



Quantifying the legacy of foliar winter injury on woody aboveground carbon sequestration of red spruce trees



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ABSTRACT

Red spruce (*Picea rubens* Sarg.) decline has been quantitatively attributed to foliar winter injury caused by freezing damage. The results of this injury include foliar mortality, crown deterioration, and negative carbon (C) balances that can lead to tree health declines and eventual mortality. In 2003, a severe region-wide event damaged over 90% of red spruce in the northeastern United States (US). We assessed the influence of the 2003 winter injury event on long-term growth and C sequestration of red spruce trees by measuring the xylem growth (basal area increment) in forest stands in Vermont (VT), New Hampshire (NH), and Massachusetts (MA) where winter injury was quantified in 2003. Although previous work reported 2 years of significant linear relationships between winter injury and growth declines, here we show that growth declines relative to pre-injury (average for 2001 and 2002) growth persisted for an additional (third) year. Using 3 years of significantly reduced growth, we estimated that the 2003 winter injury event reduced the regional C sequestration of red spruce trees >17.78 cm diameter at breast height (DBH) by about 673,000 metric tons (t) of C (approximately 2,465,000 t of CO₂) – approximately 70% larger than the previous estimate. Because winter injury in 2003 was positively and significantly related to plot elevation, we also examined relative changes in red spruce growth for three elevation groups: low (<765 m), mid- (765–920 m) and high (>920 m). Relative growth was below pre-injury levels and significantly less for high compared to low elevation groups from 2003 to 2006, after which growth between these groups was indistinguishable through 2010. In 2007, and continuing through 2010, trees in mid-elevation plots exhibited significantly higher growth relative to pre-winter injury levels. Eight years after the winter injury event, mid-elevation plots had significantly higher net growth than high elevation plots and had rebounded from growth declines following the 2003 winter injury event. As of 2010, trees in the high elevation plots continued to show net C reductions – an enduring legacy of the 2003 winter injury event. The long-lasting reductions in growth subsequent to the 2003 winter injury event were followed by an unprecedented upsurge of growth in recent years, particularly in 2009 and 2010 at mid-elevation plots. This growth increase could reflect the dominance and established ecological niche of red spruce at these elevations, but it could also be influenced by more moderate temperature trends during fall through spring in recent years.

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1. Introduction

Red spruce (*Picea rubens* Sarg.) decline is one of the most intensively studied examples of forest decline in the northeastern US (Eagar and Adams, 1992); however, little is known about the long-term effects of the loss of current-year foliage to the growth of red spruce trees. Red spruce decline has been quantitatively attributed to foliar winter injury (Friedland et al., 1984; Johnson, 1992; Lazarus et al., 2004) resulting from freezing damage that leads to death of affected foliage and crown deterioration (Schaberg and DeHayes, 2000).

When injury is severe, trees may lose up to 100% of their current-year foliage and experience elevated bud mortality (Lazarus et al., 2004), which can cause apical and lateral branch loss (Siccama et al., 1982; Friedland et al., 1984). Such losses result in negative C balances that can lead to tree health declines and eventual mortality (DeHayes, 1992; Lazarus et al., 2004). Indeed, the decline of red spruce has resulted in a large negative departure from predictions of radial growth since the 1960s (McLaughlin et al., 1987; Johnson et al., 1988).

Due to a combination of red spruce's inherently marginal cold tolerance (DeHayes, 1992; DeHayes et al., 2001), variations in weather that can either predispose or incite foliar injury (Schaberg et al., 2011), and acidic deposition-induced calcium (Ca) depletion that further reduces foliar cold tolerance (DeHayes et al., 1999;

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Halman et al., 2008), there is now an increased risk of severe, region-wide winter injury events that may occur roughly every 4 years, with more moderate, localized injury occurring more frequently (Schaberg and DeHayes, 2000). In 2003, there was a severe region-wide winter injury event that affected over 90% of red spruce in VT, NH, MA, and New York (NY) (Lazarus et al., 2004). Mean injury to red spruce current-year foliage for all canopy classes was 46%, while dominant and co-dominant trees experienced the greatest amount of mean injury at 65% (Lazarus et al., 2004). Past analysis of xylem annual increment cores from red spruce trees showed significant linear relationships between winter injury and radial growth reductions for 2 years after this winter injury event (Schaberg et al., 2011), though other red spruce decline studies have indicated that growth reductions may persist longer (e.g. Johnson et al., 1988). Results from that assessment showed that foliar injury significantly reduced radial growth both the year of and the year following injury (Schaberg et al., 2011), but failed to show how long growth reductions persisted and when, if at all, a recovery of growth relative to pre-injury rates occurred. In addition, although winter injury increased with elevation in 2003 (Lazarus et al., 2006), it is unknown if growth response to injury also varied among elevations. A differential response to injury with elevation could be particularly consequential in high elevation forests that already have a simplified species composition following the widespread mortality of red spruce at the end of the last century (Eagar and Adams, 1992), and in mid-elevation forests where red spruce loss may lead to the upslope encroachment of the northern hardwood forest (Beckage et al., 2008).

Here, we use the 2003 winter injury event to examine possible long-term growth reductions and recovery subsequent to this event across the northeastern US. We hypothesized that (i) growth reductions persisted for an additional 1–2 years beyond what the previous data showed, (ii) long-term recovery from the event was likely related to the severity of foliar loss due to winter injury, and (iii) recovery varied with elevation, which influences the duration and magnitude of photosynthetic C capture used for compensatory growth. Because forests are a critical component of global C budgets, due in part to the large quantities of C stored in living biomass (Fahey et al., 2010), changes in the growth and vigor of trees can have a substantial impact on forest C pools. The aboveground biomass of living trees is the most dynamic forest C pool (Fahey et al., 2010) and can be readily assessed using allometric equations to estimate biomass based on tree DBH (Jenkins et al., 2003). Although short-term reductions in woody growth and C sequestration have been documented (Schaberg et al., 2011), any long-term reduction in growth and possible rebounds from winter injury must be examined to understand the net influences of severe winter injury events. Here, we present a novel analysis of 8 years of radial growth data for red spruce trees in 30 plots at 14 locations across 3 New England states to provide a uniquely comprehensive analysis of the broad-scale and long-term influence of severe crown injury on aboveground woody C dynamics for an important tree species in the region. Emphasized are cumulative C losses that follow injury, rebounds in growth after initial losses, differences in both of these patterns with stand elevation, and the integration of long-term changes in growth – especially for sensitive high elevation sites.

