988). Based on examination of satellite data captured in early June 1984, the summer following a severe, region-wide winter injury event, Vogelmann and Rock (1988) detected greater damage (defined as visually apparent foliar loss on both spruce and fir) to spruce–fir forests at nine high-elevation sites in the Green Mountains of Vermont than at 11 high-elevation sites in the White Mountains of New Hampshire. They also noted that damage appeared worse on west-facing slopes than on east-facing slopes. Because this study was conducted at the height of forest decline in the 1980s and included damage to fir, it is likely that the measured damage was not only the result of a single year of heavy foliar winter injury (which primarily impacts spruce), but several compounded years of damage, including winter injury, which led to dieback and mortality.

Greater injury in the western portion of the study region suggests an E–W gradient in some predisposing or stress factor. Visual inspection of regional temperature, precipitation (Daly et al. 2004), and O_3 (Northeastern States for Coordinated Air Use Management 2004) models constructed with monitoring data from summer 2002 through winter 2003 reveals no strong E–W trend in any of these variables. Richardson et al. (2004) observed a slight increase in mean annual temperature (0.29 ± 0.11 °C per degree of longitude) from east to west across the region, though one would expect the opposite pattern if low temperatures explained the E–W trend in injury. H^+ wet deposition does show a general decrease from southwest to northeast across the region (National Atmospheric Deposition Program 2002), though this trend is based on interpolation among a relatively small number of monitoring stations. Nonetheless, the limited localized data available for the study area are consistent with the regional pattern of greater H^+ loading in western locations. For example, an analysis of 5 years (1992–1997) of data from the Vermont Precipitation Monitoring Program's St. Johnsbury station indicated that storms originating from the southwest were both the most acidic and the most frequent (46%) of all storms (Pembrook 1999). Also, for data collected between 1984 and 1995, Morrisville, on the east side of the Green Mountains of Vermont, had a significantly higher pH than Underhill, on the west side of the Green Mountains (Pembrook 1999), although this trend was confounded with the potential effects of elevation, (Morrisville 700 m vs. Underhill 1300 m). In addition to H^+, nitrate and ammonium wet deposition are also greater in western than eastern portions of the region (McNulty et al. 1991; National Atmospheric Deposition Program 2002). Combining wet and dry deposition and accounting for elevation, Ollinger et al. (1993) found a significant decrease in total deposition from southwestern Pennsylvania and New York to northeastern Maine.

Although results of least squares regression with latitude and longitude (model 1, Table 2) and GWR software's ordinary least squares global regression model (model 2, Table 3) both indicated a general tendency for greater injury on west-facing slopes, GWR's global model (model 2) indicated that this tendency did not occur at the highest elevations, where injury was more uniformly severe (Fig. 2). Climate descriptions indicate that much of the area is under the influence of "prevailing westerlies", which cause the atmospheric flow to follow a predominantly west to east pattern (Lautzenheiser 1959). This flow brings with it pollutants that may be deposited in higher concentrations on the west-facing slopes they encounter first, although exposure to pollutant-laden cloud water at the highest elevations may be more uniform.

Although east- and west-facing slopes receive the same amount of solar radiation on any given day of the year, the timing of that insolation is different, with west-facing slopes receiving their greatest insolation levels in the afternoon, when the air temperature is generally higher (Geiger 1965). Data collected at smaller scales (e.g., tree trunks, earth mounds) show that on clear days, west-facing surfaces may reach higher temperatures than east-facing surfaces at their time of peak insolation (Geiger 1965) and thus may be subject to greater temperature swings. See the subsequent section on southern exposure for discussion of the potential effects of insolation on injury.

Elevation and slope

The interaction between elevation and slope (Fig. 3) indicated an increase in injury with increasing slope steepness at higher elevations and a decrease in injury with increasing slope steepness at lower elevations. At high elevations, it is possible that steeper slopes disproportionately concentrate several factors that predispose red spruce to winter injury (e.g., thin, nutrient-poor soils and (or) greater crown exposure). In contrast, at lower elevations, cold-air drainage may concentrate the lowest temperatures in flatter areas (Blair 1942), slightly increasing injury expression there.

Southern exposure

Results of the global and geographically weighted models performed by GWR software (models 2 and 3), though not the ordinary least squares model that included latitude and longitude (model 1), indicated that injury increased with the degree to which plots faced south. Some previous studies have measured slightly but significantly greater injury on south-facing crowns than on other crown aspects (Hadley et al. 1991; Boyce 1995). South-facing slopes receive greater insolation in winter than north-facing slopes, subjecting south-facing slopes to greater potential temperature fluctuations (Blair 1942). As a result, trees on south-facing slopes are more likely to be warmed to above ambient temperatures and cooled rapidly, a phenomenon that has been shown to cause injury (Perkins and Adams 1995). Solar warming may also make branches more likely to freeze and thaw repeatedly, which has also been shown to increase injury (Hadley and Amundson 1992; Lund and Livingston 1998). Though injury was generally greater on south-facing slopes, this pattern was not evident in the northern portion of the study region at the highest elevations, possibly because injury was so near maximum levels (averaging 88%) that the additional stress associated with solar radiation could do little to increase injury further. Although insolation does not help account for injury on shaded foliage (DeHayes et al. 1990; Hadley et al. 1991; Peart et al. 1991) and is unlikely to be the primary cause of severe, region-wide injury (Strimbeck and DeHayes 2000), it may exacerbate injury on south-facing slopes when injury is not already severe. It is also possible that greater light exposure enhances the intensity of injury expression (red coloration) rather than the amount of injury itself. Hadley and Amundson (1992) found that visible light was needed to produce the characteristic red-brown color in needles that had already been freeze damaged, and procedures for several studies have included the use of light exposure to promote the development of red color following freezing injury (Perkins et al. 1993; Perkins and Adams 1995). Desiccation (due to loss of water from transpiring branches that cannot be replaced because of frozen xylem or soil) has been a frequent hypothesis for the greater degree of reddening on south-facing branches (e.g., Hadley et al. 1991; Herrick and Friedland 1991). However, Perkins et al. (1991) dismissed desiccation as a major cause of winter injury in red spruce, showing that treating branches with an

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