2. Materials and methods

2.1. Study area

We assessed dominant and co-dominant red spruce trees in 30 forest plots (10–15 trees per plot) from 14 locations in VT, NH, and MA (Fig. 1) that had been quantified for winter injury severity

(visual assessment of damage to current-year foliage, ranging from 0% to 100%) in 2003 (a sub-set of the 27 locations and 176 plots assessed by Lazarus et al., 2004). Though we selected plots to represent all damage classes (0–100% current-year foliar damage in 2003), winter injury in 2003 for dominant and co-dominant trees was extensive (Lazarus et al., 2004) and therefore, proportionally few plots assessed in 2003 that represented low winter injury severities were available for selection.

2.2. Dendrochronology

We collected xylem increment cores in fall 2010. Two cores per tree were collected at stem DBH (1.3 m aboveground level) with a 5 mm increment borer at 180° to each other and perpendicular to the dominant slope. Cores were mounted in grooved wooden blocks, sanded, and crossdated using the list method (Yamaguchi, 1991). Annual xylem increments were microscopically measured to 0.001 mm resolution using a Velmex sliding stage unit (Velmex Inc., Bloomfield, NY) with MeasureJ2X software (VoorTech Consulting, Holderness, NH) according to methods of Stokes and Smiley (1968). The computer program COFECHA was used to detect and correct for potential crossdating errors in ring series (Holmes, 1983).

We converted raw ring widths to basal area increments (BAI, $\text{cm}^2 \text{year}^{-1}$) assuming a circular outline of stem cross sections (Cook and Kairiukstis, 1990). BAI is considered a more meaningful indicator of tree growth as BAI standardizes annual increments relative to basal area, thus providing an indication of annual stemwood production while accounting for the effects of stem geometry on radial growth associated with tree-maturation (West, 1980; Hornbeck and Smith, 1985; LeBlanc, 1992). The dendrochronological statistics, series intercorrelation, autocorrelation, and average mean sensitivity, were calculated by COFECHA, and used to calculate the expressed population signal (EPS) based on the equation presented by Wigley et al. (1984) (see Table 1). Average changes in BAI after winter injury (2003–2010) were assessed relative to a 2-year (2001 and 2002) mean BAI for the same trees – hereafter referred to as pre-injury growth. Pre-injury growth was estimated using 2001 and 2002 to provide a baseline that avoided the influence of other growth-perturbing stresses – a severe drought in 1998–1999 (Palmer Drought Severity Index (PDSI) ranging from -2.4 to -4.7) and lesser drought and precipitation variability in 2000, which had mean PDSI values significantly lower than zero (Brewer, 2008; Dupigny-Giroux, 2009). One year (2002) of pre-injury growth was used in a previous study of short-term reductions in BAI following the 2003 winter injury event (Schaberg et al., 2011). Because growth in 2001 was slightly less than growth in 2002 (see Fig. 2), using average BAI for 2001 and 2002 as a pre-injury baseline provided a more conservative estimate of growth reductions following winter injury.

2.3. Statistical methods

Regression analyses were used to test and quantify the linear relationship between plot means of xylem growth (expressed as BAI) and 2003 foliar winter injury. We also conducted a regression analysis to test the relationship between 2003 winter injury severity and elevation. Next, we divided red spruce plots into three elevation categories set up to equalize sample sizes and align elevational groups with established ecotones (Siccama et al., 1982): low elevation, <765 m; mid-elevation, 765–920 m; and high elevation, >920 m. For this, an ANOVA followed by Tukey–Kramer multiple comparison tests were used to examine differences in BAI for each year after winter injury (2003–2010) relative to pre-injury growth for the three elevation categories. We then calculated the mean net change in relative BAI from

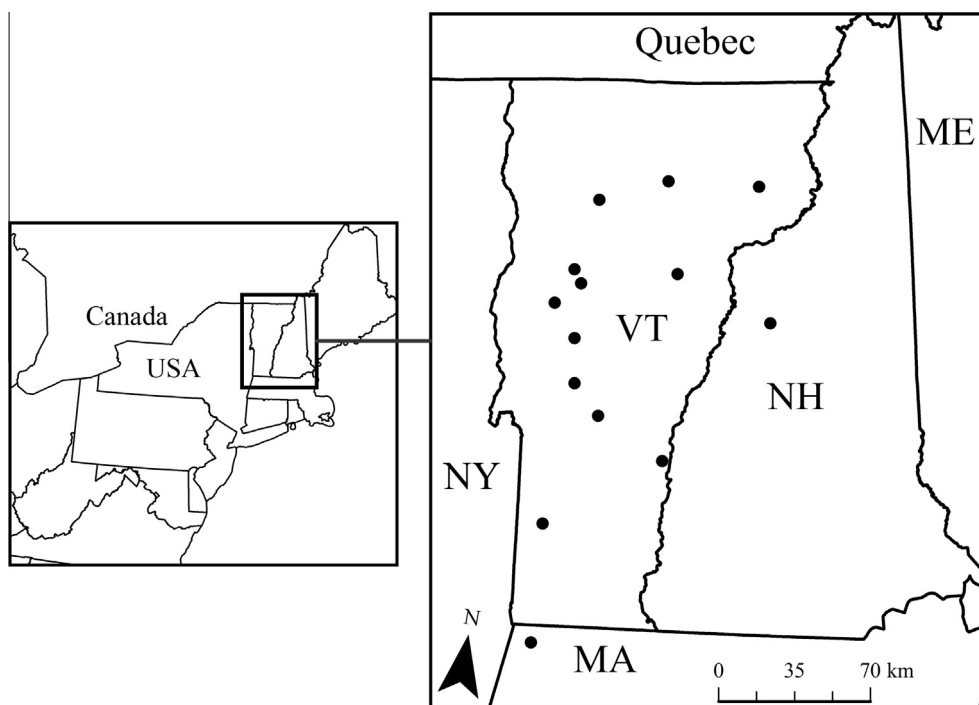


Fig. 1. Locations of 14 red spruce (*Picea rubens* Sarg.) study areas in Vermont (VT), New Hampshire (NH), and Massachusetts (MA), each containing 1–5 plots with 10–15 dominant and co-dominant red spruce trees per plot.

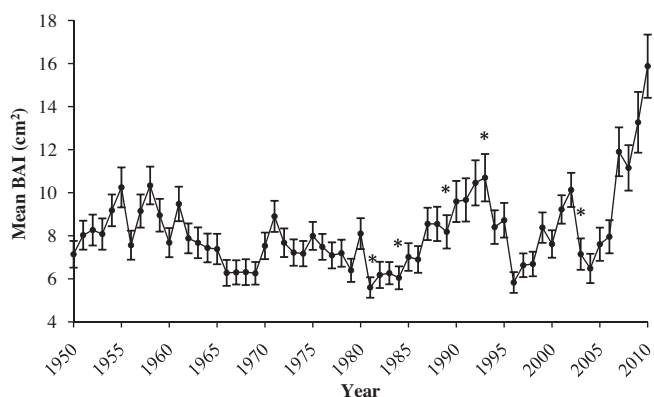


Fig. 2. Mean (\pm SE) basal area increment (BAI) for 30 red spruce (*Picea rubens* Sarg.) plots at 14 locations in Vermont (VT), New Hampshire (NH) and Massachusetts (MA) from 1950 to 2010. Asterisks mark known winter injury events in the region, which are visible mid-winter to early spring (Friedland et al., 1984; Adams et al., 1991; Boyce, 1995; Lazarus et al., 2004).

2003 to 2010 for trees from low, mid-, and high elevation plots in order to assess if they had rebounded in net growth by 2010 following initial injury-associated growth reductions. Student's *t*-tests (with a Bonferroni correction) were used to assess if the mean net change in relative BAI from 2003 to 2010 was significantly different from a hypothesized mean of zero for the three elevation groups. Results from *t*-tests were used to examine broad trends in growth reductions and rebound over time, and were not included in additional C computations. The statistical package JMP 9 (SAS Institute, Inc., Cary, NC) was used for all statistical analyses and results were considered significant if $P \leq 0.05$ unless otherwise noted.

Allometric equations (Jenkins et al., 2003) were used to estimate the influence of the 2003 winter injury event on a single year's growth, aboveground biomass accumulation, woody

biomass, C gain, and CO₂ equivalents for a 30 cm DBH red spruce tree (see Section 3.3 for details). Aboveground biomass values were converted to sequestered C based on measures of the chemical composition of spruce wood (Bertaud and Holmbom, 2004) and to CO₂ assuming a 1:1 conversion of C–CO₂. Estimates of the total number of red spruce stems, both living and dead, were gathered for VT, NH, MA, NY, and Maine (ME), for years 2002–2006, using the USDA Forest Service Forest Inventory and Analysis (FIA) online EVALIDator (Version 4.01.01) (USDA Forest Service, 2011). These estimates were used to calculate potential reduction in C sequestration associated with winter injury for red spruce trees. Following the example for a 30 cm DBH tree, we used the mid-points of tree diameter size classes from the FIA database to estimate the impacts of the regional average loss of current-year foliage in 2003 (Lazarus et al., 2004) for an average tree from each diameter class >17.78 cm DBH. We then multiplied C estimates for each tree diameter class by FIA estimates of the number of red spruce per size class in the region.

3. Results and discussion

3.1. Reductions in growth

The dendrochronological statistics (Table 1) indicate that the red spruce plots used for this study appear sensitive to environmental influences for temporal analysis and have a coherent stand-level signal (Spear, 2010). In particular, the values for series intercorrelation (a measure of the strength of the signal common to all sampled trees) and average mean sensitivity (a measure of relative change in ring-width) fall within the accepted range for red spruce chronologies (0.42–0.68 and 0.08–0.32, respectively) (NOAA National Climatic Data Center, 2008). Autocorrelation is a measure of the relationship between the current-year growth and growth in previous years; it typically ranges from 0.3 to 0.8 and high values suggest a relative conformity of genetic and microsite influences over time (NOAA National Climatic Data

Table 1
Dendrochronological statistics for red spruce (*Picea rubens* Sarg.) radial xylem increment measurements from 30 forest plots in 14 locations in Vermont (VT), New Hampshire (NH), and Massachusetts (MA) that had been quantified for winter injury severity in 2003 (Lazarus et al., 2004). The year listed in parentheses beside the expressed population signal indicates when the value fell below 0.85 for that site and is less likely to be a reliable indicator of stand-level response (Spear, 2010).

Plot location	State	N trees	Length of chronology	Series inter-correlation ^a	Average mean sensitivity ^a	Auto-correlation ^a	Expressed population signal ^b
Mt. Ascutney	VT	10	1928–2010	0.585	0.211	0.804	0.934 (1938)
Burke Mtn.	VT	10	1753–2010	0.555	0.267	0.818	0.926 (1880)
Burnt Mtn.	VT	10	1891–2010	0.485	0.236	0.858	0.904 (1923)
Burnt Mtn.	VT	10	1920–2010	0.603	0.241	0.732	0.938 (1948)
Bristol Cliffs	VT	10	1713–2010	0.510	0.263	0.746	0.912 (1923)
Mt. Carmel	VT	11	1905–2010	0.562	0.339	0.890	0.934 (1920)
Mt. Carmel	VT	10	1795–2010	0.506	0.251	0.886	0.911 (1851)
Mt. Ellen	VT	11	1824–2010	0.602	0.242	0.851	0.943 (1917)
Mt. Ellen	VT	10	1915–2010	0.453	0.289	0.861	0.892 (1934)
Mt. Equinox	VT	11	1920–2010	0.672	0.308	0.830	0.958 (1923)
Mt. Equinox	VT	12	1857–2010	0.551	0.277	0.918	0.936 (1879)
Mt. Equinox	VT	11	1909–2010	0.480	0.243	0.813	0.910 (1937)
Mt. Equinox	VT	11	1879–2010	0.453	0.306	0.917	0.901 (1930)
Mt. Greylock	MA	12	1911–2010	0.580	0.270	0.859	0.943 (1931)
Mt. Greylock	MA	10	1919–2010	0.505	0.204	0.775	0.911 (1925)
Killington Mtn.	VT	11	1817–2010	0.649	0.258	0.881	0.953 (1925)
Killington Mtn.	VT	10	1876–2010	0.445	0.266	0.815	0.889 (1924)
Killington Mtn.	VT	11	1816–2010	0.493	0.249	0.865	0.915 (1901)
Killington Mtn.	VT	11	1742–2010	0.502	0.285	0.861	0.917 (1873)
Killington Mtn.	VT	13	1793–2010	0.491	0.260	0.838	0.926 (1881)
Middlebury Gap	VT	10	1860–2010	0.598	0.253	0.740	0.937 (1924)
Mt. Mansfield	VT	14	1925–2010	0.613	0.238	0.902	0.957 (1927)
Mt. Mansfield	VT	14	1744–2010	0.550	0.254	0.836	0.945 (1803)
Mt. Mansfield	VT	10	1899–2010	0.423	0.215	0.806	0.880 (1936)
Mt. Moosilauke	NH	10	1923–2010	0.448	0.192	0.791	0.890 (1937)
Mt. Moosilauke	NH	10	1760–2010	0.599	0.258	0.817	0.937 (1904)
Mt. Moosilauke	NH	11	1890–2010	0.450	0.278	0.885	0.900 (1919)
Mad River Glen	VT	10	1927–2010	0.649	0.239	0.731	0.949 (1930)
Mad River Glen	VT	10	1930–2010	0.570	0.225	0.684	0.930 (1935)
Wolcott Forest	VT	10	1912–2010	0.539	0.223	0.871	0.921 (1937)

Where t is the average number of trees in the series and r_{bt} is the mean series intercorrelation (Wigley et al., 1984).

^a From COFECHA output (Holmes, 1983).

^b $EPS = (t * r_{bt}) / (t * r_{bt} + (1 - r_{bt}))$.

Center, 2008). The EPS is a measure of the common variability in a chronology and is dependent on sample size: when it falls below a predetermined value, typically 0.85, the chronology is a less reliable indicator of a coherent stand-level signal (Spear, 2010). In our dataset, the latest date for the EPS value to fall below 0.85 is 1948 (Table 1); therefore, we began our chronology in 1950 (Fig. 2).

Results from all plots indicate that woody growth (mean BAI) varied considerably from year-to-year, and that reduced growth was common for the years of and/or following documented severe winter injury events (Fig. 2). Indeed, for the 368 trees that we assessed, it appears that growth declined for as many as 4 years after the 2003 event. A regression of growth and winter injury severity (Fig. 3a) shows a significant linear reduction in mean plot BAI growth with increasing mean plot winter injury ($P = 0.02$) and a 19% reduction in 2003 growth relative to pre-injury growth even for trees with no foliar winter injury (y -intercept = -18.6). Reduced growth for trees that experienced no winter injury likely reflects the influence of poor growing season conditions in 2002, as was seen in an earlier study (Schaberg et al., 2011). In general, factors that reduce the functional length of the growing season (e.g., cold spring and fall temperatures, summer drought) also seem to predispose red spruce to winter injury, potentially because these conditions restrict accumulation of foliar Ca and sugars that enhance cold tolerance (Schaberg et al., 2011).

Compared to pre-injury levels, BAI data for 2004 (Fig. 3b) also showed a significant relationship between increasing winter injury and decreased growth ($P < .0001$). For 2004/pre-injury growth, there was a diminished influence of non-winter injury-associated growth reductions (growth at 0% winter injury), suggesting that the effects of a poor growing season had lessened by this time.

These results are similar to previous work that showed 2-years of significant linear relationships between winter injury and growth (Schaberg et al., 2011). However, the broader current analysis indicates that this relationship continued for an additional year: BAI data for 2005/pre-injury growth was significantly and linearly related to 2003 winter injury ($P = 0.0087$; Fig. 3c). Beginning in 2006 and continuing through 2010, the linear relationship between BAI growth and winter injury was not significant (e.g., for 2006 $P = 0.76$; Fig. 3d – data for 2007–2010 not shown).

Because regression analyses only examined the linear relationship between growth and winter injury, we also examined if changes in growth for each post-injury year was significantly lower than pre-winter injury growth for these same plots via Student's t -tests. When a general reduction in growth was examined (Table 2, all plots), an additional (fourth) year of reduced growth relative to pre-injury growth was detected, which is consistent with the trend apparent in Fig. 2 and supported by other red spruce growth decline studies in the region (see Johnson et al., 1988). This additional year of reduced growth could represent a persistent, but nonlinear, influence of winter injury on growth. However, because no relationship between increasing winter injury in 2003 and growth in 2006 was evident (Fig. 3d) it is impossible to verify that these growth reductions were specifically related to winter injury. Indeed, plots that experienced 0–40% loss of current-year foliage in 2003 were indistinguishable from plots that experienced 60–100% loss of current-year foliage in 2003 in terms of growth in 2006 (Fig. 3d). Therefore, for some reason likely unrelated to winter injury in 2003 growth remained low and comparable to 2005 levels for most plots in 2006. Data for all plots show that growth in 2009 and 2010 exceeded pre-injury levels (Table 2).

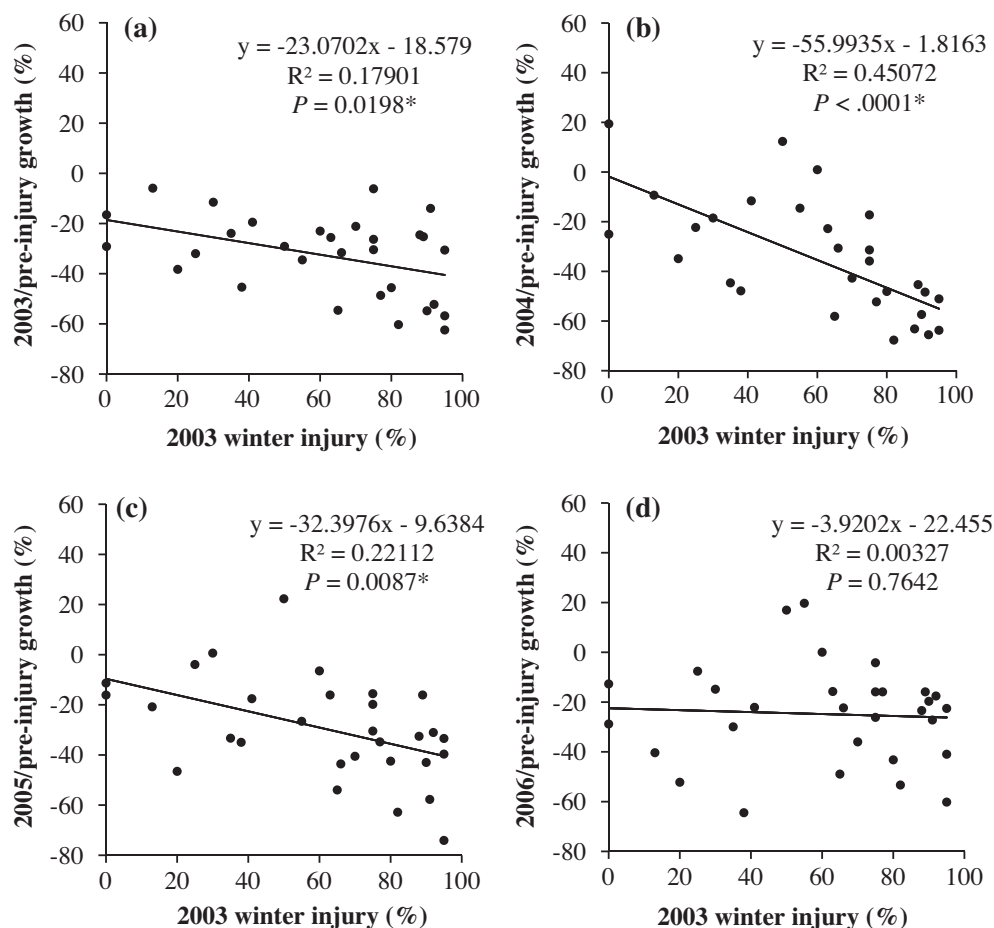


Fig. 3. Results of regression analyses showing the association between increasing current-year foliar winter injury in 2003 and basal area increment (BAI) growth in (a) 2003, (b) 2004, (c) 2005, and (d) 2006 – all relative to the 2-year mean (2001 and 2002) of growth before injury (pre-injury growth) for red spruce (*Picea rubens* Sarg.) trees at 30 plots at 14 locations in Vermont (VT), New Hampshire (NH), and Massachusetts (MA) assessed for winter injury in 2003 (Lazarus et al., 2004). Means are for 10–15 trees from an average 0% to 95% loss of current-year foliage. After 2006, results of regression analyses continued to have a non-significant linear relationship similar to results for 2006/ pre-injury growth. Asterisks indicate significant P-values (≤ 0.05).

Table 2

Percent mean change in basal area increment (BAI (%)) \pm SE compared to the 2-year mean (2001 and 2002) of growth before injury (pre-injury growth) from 2003 to 2010 for all plots and divided into three elevation groups to test whether mean is significantly different from a hypothesized mean of zero (Student's *t*-test with Bonferroni correction, overall $\alpha = 0.1$ for the eight years for which growth was assessed) for 30 red spruce (*Picea rubens* Sarg.) plots at 14 locations in Vermont (VT), New Hampshire (NH), and Massachusetts (MA) assessed for winter injury in 2003 (Lazarus et al., 2004). Negative mean BAI (%) indicates a reduction in growth relative to pre-injury levels, while positive values indicate growth exceeds pre-injury growth. Asterisks indicate significant P-values (≤ 0.0125 for any 1 year).

Year	All plots		Low elevation (<765 m)		Mid-elevation (765–920 m)		High elevation (>920 m)	
	BAI (%) \pm SE	P-value	BAI (%) \pm SE	P-value	BAI (%) \pm SE	P-value	BAI (%) \pm SE	P-value
2003	-32.65 \pm 2.92	<.0001*	-22.10 \pm 4.12	0.0002*	-34.47 \pm 3.47	<.0001*	-40.76 \pm 5.34	<.0001*
2004	-35.97 \pm 4.46	<.0001*	-18.54 \pm 6.18	0.0075*	-31.78 \pm 7.22	0.0011*	-55.25 \pm 5.09	<.0001*
2005	-29.40 \pm 3.68	<.0001*	-18.47 \pm 4.28	0.0010*	-23.26 \pm 7.07	0.0055*	-44.37 \pm 4.84	<.0001*
2006	-24.85 \pm 3.67	<.0001*	-26.71 \pm 6.30	0.0011*	-8.77 \pm 5.71	0.0816	-36.31 \pm 4.25	<.0001*
2007	11.44 \pm 5.74	0.0278	-3.98 \pm 10.50	0.3569	39.85 \pm 8.08	0.0006*	-5.01 \pm 5.40	0.1877
2008	4.46 \pm 5.57	0.2150	-10.62 \pm 10.97	0.1792	34.42 \pm 5.50	0.0001*	-6.34 \pm 4.65	0.1012
2009	21.22 \pm 7.81	0.0055*	19.50 \pm 17.15	0.1429	47.34 \pm 10.39	0.0009*	1.45 \pm 8.68	0.4355
2010	50.42 \pm 7.60	<.0001*	33.22 \pm 15.23	0.0285	77.05 \pm 12.96	0.0002*	44.28 \pm 8.26	0.0002*

3.2. Elevation-based differences in response

To test for a more nuanced and ecologically specific response of red spruce to winter injury, we examined how growth responses varied with elevation. Past work has shown that red spruce winter injury generally increases with elevation (Lazarus et al., 2004, 2006). This was also evident in our data: there was a strong relationship between plot elevation and winter injury severity in 2003 ($P < .0001$; Fig. 4). When we divided plots into three elevation

categories and examined the change in BAI compared to pre-injury growth, we detected a general reduction in growth for 2003–2006 followed by moderate increases in growth that varied by elevation (Fig. 5). For 2003–2005 the most prominent differences in growth occurred between low and high elevation groups, which were consistent with the overall strong and positive relationship between winter injury severity and elevation (Fig. 4). Interestingly, even though they experienced vastly dissimilar winter injury levels in 2003, relative growth for the low and high elevation groups con-

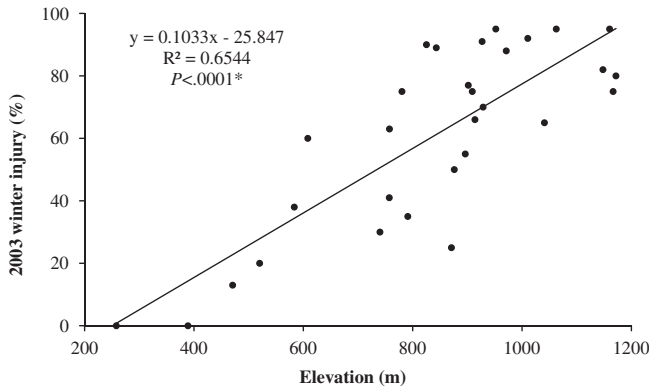


Fig. 4. Results of regression analysis showing the relationship between plot elevation and mean current-year foliar winter injury assessed in 2003 (%) for 30 red spruce (*Picea rubens* Sarg.) plots at 14 locations in Vermont (VT), New Hampshire (NH), and Massachusetts (MA) assessed for winter injury in 2003 (Lazarus et al., 2004). Asterisks indicate significant P-values (≤ 0.05).

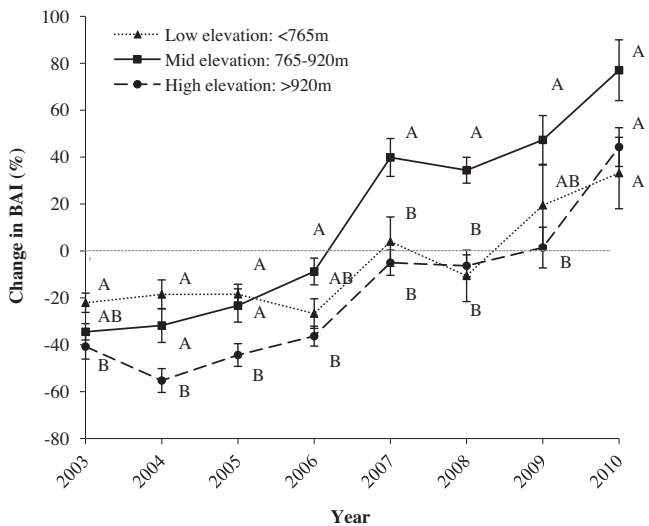


Fig. 5. Mean (\pm SE) change in basal area increment from 2003 to 2010 compared to the two-year mean (2001 and 2002) of basal area increment (BAI) growth before injury (pre-injury growth) by plot elevation, divided into three categories – low elevation (<765 m), mid-elevation (765–920 m), and high elevation (>920 m) – for 30 red spruce (*Picea rubens* Sarg.) plots at 14 locations in Vermont (VT), New Hampshire (NH), and Massachusetts (MA) assessed for winter injury in 2003 (Lazarus et al., 2004). Different letters denote significant differences ($P < 0.05$, ANOVA followed by Tukey–Kramer multiple comparison test). Solid horizontal line denotes no change in radial growth compared to pre-injury growth (0% change).

verged in 2006 and remained indistinguishable through 2010 – chiefly because growth reductions at high elevations lessened slightly around this time (Fig. 5). In 2007 and 2008 mid-elevation plots had significantly higher growth compared to both the low and high elevation groups.

For all elevation categories, growth was lower than pre-injury growth levels for each of the 3 years following winter injury (2003–2005; Table 2). For both low and high elevations, significantly lower growth persisted for an additional year (2006), but growth was not significantly different from pre-winter injury levels for 2007, 2008, and 2009. In 2010, high elevation plots experienced some rebound in growth. Starting in 2007, mid-elevation plots showed a strong increase in growth relative to the other two elevation categories; indeed, this elevation group showed strong growth through the end of the sampling period (2010).

In 2007, and continuing through 2010, red spruce trees in mid-elevation plots exhibited significantly higher BAI growth relative to pre-winter injury levels (Fig. 5, Table 2). There are a number of possible reasons why trees in the mid-elevation plots performed well, particularly compared to those from low and high elevation plots. High elevation plots experienced the greatest level of foliar and bud mortality in the 2003 injury event (Lazarus et al., 2004) and therefore, would be expected to have the greatest lingering growth reductions. In addition, high elevation spruce live on poorer sites – experiencing a shortened growing season, increased cloud cover, thinner soils, and harsher winter conditions than red spruce at lower elevations – thus, environmental constraints there would likely slow growth rebound following injury. Low elevation plots, while they suffered less winter injury, are subject to the greatest competition from hardwoods, which likely took advantage of the foliar and branch damage to red spruce associated with the 2003 winter injury event. Although trees on mid-elevation plots experienced moderate injury, red spruce are a dominant canopy species there and experience less competition from hardwoods. Also, compared to high elevations, growing conditions are more moderate and favorable at mid-elevations.

Because both initial reductions and apparent rebounds in growth vary with elevation (Fig. 5, Table 2), we calculated net growth (the summation of BAI growth reductions and increases relative to pre-injury growth per tree) following the 2003 injury event, averaged by elevation category (Fig. 6). Eight years after the winter injury event, mid-elevation plots had compensated for initial reductions in growth (i.e., mean significantly greater than zero, $P = 0.03$, Fig. 6). Mean net growth of red spruce at mid-elevation plots were also significantly greater than for red spruce at high elevation plots, where trees retained net negative growth relative to pre-injury levels (i.e., mean significantly less than zero, $P = 0.0004$, Fig. 6). Mean net growth for trees at low elevation plots was intermediate to other elevation groups, but was not significantly different from zero. Recent increases in growth have allowed trees at low and mid-elevations to overcome growth reductions associated with winter injury (Fig. 6). However, despite improved growth in 2010 (Table 2), trees at high elevations have still not rebounded in mean net growth following injury (Fig. 6).

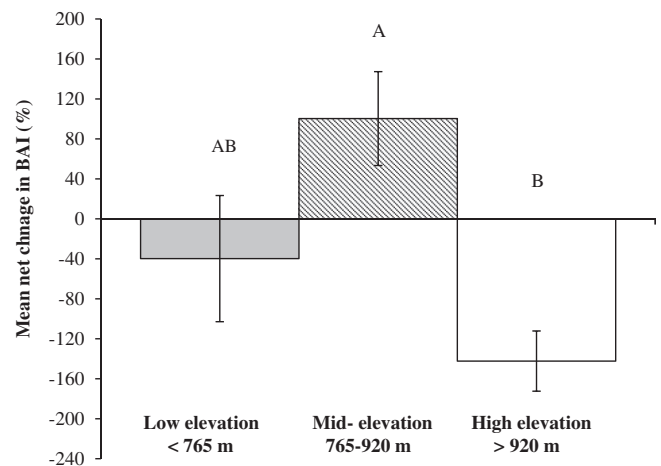


Fig. 6. Mean (\pm SE) net change in basal area increment (BAI) from 2003 to 2010 compared to the 2-year mean (2001 and 2002) of growth before injury (pre-injury growth) divided into elevation categories ($P = 0.0038$, ANOVA followed by a Tukey–Kramer multiple comparison test) for 30 red spruce (*Picea rubens* Sarg.) plots at 14 locations in Vermont (VT), New Hampshire (NH), and Massachusetts (MA) assessed for winter injury in 2003 (Lazarus et al., 2004). Both the mid- and high elevation categories are significantly different from a hypothesized mean of zero ($P = 0.0325$ and $P = 0.0004$, respectively; Student’s *t*-test), while the low elevation category is not.

This data uniquely quantifies the persistent influence of winter injury on the C relations of red spruce, and highlights the basis whereby severe foliar loss can lead to long-term C disruptions – the sort that initiated red spruce decline and mortality that was prevalent in high elevation forests in the region in recent decades (Eagar and Adams, 1992). The high elevation trees in our study were among the survivors of this wave of mortality. However, even for these presumably less vulnerable specimens, persistent reductions in growth following winter injury remain and likely influence the dynamics of high elevation forests where red spruce has historically been a keystone species central to the production of critical ecosystem services (Schaberg et al., 2011).

3.3. Estimating impacts on aboveground C sequestration

In order to improve upon past estimates of the effects of winter injury on red spruce C sequestration, we used the linear associations between winter injury and growth depicted in Fig. 3 and combined this information with established 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 relations of a hypothetical 30 cm DBH red spruce tree (Table 3). In particular, because we now know that growth reductions associated with the 2003 winter injury event continued for at least 3 years (Fig. 3), inclusion of a third year of growth reductions should clarify the legacy of winter injury on C sequestration in living trees following winter injury. The slope of the regression of relative growth in 2004 with 2003 winter injury was used to estimate C reductions for both 2003 and 2004 because this year showed less of an influence of factors other than winter injury on growth (e.g., y-intercept was closer to zero). This approach was also used by Schaberg et al. (2011), so its use here allowed for a direct comparison to a previous estimate. However, the slope of the regression of winter injury and growth from 2005 was used for our third year of winter injury associated reductions in growth in order to more specifically estimate growth for that year.

The data in Table 3 highlight apparently minor reductions in long-term aboveground woody C stores that occur for a representative 30 cm DBH red spruce following winter injury. For example, even with near 100% loss of current-year foliage, the tree depicted in Table 3 would contain only 0.63 kg less aboveground woody biomass than a similar tree that experienced no winter injury. This number would increase to 1.89 kg of biomass if 3 years of growth reduction were included (Fig. 3). However, it was estimated that there were 346,414,300 living red spruce trees 17.78 cm (7 in.)

DBH or greater in NY and northern New England from 2002 to 2006 (USDA Forest Service, 2011). Obviously, the minor reductions in C sequestration estimated for a single tree become more consequential when expanded to include trees across the region.

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 FIA data regarding the number and size of living red spruce trees in the region (USDA Forest Service, 2011). The resulting estimate has four refinements over the past regional estimate of winter injury's influence on C sequestration (Schaberg et al., 2011). First, it includes an additional year (2005) of growth reductions linearly associated with winter injury in 2003. Second, it uses an improved estimate of the number of living red spruce in the region – one that is smaller than the one used by Schaberg et al. (2011) because recent tree mortality has been excluded. This mortality is not included in C estimates because it cannot be verified as being caused by winter injury. Third, the FIA data included improved and increased estimates of red spruce in the largest size class (>26 in DBH). Finally, measurements of BAI were obtained from more trees, plots, and elevations than in previous research in order to better estimate baseline (pre-injury) growth.

Results of this analysis indicate that a winter injury event like the one experienced in 2003 would reduce the regional C sequestration of living red spruce trees 17.78 cm DBH and larger by about 673,000 t of C (approximately 2,465,000 t of CO₂) when a 3-year growth reduction (Fig. 3) is calculated – a value that is approximately 70% larger than the previous estimate using 2 years of reduced growth (see Schaberg et al., 2011) due to the refinements listed previously. Although this 3-year estimate only represents a 1% reduction in aboveground C sequestration for affected trees, it is equivalent to the CO₂ emissions resulting from the combustion of approximately 280,000,000 gallons of gasoline (Coe, 2005).

Though this value is updated, it is a conservative estimate since it (i) does not account for the persistent loss of C capture potential (Fig. 6) for the approximate 16% of red spruce that exist at high elevations in northern New England and New York (USDA Forest Service, 2011), (ii) does not include repeated winter injury events, (iii) excludes C losses on smaller trees, which are less likely to be injured during an event, but are more numerous across the landscape (Lazarus et al., 2004), (iv) excludes winter injury-induced mortality, (v) does not include reductions in belowground biomass of trees that likely coincide with aboveground losses, and (vi) does not include lost growth in dead leaders or broken lateral branches that accompany winter injury. Even for living trees, it was common for red spruce in this study to have dead leaders: 73.4% of the trees

Table 3

Estimates of the influence of the 2003 winter injury event on a single year's growth, aboveground biomass accumulation, woody biomass, C gain and CO₂ equivalents for a 30 cm DBH (diameter breast height: 1.3 m aboveground level) red spruce (*Picea rubens* Sarg.) tree.

Winter injury (%)	Annual radial growth reduction ^a (%)	BAI (cm ²)	Aboveground biomass ^b (kg)	Woody biomass ^b (kg)	C content of wood ^c (kg)	CO ₂ sequestration of woody growth ^d (kg)
0	0.00	10.13	349.08	226.20	113.10	414.41
10	7.42	9.38	348.96	226.12	113.06	414.26
20	13.02	8.81	348.87	226.06	113.03	414.15
30	18.61	8.24	348.78	226.00	113.00	414.04
40	24.21	7.68	348.69	225.94	112.97	413.93
50	29.81	7.11	348.59	225.88	112.94	413.81
60	35.41	6.54	348.50	225.81	112.91	413.70
70	41.01	5.98	348.41	225.75	112.88	413.59
80	46.61	5.41	348.32	225.69	112.85	413.48
90	52.21	4.84	348.22	225.63	112.82	413.37
100	57.81	4.27	348.13	225.57	112.78	413.25

^a Based on the equation in Fig. 3b.

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

^c Based on measures of the chemical composition of spruce wood by Bertaud and Holmbom (2004).

^d Assuming a 1:1 conversion of sequestered C–CO₂.

in this study had a dead leader of varying length. Though we detected some mortality in plots (data not shown), our plots were a small subsample of all red spruce forests in the region. FIA estimates indicate there were 40,980,100 standing dead red spruce in the region (>17.78 cm DBH) between 2002 and 2006, or about 11% of all red spruce stems. In comparison, 6% of sugar maple (*Acer saccharum* Marsh.), another declining tree species in the region (Bauce and Allen, 1991; Duchesne et al., 2003), were standing dead during this period (USDA Forest Service, 2011). Regardless of the various limitations to the current estimate, our current calculations show a persistent impact of winter injury on red spruce C sequestration.

3.4. Recent growth increases

Although these calculations focus on C losses in the 3 years following the 2003 winter injury event, what is perhaps more interesting and novel is the recent upsurge in red spruce growth relative to the past 60 years (Fig. 2). Indeed this growth is unusual for red spruce BAI measurements for these trees since the start of the 20th century (data not shown). The superlative growth for 2009 and 2010 (Fig. 2) incorporates all plots and elevations, including both low and high elevation plots whose growth increases were more moderate than mid-elevation plots (Fig. 5). Causes for recent increases in red spruce growth have not yet been examined. However, one possible explanation is that warmer winter, spring, and fall temperatures have enhanced red spruce C capture at a time when competitor hardwoods remain leafless and sympatric balsam fir (*Abies balsamea* (L.) Mill.) are physiologically dormant (Schaberg, 2000; Schaberg and DeHayes, 2000). Red spruce has a unique capacity to photosynthesize during the traditional dormant season when temperatures moderate (Schaberg et al., 1995, 1998; Schwarz et al., 1997) and can increase soluble carbohydrate stores at a time when other species are losing C via respiration (Schaberg et al., 2000).

In the northeastern US, both 2009 and 2010 contained anomalously warm spring and/or fall temperatures; higher than average temperatures were recorded in February and March of 2009, and this year contained the fourth warmest November on record (NOAA National Climatic Data Center, 2010). Atypically warm temperatures were also recorded from February to April, 2010, allowing for an earlier than normal arrival of spring; indeed, 2010 had the warmest January–November on record for the northeast (NOAA National Climatic Data Center, 2010). Furthermore, 2009 and 2010 appear to be part of a broader warming trend. In Vermont, the length of the growing season has increased an average of 3.7 ± 1.1 days per decade from 1960 to 2008, with a coinciding 0.2 ± 0.07 °C increase in summer temperatures and 0.5 ± 0.16 °C increase in winter temperatures (Betts, 2011). The influence of changing climate (e.g., warming trends, greater variability, and extreme events during traditionally cold seasons) on tree growth, including mid-elevation red spruce, has yet to be determined (Fahey et al., 2010).

3.5. Conclusions

Analysis at a broad spatial scale shows that the influence of winter injury on red spruce growth is a generalized phenomenon and is not site-specific. Indeed, despite the numerous factors that can alter tree growth for any one stand (e.g., differences in local soils and climate, different stand ages and densities, etc.), the influence of winter injury on xylem growth reductions after winter injury can be consistent and strong. Our data indicate that reductions in growth for red spruce growing at a variety of sites in VT, NH and MA, persisted for 3 years. There is evidence that growth reductions may have persisted longer, but we cannot verify that those reduc-

tions were attributable to winter injury in 2003. Using 3 years of significantly reduced growth and refined estimates of red spruce in the region, we calculated reductions in regional aboveground biomass C sequestration approximately 70% greater than the previous estimate.

Growth impacts following winter injury, particularly recovery from growth declines, were not uniform across all elevations. Eight growing seasons after the winter injury event, red spruce at low and mid-elevation sites have rebounded in mean net growth. However, as of 2010, high elevation spruce still had negative mean net growth relative to pre-injury levels. Persistent growth reductions at high elevations likely reflect the synergistic effects of harsh environmental conditions and elevated inputs of acidic deposition there – factors that contributed to the decline and mortality of red spruce at these locations in the 1970s and 1980s (Eagar and Adams, 1992).

Surprisingly, red spruce trees at mid-elevations, where injury in 2003 was substantial, rebounded robustly in growth starting in 2007 and have significantly surpassed growth declines associated with injury. Although this growth increase may be explained by red spruce's dominance and established ecological niche at these altitudes, it is also possible that changes in climate could help explain this recent surge in growth (Schwarz et al., 1997).

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